

# Stochastic Fokker-Planck equation in random environments

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We analyze the stochastic dynamics of a large population of noninteracting particles driven by a common environmental input in the form of an Ornstein-Uhlenbeck (OU) process. The density of particles evolves according to a stochastic Fokker-Planck (FP) equation with respect to different realizations of the OU process. We then exploit the connection with previous work on diffusion in randomly switching environments in order to derive moment equations for the distribution of solutions to the stochastic FP equation. We use perturbation theory and Green's functions to calculate the mean and variance of the distribution when the relaxation rate of the OU process is fast (close to the white-noise limit). Finally, we show how the theory of noise-induced synchronization can be recast into the framework of a stochastic FP equation.

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## I. INTRODUCTION

A number of recent modeling studies have considered stochastic partial differential equations (SPDEs) that describe the evolution of the density of particles diffusing in a domain with randomly switching boundary conditions [1–3]. The environmental variables that determine the boundary conditions are taken to switch between a finite number of states according to a continuous-time Markov chain. The resulting SPDE is thus piecewise deterministic. This type of model has recently been applied to several problem domains in biology and biophysics, including diffusion-limited reactions [4], neurotransmission [5], insect physiology [6], and stochastically gated gap junctions [7].

Suppose, for the sake of illustration, that particles are diffusing in some bounded domain  $\Omega \subset \mathbb{R}^d$  and that the current state of the environment is  $n(t) = n$ , with  $n \in \Gamma \subset \mathbb{Z}$ . Each realization of the environment up to time  $t$ ,  $\sigma(t) = \{n(\tau), 0 \leq \tau < t\}$ , will tend to generate a different solution of the underlying SPDE, which we denote by the density  $P(x, t)$ —this represents the density of particles in state  $x$  at time  $t$ . The presence of the random environment means that the particle density  $P(x, t)$  is itself a random field, so there is a distribution of densities. Introducing the  $r$ th order moments of the corresponding distribution of  $P$ ,

$$C^{(r)}(x_1, \dots, x_r, n) = \mathbb{E}_\sigma [P(x_1, t) \cdots P(x_r, t) \mathbf{1}_{n(t)=n}],$$

where expectation is taken with respect to realizations  $\sigma$ , one can derive a closed hierarchy of moment equations in the form of deterministic PDEs. This then establishes a relationship between  $C^{(r)}(x_1, \dots, x_r, n)$  and the joint probability density for  $r$  diffusing particles having positions  $x_1, \dots, x_r$  at time  $t$ , given that the random environment is currently in state  $n(t) = n$ .

Although the relationship between the moments of the distribution of solutions to an SPDE and the joint statistics of a finite number of particles evolving in the same random environment has been investigated primarily for diffusion-like processes, it is in fact a much more general principle. For example, rather than considering diffusing particles, one could model a population of random walkers in a randomly switching environment [8]. The diffusion equation for particle density is replaced by a stochastic birth-death master equation for the distribution of particles on a lattice, where the hopping rates

between neighboring lattice sites are themselves stochastic. In this paper we focus on another example, namely a large population of noninteracting particles driven by a common environmental input in the form of an Ornstein-Uhlenbeck (OU) process [9]. At the population level the density of particles evolves according to a stochastic Fokker-Planck (FP) equation that depends on the particular realization of the random environment. It should be noted that we use the term “particle” loosely here. That is, although  $x \in \mathbb{R}^d$  could denote the position of a physical particle, it could also represent a set of concentrations for some biochemical network evolving according to mass action kinetics. In the latter case, a particle might be a single gene or cell and the environmental variable might control the switching on and off of genes. Alternatively,  $x$  could represent voltage and ion-channel gating variables in the case of a neuron [10].

We take as our starting point the classical problem of a Brownian particle driven by colored noise in the form of an OU process [9] (Sec. II). In the white-noise limit the associated two-dimensional FP equation reduces to a scalar FP equation of the Stratonovich form. We then consider a population of identical particles driven by a common OU process, with the latter identified as some environmental variable  $\alpha(t)$ . For a given realization of the OU process, the population density evolves according to an FP equation that depends on  $\alpha(t)$ , which implies that the density is itself a random field with respect to different realizations of the OU process. We then exploit the connection with previous work on diffusion in randomly switching environments [2] in order to derive moment equations for the distribution of solutions to the stochastic FP equation (Sec. III). We thus show how the  $r$ th moment is related to the joint probability density of  $r$  identical particles driven by the same OU process. We highlight the fact that the two quantities are not necessarily equivalent, particularly in the case of boundary value problems. In Sec. IV we use perturbation theory and Green's functions to calculate the steady-state solution of the first and second-order moment equations when the relaxation rate of the OU process is fast (close to the white-noise limit). Finally, in Sec. V we apply our stochastic FP formulation to recent work on noise-induced synchronization [11–18]. In particular, we emphasize how the SPDE perspective allows one to establish synchronization of a population of

oscillators under a single realization of the common random input.

## II. A CLASSICAL SDE WITH NONWHITE NOISE: AN SPDE PERSPECTIVE

A classical problem in stochastic processes is the derivation of the Stratonovich version of the FP equation for a single particle driven by external white noise [9]. Let  $X(t)$  denote the position of the particle at time  $t$ , which is taken to evolve according to the stochastic differential equation (SDE),

$$dX(t) = [F(X) + \gamma b(X)\alpha(t)]dt + \sqrt{2D}dW(t), \quad (2.1)$$

where  $\alpha(t)$  is a stochastic external input evolving according to the OU process

$$d\alpha(t) = -\gamma^2\alpha(t)dt + \gamma d\widehat{W}(t). \quad (2.2)$$

Here  $W(t)$  and  $\widehat{W}(t)$  are independent Wiener processes with

$$\langle dW(t) \rangle = 0 = \langle d\widehat{W}(t) \rangle, \quad \langle dW(t)dW(t') \rangle = \delta(t-t')dt dt'$$

and

$$\langle d\widehat{W}(t)d\widehat{W}(t') \rangle = \delta(t-t')dt dt', \quad \langle dW(t)d\widehat{W}(t') \rangle = 0.$$

For simplicity, we take the intrinsic noise to be additive and independent of  $\alpha(t)$ . Heuristically speaking, in the limit  $\gamma \rightarrow \infty$ , we can set  $\alpha(t)dt = dW(t)/\gamma$  such that we obtain the scalar SDE

$$dX(t) = F(X)dt + \sqrt{2D}dW(t) + b(X)d\widehat{W}(t). \quad (2.3)$$

However, since we have a multiplicative noise term, there is an ambiguity with regards to the interpretation of this term from the perspective of stochastic calculus, that is, whether one should choose the Ito or Stratonovich versions. This means that the form of the corresponding FP equation is also ambiguous. [For the moment, we will assume that  $X(t) \in \mathbb{R}$  so boundary conditions can be ignored.] One way to resolve the above issue is to start with the full two-dimensional (2D) Fokker-Planck equation and to reduce it to a scalar FP equation in the limit  $\gamma \rightarrow \infty$  using an adiabatic reduction and projection

methods [9]. This yields a Fokker-Planck equation for  $x$  that is in the Stratonovich form [9]:

$$\begin{aligned} \frac{\partial \rho_\infty}{\partial t} = & -\frac{\partial}{\partial x} F(x)\rho_\infty(x,t) + D \frac{\partial^2}{\partial x^2} \rho_\infty(x,t) \\ & + \frac{1}{2} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x)\rho_\infty(x,t). \end{aligned} \quad (2.4)$$

