

A stochastic field theory for the evolution of quantitative traits in finite populations

Ananda Shikhara Bhat *

Department of Biology, Indian Institute of Science Education and Research Pune, Maharashtra 411008, India

Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, Karnataka 560012, India

Institute of Organismic and Molecular Evolution (iomE) and Institute for Quantitative and Computational Biosciences (IQCB), Johannes Gutenberg University, 55128 Mainz, Germany

ARTICLE INFO

MSC:

92D15

92D25

60H15

60J68

60J70

Keywords:

Evolutionary theory

Demographic stochasticity

Noise-induced selection

Finite populations

Eco-evolutionary dynamics

Quantitative genetics

ABSTRACT

Infinitely many distinct trait values may arise in populations bearing quantitative traits, and modeling their population dynamics is thus a formidable task. While classical models assume fixed or infinite population size, models in which the total population size fluctuates due to demographic noise in births and deaths can behave qualitatively differently from constant or infinite population models due to density-dependent dynamics. In this paper, I present a stochastic field theory for the eco-evolutionary dynamics of finite populations bearing one-dimensional quantitative traits. I derive stochastic field equations that describe the evolution of population densities, trait frequencies, and the mean value of any trait in the population. These equations recover well-known results such as the replicator-mutator equation, Price equation, and gradient dynamics in the infinite population limit. For finite populations, the equations describe the intricate interplay between natural selection, noise-induced selection, eco-evolutionary feedback, and neutral genetic drift in determining evolutionary trajectories. My work uses ideas from statistical physics, calculus of variations, and SPDEs, providing alternative methods that complement the measure-theoretic martingale approach that is more common in the literature.

1. Introduction

The success of the Modern Synthesis (Provine, 2001; Thompson, 2014) illustrates the value of abstract mathematical modeling in evolutionary biology. Several major modeling paradigms of eco-evolutionary dynamics — such as evolutionary game theory and adaptive dynamics — as well as the standard equations of population genetics and quantitative genetics, can be recovered (in a very general sense) from a small number of ‘fundamental’ equations such as the replicator-mutator equation and Price equation (Page and Nowak, 2002; Lion, 2018; Lehtonen, 2018). Historically, these ‘fundamental equations’ have been formulated in deterministic terms through difference equations and ordinary/partial differential equations (Page and Nowak, 2002; Lion, 2018; Lehtonen, 2018), and stochastic effects due to finite population sizes have been studied through more specific models such as the Wright–Fisher or Moran process (Ewens, 2004). Most classic stochastic models in population and quantitative genetics, such as the Wright–Fisher and Moran models, assume the total number of individuals in the population either remains strictly constant or varies deterministically according to ‘top-down’ rules that allow us to define the notion of a constant ‘effective population size’ (Lambert, 2010). However, the

total population size in real populations is often an emergent property of individual-level ecological and demographic processes (Metcalf and Pavard, 2007b; Lambert, 2010), and changes in the total population size due to these processes can cause qualitative changes in evolutionary dynamics relative to the expectations of constant population size models due to density-dependence (Lambert, 2010; Papkou et al., 2016; Kokko et al., 2017; Mazzolini and Grilli, 2023; de Vries et al., 2023). For instance, one important consequence of stochastic fluctuations of total population size is ‘noise-induced selection’, an evolutionary force that can reverse the direction of evolution predicted by natural selection (Gillespie, 1974; Parsons et al., 2010; Constable et al., 2016; McLeod and Day, 2019a; Week et al., 2021; Kuosmanen et al., 2022; Mazzolini and Grilli, 2023; Bhat and Guttal, 2024). Finite population models in population biology also typically incorporate stochasticity by adding noise to a ‘deterministic skeleton’ rather than deriving the complete stochastic dynamics from first principles (Coulson et al., 2004; Lambert, 2010; Doebeli et al., 2017). Unfortunately, incorporating stochasticity in this manner is known to sometimes yield inconsistent

* Correspondence to: Institute of Organismic and Molecular Evolution (iomE), Johannes Gutenberg University, 55128 Mainz, Germany.

E-mail address: abhat@uni-mainz.de.

predictions that disappear if the stochastic dynamics of finite population systems are instead systematically derived from individual-based rules (Black and McKane, 2012; Strang et al., 2019).

Stochastic individual-based models, in which (probabilistic) rules are specified at the level of the individual and population level dynamics are systematically derived from first principles, provide a natural way to describe eco-evolutionary dynamics of finite populations from first principles and avoid the potential pitfalls of ad-hoc implementations of stochasticity on one hand, and those of ignoring density-dependent ecological/demographic processes on the other. The process of systematically deriving equations of eco-evolutionary population dynamics from demographic first principles also provides a more mechanistic description of evolutionary dynamics (Lambert, 2010; Doebeli et al., 2017) because ‘all paths to fitness lead through demography’ (Metcalfe and Pavard, 2007a). While such a mechanistic description of eco-evolutionary dynamics can be carried out for populations bearing discrete traits without using too much mathematical machinery (Parsons et al., 2010; Kuosmanen et al., 2022; Bhat and Guttal, 2024), studies that work with quantitative traits are currently grounded in the theory of measure-valued branching processes and their characterization via martingale theory and related fields (Fournier and Méléard, 2004; Champagnat et al., 2006; Champagnat and Lambert, 2007; Champagnat et al., 2008; Champagnat and Méléard, 2011; Week et al., 2021; Boussange and Pellissier, 2022). As such, working with quantitative trait stochastic individual-based models analytically currently requires a considerable mathematical background in stochastic analysis and measure theory.

It has long been recognized that the equations governing the population level behavior of Markov processes based on stochastic individual-based dynamics are often very similar to the equations describing the behavior of many interacting particles in statistical physics (Gardiner, 2009; Black and McKane, 2012) and quantum mechanics (Martin et al., 1973; Hochberg et al., 1999; Baez and Biamonte, 2018). As a consequence, powerful heuristic tools originally developed in physics can be leveraged, under many situations, to study the behavior of systems in which a large number of individuals interact in a stochastic manner (Martin et al., 1973; Doi, 1976; Peliti, 1985; Hochberg et al., 1999; Thomas et al., 2014; Chow and Buice, 2015; Weber and Frey, 2017; Baez and Biamonte, 2018). Indeed, various tools from statistical and quantum mechanics have already been successfully applied to study stochasticity in biological populations (O’Dwyer et al., 2009; de Vlader and Barton, 2011; Black and McKane, 2012; Schraiber, 2014). However, most studies that apply ideas from statistical physics to biological populations focus on modeling finite-dimensional systems. In contrast, populations bearing quantitative traits must be characterized by a function or distribution, and the object describing the state of the system at any given point is thus, in general, infinite-dimensional. In infinite dimensions, the analogy between statistical/quantum mechanics and Markov processes becomes an analogy between statistical/quantum field theory and infinite-dimensional stochastic processes such as SPDEs (Hochberg et al., 1999; García-Ojalvo and Sancho, 1999). While such ‘stochastic field equations’ have been introduced to theoretical biology in the context of neurobiology (Buice and Cowan, 2007; Bressloff, 2010; Coombes et al., 2014) and collective motion (Ó Laighléis et al., 2018), they are as yet largely unused in population biology.

In this paper, I present a general approach to modeling the evolution of one-dimensional quantitative traits in an arbitrary closed finite, fluctuating population starting from the demographic first principles of birth and death. My approach consists of describing the population as a stochastic ‘field’ (function over space of allowed traits and time), assuming that birth and death rates scale according to a population size measure (Czuppon and Traulsen, 2021), and then using ideas from statistical physics to derive stochastic equations that describe how this field changes over time when the carrying capacity is not too small. My framework largely only uses tools from calculus, calculus

of variations, and some heuristics for spacetime white noise. It also yields stochastic partial differential equations (SPDEs) that are more amenable to direct attack using tools from statistical and quantum field theory than the more ‘analytic’ formulation in terms of martingale problems. As such, my work is intended to complement the rigorous framework presented in previous studies (Champagnat et al., 2006, 2008) with an alternative, heuristic formalism. In the next section, I present the general formalism and describe the exact stochastic population dynamics via a functional master equation (Kolmogorov forward equation). These dynamics can then be approximated via an infinite-dimensional system size approximation to arrive at SPDEs describing the stochastic dynamics of biologically important quantities such as population abundances, trait frequencies, and trait means. I present the main results and their biological implications in the main text, and delegate detailed derivations to the Supplementary.

2. General field equation formalism

Consider a closed population of individuals bearing a trait that takes values in a set $\mathcal{T} \subseteq \mathbb{R}$. I assume that the trait value of an individual cannot change over its lifetime. I will say that individuals that have the same value of the trait are of the same ‘type’ and are all identical for the purposes of our model. Each individual with a trait value $x \in \mathcal{T}$ can be characterized as a single Dirac delta mass centered at x , defined indirectly as the object which satisfies, for any one-dimensional real function f and any set $A \subseteq \mathcal{T}$,

$$\int_A f(y) \delta_x dy = \begin{cases} f(x) & x \in A \\ 0 & x \notin A \end{cases}$$

Intuitively, δ_x should be thought of as analogous to an indicator function: Given any set $A \subseteq \mathcal{T}$, integrating δ_x over A returns 1 if $x \in A$ and 0 otherwise, and thus tells us whether or not the individual in question has a trait value that lies within the set A . Note that in physics notation, the Dirac mass centered at x would be $\delta(y - x)$, where y is a dummy variable, and the integral would be written $\int_A f(y) \delta(y - x) dy$.

If the population at any time t consists of $N(t)$ individuals with trait values $\{x_1, x_2, \dots, x_{N(t)}\}$, it can then be completely characterized (Fig. 1) by the ‘stochastic field’ (finite measure)

$$\nu_t = \sum_{i=1}^{N(t)} \delta_{x_i}$$

Thus, we are interested in formulating and studying a stochastic process taking values in

$$\mathcal{M}(\mathcal{T}) = \left\{ \sum_{i=1}^n \delta_{x_i} \mid n \in \mathbb{N}, x_i \in \mathcal{T} \right\}$$

The elements of $\mathcal{M}(\mathcal{T})$ are formally so-called ‘finite measures’. For our purposes, $\nu \in \mathcal{M}(\mathcal{T})$ can be thought of as analogous to a ‘density function’ in the sense that for any subset $A \subset \mathcal{T}$ of the trait space, the quantity $\int_A \nu dx$ gives the number of individuals that have trait values that lie within the set A in the population ν . I will use the notation $\nu(x, t)$ to denote the field at time t to help the reader remember this interpretation of ν as a ‘density’ over the trait space. It is important to note that just like with probability densities, the ‘value of the field at trait value x ’ is undefined, and thus it only makes sense to speak of quantities of the form $\int f(x, \nu) \nu(x, t) dx$ for some function $f(x, \nu)$ (Note that in measure-theoretic notation, ν is viewed as a measure and thus integration of f against ν is usually written $\langle f, \nu \rangle = \int f(x, \nu) \nu(dx)$). In this sense, the variable x in $\nu(x, t)$ is a dummy variable that will be integrated over, but I retain it in the interest of suggestive notation. It is easy to see from the definition of the Dirac mass that when the population is given by $\nu(y, t) = \sum_{i=1}^{N(t)} \delta_{x_i}$, we have $\int_{\mathcal{T}} f(y) \nu(y, t) dy = \sum_{i=1}^{N(t)} f(x_i)$. Thus, $\int_{\mathcal{T}} f(y) \nu(y, t) dy$ simply evaluates the function f for each trait value x_i that is currently present in the population.

