

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

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## Abstract

Infinitely many distinct trait values may arise in populations bearing quantitative traits, and modelling 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 methods use ideas from statistical physics and present an alternative to some recently proposed measure-theoretic frameworks.

**Keywords:** Evolutionary theory; Demographic stochasticity; Noise-induced selection; Finite populations; Eco-evolutionary dynamics; Quantitative genetics

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# Introduction

The success of the Modern Synthesis (Provine, 2001; Thompson, 2014) illustrates the value of abstract mathematical modelling in evolutionary biology. Several major modelling 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, 2007a; 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 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 princi-

ples, 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’ (Metcalf and Pavard, 2007b). 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 Vladar and Barton, 2011; Black and McKane, 2012; Schraiber, 2014). However, most studies that apply ideas from statistical physics to biological populations focus on modelling 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 intro-

duced 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 modelling 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 there exists an ecological carrying capacity, 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 measure-theoretic framework presented in previous studies (Champagnat et al., 2006; Champagnat et al., 2008) with a formalism that may be more accessible to readers without a background in stochastic analysis. 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.

## 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,  $\delta_x$  should be thought of as analogous to an indicator function: Given any set  $A \subseteq \mathcal{T}$ , integrating  $\delta_x$  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  $\int_A f(y)\delta(y - x)dy$ .

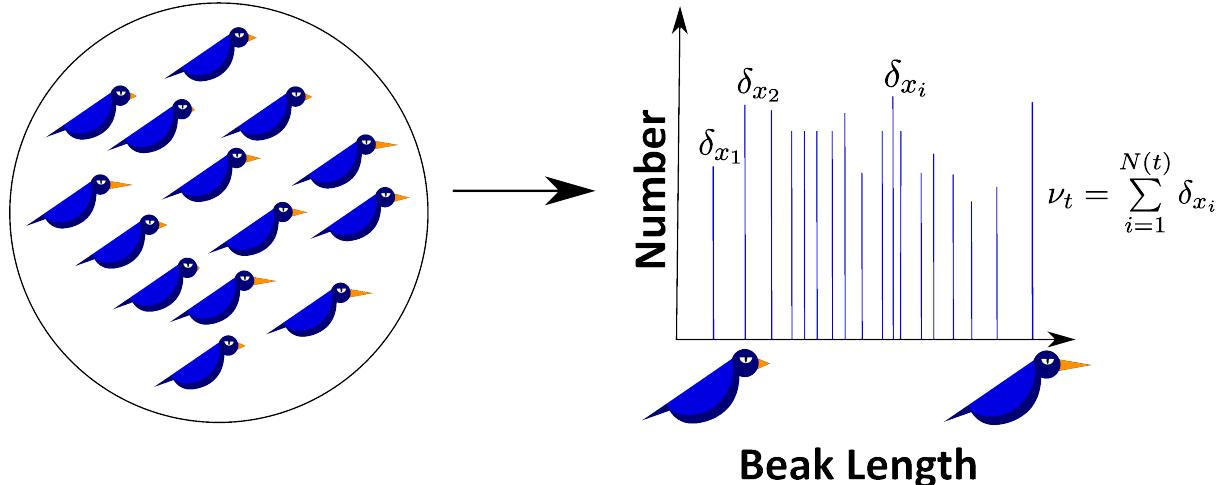
If the population at any time  $t$  consists of  $N(t)$  individuals with trait values  $\{x_1, x_2, \dots, x_{N(t)}\}$ , it can then be completely characterized (Fig. 1) by the ‘stochastic field’

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

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  $\nu$ . I will use the notation  $\nu(x, t)$  to denote the field at time  $t$  to help the reader remember this interpretation of  $\nu$  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,  $\nu$  is viewed as a measure and thus integration of  $f$  against  $\nu$  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.



**Figure 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.

Now that we have described the population, we must define the rules for how it changes over time. I assume that the probability of 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  $\nu$ . That is, if we know that the population was in the state  $\nu$  and we know that *either a birth or a death* has occurred and changed the population to some state other than  $\nu$ , 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

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

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

the set  $A$  is

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

where  $\mathcal{N} = \int_{\mathcal{T}} b(x|\nu) + d(x|\nu) dx$  is the normalizing constant in both cases. I assume  $\mathcal{N}$  is always finite and non-zero. Our description of population dynamics is thus a ‘function’-valued Markov process (and more precisely a function-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 scale linearly with the total population size, *i.e.* that for a given population  $\nu$ , 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  $\nu$ .