Now suppose that  $\gamma$  is finite and treat the system given by Eqs. (2.1) and (2.2) as a two-dimensional SDE for the variables  $\alpha(t), X(t)$ . One then has to deal with the full 2D FP equation for the probability density  $p(x, \alpha, t | x_0, \alpha_0, 0)$ . This takes the form (after dropping the explicit dependence on initial conditions)

$$\begin{aligned} \frac{\partial p}{\partial t} = & \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) p - \gamma \left[ \frac{\partial}{\partial x} b(x)\alpha \right] p \\ & + \left[ -\frac{\partial}{\partial x} F(x) + D \frac{\partial^2}{\partial x^2} \right] p. \end{aligned} \quad (2.5)$$

Note that from a computational perspective, the probability  $p(x, \alpha, t)$  can be determined by numerically solving Eqs. (2.1) and (2.2) for an ensemble of independent particles each evolving in a different realization of the environment, see Fig. 1(a). It is convenient to rewrite (2.1) in the more suggestive form

$$dX = F(X, \alpha)dt + \sqrt{2D}dW(t), \quad (2.6)$$

with  $F(X, \alpha) = F(X) + \gamma b(X)\alpha(t)$  and  $\alpha$  evolving according to the OU process (2.2). We can then view  $\alpha(t)$  as some stochastic environmental variable, while  $x(t)$  is an internal state variable. For a given realization  $\sigma(t) = \{\alpha(\tau), 0 \leq \tau < t\}$  of the stochastic process  $\alpha(t)$ , Eq. (2.6) is an SDE that reduces to a deterministic, nonautonomous ordinary differential equation (ODE) when  $D = 0$  (no intrinsic noise).

Let us now consider an ensemble of identical particles labeled by  $i = 1, \dots, \mathcal{N}$  with internal variables  $X_i(t)$  all being driven by the same external or environmental variable  $\alpha(t)$ , see Fig. 1(b). Equation (2.6) becomes

$$dX_i(t) = F(X_i, \alpha(t))dt + \sqrt{2D}dW_i(t), \quad (2.7)$$

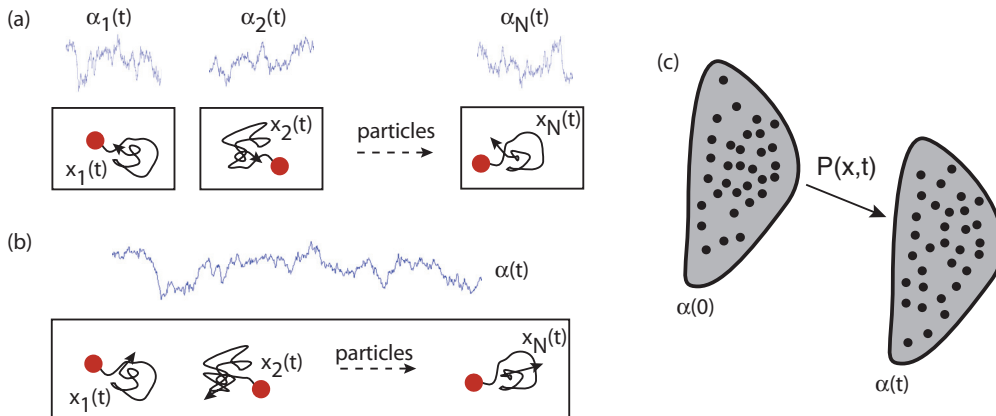


FIG. 1. Diagram illustrating the difference between the particle and population perspectives. (a) Multiple realizations of a single particle moving in a random environment generates the probability density  $p(x, \alpha, t)$ . (b) Large population ( $N \rightarrow \infty$ ) of particles evolving in a single realization  $\sigma$  of the common random environment generates the population density  $P(x, t)$ . (c) The stochastic FP equation describes the evolution of the population density  $P(x, t)$  for a given realization  $\sigma$  of the noisy input  $\alpha(t)$ .

for  $i = 1, \dots, \mathcal{N}$  and independent Wiener processes  $W_i(t)$ , with the stochastic variable  $\alpha(t)$  independent of  $i$  and evolving according to Eq. (2.2). Assume that the initial positions of the particles,  $x_i(0)$ , are randomly generated from a density  $p_0(x)$ . Take the thermodynamic limit  $\mathcal{N} \rightarrow \infty$ , and let  $P(x, t)$  denote the density of particles in state  $x$  at time  $t$  given a particular realization  $\sigma(t)$  of the OU process. The population density evolves according to the stochastic FP equation

$$\frac{\partial}{\partial t} P(x, t) = \left[ -\frac{\partial}{\partial x} F(x, \alpha(t)) + D \frac{\partial^2}{\partial x^2} \right] P(x, t), \quad (2.8)$$

with  $P(x, 0) = p_0(x)$ . An important observation is that the density  $P(x, t)$  is a random field with respect to realizations  $\sigma$ .

In the following we will refer to the deterministic FP Eq. (2.5) for  $p(x, \alpha, t)$  as representing a particle perspective, whereas the SPDE given by (2.8) for  $P(x, t)$  represents a population or continuum perspective. [This should not be confused with the distinction between particle (Lagrangian) and population (Eulerian) descriptions corresponding, respectively, to SDEs and their associated deterministic FP equations.] A similar classification has recently arisen in other problem domains. One example is the diffusion of particles in a randomly switching environment, specifically, a finite domain with randomly switching boundary conditions [1–4,6]; a related study looks at random walks in random environments [8].

### III. MOMENT EQUATIONS OF THE SPDE

Consider an ensemble of particles evolving according to Eqs. (2.7) and (2.2) in the thermodynamic limit  $\mathcal{N} \rightarrow \infty$ . For the sake of illustration, suppose that  $X \in [0, L]$  and there are reflecting boundary conditions at  $x = 0, L$ . In order to analyze the corresponding stochastic FP Eq. (2.8), we follow the approach of Ref. [2] by discretizing  $x$  using a finite-difference scheme so (2.8) is converted to a higher-level SDE. Introduce the lattice spacing  $a$  such that  $x = ja$  for  $j = 0, \dots, N+1$  with  $(N+1)a = L$ . Let  $P_j(t) = P(ja, t)$  and  $F_j(\alpha) = F(ja, \alpha) = F(ja) + \gamma b(ja)\alpha$ . Then

$$\frac{dP_i}{dt} = -\sum_{j=1}^N K_{ij}(\alpha) P_j, \quad \text{if } \alpha(t) = \alpha. \quad (3.1)$$

Away from the boundaries ( $i \neq 1, N$ ),

$$K_{ij}(\alpha) = \frac{1}{a} [\delta_{i,j-1} - \delta_{i,j}] F_j(\alpha) - \Delta_{ij}, \quad (3.2)$$

where  $\Delta_{ij}$  is the discrete Laplacian

$$\Delta_{ij} = \frac{D}{a^2} [\delta_{i,j+1} + \delta_{i,j-1} - 2\delta_{i,j}]. \quad (3.3)$$

At the two ends we have

$$u_1 F_1(\alpha) - \frac{D}{a} [u_1 - u_0] = 0,$$

$$u_{N+1} F_{N+1}(\alpha) - \frac{D}{a} [u_{N+1} - u_N] = 0.$$

These boundary conditions can be implemented by taking

$$K_{1j}(\alpha) = \frac{F_2(\alpha)}{a} \delta_{2,j} - \frac{D}{a^2} [\delta_{2,j} - \delta_{1,j}]$$

and

$$K_{Nj}(\alpha) = -\frac{F_N(\alpha)}{a} \delta_{N,j} - \frac{D}{a^2} [\delta_{N-1,j} - \delta_{N,j}].$$

Let  $\mathbf{P}(t) = (P_j(t), j = 1, \dots, N)$  and introduce the joint probability density

$$\varrho(\mathbf{P}, \alpha, t) d\mathbf{P} d\alpha = \mathbb{P}[\mathbf{P}(t) \in (\mathbf{P}, \mathbf{P} + d\mathbf{P}), \alpha(t) \in \{\alpha, \alpha + d\alpha\}], \quad (3.4)$$

where we have dropped the explicit dependence on initial conditions. The resulting FP equations for the SDE given by Eqs. (3.1) and (2.2) is

$$\begin{aligned} \frac{\partial \varrho}{\partial t} = & \sum_{i=1}^N \frac{\partial}{\partial P_i} \left[ \left( \sum_{j=1}^N K_{ij}(\alpha) P_j \right) \varrho(\mathbf{P}, \alpha, t) \right] \\ & + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) \varrho(\mathbf{P}, \alpha, t). \end{aligned} \quad (3.5)$$

Since the FP Eq. (3.5) is linear in  $\varrho$ , we can derive a closed set of equations for the moments of  $\varrho$ . (Discretizing space allows us to avoid dealing with a functional FP equation.)