Now that we have described the population, we must define the rules for how it changes over time. I assume that the probability of

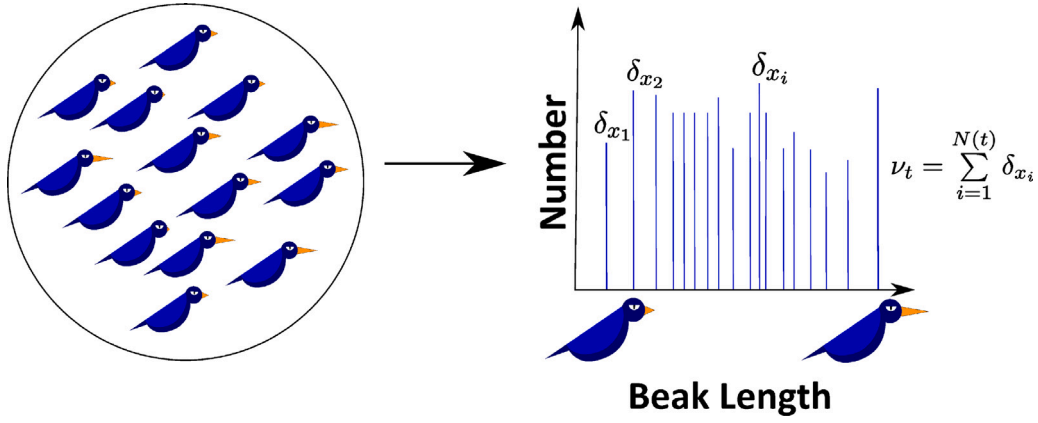


Fig. 1. Schematic description of the state space of our stochastic process. Consider a population of birds in which individuals have varying beak lengths. Since each individual has a single beak length, it can be characterized as a Dirac mass centered at its beak length. Thus, if the population has $N(t)$ individuals, it can be described as a distribution obtained as the sum of $N(t)$ (not necessarily distinct) Dirac masses.

observing two or more simultaneous events (births or deaths) at the same instant of time is negligible. Thus, the population changes in units of a single individual. Since we assumed the population is closed, changes in the population can now be described using two non-negative functionals $b(x|\nu)$ and $d(x|\nu)$ from $\mathcal{T} \times \mathcal{M}(\mathcal{T})$ to $[0, \infty)$ that specify the absolute (rather than per-capita) rate at which individuals with trait value x are born and die respectively in a population ν . That is, if we know that the population was in the state ν and we know that *either a birth or a death* has occurred and changed the population to some state other than ν , then the probability that the event which occurred is the birth of an individual whose phenotype is within the set $A \subset \mathcal{T}$ is given by

$$\mathbb{P}[\text{Birth with offspring in } A \mid \text{something happened}] = \frac{1}{\mathcal{N}(\nu)} \int_A b(x|\nu) dx$$

and the probability that the event is the death of an individual whose phenotype is within the set A is

$$\mathbb{P}[\text{Death of an individual in } A \mid \text{something happened}] = \frac{1}{\mathcal{N}(\nu)} \int_A d(x|\nu) dx$$

where $\mathcal{N}(\nu) = \int_{\mathcal{T}} b(x|\nu) + d(x|\nu) dx$ is a normalizing constant that could depend on the current state ν . I assume $\mathcal{N}(\nu)$ is always finite and non-zero. Our description of population dynamics is thus a ‘function’-valued Markov process (and more precisely a measure-valued birth–death process) with transition probabilities given by the birth and death rate functionals $b(x|\nu)$ and $d(x|\nu)$. I further assume that the total birth and death rates do not scale faster than linearly with the total population size, i.e. that for a given population ν , the quantities $\int_{\mathcal{T}} b(x|\nu) dx$ and $\int_{\mathcal{T}} d(x|\nu) dx$ are $\mathcal{O}(\int_{\mathcal{T}} \nu dx)$. This latter assumption will be used in the section below when conducting a system-size expansion.

Let us now define, for each $x \in \mathcal{T}$, two *step operators* \mathcal{E}_x^\pm defined by their action on any function $f(y, \nu) : \mathcal{T} \times \mathcal{M}(\mathcal{T}) \rightarrow \mathbb{R}$ as:

$$\mathcal{E}_x^\pm f(y, \nu) = f(y, \nu \pm \delta_x)$$

In other words, the step operators \mathcal{E}_x^\pm simply describe the effect of adding or removing a single individual with trait value x from the population ν .

Let $P(\nu, t | \nu_0, 0)$ be the (conditional) probability density function of the process, i.e. the probability that the population is described by ν at time t given that it is described by ν_0 at time 0. From now on, I omit the conditioning and simply write $P(\nu, t)$ for notational simplicity. Recall that any change to the population must be through the birth or death of a single individual, i.e. through addition or subtraction of a single Dirac mass. For any state $\nu \in \mathcal{M}(\mathcal{T})$, a population could end up in the state ν either through a birth of an individual δ_x in a population $\nu - \delta_x$, or through the death of an individual δ_x in a population $\nu + \delta_x$, for any

possible $x \in \mathcal{T}$. Transitions of the form $\nu - \delta_x \rightarrow \nu$ occur through the birth of an individual with trait value x , and by the definition of our birth rates above, the transition rate from $\nu - \delta_x$ to ν is thus given by $b(x|\nu - \delta_x)$. To find the total transition probability into the state ν , we must now ‘sum over’ (integrate) the contributions of transitions due to births of individuals of all possible trait values $x \in \mathcal{T}$. Thus, the transition rate into the state ν at time t due to births is

$$R_{\text{in}}^{\text{births}}(\nu, t) = \underbrace{\int_{\mathcal{T}}}_{\text{‘sum over’ all possible } x} \underbrace{b(x|\nu - \delta_x)}_{\text{Rate of } (\nu - \delta_x) \rightarrow \nu \text{ transition}} \underbrace{P(\nu - \delta_x, t)}_{\text{Probability of finding the population } \nu - \delta_x} dx = \int_{\mathcal{T}} [\mathcal{E}_x^- b(x|\nu) P(\nu, t)] dx \quad (1)$$

where we have rewritten the term within the integral on the RHS of Eq. (1) as $b(x|\nu - \delta_x) P(\nu - \delta_x, t) = \mathcal{E}_x^- b(x|\nu) P(\nu, t)$ using the definition of the step operator \mathcal{E}_x^- . Similarly, the transition from $\nu + \delta_x$ to ν is through death of type x individuals and thus has transition rate $d(x|\nu + \delta_x)$. The total transition probability into the population ν at time t due to deaths of individuals can thus be written

$$R_{\text{in}}^{\text{deaths}}(\nu, t) = \underbrace{\int_{\mathcal{T}}}_{\text{‘sum over’ all possible } x} \underbrace{d(x|\nu + \delta_x)}_{\text{Rate of } (\nu + \delta_x) \rightarrow \nu \text{ transition}} \underbrace{P(\nu + \delta_x, t)}_{\text{Probability of finding the population } \nu + \delta_x} dx = \int_{\mathcal{T}} [\mathcal{E}_x^+ d(x|\nu) P(\nu, t)] dx \quad (2)$$

The transition rate out of ν to a state $\nu + \delta_x$ due to births of type x individuals is $b(x|\nu)$, and transition out to a state $\nu - \delta_x$ due to death of type x individuals is $d(x|\nu)$. Thus, the transition probabilities of exiting the state ν at time t are given by

$$R_{\text{out}}^{\text{births}}(\nu, t) = \int_{\mathcal{T}} b(x|\nu) P(\nu, t) dx \quad (3)$$

$$R_{\text{out}}^{\text{deaths}}(\nu, t) = \int_{\mathcal{T}} d(x|\nu) P(\nu, t) dx \quad (4)$$

Now, the total probability flux through the state ν must be given by the difference between the rate of inflow and the rate of outflow of probability, or, in equations,

$$\underbrace{\frac{\partial P}{\partial t}(\nu, t)}_{\text{Rate of change of probability of the population being described by } \nu} = \underbrace{[R_{\text{in}}^{\text{births}}(\nu, t) + R_{\text{in}}^{\text{deaths}}(\nu, t)]}_{\text{Total rate of ‘inflow’ into the population } \nu \text{ due to births and deaths}} - \underbrace{[R_{\text{out}}^{\text{births}}(\nu, t) + R_{\text{out}}^{\text{deaths}}(\nu, t)]}_{\text{Total rate of ‘outflow’ from the population } \nu \text{ due to births and deaths}} \quad (5)$$

Substituting Eqs. (1)–(4) into Eq. (5) and rearranging, we thus see that $P(v, t)$ must satisfy:

$$\frac{\partial P}{\partial t}(v, t) = \int_{\mathcal{T}} [(\mathcal{E}_x^- - 1)b(x|v)P(v, t) + (\mathcal{E}_x^+ - 1)d(x|v)P(v, t)] dx \quad (6)$$

Eq. (6) completely describes the stochastic evolution of the population, and can be thought of as an infinite-dimensional ‘master equation’ (Van Kampen, 1981, Equation 5.1.5) or Kolmogorov Forward Equation (Karatzas and Shreve, 1998, Equation 5.1.6).

2.1. The population density field

On ecological grounds, I assume the birth–death process admits a carrying capacity, or more generally a *population size measure* (Czuppon and Traulsen, 2021) $K > 0$ such that the expected population growth rate of every type is negative whenever the total population size exceeds K . In other words, I assume that the functionals $b(x|v)$ and $d(x|v)$ are such that there exists a $K > 0$ such that for any set $A \subseteq \mathcal{T}$, $\int_A [b(x|v) - d(x|v)] dx < 0$ whenever $\int_{\mathcal{T}} v dx > K$. In this case, we expect the stochastic process to remain in the domain where the total population size $\int_{\mathcal{T}} v dx$ is $\mathcal{O}(K)$. Thus, $K = \infty$ corresponds to an infinitely large population. By dividing $v(\cdot, t)$ by K , we can now obtain a new field $\phi(x, t) = v(x, t)/K$. For any set $A \subset \mathcal{T}$, $\int_A \phi(x, t) dx$ gives the ‘population density’ of individuals that have trait values that lie within the set A . I will call ϕ the population density field. The field at time t is defined as

$$\phi(\cdot, t) := \frac{1}{K} v(\cdot, t) = \frac{1}{K} \sum_{i=1}^{N(t)} \delta_{x_i}$$

Note that since the total population size $\int_{\mathcal{T}} v(x, t) dx$ is $\mathcal{O}(K)$, the total population density $\int_{\mathcal{T}} \phi(x, t) dx$ is $\mathcal{O}(1)$. The parameter K , along with the scaling assumptions on the birth and death rate functionals, are such that, for any $t > 0$, $\int_{\mathcal{T}} \phi(x, t) dx \rightarrow 1$ as $K \rightarrow \infty$. Thus, the limit $K \rightarrow \infty$ corresponds to finite population densities but infinite population sizes. Mathematically, I assume we can find two non-negative $\mathcal{O}(1)$ functionals b_K and d_K such that the birth and death rate functionals $b(x|v)$ and $d(x|v)$ can be rewritten as:

$$\begin{aligned} b(x|v) &= K b_K(x|v/K) = K b_K(x|\phi) \\ d(x|v) &= K d_K(x|v/K) = K d_K(x|\phi) \end{aligned} \quad (7)$$

. The new stochastic field $\{\phi(\cdot, t)\}_{t \geq 0}$ takes values in

$$\mathcal{M}_K(\mathcal{T}) := \left\{ \frac{1}{K} \sum_{i=1}^n \delta_{x_i} \mid n \in \mathbb{N}, x_i \in \mathcal{T} \right\}$$

As before, $\phi(x, t)$ can be thought of as analogous to a ‘probability density function’ for the population density in the sense that the population density of individuals with trait values that lie within the (infinitesimal) interval $(x, x + dx)$ is informally $\phi(x, t) dx$. If K is large, each individual contributes a negligible amount to the total density field and the field as a whole begins to look approximately continuous (over the trait space), allowing us to now speak about the value of the field at a particular trait value x instead of merely speaking about the density of individuals within subsets of the trait space. I take this continuity as an assumption, but it can be shown to rigorously hold under various technical conditions using more sophisticated mathematical tools (Champagnat et al., 2006; Week et al., 2021). Let $P(\phi, t | \phi_0, 0)$ be the probability that the population density field is given by $\phi \in \mathcal{M}_K(\mathcal{T})$ at time t if the stochastic process was initialized with the field $\phi_0 \in \mathcal{M}_K(\mathcal{T})$ at time 0. As before, I omit the conditioning below for notational simplicity. We are interested in finding an equation for how $P(\phi, t)$ changes over time.