Let  $P(\nu, t|\nu_0, 0)$  be the (conditional) probability density function of the process. 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  $\nu$  either through a birth of an individual  $\delta_x$  in a population  $\nu - \delta_x$ , or through the death of an individual  $\delta_x$  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  $\nu$  is thus given by  $b(x|\nu - \delta_x)$ . To find the total transition probability into the state  $\nu$ , 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  $\nu$  at time  $t$  due to births is

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

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  $\nu$  is through death of type  $x$  individuals and thus has transition rate  $d(x|\nu + \delta_x)$ . The total transition probability into the population  $\nu$  at time  $t$  due to deaths of individuals can thus be written

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

The transition rate out of  $\nu$  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  $\nu$  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  $\nu$  must be given by the difference between the rate of inflow and the rate of outflow of probability, or, in equations,

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

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

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

Equation 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).

## The population density field

On ecological grounds, I assume that 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  $b(x|\nu)$  and  $d(x|\nu)$  are such that there exists a  $K > 0$  such that for any set  $A \subseteq \mathcal{T}$ ,  $\int_A [b(x|\nu) - d(x|\nu)] dx < 0$  whenever  $\int_{\mathcal{T}} \nu dx > K$ . In this case, we expect the stochastic process to remain in the domain where the total population size  $\int_{\mathcal{T}} \nu dx$  is  $\mathcal{O}(K)$ . Thus,  $K = \infty$  corresponds to an infinitely large population. By dividing the population number field  $\nu(\cdot, t)$  by  $K$ , we can now obtain a new process  $\{\phi(\cdot, t)\}_{t \geq 0}$  such that 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  $\phi$  the population density field. The field at time  $t$  is defined as

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

Note that since the total population size  $\int_{\mathcal{T}} \nu(x, t) dx$  is  $\mathcal{O}(K)$ , the total population density  $\int_{\mathcal{T}} \phi(x, t) dx$  is  $\mathcal{O}(1)$ . I assume that the density process scales such that  $\int_{\mathcal{T}} \phi(x, t) dx \rightarrow 1$  as  $K \rightarrow \infty$  so that we may still speak of population density dynamics in the infinite population limit. 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  $b(x|\nu)$  and  $d(x|\nu)$  can be rewritten as:

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

. 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. 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.

## Functional forms of the birth and death rates

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

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

where  $b^{(\text{ind})}(x|\phi)$ ,  $d^{(\text{ind})}(x|\phi)$ , and  $\mu Q(x|\phi)$  are all  $\mathcal{O}(1)$  and continuous in both  $x$  and  $\phi$ . 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  $\phi$  at an individual (per-capita) level. When there are no type  $x$  individuals in the population ( $\phi(x, \cdot) = 0$ ), 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  $\phi(x, \cdot)b^{(\text{ind})}(x|\phi)$  vanishes whenever  $\phi(x, \cdot) = 0$ . 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  $\phi(y, \cdot)$ ), but does *not* depend on the density of type  $x$  individuals (i.e.  $\phi(x, \cdot)$ ). The function  $Q(x|\phi)$  accounts for this possibility of birth due to mutations or immigration. 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  $\mathcal{O}(1)$ ) and could in principle model several ecological phenomena.

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

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

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  $\phi$  due to non-mutational effects. I also

define  $\tau(x|\phi)$ , the *per-capita turnover* rate of type  $x$  in a population  $\phi$ , 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  $\phi$  due to non-mutational effects.

## 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

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

Thus,  $K N_K(t)$  is the total population size at time  $t$ . When the population is at carrying capacity,  $N_K = 1$ . Further, by the assumption I made when first introducing the carrying capacity above,  $\int_{\mathcal{T}} \phi dx = N_K \rightarrow 1$  as  $K \rightarrow \infty$  so that we can still speak of population density dynamics in the infinite population size limit.

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

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

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  $f(x|\phi)$  be a field describing the value of any quantitative ‘type’ level quantity in a population  $\phi$  (*i.e.* a field defined at every point  $x \in \mathcal{T}$ ). For example,  $f$  could describe a phenotype, a quantity such as fitness or turnover rate, or simply a label defined at each trait value  $x$ . I assume  $f(x|\phi)$  takes values in  $\mathbb{R}$ . Given any such type-level quantity, We can define the mean value of  $f$  in the population  $\phi$  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

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

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  $\phi$ . 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  $\mathbb{E}[\cdot]$ .

## 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  $\overline{f}$  of any field describing a type-level quantity  $f(x|\phi)$  (of particular interest will be  $\overline{x}$ , 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.