First, let

$$V_j(\alpha, t) = \mathbb{E}_\sigma [P_j(t) 1_{\alpha(t)=\alpha}] = \int \varrho(\mathbf{P}, \alpha, t) P_j(t) d\mathbf{P}, \quad (3.6)$$

where

$$\int F(\mathbf{P}) d\mathbf{P} = \left[ \prod_{i=1}^N \int_0^\infty dP_i \right] f(\mathbf{P}).$$

The subscript  $\sigma$  denotes taking expectations with respect to realizations of the OU process. Multiplying both sides of Eq. (3.5) by  $P_k(t)$  and integrating by parts with respect to  $\mathbf{P}$  gives [for  $\varrho(\mathbf{P}, \alpha, t) \rightarrow 0$  as  $\mathbf{P} \rightarrow \infty$ ]

$$\frac{\partial V_k}{\partial t} = -\sum_{j=1}^N K_{kj}(\alpha) V_j + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) V_k.$$

We have assumed that the initial variable  $\alpha(0)$  is distributed according to the stationary distribution  $p_s(\alpha)$ . If we now retake the continuum limit  $a \rightarrow 0$ , then we obtain the FP equation

$$\frac{\partial V}{\partial t} = \left[ -\frac{\partial}{\partial x} F(x, \alpha) + D \frac{\partial^2}{\partial x^2} \right] V + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) V, \quad (3.7)$$

for  $V(x, \alpha, t) = \mathbb{E}_\sigma [P(x, t) 1_{\alpha(t)=\alpha}]$ .

Next we consider the second-order moments

$$\begin{aligned} C_{kl}(\alpha, t) &= \mathbb{E}_\sigma [P_k(t) P_l(t) 1_{\alpha(t)=\alpha}] \\ &= \int \varrho(\mathbf{P}, \alpha, t) P_k(t) P_l(t) d\mathbf{P}. \end{aligned}$$

Multiplying both sides of Eq. (3.5) by  $P_k(t) P_l(t)$  and integrating by parts with respect to  $\mathbf{P}$  gives

$$\begin{aligned} \frac{dC_{kl}}{dt} = & -\sum_{j=1}^N K_{kj}(\alpha) C_{jl} - \sum_{j=1}^N K_{lj}(\alpha) C_{jk} \\ & + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) C_{kl}. \end{aligned}$$

If we now retake the continuum limit  $a \rightarrow 0$ , then we obtain an FP equation for the equal-time two-point correlations,

$$C(x, y, \alpha, t) = \mathbb{E}_\sigma[P(x, t)P(y, t)1_{\alpha(t)=\alpha}], \quad (3.8)$$

given by

$$\begin{aligned} \frac{\partial C}{\partial t} = & -\frac{\partial}{\partial x}(F(x, \alpha)C) - \frac{\partial}{\partial y}(F(y, \alpha)C) \\ & + D\frac{\partial^2 C}{\partial x^2} + D\frac{\partial^2 C}{\partial y^2} + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) C. \end{aligned} \quad (3.9)$$

Similarly, the  $r$ th moments of  $\varrho$ ,  $r > 2$ , are

$$C^{(r)}(x_1, \dots, x_r, \alpha, t) \equiv \mathbb{E}_\sigma[P(x_1, t) \cdots P(x_r, t)1_{\alpha(t)=\alpha}]$$

and evolve according to an  $r$ -dimensional FP equation.

Formally speaking, Eq. (3.7) for the first-order moments  $V(x, \alpha, t)$  is identical in form to the deterministic FP Eq. (2.5) for the single-particle probability density  $p(x, \alpha, t)$ . Similarly, Eq. (3.9) for the second moment  $C(x, y, \alpha, t)$  is identical in form to the FP equation that would be written down for the joint probability density of two particles with positions  $x$  and  $y$  at time  $t$ . More generally,  $C^{(r)}$  is related to the joint probability density of  $r$  particles. [The latter would correspond to having  $r$  particles in each of the boxes in Fig. 1(a).] However, these two representations are not equivalent, particularly in the case of bounded domains [2]. From a physical perspective, there is a much wider class of boundary conditions that one can impose on the SPDE (2.8) compared to the SDE (2.1) or its finite-particle extension (2.7). This reflects the fact that particle conservation need not hold at the SPDE level. For example, if  $X \in [0, L]$ , then one could impose an inhomogeneous boundary condition at  $x = L$ , say, of the form (i)  $P(L, t) = \eta$  or (ii)  $J(L, t) = \eta$ , where

$$J(x, t) = \left[ F(x) + \gamma \alpha(t) b(x) - D \frac{\partial}{\partial x} \right] P(x, t). \quad (3.10)$$

These represent, respectively, maintenance of a bath of particles or a constant flux at  $x = L$ , which does not make sense at the single-particle level. One of the major benefits of the discretization scheme used to derive Eq. (3.5) is that boundary conditions can be absorbed into the discrete operator  $K_{ij}(\alpha)$ . Hence, the boundary conditions are maintained when one takes moments and retakes the continuum limit  $a \rightarrow 0$ .

#### IV. STEADY-STATE SOLUTIONS OF MOMENT EQUATIONS

In this section we use a combination of perturbation theory and Green's functions to obtain general approximate expressions for the steady-state solutions of the first-order and second-order moment Eqs. (3.7) and (3.9), respectively.

##### A. Perturbation expansion in $\gamma^{-1}$

We begin by carrying out a perturbation series expansion in the small parameter  $\epsilon = \gamma^{-1}$  for large  $\gamma$ . We use a more direct method than the use of projection operators in Ref. [9] and include higher-order terms. Suppose that we rescale time according to  $\tau = \gamma^2 t$  and set  $\epsilon = \gamma^{-1}$ . [We nondimensionalize time by taking the relaxation dynamics of the ODE  $\dot{x} = F(x)$

to be  $O(1)$ .] Equation (3.7) for the first-order moments  $V(x, \alpha, t)$  now becomes

$$\frac{\partial V}{\partial \tau} = \mathbb{L}_\epsilon V \equiv (\mathbb{L}_1 + \epsilon \mathbb{L}_2 + \epsilon^2 \mathbb{L}_3) V, \quad (4.1)$$

with the operators  $\mathbb{L}_j$  given by

$$\mathbb{L}_1 = \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2}, \quad (4.2a)$$

$$\mathbb{L}_2 = -\frac{\partial}{\partial x} b(x) \alpha, \quad (4.2b)$$

$$\mathbb{L}_3 = -\frac{\partial}{\partial x} F(x) + D \frac{\partial^2}{\partial x^2}. \quad (4.2c)$$