2.2. Functional forms of the birth and death rates

I assume that the birth and death functions take the form:

$$\begin{aligned} b_K(x|\phi) &= \phi(x, t) b^{(\text{ind})}(x|\phi) + \mu Q(x|\phi) \\ d_K(x|\phi) &= \phi(x, t) d^{(\text{ind})}(x|\phi) \end{aligned} \quad (8)$$

where $\mu \geq 0$ is a constant and $b^{(\text{ind})}(x|\phi)$, $d^{(\text{ind})}(x|\phi)$, and $Q(x|\phi)$ are all $\mathcal{O}(1)$ and continuous in both x and ϕ . Here, the functionals $b^{(\text{ind})}(x|\phi)$ and $d^{(\text{ind})}(x|\phi)$ can be thought of as describing the birth and death rate of type x organisms in a population ϕ at an individual (per-capita) level. The term $Q(x|\phi)$ describes contributions to the birth rate that are not of the form $\phi F[x|\phi]$. If at some time t there are no type x individuals in the population ($\phi(x, t) = 0$), type x individuals may still arise in the population due to immigration or mutations of other types during birth. However, such births cannot be incorporated into $b^{(\text{ind})}$ since the product $\phi(x, t) b^{(\text{ind})}(x|\phi)$ vanishes whenever $\phi(x, t) = 0$. For instance, if individuals of type x are born due to mutations at birth of a different type y , the contribution to the birth rate of type x depends on a mutation rate and on the value of the density field at y (i.e. on $\phi(y, t)$), but does *not* depend on the density of type x individuals (i.e. $\phi(x, t)$). For simplicity, I will henceforth assume that the population is closed and Q describes the effects of potential mutational effects during birth, with $\mu \geq 0$ being a constant mutation rate. Note that we do not need to include such a term for the death rate, since we must necessarily have $d_K(x|\phi) = 0$ when $\phi(x, \cdot) = 0$ to avoid negative population density values and thus mutation/emigration that leads to loss of individuals can be subsumed into $d^{(\text{ind})}$. The functionals $b^{(\text{ind})}(x|\phi)$, $d^{(\text{ind})}(x|\phi)$, and $Q(x|\phi)$ may be quite complex (as long as they are all bounded for all x, ϕ as $t \rightarrow \infty$) and could in principle model several ecological phenomena.

I define $w(x|\phi)$, the *Malthusian fitness* of type x in a population ϕ as

$$w(x|\phi) := b^{(\text{ind})}(x|\phi) - d^{(\text{ind})}(x|\phi) \quad (9)$$

In words, $w(x|\phi)$ is a measure of the (stochastic) growth rate of type x individuals in the population defined by the population density field ϕ due to non-mutational effects. I also define $\tau(x|\phi)$, the *per-capita turnover* rate of type x in a population ϕ , as

$$\tau(x|\phi) := b^{(\text{ind})}(x|\phi) + d^{(\text{ind})}(x|\phi) \quad (10)$$

The quantity $\tau(x|\phi)$ is a measure of the expected total number of (stochastic) changes to the density field at point x in a population ϕ due to non-mutational effects.

2.3. Statistical measures for type-level quantities

So far, we have been speaking entirely in terms of population densities. However, evolution is not in terms of population densities, but in terms of trait frequencies. To track population sizes, I compute the scaled population size N_K as

$$N_K(t) := \int_{\mathcal{T}} \phi(x, t) dx = \frac{1}{K} \int_{\mathcal{T}} v(x, t) dx \quad (11)$$

Thus, $K N_K(t)$ is the total population size at time t . When the population is at carrying capacity, $N_K = 1$. Further, recall that we assumed $\int_{\mathcal{T}} \phi(x, t) dx = N_K(t) \rightarrow 1$ as $K \rightarrow \infty$ for any fixed t .

I now define the *trait frequency field* $p(x, t)$, a stochastic field given by

$$p(x, t) := \frac{v(x, t)}{\int_{\mathcal{T}} v(y, t) dy} = \frac{\phi(x, t)}{N_K(t)} \quad (12)$$

Integrating the $p(x, t)$ field in the x variable over any set $A \subseteq \mathcal{T}$ gives us the frequency of individuals bearing trait values that lie in the set A .

Now, let $f(x|\phi) : \mathcal{T} \times \mathcal{M}(\mathcal{T}) \rightarrow \mathbb{R}$ be a real function. For example, f could describe a phenotype, a quantity such as fitness or turnover rate, or simply a label defined at each trait value x . Given any such type-level quantity, We can define the mean value of f in the population ϕ at time t as

$$\bar{f}(t) = \int_{\mathcal{T}} f(x|\phi) p(x, t) dx \quad (13)$$

the statistical covariance of two quantities f and g as

$$\text{Cov}(f, g) = \overline{fg} - \bar{f}\bar{g} \quad (14)$$

Table 1
Table of notation.

| Symbol | Meaning |
|--------------------------------------|---|
| \mathcal{T} | Trait space, assumed a subset of \mathbb{R} . |
| δ_x | Dirac mass centered at $x \in \mathcal{T}$. We will use this to characterize a single individual. |
| $v(y, t)$ | A stochastic field describing the population at time t . If the population at time t consists of individuals having trait values $\{x_1, x_2, x_3, \dots\}$, then $v(y, t) = \sum_i \delta_{x_i}$ describes the entire population. |
| $\mathcal{M}(\mathcal{T})$ | The set $\left\{ \sum_{i=1}^n \delta_{x_i} \mid n \in \mathbb{N}, x_i \in \mathcal{T} \right\}$. This is the state space of our stochastic process. |
| $b(x \nu), d(x \nu)$ | Birth and death rate functionals for the birth–death process $\{v(\cdot, t)\}_{t \geq 0}$. |
| K | Population size measure (Czuppon and Traulsen, 2021). A non-negative number that controls the expected total population size. $K \rightarrow \infty$ yields the infinite population size (but finite population density) limit. |
| $\phi(y, t)$ | Population density field, $v(y, t)/K$. |
| $\mathcal{M}_K(\mathcal{T})$ | The set $\left\{ \frac{1}{K} \sum_{i=1}^n \delta_{x_i} \mid n \in \mathbb{N}, x_i \in \mathcal{T} \right\}$. This is the state space of our rescaled stochastic process $\{\phi(\cdot, t)\}_{t \geq 0}$. |
| $N_K(t)$ | The rescaled population size $\int_{\mathcal{T}} \phi(y, t) dy$. $KN_K(t)$ is the total population size at time t . |
| $p(x, t)$ | The trait frequency field $\phi(x, t)/N_K(t)$. |
| $b_K(x \phi), d_K(x \phi)$ | Birth and death rate functionals for the rescaled process $\{\phi(\cdot, t)\}_{t \geq 0}$. I assume the functional forms $b_K(x \phi) = \phi(x, t)b^{(\text{ind})}(x \phi) + \mu Q(x \phi)$, $d_K(x \phi) = \phi(x, t)d^{(\text{ind})}(x \phi)$. |
| $P(\nu, t)$ | Shorthand for $P(\nu, t \nu_0, 0)$, Probability of finding the population in a state ν at time t if it begins in a state ν_0 at time 0. |
| $b^{(\text{ind})}, d^{(\text{ind})}$ | Per-capita birth and death rates, excluding potential mutational effects (see below) |
| $Q(x \phi)$ | Function to model contributions to birth rate that cannot be written in terms of per-capita rates. The strength is parameterized by a constant $\mu > 0$. The analogy is with mutation (parameterized by a mutation rate) or immigration (parameterized by a migration rate). See main text for details. |
| $w(x \phi)$ | Malthusian fitness $b^{(\text{ind})}(x \phi) - d^{(\text{ind})}(x \phi)$ of trait value x in a population ϕ . |
| $\tau(x \phi)$ | Per-capita turnover rate $b^{(\text{ind})}(x \phi) + d^{(\text{ind})}(x \phi)$ of trait value x in a population ϕ . |
| \bar{f} | Statistical mean of $f(x \phi)$ in the population, computed as $\int_{\mathcal{T}} f(x \phi)p(x, t)dx$. |
| $\text{Cov}(f, g)$ | Statistical covariance between $f(x \phi)$ and $g(x \phi)$ in the population, computed as $\overline{fg} - \bar{f}\bar{g}$. |
| $\dot{W}(x, t)$ | A spacetime white noise process on $\mathcal{T} \times [0, \infty)$. |

and the statistical variance of a quantity f as $\sigma_f^2 = \text{Cov}(f, f)$. Note that these three quantities are all statistical measures that describe how traits are distributed in a given population ϕ . They are distinct from the *probabilistic* expectation, variance, and covariance obtained by integrating over an ensemble of populations that represent different realizations of the stochastic process. I denote the probabilistic expectation by $\mathbb{E}[\cdot]$ (see Table 1).

3. Results

In principle, Eq. (6) exactly describes the complete stochastic population dynamics of our population of interest. However, in practice, the exact stochastic process is usually much too complicated to be studied directly on an exact level. Instead, we will look for approximate continuous field equations that describe the density field $\phi(x, t)$, the trait frequency field $p(x, t)$, and the mean value \bar{f} of any field describing a type-level quantity $f(x|\phi)$ (of particular interest will be \bar{x} , the mean value of the trait itself). I relegate the detailed calculations to the supplementary material, which is entirely mathematically self-contained (except for using Eq. (6) as a starting point). I provide the big picture (on a mathematical level) outlining the reasoning behind the calculations in supplementary section S1. In the main text, I instead focus on discussing the major results, their biological implications and interpretations, and connections to various existing formal descriptions of the evolution of quantitative traits.