In the limit  $\epsilon \rightarrow 0$ , we obtain the steady-state equation  $\mathbb{L}_1 V = 0$ , which has the (normalized solution)  $V(x, \alpha) = e^{-\alpha^2} / \sqrt{\pi}$ . In order to solve the corresponding steady-state equation  $\mathbb{L}_\epsilon V = 0$  for  $\epsilon > 0$ , we will carry out a perturbation expansion of  $V$  in terms of the eigenvalues  $\lambda$  and eigenfunctions  $\phi_\lambda$  of the linear operator  $\mathbb{L}_1$  for the OU process:

$$\mathbb{L}_1 \phi_\lambda(\alpha) = -\lambda \phi_\lambda(\alpha).$$

Noting that this eigenvalue equation can be transformed into a time-independent Schrodinger equation with a harmonic potential, one obtains a discrete spectrum with  $\lambda_n = n = 0, 1, 2, \dots$  and

$$\phi_n(\alpha) = \sqrt{\frac{1}{2^n n! \pi}} e^{-\alpha^2} H_n(\alpha), \quad (4.3)$$

where  $H_n(\alpha)$  are Hermite polynomials. In particular, the first few polynomials are

$$H_0(\alpha) = 1, \quad H_1(\alpha) = 2\alpha, \quad H_2(\alpha) = 4\alpha^2 - 2. \quad (4.4)$$

It is also necessary to determine the eigenfunction  $\psi_n$  of the adjoint operator  $\mathbb{L}_1^\dagger$ , defined by

$$\mathbb{L}_1^\dagger \psi_n = -\lambda_n \psi_n, \quad \mathbb{L}_1^\dagger = -\alpha \frac{\partial}{\partial \alpha} + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2}.$$

It is easy to show that  $\psi_n$  and  $\phi_n$  are related according to

$$\phi_n(\alpha) = p_s(\alpha) \psi_n(\alpha), \quad p_s(\alpha) = \sqrt{\frac{1}{\pi}} e^{-\alpha^2}, \quad (4.5)$$

and satisfy the biorthogonality relation

$$\int_{-\infty}^{\infty} \psi_n(\alpha) \phi_m(\alpha) d\alpha = \delta_{n,m}.$$

In particular, setting  $n = 0$  or  $n = 1$ , we have the normalization conditions

$$\int_{-\infty}^{\infty} \phi_m(\alpha) d\alpha = \delta_{m,0}, \quad \int_{-\infty}^{\infty} \alpha \phi_m(\alpha) d\alpha = \frac{1}{\sqrt{2}} \delta_{m,1}. \quad (4.6)$$

We now introduce the following perturbation series expansion of the steady-state solution of Eq. (4.1):

$$\begin{aligned} V(x, \alpha) = & A_0(x) \phi_0(\alpha) + \sum_m \phi_m(\alpha) [\epsilon A_m^{(1)}(x) \\ & + \epsilon^2 A_m^{(2)}(x) + O(\epsilon^3)]. \end{aligned} \quad (4.7)$$

Substituting Eq. (4.7) into Eq. (4.1) and collecting  $O(\varepsilon)$  terms gives

$$\sum_m m A_m^{(1)}(x) \phi_m(\alpha) = \mathbb{L}_2 A_0(x) \phi_0(\alpha). \quad (4.8)$$

Multiplying Eq. (4.8) by the adjoint  $\psi_k(\alpha)$ , integrating with respect to  $\alpha$  and using Eq. (4.2b) yields ( $k \neq 0$ )

$$A_k^{(1)}(x) = -\frac{R_{0k}}{k} \frac{\partial}{\partial x} b(x) A_0(x). \quad (4.9)$$

Note that we have used the completeness of the eigenfunctions  $\phi_n(x)$  to write

$$\alpha \phi_n(\alpha) = \sum_l R_{nl} \phi_l(\alpha). \quad (4.10)$$

Proceeding to  $O(\varepsilon^2)$  we obtain the equation

$$\sum_m m \phi_m(\alpha) A_m^{(2)}(x) = \mathbb{L}_2 \left( \sum_m \phi_m(\alpha) A_m^{(1)}(x) \right) + \phi_0(\alpha) \mathbb{L}_3 A_0(x). \quad (4.11)$$

Again taking the inner product with respect to  $\phi_k(\alpha)$ , and using Eqs. (4.2b), (4.2c), and the expansion (4.10), we have

$$-k A_k^{(2)}(x) = \sum_m R_{mk} \frac{\partial}{\partial x} b(x) A_m^{(1)}(x) - \delta_{k,0} \mathbb{L}_3 A_0(x). \quad (4.12)$$

Substituting for  $A_m^{(1)}$  shows that for  $k \neq 0$  we have

$$\begin{aligned} A_k^{(2)}(x) &= \mathbb{L}_k^{(2)} A_0(x) \\ &= \left[ \sum_{m \neq 0} \frac{R_{0m} R_{mk}}{km} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x) \right] A_0(x). \end{aligned} \quad (4.13)$$

Similarly, setting  $k = 0$  in Eq. (4.12) yields a differential equation for  $A_0(x)$ :

$$\mathbb{L}_3 A_0(x) = \sum_{m \neq 0} \frac{R_{0m} R_{m0}}{m} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x) A_0(x). \quad (4.14)$$

In the case of an OU process, one can use standard recursion relations for Hermite polynomials to show that

$$R_{nm} = R_{mn} = \delta_{n,m-1} \sqrt{\frac{n+1}{2}} + \delta_{n,m+1} \sqrt{\frac{n}{2}}, \quad (4.15)$$

and  $\sum_{m \neq 0} R_{0m} R_{m0} / m = 1/2$ . Comparing Eq. (4.14) with the Stratonovich FP Eq. (2.4) we deduce that  $A_0(x) = V_\infty(x)$ , where  $V_\infty(x)$  is the steady-state solution of the latter. Finally, combining Eqs. (4.7), (4.9), and (4.13), we obtain the following approximation of the steady-state solution of Eq. (4.1):

$$\begin{aligned} V(x, \alpha) &= \left\{ \phi_0(\alpha) - \varepsilon \sum_{n>0} \phi_n(\alpha) \left[ \frac{R_{0n}}{n} \frac{\partial}{\partial x} b(x) \right. \right. \\ &\quad \left. \left. - \varepsilon \sum_{m \neq n} \frac{R_{0m} R_{mn}}{nm} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x) \right] \right\} V_\infty(x). \end{aligned} \quad (4.16)$$

Multiplying Eq. (4.16) by  $\alpha^l$ ,  $l = 0, 1$ , integrating with respect to  $\alpha$ , and using Eq. (4.6) gives

$$\begin{aligned} \int_{-\infty}^{\infty} V(x, \alpha) d\alpha &= V_\infty(x), \\ \int_{-\infty}^{\infty} \alpha V(x, \alpha) d\alpha &= -\frac{1}{2} \frac{\partial}{\partial x} b(x) V_\infty(x), \end{aligned} \quad (4.17)$$

which hold for all  $\gamma$ . Incidentally, these results provide an alternative derivation of the (steady-state) Stratonovich FP Eq. (2.4), based on integrating (2.4) with respect to  $\alpha$ . Finally, using Eqs. (4.4) and (4.15),

$$\begin{aligned} V(x, \alpha) &= p_s(\alpha) \left\{ 1 - \varepsilon \alpha \frac{\partial}{\partial x} b(x) \right. \\ &\quad \left. + \varepsilon^2 \left[ \frac{2\alpha^2 - 1}{4} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x) \right] \right\} V_\infty(x). \end{aligned} \quad (4.18)$$