3.1. A field equation for population densities

In supplementary section S2, I obtain an approximate equation describing the behavior of the density field ϕ using an infinite-dimensional analog of the system-size expansion (Gardiner, 2009, Chapter 13), also called the diffusion approximation in the population genetics literature (Crow and Kimura, 1970; Ewens, 2004). I show that if K is reasonably large, $P(\phi, t)$ approximately evolves according to the equation:

$$\begin{aligned} \frac{\partial P}{\partial t}(\phi, t) = & \int_{\mathcal{T}} \left[-\frac{\delta}{\delta \phi(x)} \{ [\phi(x)w(x|\phi) + \mu Q(x|\phi)] P(\phi, t) \} \right. \\ & \left. + \frac{1}{2K} \frac{\delta^2}{\delta \phi(x)^2} \{ [\phi(x)\tau(x|\phi) + \mu Q(x|\phi)] P(\phi, t) \} \right] dx \end{aligned} \quad (15)$$

where I have suppressed the t dependence of ϕ for conciseness. Here, $\delta F / \delta \rho$ denotes the *functional derivative* of the functional F with respect

to the function ρ , defined indirectly as the unique object that satisfies for any function ξ

$$\int \frac{\delta F}{\delta \rho(x)} \xi(x) dx = \lim_{h \rightarrow 0} \frac{F[\rho + h\xi] - F[\rho]}{h}. \quad (16)$$

Eq. (15) is a functional Fokker–Planck equation (Gardiner, 2009, Equation 13.1.25; García-Ojalvo and Sancho (1999), Equation 2.54) or Kolmogorov forward equation (Karatzas and Shreve, 1998, Equation 5.1.6) for $P(\phi, t)$, the probability of finding the population in a state ϕ at time t . We now recall that a finite-dimensional Markov process whose density is described by a Fokker–Planck equation can always equivalently be represented as the solution to an Itô stochastic differential equation (Gardiner, 2009, section 4.3.5). Exactly analogously, infinite-dimensional Markov processes whose density functions are described by functional Fokker–Planck equations can be represented as solutions to Itô stochastic partial differential equations (Konno and Shiga, 1988, theorem 1.4; Dawson et al., 2000, theorem 1.2 with $g \equiv 0, \gamma = \sigma^2 = 1, e^2 = 2$). Thus, the stochastic process whose probability density is described by Eq. (15) must satisfy the stochastic partial differential equation (SPDE):

$$\frac{\partial \phi}{\partial t}(x, t) = [\phi(x, t)w(x|\phi) + \mu Q(x|\phi)] + \frac{1}{\sqrt{K}} \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(x|\phi)} \dot{W}(x, t) \quad (17)$$

where $\dot{W}(x, t)$ is the *spacetime white noise* on $\mathcal{T} \times [0, \infty)$, defined indirectly (Pardoux, 2021) as the object that satisfies for any two square-integrable functions f, g on $\mathcal{T} \times [0, \infty)$ and any time $t > 0$:

$$\begin{aligned} \mathbb{E} \left[\int_0^t \int_{\mathcal{T}} f(u, s) \dot{W}(u, s) du ds \right] &= 0 \\ \mathbb{E} \left[\int_0^t \int_{\mathcal{T}} f(u, s) \dot{W}(u, s) du ds \int_0^t \int_{\mathcal{T}} g(u, s) \dot{W}(u, s) du ds \right] &= \int_0^t \int_{\mathcal{T}} f(u, s) g(u, s) du ds. \end{aligned} \quad (18)$$

(Week et al., 2021) provide an excellent introduction to spacetime white noise processes. In supplementary section S8, I show how the equation for the density field can be combined with a weak noise approximation and Fourier techniques to study phenotypic clustering and adaptive diversification/speciation. The analytic pipeline for studying phenotypic clustering via Fourier techniques has already been developed for some specific models in previous studies (Rogers et al., 2012; Rogers and McKane, 2015), but to the best of my knowledge, supplementary section S8 provides the first general treatment.

3.1.1. The infinite population limit

Taking the infinite population limit ($K \rightarrow \infty$) in Eq. (17) yields a deterministic process whose evolution is described by the PDE:

$$\frac{\partial \phi}{\partial t}(x, t) = \underbrace{\phi(x, t)w(x|\phi)}_{\text{Growth rate due to ecological interactions}} + \underbrace{\mu Q(x|\phi)}_{\text{Additional growth rate due to mutations}} \quad (19)$$

Eq. (19) describes the change in population densities as the sum of two terms. The first term is the difference between the per-capita birth and death rates of type x individuals ($w(x|\phi)$) multiplied by the current population density at the point x , and represents growth due to ecological interactions in the absence of mutation; This can be seen by comparing Eq. (19) (with $\mu = 0$) to one-dimensional ecological models of the form $\dot{N}_t = N_t f(N_t)$ (ex: $f(N_t) = r$ gives exponential growth, $f(N_t) = (1 - N_t/K)$ gives logistic growth, and so on). The second term on the RHS of Eq. (19) describes the effects of mutation on growth rate; This term is always non-negative because we only incorporated the effects of mutation in the birth rate in Eq. (8). Models of this form are precisely the non-spatial ‘PDE models’ discussed in studies of adaptive diversification (Doebeli, 2011). Eq. (19) is also the starting point of ‘oligomorphic dynamics’ if one assumes the population is composed of a small number of ‘morphs’, i.e. $\phi(x, t) = \sum_{k=1}^S n_k(t) \phi_k(x, t)$, where $n_k \geq 0$ is the abundance of the k th morph, $\phi_k(x, t)$ is the phenotypic distribution of the k th morph, and S is the total number of distinct morphs in the population (Sasaki and Dieckmann, 2011; Lion et al., 2023). Finally, equations of the form Eq. (19) have also recently been proposed as models to study the effects of intraspecific trait variation in ecological communities (Nordbotten et al., 2020; Wickman et al., 2023).

3.2. A stochastic replicator equation for the trait frequency field

The dynamics of the per-capita population growth rate can be studied using Eq. (17). By integrating Eq. (17) in the x variable and dividing throughout by N_K , I find

$$\frac{1}{N_K} \frac{dN_K}{dt} = \left[\bar{w}(t) + \frac{\mu}{N_K(t)} \int_{\mathcal{T}} Q(x|\phi) dx \right] + \frac{1}{\sqrt{K} N_K(t)} \int_{\mathcal{T}} \sqrt{\phi(x, t) \tau(x|\phi) + \mu Q(x|\phi)} \dot{W}(x, t) dx \quad (20)$$

Thus, mean fitness controls the expected per-capita population growth rate, mean turnover rate controls the variance in the per-capita population growth rate, and mutations contribute to both mean and variance. Note that the stochastic term here is a simple purely temporal white noise rather than a spacetime white noise due to the integration over the x variable.

To describe evolutionary dynamics, we need an equation for trait frequencies. In supplementary section S3, I derive an SPDE for the trait frequency field using a heuristic infinite-dimensional Itô formula (Curtain and Falb, 1970, theorem 3.8; Da Prato and Zabczyk, 2014, theorem 4.32). Given a type-level quantity $f[x|\phi]$, I define the selection–mutation operator $S_f[x|\phi]$ for f in the population ϕ as:

$$S_f[x|\phi] = \underbrace{(f[x|\phi] - \bar{f}(t))p(x, t)}_{\text{Selection for higher values of } f} + \underbrace{\frac{\mu}{N_K(t)} \left(Q(x|\phi) - p(x) \int_{\mathcal{T}} Q(y|\phi) dy \right)}_{\text{Mutation biases/transmission biases}} \quad (21)$$

The operator $S_f[x|\phi]$ represents how the trait frequency field p changes at the point x in a population ϕ as a balance between two evolutionary processes: (i) *selection* for those trait values x that are associated with higher values of f than the population mean \bar{f} , and (ii) *mutation* that can potentially bias which trait values x arise in the population and thus how the trait frequency field changes over time. I show in section S3 of

the supplementary that the stochastic dynamics of the trait frequency field $p(x, t)$ are described by the remarkably compact equation:

$$\frac{\partial p}{\partial t}(x, t) = \underbrace{S_w[x|\phi]}_{\text{Classical selection-mutation}} - \underbrace{\frac{1}{K N_K(t)} S_{\tau}[x|\phi]}_{\text{Noise-induced selection-mutation}} + \underbrace{\frac{1}{\sqrt{K} N_K(t)} \dot{W}_p(x, t)}_{\text{Undirected stochastic fluctuations}} \quad (22)$$

where

$$\dot{W}_p(x, t) := \sqrt{\phi(x, t) \tau(x|\phi) + \mu Q(x|\phi)} \dot{W}(x, t) - p(x) \int_{\mathcal{T}} \sqrt{\phi(y, t) \tau(y|\phi) + \mu Q(y|\phi)} \dot{W}(y, t) dy \quad (23)$$

is a spacetime white noise that vanishes upon taking probabilistic expectations.

Thus, the trait frequency field is influenced by three distinct evolutionary forces. $S_w[x|\phi]$ quantifies the selection–mutation balance for higher fitness w in the population and thus represents the effects of classical selection and mutation. The $-(S_{\tau}[x|\phi]/K N_K)$ term quantifies the balance between mutation and selection for *lower* turnover rates τ (notice the minus sign), and the strength of this force depends inversely on the total population size $K N_K$. This force is called noise-induced selection, and has been shown to play an important role in diverse finite population eco-evolutionary systems (Constable et al., 2016; McLeod and Day, 2019a; Week et al., 2021; Kuosmanen et al., 2022; Mazzolini and Grilli, 2023; Bhat and Guttal, 2024). Notice that even if a trait is in complete selection–mutation balance for Malthusian fitness w (i.e. $S_w[x|\phi] = 0$), the trait frequency field could experience directional changes arising from a lack of selection–mutation balance for turnover rates $S_{\tau}[x|\phi]$ due to noise-induced selection. Finally, $\dot{W}_p(x, t)$ captures the effects of stochastic fluctuations to the trait frequency field due to demographic stochasticity. This term exhibits the $1/\sqrt{K}$ scaling that is characteristic of genetic drift. Though the term disappears upon taking probabilistic expectations $\mathbb{E}[\cdot]$ and thus does not influence the expected behavior over short time scales, discrete trait analogs of this term are known to be able to directionally bias evolutionary dynamics over long timescales (McLeod and Day, 2019a,b; Bhat and Guttal, 2024). Eq. (22) is a stochastic version of the replicator-mutator equation for quantitative traits in finite, fluctuating populations, as will become clear upon taking the infinite population limit.

3.2.1. The infinite population limit

If we take the infinite population limit ($K \rightarrow \infty$) of Eq. (22), all terms other than the selection–mutation operator for fitness drop out of the equation. Thus, the infinite population limit is the deterministic process described by the PDE

$$\frac{\partial p}{\partial t}(x, t) = [w(x|\phi) - \bar{w}(t)] p(x, t) + \mu \left[Q(x|\phi) - p(x) \int_{\mathcal{T}} Q(y|\phi) dy \right] \quad (24)$$

Eq. (24) is a version of the replicator-mutator equation from evolutionary game spaces (Cressman and Tao, 2014). In supplementary section S4, I show that Eq. (24) also recovers Kimura’s continuum-of-alleles model (Kimura, 1965) when the trait space is the real line and the mutational effects in $Q(x|\phi)$ are modeled via convolution with a mutation kernel (i.e. modeled such that mutations are symmetric, more extreme mutational effects are less likely, and the probability of a mutation of a given mutational effect size is parameterized by a mutation kernel function). The replicator-mutator equation can also be derived from a stochastic individual-based model using measure-theoretic martingale techniques (Champagnat et al., 2006; Wakano et al., 2017).

3.3. A stochastic price equation

In supplementary section S5, I use the equation for the trait frequency field (Eq. (22)) to show that the statistical mean value of any

function f (now possibly also varying over time) in the population obeys the one-dimensional SDE:

$$\frac{d\bar{f}}{dt} = \underbrace{\text{Cov}(w, f)}_{\text{Classical selection}} - \underbrace{\frac{1}{KN_K(t)} \text{Cov}(\tau, f)}_{\text{Noise-induced selection}} + \underbrace{\left(\frac{\partial f}{\partial t}\right)}_{\text{Ecological effects}} + \underbrace{M_{\bar{f}}(p, N_K)}_{\text{Mutational effects}} + \underbrace{\frac{1}{\sqrt{KN_K(t)}} \frac{dW_{\bar{f}}}{dt}}_{\text{Stochastic fluctuations}} \quad (25)$$

where

$$M_{\bar{f}}(p, N_K) = \frac{\mu}{N_K} \left(1 - \frac{1}{KN_K(t)}\right) \left(\int_{\mathcal{T}} f(x|\phi) Q(x|\phi) dx - \bar{f}(t) \int_{\mathcal{T}} Q(y|\phi) dy\right) \quad (26)$$

is a term describing the effects of mutation/transmission biases and

$$\frac{dW_{\bar{f}}}{dt} = \int_{\mathcal{T}} \left(f(x|\phi) - \bar{f}(t)\right) \sqrt{\phi(x, t) \tau(x|\phi) + \mu Q(y|\phi)} \dot{W}(x, t) dx \quad (27)$$

is a purely temporal white noise.

Eq. (25) once again reveals the effects of mutation and selection in a clear manner: The mean value of f increases due to classical natural selection if f covaries positively with fitness, and increases due to noise-induced selection if f covaries negatively with turnover rate. Mutational biases are captured in the $M_{\bar{f}}$ term. The third term on the RHS of Eq. (25) is non-zero whenever the function f changes over time through mechanisms other than through changes in the field ϕ itself, and thus represents the effects of eco-evolutionary feedbacks due to factors such as plasticity and environmental heterogeneity leading to changes in the function f over time. This term also generically occurs in the Price equation and Fisher's fundamental theorem for discrete traits (Lion, 2018; Kokko, 2021). Finally, the last term on the RHS of Eq. (25) represents the effects of undirected stochastic fluctuations that incorporate the effects of genetic/ecological drift. Note that Eq. (25) holds for any type level field $f(x|\phi)$. In supplementary section S6, I present a stochastic analog of Fisher's fundamental theorem that arises upon substituting $f(x|\phi) = w(x|\phi)$ and $\mu = 0$ into Eq. (25).

3.3.1. The infinite population limit

If we take the infinite population limit in Eq. (25), we obtain a deterministic ODE that reads

$$\frac{d\bar{f}}{dt} = \text{Cov}(w, f) + \left(\frac{\partial f}{\partial t}\right) + \mu \left(\int_{\mathcal{T}} f(x|\phi) Q(x|\phi) dx - \bar{f}(t) \int_{\mathcal{T}} Q(y|\phi) dy\right) \quad (28)$$

Eq. (28) is a (dynamic) version of the Price equation for quantitative traits. For the special case $f(x|\phi) = x$, the quantity $\partial f / \partial t$ is identically 0, and Eq. (28) reduces to a more familiar version of the Price equation (Page and Nowak, 2002; Lion, 2018):

$$\frac{d\bar{x}}{dt} = \text{Cov}(w, x) + \mu \left(\int_{\mathcal{T}} x Q(x|\phi) dx - \bar{x}(t) \int_{\mathcal{T}} Q(y|\phi) dy\right) \quad (29)$$

3.4. A stochastic equation of gradient dynamics in finite populations

Consider now the special case $f(x|\phi) = x$ in Eq. (25). In this section, I restrict myself to the strong selection, weak mutation limit. Specifically, I assume:

- Rare mutations, i.e. μ is infinitesimally small.
- Small mutational effects with 'almost faithful' reproduction, meaning $Q(x|\phi)$ is infinitesimally small.
- Strong selection, meaning that types with low relative fitness are immediately eliminated and the population is sharply peaked around a few trait values.

Mathematically, these assumptions mean that if we begin with a monomorphic population $\phi(x, 0) = N_K(0)\delta_{y_0}$, the population (at least initially) remains strongly peaked about the mean value of the trait, with some small spread due to the (infinitesimal) mutational effects;

Thus, I assume mathematically that $\sigma_x^2(t)$, the variance of the trait in the population at time t , is infinitesimal but non-zero. The density field $\phi(x, t)$ can then be approximated by a scaled Dirac delta mass $N_K(t)\delta_{y(t)}$ moving across the trait space according to a trajectory governed by a function $y(t)$ (to be found). I show in supplementary section S7 that under these assumptions, the trajectory $y(t)$ of a monomorphic population $\phi(x, t) = N_K(t)\delta_{y(t)}$ is approximately given by

$$\frac{dy}{dt} = \underbrace{\sigma_x^2(t) \frac{\partial G(x; y)}{\partial x} \Big|_{x=y}}_{\text{Finite population Selection Gradient}} + \underbrace{\frac{dW_y}{dt}}_{\text{Stochastic Fluctuations}} \quad (30)$$

The quantity $G(x; y)$ is given by

$$G(x; y) = \underbrace{w(x|N_K\delta_y)}_{\text{Classical Selection}} - \underbrace{\frac{1}{KN_K(t)} \tau(x|N_K\delta_y)}_{\text{Noise-induced Selection}} \quad (31)$$

and represents the balance between classical natural selection and noise-induced selection. $\partial G / \partial x$ is thus a modified selection gradient that not only accounts for classical selection, but also incorporates noise-induced selection. The white noise term in Eq. (30) is given by

$$\frac{dW_y}{dt} = \int_{\mathcal{T}} (x - y(t)) \sqrt{\tau(x|N_K(t)\delta_{y(t)})} \dot{W}(x, t) dx \quad (32)$$

and vanishes upon taking probabilistic expectations over realizations. Note that the expected dynamics in the finite population do not follow the classic natural selection gradient as occurs in infinite population models, but instead follow a gradient that represents the balance between classical selection and noise-induced selection. Champagnat and Lambert (2007) have also obtained an SDE for adaptive dynamics in finite populations that they call the 'canonical diffusion' of adaptive dynamics.

3.4.1. The infinite population limit

Taking $K \rightarrow \infty$ in Eq. (30), we obtain

$$\frac{dy}{dt} = \sigma_x^2(t) \frac{\partial w(x|\delta_y)}{\partial x} \Big|_{x=y} \quad (33)$$

The term $w(x|\delta_{y(t)})$ is the expected growth rate of an individual with trait value x in a population in which (almost) every individual has trait value y . This quantity is referred to as the invasion fitness of a 'mutant' x in a population of 'resident' y individuals. Eq. (33) is the canonical form of a broad class of models captured under the name of 'gradient dynamics' (Abrams et al., 1993; Taylor and Day, 1997; Lehtonen, 2018). It is also deeply related to the canonical equation of adaptive dynamics (Lion, 2018; Lehtonen, 2018).

4. Discussion

The stochastic field theoretic formalism I present provides a method for studying eco-evolutionary dynamics of populations bearing a single one-dimensional quantitative trait from the biological first principles of birth and death. In particular, I have derived an equation for studying ecological dynamics by tracking population densities (Eq. (17)) and have also derived SDE/SPDEs for evolutionary dynamics that generalize the replicator-mutator equation (Eq. (22)), Price equation (Eq. (25)), and gradient dynamics (Eq. (30)). Along with describing the effects of natural selection, mutation/transmission bias, and genetic drift, these equations also provide a general description of the role of noise-induced selection in affecting the evolutionary trajectories of finite, fluctuating populations (Gillespie, 1974; Constable et al., 2016; McLeod and Day, 2019a; Week et al., 2021). As a concrete example of the utility of these equations, I present a simple asexual model of resource competition in section S9 of the Supplementary that recovers the quantitative logistic equation (Doebeli, 2011) in the infinite population limit, and a second example in section S10 that recovers as the Fisher-KPP equation in

the infinite population limit but whose finite population dynamics does not correspond to the ‘stochastic Fisher–KPP equation’ (Doering et al., 2003) (but is the SPDE expected by Champagnat et al., 2006).

One intriguing application of the general formalism outlined in this paper is in the study of the emergence of sympatric polymorphism for quantitative traits via evolutionary branching (Doebeli, 2011). Adaptive dynamics, the primary theoretical framework for studying evolutionary branching, is typically formulated in an infinite population setting (Geritz et al., 1998; Doebeli, 2011; Avila and Mullan, 2023) obtained as a deterministic limit of an underlying stochastic model (Dieckmann and Law, 1996; Champagnat and Lambert, 2007). However, studies show that finite populations exhibit a systematically lower tendency to undergo evolutionary branching and/or take longer to branch than predicted by infinite population frameworks, and may remain monomorphic if the population size is too small (Johansson and Ripa, 2006; Claessen et al., 2007; Wakano and Iwasa, 2013; Débarre and Otto, 2016; Johnson et al., 2021). SPDEs can often exhibit noise-induced phase transitions where stochasticity causes qualitative changes in the behavior of the system as a parameter controlling the strength of noise in the system is varied. Such transitions can be systematically studied using the language of non-equilibrium statistical physics (García-Ojalvo and Sancho, 1999, Chapter 3). The SPDEs I formulate in this paper, where the strength of stochastic fluctuations scales as $K^{-1/2}$, suggest that the failure of evolutionary branching in small populations could be reformulated and studied very generally in terms of a noise-induced phase transition in which the population size measure K is the driving parameter. Alternatively, the stochastic version of the gradient equation (Eq. (30)) could be used to study evolutionary branching in finite, fluctuating populations exactly analogously to how invasion fitness functions and their effects on population dynamics are used to study branching in infinite population models via the canonical equation of adaptive dynamics (Doebeli, 2011). In fact, Eq. (30) directly shows that evolutionarily singular points (points at which the RHS of Eq. (33) vanishes) need not be fixed points for finite populations when noise-induced selection is present. This fact could be a general factor hindering evolutionary branching in finite populations, since a population may not stay at an evolutionary branching point for long enough to allow polymorphisms to become established in the population. I also provide a general method to study evolutionary branching using the density field and a ‘weak noise approximation’ in section S8.

4.1. Connections with previous studies

Lande (1976) has used tools from probability theory to study the effects of demographic stochasticity in populations bearing quantitative traits and evolving in discrete time. My work can be viewed as an extension of Lande’s framework to fluctuating populations evolving in continuous time. Alternatively, the formalism can be seen as a generalization of Lion (2018)’s conceptual synthesis of eco-evolutionary dynamics to finite, fluctuating populations: Taking the infinite population limit of the equations presented in this paper yields the quantitative trait versions of the equations presented in Lion (2018). Just like in Lion (2018), equations for moments such as the mean value (Eq. (25)) and variance of any field can be iteratively obtained from the stochastic replicator-mutator equation (Eq. (22)) using Itô’s formula.

The first study of noise-induced selection for reduced turnover rates is generally attributed to Gillespie (1974) (see Veller et al. (2017)). Gillespie was interested in variance in offspring numbers, and the effect I identify as noise-induced selection is therefore often referred to as a selection ‘for reduced variance’ in the bet-hedging and life-history evolution literature since τ_i controls the infinitesimal variance of the density process through Eq. (17) (but note that the variance in this case is variance in per capita growth rate rather than variance in number of offspring, and that the stochasticity here is intrinsic to the population rather than being the result of a fluctuating external environment). My

formulation can be connected with the bet-hedging literature in three distinct ways: (1) while Gillespie (1974) worked with simple models in which individuals could have only one of two possible phenotype values, the formalism I present in this paper provides equations describing noise-induced selection in populations bearing quantitative traits in which infinitely many distinct phenotypes may arise over time. (2) Later models of bet-hedging literature in life-history evolution often use an approach that is ‘dynamically insufficient’: rather than finding dynamical equations that are forward-looking in time, these studies instead partition a given amount of phenotypic change between two successive generations into various components in the style of the Price equation (Frank and Slatkin, 1990). In contrast, my approach is dynamic, providing SDEs and SPDEs that are ‘forward-looking’ in time. In this sense, the paper can be considered as a generalization of some of the ideas studied in Parsons et al. (2010) and Bhat and Guttal (2024) to the study of quantitative traits. (3) The equations I derive in this paper also model a second noise-induced effect that is often not discussed in bet-hedging literature: The ‘noise’ terms (stochastic integral terms in the SDEs/SPDEs) have recently been shown to contribute to systematic directional biases in long-term evolutionary trajectories through a mechanism that is distinct from the ‘Gillespie effect’ from bet-hedging theory (McLeod and Day, 2019a). However, McLeod and Day (2019a) work with discrete traits, and my work can thus also be viewed as an extension of McLeod and Day (2019a) to populations bearing quantitative traits.