It is straightforward to extend the above perturbation analysis to steady-state solution of Eq. (3.9) and we find that

$$\begin{aligned} C(x, y, \alpha) &= p_s(\alpha) \left\{ 1 - \varepsilon \alpha \left[ \frac{\partial}{\partial x} b(x) + \frac{\partial}{\partial y} b(y) \right] \right. \\ &\quad \left. + \varepsilon^2 \frac{2\alpha^2 - 1}{4} \left[ \frac{\partial}{\partial x} b(x) + \frac{\partial}{\partial y} b(y) \right]^2 \right\} C_\infty(x, y), \end{aligned} \quad (4.19)$$

where

$$C_\infty(x, y) = \int_{-\infty}^{\infty} C(x, y, \alpha) d\alpha$$

is the steady-state solution of the two-dimensional Stratonovich equation

$$\begin{aligned} \frac{\partial C_\infty}{\partial t} &= \left[ -\frac{\partial}{\partial x} F(x) - \frac{\partial}{\partial y} F(y) + D \frac{\partial^2}{\partial x^2} + D \frac{\partial^2}{\partial y^2} \right] C_\infty \\ &\quad + \frac{1}{2} \frac{\partial}{\partial x} b(x) \frac{\partial}{\partial x} b(x) C_\infty + \frac{1}{2} \frac{\partial}{\partial y} b(y) \frac{\partial}{\partial y} b(y) C_\infty \\ &\quad + \frac{\partial}{\partial y} b(y) \frac{\partial}{\partial x} b(x) C_\infty. \end{aligned} \quad (4.20)$$

[The latter could also be derived by extending the projection method of Gardiner [9] to the second-order FP Eq. (3.9).] The mixed-derivative terms in Eqs. (4.19) and (4.20) reflect the emergence of statistical correlations due to the randomly switching environment: it prevents us from decomposing the solution into the product form  $C_\infty(x, y, t) = V_\infty(x, t) V_\infty(y, t)$  where  $V$  is the solution to Eq. (3.7).

## B. Eigenfunction expansion for $C_\infty$

So far we have expressed the steady-state solutions of the first-order and second-order moment equations in terms of a perturbation expansion with respect to  $\gamma^{-1}$ , which takes the form of a linear operator acting on the steady-state solution ( $V_\infty$  or  $C_\infty$ ) of the corresponding Stratonovich FP equation obtained in the limit  $\gamma \rightarrow \infty$ . When dealing with second-order (and higher-order) moment equations, one has to solve a multivariate FP equation, which generally does not have an explicit solution. However, in certain limits, it is possible to

proceed using another form of eigenfunction expansion. In order to illustrate this, consider the stochastic FP Eq. (2.8) on the bounded domain  $[0, L]$  with boundary conditions

$$P(0, t) = 0, \quad P(L, t) = \eta,$$

and additive environmental noise,  $b(x) = \sqrt{2\sigma}$ . Set  $D_{\text{eff}} = D + \sigma$ . We proceed by finding the steady-state solutions of Eqs. (2.4) and (4.20) for  $p_\infty = V_\infty$  and  $C_\infty$ . First, Eq. (2.4) becomes

$$0 = -\frac{d}{dx}F(x)V_\infty(x) + D_{\text{eff}}\frac{d^2}{dx^2}V_\infty(x), \quad (4.21)$$

with  $V_\infty(0) = 0$  and  $V_\infty(L) = \eta$ . Integrating once yields

$$\frac{dV_\infty}{dx} - \frac{F(x)}{D_{\text{eff}}}V_\infty = \frac{J_0}{D_{\text{eff}}},$$

where the integration constant  $J_0$  is the flux flowing from the right to the left boundary. Setting  $F(x) = -U'(x)$ , integrating again, and using the boundary conditions shows that

$$V_\infty(x) = \eta \exp\left[\frac{-[U(x) - U(L)]}{D_{\text{eff}}}\right] \frac{\int_0^x e^{U(y)/D_{\text{eff}}} dy}{\int_0^L e^{U(y)/D_{\text{eff}}} dy}. \quad (4.22)$$

Next, Eq. (4.20) becomes

$$0 = -\frac{\partial}{\partial x}F(x)C_\infty - \frac{\partial}{\partial y}F(y)C_\infty + D_{\text{eff}}\frac{\partial^2 C_\infty}{\partial x^2} + D_{\text{eff}}\frac{\partial^2 C_\infty}{\partial y^2} + 2\sigma\frac{\partial^2 C_\infty}{\partial y\partial x}, \quad (4.23)$$

with the boundary conditions  $C_\infty(x, 0) = C_\infty(0, y) = 0$  and  $C_\infty(x, L) = \eta V_\infty(x)$ ,  $C_\infty(L, y) = \eta V_\infty(y)$ . Unfortunately, the give boundary value problem cannot be solved explicitly. (For an example that can be solved, see Sec. V.) Therefore, we will proceed using a perturbation expansion in the noise term  $\sigma$ . That is, we set

$$C_\infty(x, y) = V_\infty(x)V_\infty(y) + \sigma\phi(x, y) + O(\sigma^2)$$

and substitute into (4.23). Collecting  $O(\sigma)$  terms yields

$$0 = -\frac{\partial}{\partial x}F(x)\phi - \frac{\partial}{\partial y}F(y)\phi + D_{\text{eff}}\frac{\partial^2 \phi}{\partial x^2} + D_{\text{eff}}\frac{\partial^2 \phi}{\partial y^2} + 2\frac{\partial V_\infty(y)}{\partial y}\frac{\partial V_\infty(x)}{\partial x}, \quad (4.24)$$

with boundary conditions  $\phi(0, y) = \phi(x, 0) = \phi(L, y) = \phi(x, L) = 0$ . Equation (4.24) can be solved using Green's functions.

Let

$$\mathbb{L}_x = \frac{\partial}{\partial x}F(x) + D_{\text{eff}}\frac{\partial^2}{\partial x^2}$$

and consider the following eigenvalue equation on  $[0, L]$ :

$$\mathbb{L}_x \Phi_n(x) = \lambda_n \Phi_n(x),$$

for integers  $n$  with the boundary conditions  $\Phi(x) = 0 = \Phi(L)$ . Clearly,  $\lambda_n \neq 0$  for all  $n$ . We can now rewrite Eq. (4.24) as

$$\mathbb{L}_x \phi(x, y) + \mathbb{L}_y \phi(x, y) = \Sigma(x, y) \equiv -2\frac{\partial V_\infty(y)}{\partial y}\frac{\partial V_\infty(x)}{\partial x}.$$

Next, consider the eigenvalue equation

$$\mathbb{L}_x \phi(x, y) + \mathbb{L}_y \phi(x, y) = \Lambda \phi(x, y).$$

This can be solved using separation of variables:  $\phi(x, y) = A(x)B(y)$  such that

$$\mathbb{L}_x A(x) = CA(x), \quad \mathbb{L}_y B(y) = (C - \Lambda)B(y),$$

for some constant  $C$ . It follows that  $A(x) = \Phi_n(x)$  and  $B(y) = \Phi_m(y)$  for integers  $m, n$  with  $C = \lambda_n$  and  $C - \Lambda = \lambda_m$ , that is,  $\Lambda = \lambda_m + \lambda_n$ . Assuming that the eigenfunctions  $\Phi_n(x)$  form a complete biorthonormal set on  $[0, L]$ , we can write down an eigenfunction expansion for the Green's function of the operator  $\mathbb{L}_x + \mathbb{L}_y$ :

$$(\mathbb{L}_x + \mathbb{L}_y)G(x, y|x_0, y_0) = \delta(x - x_0)\delta(y - y_0),$$

with  $G$  vanishing at  $x = 0, L$  and  $y = 0, L$ . That is,

$$G(x, y|x_0, y_0) = \sum_{n,m} \frac{\Phi_n(x)\Phi_n(x_0)\Phi_m(y)\Phi_m(y_0)}{\lambda_n + \lambda_m}. \quad (4.25)$$

Given the Green's function  $G$ , the  $O(\sigma)$  contribution to the second moment is

$$\phi(x, y) = \int_0^L \int_0^L G(x, y|x_0, y_0)\Sigma(x_0, y_0)dx_0dy_0. \quad (4.26)$$

Combining our various results we find that to  $O(\sigma)$

$$C_\infty(x, y) = V_\infty(x)V_\infty(y) + \sigma \sum_{n,m} C_n C_m \frac{\Phi_n(x)\Phi_n(y)}{\lambda_n + \lambda_m}, \quad (4.27)$$

where

$$C_n = \left[ \int_0^L \Phi_n(z) \frac{\partial V_\infty(z)}{\partial z} dz \right]. \quad (4.28)$$

## V. STOCHASTIC SYNCHRONIZATION OF AN ENSEMBLE OF POPULATION OSCILLATORS

So far we have considered one-dimensional particle dynamics,  $X(t) \in \mathbb{R}$ . However, all of the analysis carries over to higher spatial dimensions where more complicated dynamics can occur in the deterministic limit, in particular limit cycle oscillations. The  $d$ -dimensional version of Eq. (2.7) is

$$dX_j^\mu = F_\mu(\mathbf{X}_j)dt + \gamma b_\mu(\mathbf{X}_j)\alpha(t)dt + \sqrt{2D}dW_j^\mu(t) \quad (5.1)$$

for  $j = 1, \dots, \mathcal{N}$  and  $\mu = 1, \dots, d$ , where  $\mu$  labels the components of the vector  $\mathbf{X}_j \in \mathbb{R}^d$  for the  $j$ th particle. We associate an independent set of Wiener processes  $W_j^\mu, \mu = 1, \dots, d$  with each particle (independent noise) but take the extrinsic environmental noise to be given by a common OU

process  $\alpha(t)$  evolving according to Eq. (2.2). Hence,

$$\langle dW_k^\mu(t)dW_l^\nu(t') \rangle = \delta_{k,l}\delta_{\mu,\nu}\delta(t-t')dt, \quad (5.2)$$

$$\langle dW_k^\mu(t)d\widehat{W}(t) \rangle = 0. \quad (5.3)$$

SDEs of the form (5.1) have been the starting point for a number of recent studies of noise-induced synchronization of uncoupled limit cycle oscillators [11–18]. Here  $\mathbf{X}_j$  represents a set of state variables for a single oscillator, which could be the concentrations of reacting chemical species in the case of a chemical oscillator or voltage and ion-channel gating variables in the case of neural oscillators. It is assumed that the deterministic ODE,  $\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x})$ , supports a stable limit cycle. Most previous studies of noise-induced synchronization have taken the white-noise limit  $\gamma \rightarrow \infty$  and have carried out a stochastic phase reduction of the resulting SDEs for finite  $\mathcal{N}$ , taking care of the subtle features of stochastic calculus. One exception is Ref. [15], where the authors carry out a careful phase reduction of a single-limit-cycle oscillator with colored external noise, which takes into account the different time scales of the system. Here we will also keep  $\gamma$  finite and explore the issue of noise-induced synchronization from the perspective of stochastic FP equations.

### A. Stochastic phase reduction

Introduce the phase variable  $\theta \in (-\pi, \pi]$  such that the dynamics of an individual limit cycle oscillator (in the absence of noise) reduces to the simple phase equation  $\dot{\theta} = \omega$ , where  $\omega = 2\pi/T$  is the natural frequency of the oscillator and denote the limit cycle solution by  $\mathbf{x} = \mathbf{x}^*[\theta(t)]$ . The phase reduction method [19,20] exploits the observation that the notion of phase can be extended into a neighborhood  $\mathcal{M} \subset \mathbb{R}^d$  of each deterministic limit cycle, that is, there exists an isochronal mapping  $\Psi : \mathcal{M} \rightarrow [-\pi, \pi]$  with  $\theta = \Psi(\mathbf{x})$ . This allows us to define a stochastic phase variable according to  $\Theta_j(t) = \Psi_j(t) \in [-\pi, \pi]$  with  $\mathbf{X}_j(t)$  evolving according to Eq. (5.1). Since the extrinsic noise is colored and the intrinsic noise is additive, we do not have to worry about Ito vs. Stratonovich in carrying out the phase reduction. However, it is necessary to take the noise terms to be sufficiently weak so the probability of large deviations from the attracting limit cycle can be ignored. We thus obtain the stochastic phase equations [11,13,15]:

$$d\Theta_j = \omega + \epsilon \sum_{\mu=1}^d Z_\mu(\Theta_j) [\gamma b_\mu(\Theta_j) \alpha(t) dt + \sqrt{2D} dW_j^\mu]. \quad (5.4)$$

Here  $Z_\mu(\theta)$  is the  $\mu$ th component of the infinitesimal phase resetting curve (PRC) defined as

$$Z_\mu(\theta) = \left. \frac{\partial \Psi(\mathbf{x})}{\partial x_\mu} \right|_{\mathbf{x}=\mathbf{x}^*(\theta)} \quad (5.5)$$

with  $\sum_{\mu=1}^d Z_\mu(\theta) F_{\mu,s}[\mathbf{x}^*(\theta)] = \omega$ . We have also scaled the intrinsic and extrinsic noise terms by a small factor  $\epsilon$  to ensure that we are operating in the weak-noise regime. (This factor is distinct from  $\varepsilon = \gamma^{-1}$ .) All the terms multiplying  $Z_k(\theta)$  are evaluated on the limit cycle. Note that Eq. (5.4) is valid provided that the rate of relaxation  $\gamma_p$  to the limit cycle is must faster than the relaxation rate  $\gamma$  of the colored noise [15]. Now

introduce the joint probability density  $p(\boldsymbol{\theta}, \alpha, t)$  according to  $p(\boldsymbol{\theta}, \alpha, t) d\boldsymbol{\theta} d\alpha = \mathbb{P}[\boldsymbol{\theta} < \boldsymbol{\Theta}(t) < \boldsymbol{\theta} + d\boldsymbol{\theta}, \alpha < \alpha(t) < \alpha + d\alpha]$ .

This satisfies the multivariate FP equation of the form

$$\begin{aligned} \frac{\partial p(\boldsymbol{\theta}, \alpha, t)}{\partial t} = & - \sum_{j=1}^{\mathcal{N}} \frac{\partial}{\partial \theta_j} [\mathcal{F}(\theta_j, \alpha) p(\boldsymbol{\theta}, \alpha, t)] \\ & + \epsilon^2 D \sum_{j=1}^{\mathcal{N}} \frac{\partial^2 p(\boldsymbol{\theta}, \alpha, t)}{\partial \theta_j^2} \\ & + \gamma^2 \left( \frac{\partial}{\partial \alpha} \alpha + \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} \right) p(\boldsymbol{\theta}, \alpha, t), \end{aligned} \quad (5.6)$$

where

$$\mathcal{F}(\boldsymbol{\theta}, \alpha) = \omega + \gamma \epsilon B(\boldsymbol{\theta}) \alpha \quad (5.7)$$

and

$$B(\boldsymbol{\theta}) = \sum_{\mu=1}^d Z_\mu(\boldsymbol{\theta}) b_\mu(\boldsymbol{\theta}). \quad (5.8)$$