Week et al. (2021) have recently independently arrived at the equations for trait frequencies (Eq. (22)) and mean trait value (Eq. (25)) for the special case $f(x|\phi) = x$ by studying the scaling limits of measure-valued branching processes using certain heuristics for space-time white noise (Week et al., 2021). My formalism and Week et al. (2021)’s formalism are complementary to each other. My formulation provides an alternate method of attack for the study of quantitative traits in finite fluctuating populations that may be more appropriate for some particular problems (such as phenotypic clustering; see section S8), while the approach in Week et al. (2021) may be more appropriate for others. Etheridge et al. (2024) have also recently studied similar infinite-dimensional stochastic processes and their scaling limits in the context of spatial ecology. Though the focus of their work is ecological, many of the technical tools used and scaling limits studied are complementary to this paper as well as the more rigorous work of Champagnat et al. (2006) and Week et al. (2021).

4.2. The utility of the SPDE approach

In this paper, I have used an analytical pipeline that consists of modeling the population as an infinite-dimensional birth–death process, describing the dynamics via a master equation, and then finding an approximate continuous approximation using a so-called ‘system size expansion’ (Fig. 2). This general approach first arose in statistical physics to describe the erratic motion of particles that are under the influence of a large number of forces (Kramers, 1940; Moyal, 1949; Van Kampen, 1981; for the infinite-dimensional version, see sections 13.1 and 13.2 of Gardiner, 2009). For discrete traits, the general analytical pipeline is well-known in population genetics, where it goes by the name of the ‘diffusion approximation’ (Feller, 1951; Kimura, 1964). Though most standard treatments of the diffusion approximation assume the total population size is strictly constant or varies deterministically (Crow and Kimura, 1970; Ewens, 2004; Lambert, 2010; Czappon and Traulsen, 2021), this assumption is not actually necessary (Feller, 1951, section 10), and indeed, relaxing the assumption can have important consequences for population dynamics through noise-induced selection (Gillespie, 1974; Parsons et al., 2010; Constable et al., 2016; McLeod and Day, 2019a).

I have shown how an approximation scheme that is very similar in spirit (Fig. 2) can also be used to model the evolution of quantitative traits using functional derivatives and SPDEs rather than martingale

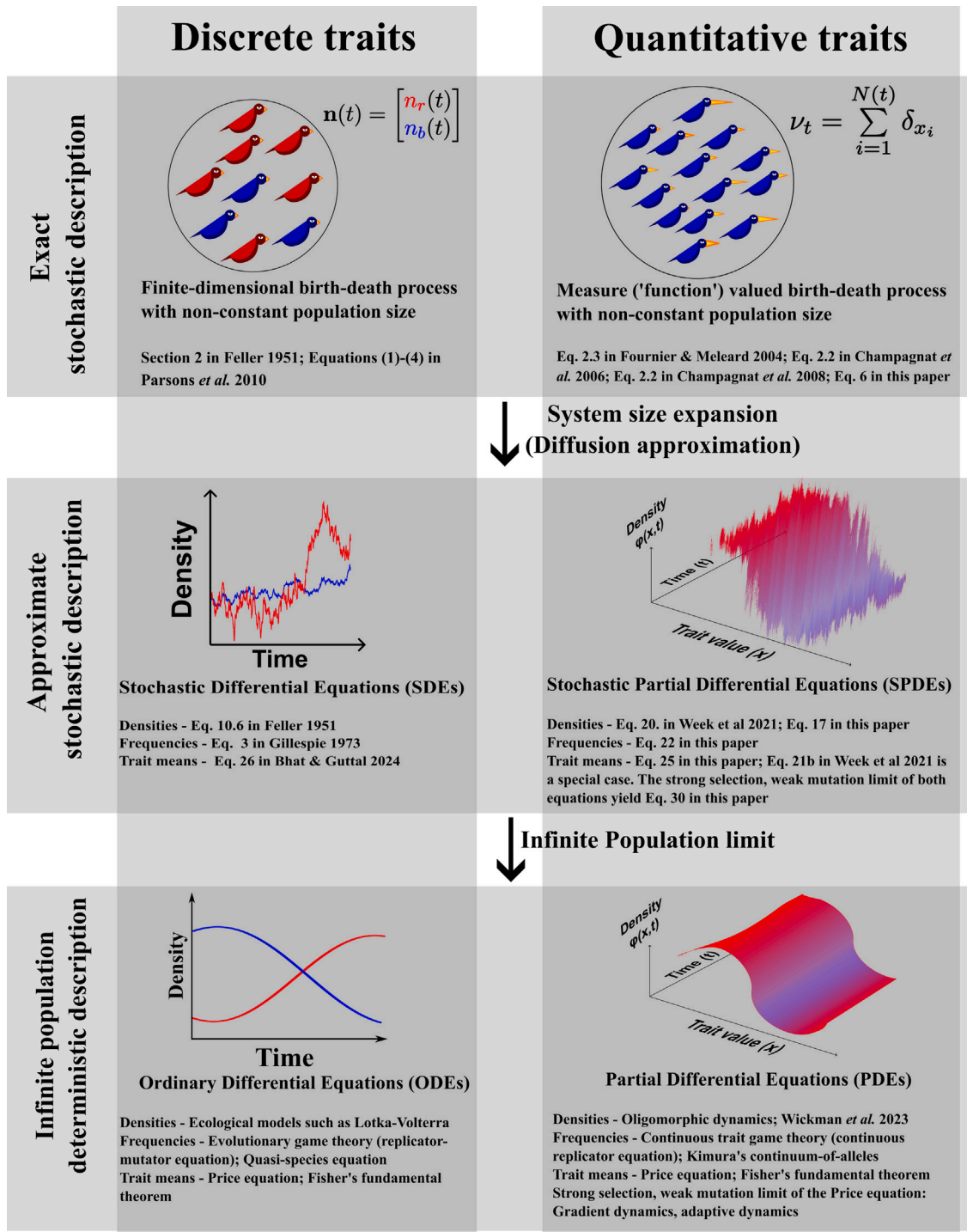


Fig. 2. Summary of the analytic pipeline used in this manuscript and a comparison with discrete trait models. Papers listed provide examples of previous studies that are situated at various points in this pipeline. I have deliberately tried to cite older papers wherever possible. Page and Nowak (2002), Lion (2018), and Lehtonen (2018) speak about the bottom most panels and the connections between the various deterministic equations. Bhat and Guttal (2024) discuss the panel on the left. Champagnat *et al.* (2006) discuss the panel on the right from the measure-theoretic perspective.

techniques. My approach also helps clarify the mathematical connections between models of the evolutionary dynamics of discrete traits and those of quantitative traits — informally, the field equations I present in this paper are the ‘ $m \rightarrow \infty$ ’ limit of equations describing the evolution of m discrete traits upon replacing sums with integrals (see Bhat and Guttal, 2024 for the discrete trait equations in the same notation as used in this paper). Conversely, discrete trait dynamics can be recovered from the field equations presented in this paper and

in Week *et al.* (2021) by discretizing the trait space, for instance by dividing the trait space $\mathcal{T} \subset \mathbb{R}$ into m disjoint intervals and treating all individuals that have trait values within the same interval as equivalent (Fig. 2).

The equations I derive in this paper also allow us to leverage tools from dynamical systems that complement the tools that come with the more probabilistic approach used in the current literature. For instance, models in theoretical population biology and population

genetics routinely assume a separation between ecological and evolutionary timescales (Parsons et al., 2010; Constable et al., 2013; Chotibut and Nelson, 2017; McLeod and Day, 2019a) to make stochastic dynamics more amenable to analysis. Parsons and Rogers (2017) have recently extended the relevant mathematical machinery (‘adiabatic elimination’ in physics language, ‘slow manifold approximation’ in mathematics language) to infinite dimensional systems (i.e. SPDEs). The SPDEs I present in this paper may thus allow us to by-pass the formidable stochastic analysis tools that are required for formulating timescale separation arguments in the more rigorous measure-theoretic martingale perspective (see, for instance, section 5 in Champagnat et al., 2008). SPDEs are also more amenable for studying noise-induced oscillations in population abundance (García-Ojalvo and Sancho, 1999, Chapter 5) using spectral methods similar to those in supplementary section S8.

Currently, stochastic field equations of the kind I derive here are primarily used by statistical physicists (García-Ojalvo and Sancho, 1999) and are attacked using ingenious heuristic tools such as the path integral formalism (Hochberg et al., 1999; Chow and Buice, 2015; Weber and Frey, 2017), Feynman diagrams (Thomas et al., 2014), Fock space methods (Del Razo et al., 2022), and the renormalization group (Täuber et al., 2005). The equations and general approach I develop are also intended to encourage the use of such techniques from physics in studying the evolution of quantitative traits.

4.3. Summary and outlook

In this paper, I have presented a field theoretic approach to modeling the eco-evolutionary population dynamics of quantitative traits in finite, fluctuating populations. The equations I derive provide a generic description of evolutionary dynamics in finite, fluctuating populations that includes the effects of noise-induced selection alongside the more standard forces of natural selection, mutation, eco-evolutionary feedbacks, and genetic/ecological drift. My approach uses techniques grounded in statistical physics and the calculus of variations that are analogous to the diffusion approximation from population genetics (Fig. 2). It supplies an alternative perspective that complements current formulations of evolutionary dynamics of quantitative traits in finite populations that typically use martingale techniques (Champagnat et al., 2006, 2008; Boussange and Pellissier, 2022; Etheridge et al., 2024).

Importantly, the formalism I develop here likely does *not* carry over to the study of population dynamics in higher dimensional trait spaces. This is because stochastic processes driven by spacetime white noise are habitually badly behaved in higher spatial dimensions, making analytical progress very difficult. For example, measure-valued birth-death processes and their scaling limits (superprocesses) often do not admit a density with respect to the Lebesgue measure in ≥ 2 dimensions (Fleming and Viot, 1979; Konno and Shiga, 1988; Dawson et al., 2000; Etheridge, 2000; also see Remark 4.1.1.2.3 in Champagnat et al., 2008 and Remark 2.20 in Etheridge et al., 2024). Even if we were to ignore this technical point, SPDEs in ≥ 2 dimensions routinely do not even admit any function valued solutions (Etheridge, 2000; Pardoux, 2021) and are thus difficult to handle analytically. It may well be the case that concrete biologically useful progress in this direction requires radically new mathematics, a situation increasingly also encountered in other areas of mathematical biology (Borovik, 2021; Vittadello and Stumpf, 2022).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This paper arose from work conducted during my Master’s thesis project in Vishwesha Guttal’s group at the Centre for Ecological Sciences (CES) at the Indian Institute of Science. During that time, Prof. Guttal’s group was supported by grants from the Science and Engineering Research Board (SERB), Government of India (MTR/2022/000273). I am grateful to Vishwesha Guttal for his guidance, advice, and several insightful discussions. Gaurav Athreya, Anish Bhattacharya, Peter Ralph, and two anonymous reviewers provided helpful comments that greatly improved an earlier draft of this manuscript. I am a recipient of a Kishore Vaigyanik Protsahan Yojana (KVPY) fellowship from the Department of Science and Technology of the Government of India (Fellowship ID: SX-1711025), and acknowledge the same for financial support. The open access fee for this publication was covered by the DEAL Consortium between Elsevier and Johannes Gutenberg University, Mainz.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2024.10.003>.