Applying the projection method of Gardiner [9], we can also derive a Stratonovich FP equation for

$$\rho(\boldsymbol{\theta}, t) = \lim_{\gamma \rightarrow \infty} p(\boldsymbol{\theta}, \alpha, t)$$

given by

$$\begin{aligned} \frac{\partial \rho(\boldsymbol{\theta}, t)}{\partial t} = & - \sum_{j=1}^{\mathcal{N}} \frac{\partial}{\partial \theta_j} [\omega \rho(\boldsymbol{\theta}, t)] + \epsilon^2 D \sum_{j=1}^{\mathcal{N}} \frac{\partial^2 p(\boldsymbol{\theta}, \alpha, t)}{\partial \theta_j^2} \\ & + \frac{\epsilon^2}{2} \sum_{i,j=1}^{\mathcal{N}} \frac{\partial}{\partial \theta_i} B(\theta_i) \frac{\partial}{\partial \theta_j} B(\theta_j) \rho(\boldsymbol{\theta}, t). \end{aligned} \quad (5.9)$$

One could also derive higher-order corrections to Eq. (5.9) by carrying out a perturbation-expansion in  $\gamma^{-1}$  along the lines highlighted in Sec. IV. Note that  $\rho(\boldsymbol{\theta}, t)$  satisfies periodic boundary conditions on the  $\mathcal{N}$ -torus  $[-\pi, \pi]^{\mathcal{N}}$ .

### B. Phase averaging

Having obtained the FP Eq. (5.9), we can now carry out the averaging procedure of Nakao *et al.* [13]. The basic idea is to introduce the slow phase variables  $\boldsymbol{\psi} = (\psi_1, \dots, \psi_{\mathcal{N}})$  according to  $\theta_j = \omega t + \psi_j$  and set  $Q(\boldsymbol{\psi}, t) = \rho(\omega t \mathbf{1} + \boldsymbol{\psi}, t)$  with  $\mathbf{1} = (1, 1, \dots, 1)$ . For sufficiently weak noise (small  $b_\mu$  and  $D$ ),  $Q$  is a slowly varying function of time so we can average Eq. (5.6) for  $Q$  over one cycle of length  $T = 2\pi/\omega$ . [One cannot apply averaging to Eq. (5.6), due to the  $\gamma^2$  term.] In order to carry out the averaging procedure, we first convert (3.9) into the Ito form

$$\begin{aligned} \frac{\partial \rho(\boldsymbol{\theta}, t)}{\partial t} = & - \sum_{j=1}^{\mathcal{N}} \frac{\partial}{\partial \theta_j} [\omega + \epsilon^2 B'(\theta_j)] \rho(\boldsymbol{\theta}, t) \\ & + \epsilon^2 D \sum_{j=1}^{\mathcal{N}} \frac{\partial^2 \rho(\boldsymbol{\theta}, t)}{\partial \theta_j^2} \\ & + \frac{\epsilon^2}{2} \sum_{i,j=1}^{\mathcal{N}} \frac{\partial}{\partial \theta_i} \frac{\partial}{\partial \theta_j} B(\theta_i) B(\theta_j) \rho(\boldsymbol{\theta}, t). \end{aligned} \quad (5.10)$$

The averaged FP equation for  $Q$  is then

$$\frac{\partial Q(\boldsymbol{\psi}, t)}{\partial t} = \sum_{i,j=1}^{\mathcal{N}} \frac{\partial^2}{\partial \psi_i \partial \psi_j} [D(\psi_i, \psi_j) Q(\boldsymbol{\psi}, t)], \quad (5.11)$$

where we have absorbed the factor  $\epsilon^2$  into  $t$  and

$$D(\psi_i, \psi_j) = g(\psi_i - \psi_j) + D\delta_{i,j} \quad (5.12)$$

with

$$g(\psi) = \frac{1}{4\pi} \int_{-\pi}^{\pi} B(\theta') B(\theta' + \psi) d\theta'. \quad (5.13)$$

Following Nakao *et al.* [13] and Ly and Ermentrout [16], one can now investigate the role of common environmental noise on the synchronization of a pair of oscillators. Setting  $\mathcal{N} = 2$  in Eq. (5.11) gives

$$\begin{aligned} \frac{\partial Q}{\partial t} &= (g(0) + D) \left[ \left( \frac{\partial}{\partial \psi_1} \right)^2 + \left( \frac{\partial}{\partial \psi_2} \right)^2 \right] Q \\ &+ \frac{\partial^2}{\partial \psi_1 \partial \psi_2} [g(\psi_1 - \psi_2) Q]. \end{aligned}$$

Performing the change of variables

$$\psi = (\psi_1 + \psi_2)/2, \quad \phi = \psi_1 - \psi_2$$

and writing  $Q(\psi_1, \psi_2, t) = \Psi(\psi, t)\Phi(\phi, t)$ , we obtain the pair of PDEs

$$\frac{\partial \Psi}{\partial t} = \frac{1}{2} [g(0) + g(\phi) + D] \frac{\partial^2 \Psi}{\partial \psi^2}$$

and

$$\frac{\partial \Phi}{\partial t} = 2 \frac{\partial^2}{\partial \phi^2} [g(0) - g(\phi) + D] \Phi.$$

These have the steady-state solution [13]

$$\Psi_s(\psi) = \frac{1}{2\pi}, \quad \Phi_s(\phi) = \frac{\Gamma_0}{[g(0) - g(\phi)] + D}, \quad (5.14)$$

where  $\Gamma_0$  is a normalization constant. A number of important results follow from (5.14). First, in the absence of a common extrinsic noise source ( $g \equiv 0$ ) and  $D > 0$ ,  $\Phi_0(\phi)$  is a uniform distribution, which means that the oscillators are completely desynchronized. On the other hand, if  $D = 0$  (no intrinsic noise), then the distribution  $\Phi_0(\phi)$  diverges at  $\theta = 0$  while keeping positive since it can be shown that  $g(0) \geq g(\theta)$  [13]. Hence, the phase difference between any pair of oscillators accumulates at zero, resulting in complete noise-induced synchronization.

### C. SPDE perspective

The analysis carried out in Sec. VA and VB was from the particle perspective, in which deterministic FP equations were derived for the joint probability densities of  $\mathcal{N}$  uncoupled oscillators evolving in the same environment. Thus Eqs. (5.6) and (5.9) for  $\mathcal{N} = 2$  are the analogs of the second-order moment Eqs. (3.9) and (4.20). An additional feature of the phase oscillator model is that under an appropriate separation of time scales, one can use phase averaging to solve the associated multivariate FP equation. However, one limitation

of the above analysis is that noise-induced synchronization was established after averaging over multiple realizations of the environmental noise. A stronger result is to show that a population of oscillators synchronizes within a single realization of the random environment. This can be achieved using the population or SPDE perspective.

Consider the phase-reduced SDE (5.4) for a given realization  $\sigma(t) = \{\alpha(\tau), 0 \leq \tau < t\}$  of the stochastic process  $\alpha(t)$ . Suppose that the initial phase of the oscillators,  $\Theta_j(0)$ , are randomly generated from a density  $p_0(\theta)$ . Taking the thermodynamic limit, the resulting population density  $P(\theta, t)$  evolves according to the stochastic FP equation

$$\frac{\partial P(\theta, t)}{\partial t} = -\frac{\partial}{\partial \theta} [\mathcal{F}(\theta, \alpha(t)) P(\theta, t)] + \epsilon^2 D \frac{\partial^2 P(\theta, t)}{\partial \theta^2} \quad (5.15)$$

with  $\mathcal{F}(\theta, \alpha)$  given by Eq. (5.7), and  $P(\theta, t)$  represents the density of oscillators that have the phase  $\theta$  at time  $t$ . As in the 1D case, we have the mapping

$$p(\theta_1, \dots, \theta_r, \alpha, t) \rightarrow \mathbb{E}_\sigma [P(\theta_1) \cdots P(\theta_r) 1_{\alpha(t)=\alpha}]. \quad (5.16)$$

That is, the  $r$ th moments of the distribution of  $P$  satisfy the same FP equation as the  $r$ th order joint probability density  $p$ .