Data availability

No data was used for the research described in the article.

References

- Abrams, P.A., Harada, Y., Matsuda, H., 1993. On the relationship between quantitative genetic and ESS models. *Evolution* 47 (3), 982–985. <http://dx.doi.org/10.2307/2410204>.
- Avila, P., Mullan, C., 2023. Evolutionary game theory and the adaptive dynamics approach: adaptation where individuals interact. *Phil. Trans. R. Soc. B* 378 (1876), 20210502. <http://dx.doi.org/10.1098/rstb.2021.0502>.
- Baez, J.C., Biamonte, J.D., 2018. *Quantum techniques in stochastic mechanics*. World Scientific, New Jersey, ISBN: 978-981-322-693-7.
- Bhat, A.S., Guttal, V., 2024. Eco-evolutionary dynamics for finite populations and the noise-induced reversal of selection. *Amer. Nat.* <http://dx.doi.org/10.1086/733196>.
- Black, A.J., McKane, A.J., 2012. Stochastic formulation of ecological models and their applications. *Trends Ecol. Evolut.* 27 (6), 337–345. <http://dx.doi.org/10.1016/j.tree.2012.01.014>.
- Borovik, A., 2021. A mathematician’s view of the unreasonable ineffectiveness of mathematics in biology. *Biosystems* 205, 104410. <http://dx.doi.org/10.1016/j.biosystems.2021.104410>.
- Boussange, V., Pellissier, L., 2022. Eco-evolutionary model on spatial graphs reveals how habitat structure affects phenotypic differentiation. *Commun. Biol.* 5 (1), 1–12. <http://dx.doi.org/10.1038/s42003-022-03595-3>.
- Bressloff, P.C., 2010. Stochastic neural field theory and the system-size expansion. *SIAM J. Appl. Math.* 70 (5), 1488–1521. <http://dx.doi.org/10.1137/090756971>.
- Buice, M.A., Cowan, J.D., 2007. Field-theoretic approach to fluctuation effects in neural networks. *Phys. Rev. E* 75 (5), 051919. <http://dx.doi.org/10.1103/PhysRevE.75.051919>.
- Champagnat, N., Ferrière, R., Méléard, S., 2006. Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models. *Theor. Popul. Biol.* 69 (3), 297–321. <http://dx.doi.org/10.1016/j.tpb.2005.10.004>.
- Champagnat, N., Ferrière, R., Méléard, S., 2008. From individual stochastic processes to macroscopic models in adaptive evolution. *Stoch. Models* 24 (sup1), 2–44. <http://dx.doi.org/10.1080/15326340802437710>.
- Champagnat, N., Lambert, A., 2007. Evolution of discrete populations and the canonical diffusion of adaptive dynamics. *Ann. Appl. Probab.* 17 (1), 102–155. <http://dx.doi.org/10.1214/105051606000000628>.
- Champagnat, N., Méléard, S., 2011. Polymorphic evolution sequence and evolutionary branching. *Probab. Theory Related Fields* 151 (1), 45–94. <http://dx.doi.org/10.1007/s00440-010-0292-9>.
- Chotibut, T., Nelson, D.R., 2017. Population genetics with fluctuating population sizes. *J. Stat. Phys.* 167 (3), 777–791. <http://dx.doi.org/10.1007/s10955-017-1741-y>.
- Chow, C.C., Buice, M.A., 2015. Path integral methods for stochastic differential equations. *J. Math. Neurosci.* 5 (1), 1–35. <http://dx.doi.org/10.1186/s13408-015-0018-5>.
- Claessen, D., Andersson, J., Persson, L., Roos, A.M.d., 2007. Delayed evolutionary branching in small populations. *Evol. Ecol. Res.* 9 (1), 51–69.

- Constable, G.W.A., McKane, A.J., Rogers, T., 2013. Stochastic dynamics on slow manifolds. *J. Phys. A* 46 (29), 295002. <http://dx.doi.org/10.1088/1751-8113/46/29/295002>.
- Constable, G.W.A., Rogers, T., McKane, A.J., Tarnita, C.E., 2016. Demographic noise can reverse the direction of deterministic selection. *Proc. Natl. Acad. Sci.* 113 (32), E4745–E4754. <http://dx.doi.org/10.1073/pnas.1603693113>.
- Coomes, S., beim Graben, P., Potthast, R., Wright, J. (Eds.), 2014. *Neural Fields: Theory and Applications*. Springer Berlin Heidelberg, Berlin, Heidelberg, ISBN: 978-3-642-54592-4, <http://dx.doi.org/10.1007/978-3-642-54593-1>.
- Coulson, T., Rohani, P., Pascual, M., 2004. Skeletons, noise and population growth: the end of an old debate? *Trends Ecol. Evolut.* 19 (7), 359–364. <http://dx.doi.org/10.1016/j.tree.2004.05.008>.
- Cressman, R., Tao, Y., 2014. The replicator equation and other game dynamics. *Proc. Natl. Acad. Sci.* 111 (supplement_3), 10810–10817. <http://dx.doi.org/10.1073/pnas.1400823111>.
- Crow, J.F., Kimura, M., 1970. *An Introduction to Population Genetics Theory*. In: Harper International Editions, Harper & Row, New York.
- Curtain, R.F., Falb, P.L., 1970. Ito's lemma in infinite dimensions. *J. Math. Anal. Appl.* 31 (2), 434–448. [http://dx.doi.org/10.1016/0022-247X\(70\)90037-5](http://dx.doi.org/10.1016/0022-247X(70)90037-5).
- Czuppon, P., Traulsen, A., 2021. Understanding evolutionary and ecological dynamics using a continuum limit. *Ecol. Evolut.* 11 (11), 5857–5873. <http://dx.doi.org/10.1002/ecs3.7205>.
- Da Prato, G., Zabczyk, J., 2014. *Stochastic Equations in Infinite Dimensions*, second ed. In: *Encyclopedia of Mathematics and its Applications*, Cambridge University Press, Cambridge, ISBN: 978-1-107-05584-1, <http://dx.doi.org/10.1017/CBO9781107295513>.
- Dawson, D.A., Vaillancourt, J., Wang, H., 2000. Stochastic partial differential equations for a class of interacting measure-valued diffusions. *Ann. l'Inst. Henri Poincaré Stat.(B) Probab.* 36 (2), 167–180. [http://dx.doi.org/10.1016/S0246-0203\(00\)00121-7](http://dx.doi.org/10.1016/S0246-0203(00)00121-7).
- de Vladar, H.P., Barton, N.H., 2011. The contribution of statistical physics to evolutionary biology. *Trends Ecol. Evolut.* 26 (8), 424–432. <http://dx.doi.org/10.1016/j.tree.2011.04.002>.
- de Vries, C., Galipaud, M., Kokko, H., 2023. Extrinsic mortality and senescence: a guide for the perplexed. *Peer Community J.* 3, <http://dx.doi.org/10.24072/pcjournal.253>.
- Débarre, F., Otto, S.P., 2016. Evolutionary dynamics of a quantitative trait in a finite asexual population. *Theor. Popul. Biol.* 108, 75–88. <http://dx.doi.org/10.1016/j.tpb.2015.12.002>.
- Del Razo, M.J., Frömberg, D., Straube, A.V., Schütte, C., Höfling, F., Winkelmann, S., 2022. A probabilistic framework for particle-based reaction–diffusion dynamics using classical Fock space representations. *Lett. Math. Phys.* 112 (3), 49. <http://dx.doi.org/10.1007/s11005-022-01539-w>.
- Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34 (5), 579–612. <http://dx.doi.org/10.1007/BF02409751>.
- Doebeli, M., 2011. *Adaptive Diversification*. Princeton University Press, Princeton, N.J., ISBN: 978-0-691-12894-8.
- Doebeli, M., Ispolatov, Y., Simon, B., 2017. Towards a mechanistic foundation of evolutionary theory. *eLife* 6, e23804. <http://dx.doi.org/10.7554/eLife.23804>.
- Doering, C.R., Mueller, C., Smereka, P., 2003. Interacting particles, the stochastic Fisher–Kolmogorov–Petrovsky–Piscounov equation, and duality. *Phys. A* 325 (1), 243–259. [http://dx.doi.org/10.1016/S0378-4371\(03\)00203-6](http://dx.doi.org/10.1016/S0378-4371(03)00203-6).
- Doi, M., 1976. Second quantization representation for classical many-particle system. *J. Phys. A: Math. Gen.* 9 (9), 1465. <http://dx.doi.org/10.1088/0305-4470/9/9/008>.
- Etheridge, A.M., 2000. *An Introduction to Superprocesses*. In: *University Lecture Series* (Providence, R.I.), American Mathematical Society, Providence, RI, ISBN: 978-0-8218-2706-2.
- Etheridge, A.M., Kurtz, T.G., Letter, I., Ralph, P.L., Tsui Ho Lung, T., 2024. Looking forwards and backwards: Dynamics and genealogies of locally regulated populations. *Electron. J. Probab.* 29, 1–85. <http://dx.doi.org/10.1214/24-EJP1075>.
- Ewens, W.J., 2004. *Mathematical Population Genetics 1: Theoretical Introduction*. Springer Science & Business Media, ISBN: 978-0-387-20191-7.
- Feller, W., 1951. Diffusion processes in genetics. In: *Proceedings of the Second Berkeley Symposium on Mathematical Statistics and Probability*, Vol. 2. University of California Press, pp. 227–247. <http://dx.doi.org/10.1525/9780520411586-018>.
- Fleming, W.H., Viot, M., 1979. Some measure-valued Markov processes in population genetics theory. *Indiana Univ. Math. J.* 28 (5), 817–843.
- Fournier, N., Méléard, S., 2004. A microscopic probabilistic description of a locally regulated population and macroscopic approximations. *Ann. Appl. Probab.* 14 (4), 1880–1919. <http://dx.doi.org/10.1214/105051604000000882>.
- Frank, S.A., Slatkin, M., 1990. Evolution in a variable environment. *Amer. Nat.* 136 (2), 244–260. <http://dx.doi.org/10.1086/285094>.
- García-Ojalvo, J., Sancho, J.M., 1999. Noise in spatially extended systems. In: *Institute for Nonlinear Science* (Springer-Verlag), Springer, New York, ISBN: 978-0-387-98855-9.
- Gardiner, C.W., 2009. *Stochastic Methods: A Handbook for the Natural and Social Sciences*. Springer, Berlin, ISBN: 978-3-540-70712-7.
- Geritz, S., Kisdi, E., Meszéna, G., Metz, J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12 (1), 35–57. <http://dx.doi.org/10.1023/A:1006554906681>.
- Gillespie, J.H., 1974. Natural selection for within-generation variance in offspring number. *Genetics* 76 (3), 601–606. <http://dx.doi.org/10.1093/genetics/76.3.601>.
- Hochberg, D., Molina-Paris, C., Pérez-Mercader, J., Visser, M., 1999. Effective action for stochastic partial differential equations. *Phys. Rev. E* 60 (6), 6343–6360. <http://dx.doi.org/10.1103/PhysRevE.60.6343>.
- Johansson, J., Ripa, J., 2006. Will sympatric speciation fail due to stochastic competitive exclusion? *Amer. Nat.* 168 (4), 572–578. <http://dx.doi.org/10.1086/507996>.
- Johnson, B., Altrock, P.M., Kimmel, G.J., 2021. Two-dimensional adaptive dynamics of evolutionary public goods games: finite-size effects on fixation probability and branching time. *Royal Soc. Open Sci.* 8 (5), 210182. <http://dx.doi.org/10.1098/rsos.210182>.
- Karatzas, I., Shreve, S.E., 1998. *Brownian Motion and Stochastic Calculus*, second ed. In: *Graduate Texts in Mathematics*, Springer-Verlag, New York, ISBN: 978-0-387-97655-6.
- Kimura, M., 1964. Diffusion models in population genetics. *J. Appl. Probab.* 1 (2), 177–232. <http://dx.doi.org/10.2307/3211856>.
- Kimura, M., 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proc. Natl. Acad. Sci.* 54 (3), 731–736. <http://dx.doi.org/10.1073/pnas.54.3.731>.
- Kokko, H., 2021. The stagnation paradox: the ever-improving but (more or less) stationary population fitness. *Proc. R. Soc. Lond. [Biol.]* 288 (1963), 20212145. <http://dx.doi.org/10.1098/rspb.2021.2145>.
- Kokko, H., Chaturvedi, A., Croll, D., Fischer, M.C., Guillaume, F., Karrenberg, S., Kerr, B., Rolshausen, G., Stapley, J., 2017. Can evolution supply what ecology demands? *Trends Ecol. Evolut.* 32 (3), 187–197. <http://dx.doi.org/10.1016/j.tree.2016.12.005>.
- Konno, N., Shiga, T., 1988. Stochastic partial differential equations for some measure-valued diffusions. *Probab. Theory Related Fields* 79 (2), 201–225. <http://dx.doi.org/10.1007/BF00320919>.
- Kramers, H.A., 1940. Brownian motion in a field of force and the diffusion model of chemical reactions. *Physica* 7 (4), 284–304. [http://dx.doi.org/10.1016/S0031-8914\(40\)90098-2](http://dx.doi.org/10.1016/S0031-8914(40)90098-2).
- Kuusmanen, T., Särkkä, S., Mustonen, V., 2022. Turnover shapes evolution of birth and death rates. <http://dx.doi.org/10.1101/2022.07.11.499527>, bioRxiv, Pages: 2022.07.11.499527 Section: New Results.
- Lambert, A., 2010. Population genetics, ecology and the size of populations. *J. Math. Biol.* 60 (3), 469–472. <http://dx.doi.org/10.1007/s00285-009-0286-3>.
- Lande, R., 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30 (2), 314–334. <http://dx.doi.org/10.2307/2407703>.
- Lehtonen, J., 2018. The price equation, gradient dynamics, and continuous trait game theory. *Amer. Nat.* 191 (1), 146–153. <http://dx.doi.org/10.1086/694891>.
- Lion, S., 2018. Theoretical approaches in evolutionary ecology: Environmental feedback as a unifying perspective. *Amer. Nat.* 191 (1), 21–44. <http://dx.doi.org/10.1086/694865>.
- Lion, S., Sasaki, A., Boots, M., 2023. Extending eco-evolutionary theory with oligomorphic dynamics. *Ecol. Lett.* n/a (n/a), <http://dx.doi.org/10.1111/ele.14183>.
- Martin, P.C., Siggia, E.D., Rose, H.A., 1973. Statistical dynamics of classical systems. *Phys. Rev. A* 8 (1), 423–437. <http://dx.doi.org/10.1103/PhysRevA.8.423>.
- Mazzolini, A., Grilli, J., 2023. Universality of evolutionary trajectories under arbitrary forms of self-limitation and competition. *Phys. Rev. E* 108 (3), 034406. <http://dx.doi.org/10.1103/PhysRevE.108.034406>.
- McLeod, D.V., Day, T., 2019a. Social evolution under demographic stochasticity. *PLoS Comput. Biol.* 15 (2), e1006739. <http://dx.doi.org/10.1371/journal.pcbi.1006739>.
- McLeod, D.V., Day, T., 2019b. Why is sterility virulence most common in sexually transmitted infections? Examining the role of epidemiology. *Evolution* 73 (5), 872–882. <http://dx.doi.org/10.1111/evo.13718>.
- Metcalfe, C.J.E., Pavard, S., 2007a. All paths to fitness lead through demography. *Trends Ecol. Evolut.* 22 (11), 563–564. <http://dx.doi.org/10.1016/j.tree.2007.07.003>.
- Metcalfe, C.J.E., Pavard, S., 2007b. Why evolutionary biologists should be demographers. *Trends Ecol. Evolut.* 22 (4), 205–212. <http://dx.doi.org/10.1016/j.tree.2006.12.001>.
- Moyal, J.E., 1949. Stochastic processes and statistical physics. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 11 (2), 150–210. <http://dx.doi.org/10.1111/j.2517-6161.1949.tb00030.x>.
- Nordbotten, J.M., Bokma, F., Hermansen, J.S., Stenseth, N.C., 2020. The dynamics of trait variance in multi-species communities. *Royal Soc. Open Sci.* 7 (8), 200321. <http://dx.doi.org/10.1098/rsos.200321>.
- Ó Laihleis, E., Evans, M.R., Blythe, R.A., 2018. Minimal stochastic field equations for one-dimensional flocking. *Phys. Rev. E* 98 (6), 062127. <http://dx.doi.org/10.1103/PhysRevE.98.062127>.
- O'Dwyer, J.P., Lake, J.K., Ostling, A., Savage, V.M., Green, J.L., 2009. An integrative framework for stochastic, size-structured community assembly. *Proc. Natl. Acad. Sci.* 106 (15), 6170–6175. <http://dx.doi.org/10.1073/pnas.0813041106>.
- Page, K.M., Nowak, M.A., 2002. Unifying evolutionary dynamics. *J. Theoret. Biol.* 219 (1), 93–98. <http://dx.doi.org/10.1006/jtbi.2002.3112>.
- Papkou, A., Gokhale, C.S., Traulsen, A., Schulerburg, H., 2016. Host–parasite coevolution: why changing population size matters. *Zoology* 119 (4), 330–338. <http://dx.doi.org/10.1016/j.zool.2016.02.001>.

- Pardoux, É., 2021. Stochastic Partial Differential Equations: An Introduction. In: SpringerBriefs in Mathematics, Springer International Publishing, Cham, ISBN: 978-3-030-89002-5, <http://dx.doi.org/10.1007/978-3-030-89002-5>.
- Parsons, T.L., Quince, C., Plotkin, J.B., 2010. Some consequences of demographic stochasticity in population genetics. *Genetics* 185 (4), 1345–1354. <http://dx.doi.org/10.1534/genetics.110.115030>.
- Parsons, T.L., Rogers, T., 2017. Dimension reduction for stochastic dynamical systems forced onto a manifold by large drift: a constructive approach with examples from theoretical biology. *J. Phys. A* 50 (41), 415601. <http://dx.doi.org/10.1088/1751-8121/aa86c7>.
- Peliti, L., 1985. Path integral approach to birth-death processes on a lattice. *J. Physique* 46 (9), 1469–1483. <http://dx.doi.org/10.1051/jphys:019850046090146900>.
- Provine, W.B., 2001. *The Origins of Theoretical Population Genetics: With a New Afterword*. University of Chicago Press, Chicago, IL, ISBN: 978-0-226-68464-2.
- Rogers, T., McKane, A.J., 2015. Modes of competition and the fitness of evolved populations. *Phys. Rev. E* 92 (3), 032708. <http://dx.doi.org/10.1103/PhysRevE.92.032708>.
- Rogers, T., McKane, A.J., Rossberg, A.G., 2012. Demographic noise can lead to the spontaneous formation of species. *Europhys. Lett.* 97 (4), 40008. <http://dx.doi.org/10.1209/0295-5075/97/40008>.
- Sasaki, A., Dieckmann, U., 2011. Oligomorphic dynamics for analyzing the quantitative genetics of adaptive speciation. *J. Math. Biol.* 63 (4), 601–635. <http://dx.doi.org/10.1007/s00285-010-0380-6>.
- Schraiber, J.G., 2014. A path integral formulation of the Wright–Fisher process with genetic selection. *Theor. Popul. Biol.* 92, 30–35. <http://dx.doi.org/10.1016/j.tpb.2013.11.002>.
- Strang, A.G., Abbott, K.C., Thomas, P.J., 2019. How to avoid an extinction time paradox. *Theor. Ecol.* 12 (4), 467–487. <http://dx.doi.org/10.1007/s12080-019-0416-5>.
- Täuber, U.C., Howard, M., Vollmayr-Lee, B.P., 2005. Applications of field-theoretic renormalization group methods to reaction–diffusion problems. *J. Phys. A: Math. Gen.* 38 (17), R79. <http://dx.doi.org/10.1088/0305-4470/38/17/R01>.
- Taylor, P., Day, T., 1997. Evolutionary stability under the replicator and the gradient dynamics. *Evol. Ecol.* 11 (5), 579–590. <http://dx.doi.org/10.1007/s10682-997-1513-2>.
- Thomas, P., Fleck, C., Grima, R., Popović, N., 2014. System size expansion using Feynman rules and diagrams. *J. Phys. A* 47 (45), 455007. <http://dx.doi.org/10.1088/1751-8113/47/45/455007>.
- Thompson, R.P., 2014. Darwin’s theory and the value of mathematical formalization. In: Walsh, D., Thompson, R.P. (Eds.), *Evolutionary Biology: Conceptual, Ethical, and Religious Issues*. Cambridge University Press, Cambridge, ISBN: 978-1-107-02701-5, pp. 109–136. <http://dx.doi.org/10.1017/CBO9781139208796.008>.
- Van Kampen, N.G., 1981. *Stochastic Processes in Physics and Chemistry*. North-Holland, Amsterdam, New York, New York, ISBN: 978-0-444-86200-6, Open Library ID: OL4265375M.
- Veller, C., Muralidhar, P., Constable, G.W.A., Nowak, M.A., 2017. Drift-induced selection between male and female heterogamety. *Genetics* 207 (2), 711–727. <http://dx.doi.org/10.1534/genetics.117.300151>.
- Vittadello, S.T., Stumpf, M.P.H., 2022. Open problems in mathematical biology. *Math. Biosci.* 354, 108926. <http://dx.doi.org/10.1016/j.mbs.2022.108926>.
- Wakano, J.Y., Funaki, T., Yokoyama, S., 2017. Derivation of replicator–mutator equations from a model in population genetics. *Jpn. J. Ind. Appl. Math.* 34, 473–488. <http://dx.doi.org/10.1007/s13160-017-0249-9>.
- Wakano, J.Y., Iwasa, Y., 2013. Evolutionary branching in a finite population: Deterministic branching vs. stochastic branching. *Genetics* 193 (1), 229–241. <http://dx.doi.org/10.1534/genetics.112.144980>.
- Weber, M.F., Frey, E., 2017. Master equations and the theory of stochastic path integrals. *Rep. Progr. Phys.* 80 (4), 046601. <http://dx.doi.org/10.1088/1361-6633/aa5ae2>.
- Week, B., Nuismer, S.L., Harmon, L.J., Krone, S.M., 2021. A white noise approach to evolutionary ecology. *J. Theoret. Biol.* 521, 110660. <http://dx.doi.org/10.1016/j.jtbi.2021.110660>.
- Wickman, J., Koffel, T., Klausmeier, C.A., 2023. A theoretical framework for trait-based eco-evolutionary dynamics: Population structure, intraspecific variation, and community assembly. *Amer. Nat.* 201 (4), 501–522. <http://dx.doi.org/10.1086/723406>.