Let us now focus on the special case of zero intrinsic noise ( $D = 0$ ). In that case, the phase of each oscillator in the population evolves according to the nonautonomous ODE,

$$\frac{d\theta}{dt} = \omega + \epsilon B(\theta)\alpha(t). \quad (5.17)$$

This has the formal solution

$$\theta(t, q) = \omega t + \epsilon \int_0^t B(\theta(s, q)) \alpha(s) ds + q, \quad (5.18)$$

with  $\theta(0, q) = q$ . Moreover,

$$P(\theta, t) = \int_0^{2\pi} \delta[\theta - \theta(t, q)] p_0(q) dq, \quad (5.19)$$

where  $p_0(q)$  is the initial distribution of phases. Synchronization can be established if the solution  $\theta(t, q)$  becomes independent of the initial phase  $q$  in the large  $t$  limit. We will proceed by carrying out a perturbation expansion in  $\epsilon$  along the lines of Ref. [17]. That is, we substitute the approximation

$$\theta(s, q) \approx \omega s + \epsilon \int_0^s B(\omega s + q) \alpha(s) ds + q$$

into the integral on the right-hand side and Taylor expand  $B$  to obtain the  $O(\epsilon^2)$  solution

$$\begin{aligned} \theta(t, q) &= \omega t + q + \epsilon \int_0^t B(\omega s + q) \alpha(s) ds \\ &+ \epsilon^2 \int_0^t B'(\omega s + q) \int_0^s B(\omega s' + q) \alpha(s') \alpha(s) ds' ds. \end{aligned} \quad (5.20)$$

Now suppose that  $\gamma \gg \omega/2\pi$  so the colored noise  $\alpha(t)$  varies much more rapidly than the phase  $\omega t$ . We can then time average



the noise so

$$\begin{aligned} \theta(t, q) &\approx \omega t + q + \epsilon \int_0^t B(\omega s + q) \langle \alpha(s) \rangle ds \\ &+ \epsilon^2 \int_0^t B'(\omega s + q) \int_0^s B(\omega s' + q) \langle \alpha(s') \alpha(s) \rangle ds' ds. \end{aligned} \quad (5.21)$$

Since we have a stationary OU process, which is ergodic, we can replace the time averages by ensemble averages with  $\langle \alpha(s) \rangle = 0$  and

$$\langle \alpha(s) \alpha(s') \rangle = C(s - s') = \frac{1}{2\gamma} e^{-\gamma|s-s'|}.$$

Shifting  $s$  and  $s'$ , we thus obtain the approximation

$$\begin{aligned} \theta(t, q) &= \omega t + q \\ &+ \epsilon^2 \int_{q/\omega}^{t+q/\omega} B'(\omega s) \int_{q/\omega}^{s+q/\omega} B(\omega s') C(s - s') ds' ds. \end{aligned} \quad (5.22)$$

Note that  $\theta(t, q)$  is no longer dependent on the particular realization  $\sigma$ . Finally, dividing through by  $t$  and taking the large- $t$  limit, we see that the dependence on the initial phase disappears such that  $\theta(t, q) \rightarrow \Theta(t)$ , where

$$\Theta(t) = (\omega + \epsilon^2 \Lambda) t, \quad (5.23)$$

with

$$\Lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t B'(\omega s) \int_0^s B(\omega s') C(s - s') ds' ds. \quad (5.24)$$

It follows from Eq. (5.19) that

$$P(\theta, t) \rightarrow \delta[\theta - \Theta(t)],$$

which is independent of the particular realization of the noise. We conclude that an ensemble of uncoupled identical phase oscillators evolving in the same random environment driven by fast colored noise synchronize their activity, and the collective oscillation has an  $O(\epsilon^2)$  correction to the natural frequency  $\omega$ . We can also take the white-noise limit in Eq. (5.24) with  $C(s - s') \rightarrow \delta(s - s')$  to obtain

$$\Lambda = \frac{1}{T} \int_0^T B'(\omega s) B(\omega s) ds = 0. \quad (5.25)$$

We have exploited the fact that  $B(\theta)$  is  $2\pi$  periodic. For an explicit numerical example of noise-induced synchronization under a single realization of a common noisy environment, see Fig. 1 of Ref. [11].

Although the above results are not new, our derivation in terms of independence of initial conditions and our explicit emphasis of the SPDE framework is distinct from previous studies [11–18]. Several of the latter establish synchrony by calculating the Lyapunov exponent of nearby trajectories for oscillators driven by the same environmental noise and showing that the Lyapunov exponent is always negative. [The expression for the Lyapunov exponent is given by the integrals in Eq. (5.24) or (5.25) after replacing  $B'$  by  $B''$ .] In summary, the major difference between the particle and population perspectives within the context of noise-induced synchronization is that the latter establishes a stronger form

of synchrony based on a single realization of the random environmental input. As noted in Sec. III, another difference between the particle and population or SPDE formulations is that the latter can incorporate a broader range of boundary conditions. For example, one could consider a more general class of model, in which the number of oscillators is not conserved.

## VI. DISCUSSION

In this paper we developed a general framework for studying SDEs in random environments, based on the idea that one can separate out the realizations (ensemble averaging) of intrinsic and environmental noise, see Fig. 1. The standard approach, which we call the particle perspective, is to simultaneously consider realizations of both sources of noise, which results in a deterministic FP equation. Here we introduced the so-called population or SPDE perspective, in which we consider multiple realizations of the intrinsic noise for a single realization of the environmental noise, which leads to a stochastic FP equation. A relationship between the particle and population perspectives was obtained by deriving moment equations for the distribution of the resulting stochastic population density by averaging over multiple realizations of the environment. We gave two examples where the two formulations are not equivalent. The first involved boundary value problems that do not conserve particle number, and the other concerned establishing noise-induced synchronization of oscillators without averaging with respect to realizations of the environment.

As we indicated in the Introduction, one could apply the same approach to systems where either or both the intrinsic and environmental noise are discrete rather than continuous stochastic processes. One example where both processes are discrete is a population of random walkers moving on a stochastically gated lattice, which has applications to the diffusion of particles in the plasma membrane of cells [8]. An example of a hybrid system with continuous intrinsic noise and discrete environmental noise is a population of stochastic gene networks in which the switching on and off of a promoter site is driven by discrete environmental noise [21].

In this paper, the particles were taken to be noninteracting so any statistical correlations arose from the fact that they were driven by a common random environment. Another mechanism for introducing correlations would be to include physical coupling between a set of  $N$  particles. One could apply our methods if each “particle” was identified with a single interacting population so  $\mathbf{x} \in \mathbb{R}^N$  and we considered an ensemble of independent populations driven by a common environmental input. We could then analyze interpopulation correlations. However, most studies of interacting particle systems focus on intrapopulation correlations in the absence of a common environmental drive. Examples include interacting Brownian particles with long-range interactions [22,23] and the Kuramoto model [19,24–26]. In the thermodynamic limit  $N \rightarrow \infty$  one can derive a mean-field model that takes the form of a nonlinear FP equation; for finite  $N$ , fluctuations about the mean-field solution can be modeled in terms of a stochastic FP equation. Note, however, there has been some work on

noise-induced synchronization of coupled phase oscillators with environmental noise, based on solutions of deterministic FP equations [16].

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