### A field equation for population densities

In supplementary section S2, I obtain an approximate equation describing the behaviour of the density field  $\phi$  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:

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

Symbol	Meaning
$\mathcal{T}$	Trait space, assumed a subset of $\mathbb{R}$ .
$\delta_x$	Dirac mass centered at $x \in \mathcal{T}$ . We will use this to characterize a single individual.
$\nu(y, t)$	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 $\nu(y, t) = \sum_i \delta_{x_i}$ 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 $\{\nu(\cdot, t)\}_{t \geq 0}$ .
$K$	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, $\nu(y, t)/K$
$\mathcal{M}_K(\mathcal{T})$	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 $\nu$ at time $t$ if it begins in a state $\nu_0$ at time 0.
$b^{(\text{ind})}, d^{(\text{ind})}$	Per-capita birth and death rates, excluding potential mutational effects (see below)
$\mu Q(x \phi)$	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 (parametrized 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 $\phi$ .
$\tau(x \phi)$	Per-capita turnover rate $b^{(\text{ind})}(x \phi) + d^{(\text{ind})}(x \phi)$ of trait value $x$ in a population $\phi$ .
$\bar{f}$	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 $\bar{fg} - \bar{f}\bar{g}$ .
$\dot{W}(x, t)$	A spacetime white noise process on $\mathcal{T} \times [0, \infty)$ .

**Table 1:** Table of Notation

where I have suppressed the  $t$  dependence of  $\phi$  for conciseness. Here,  $\delta F/\delta\rho$  denotes the *functional derivative* of the functional  $F$  with respect to the function  $\rho$ , defined indirectly as the unique object that satisfies for any function  $\xi$

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

Equation 15 is a functional Fokker-Planck equation (Gardiner, 2009, Equation 13.1.25; García-Ojalvo and Sancho, 1999, Equation 2.54) for  $P(\phi, t)$ , the probability of finding the population in a state  $\phi$  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  $g \equiv 0, \gamma = \sigma^2 = 1, \epsilon^2 = 2$ ). 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  $t > 0$ :

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

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.

### The infinite population limit

Taking the infinite population limit ( $K \rightarrow \infty$ ) in equation 17 yields a deterministic PDE:

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

Equation 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 equation 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). Equation 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  $k^{\text{th}}$  morph,  $\phi_k(x, t)$  is the phenotypic distribution of the  $k^{\text{th}}$  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).

### 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

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

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  $\mathcal{S}_f[x|\phi]$  for  $f$  in the population  $\phi$  as:

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

The operator  $\mathcal{S}_f[x|\phi]$  represents how the trait frequency field  $p$  changes at the point  $x$  in a population  $\phi$  as a balance between two evolutionary processes: (i) *selection* for those trait frequencies that are associated with higher values of  $f$  than the population mean  $\bar{f}$ , and (ii) *mutation* that can potentially bias which values of  $x$  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:

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

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.  $\mathcal{S}_w[x|\phi]$  quantifies the selection-mutation balance for higher fitness  $w$  in the population and thus represents the effects of classical selection and mutation. The  $-(\mathcal{S}_{\tau}[x|\phi]/KN_K)$  term quantifies the balance between mutation and selection for *lower* turnover rates  $\tau$  (notice the minus sign), and the strength of this force depends inversely on the total population size  $KN_K$ . 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). Notice that even if a trait is in complete selection-mutation balance for Malthusian fitness  $w$  (*i.e.*  $\mathcal{S}_w[x|\phi] = 0$ ), the trait frequency field could experience directional changes arising from a lack of selection-mutation balance for turnover rates  $\mathcal{S}_\tau[x|\phi]$  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; McLeod and Day, 2019b). Equation 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.

### ***The infinite population limit***

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

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

Equation 24 is a version of the replicator-mutator equation from evolutionary game theory for continuous strategy spaces (Cressman and Tao, 2014). In supplementary section S4, I show that equation 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 modelled via convolution with a mutation kernel (*i.e.* modelled 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).

## **A stochastic Price equation**

In supplementary section S5, I use the equation for the trait frequency field (equation 22) to show that the statistical mean value of any type-level quantity  $f$  in the population obeys

the one-dimensional SDE:

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

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

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

is a purely temporal white noise (*i.e.*  $W_{\bar{f}}$  is a Brownian motion).

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  $\phi$  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.

### The infinite population limit

If we take the infinite population limit in equation 25, we obtain a deterministic ODE that reads

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

Equation 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 equation 28 reduces to a more familiar version of the Price equation (Page and Nowak, 2002; Lion, 2018):

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

### 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.*  $\mu$  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.

### *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).

## 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 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 Mullon, 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.

## 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 traitversions 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) (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  $\tau_i$  controls the infinitesimal variance of the density process through equation 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 to the study of quantitative traits. (3) The equation I provide in this paper also models a second effect of noise-induced selection 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 measure-theoretic approach in Week et al., 2021 may be more appropriate for others.

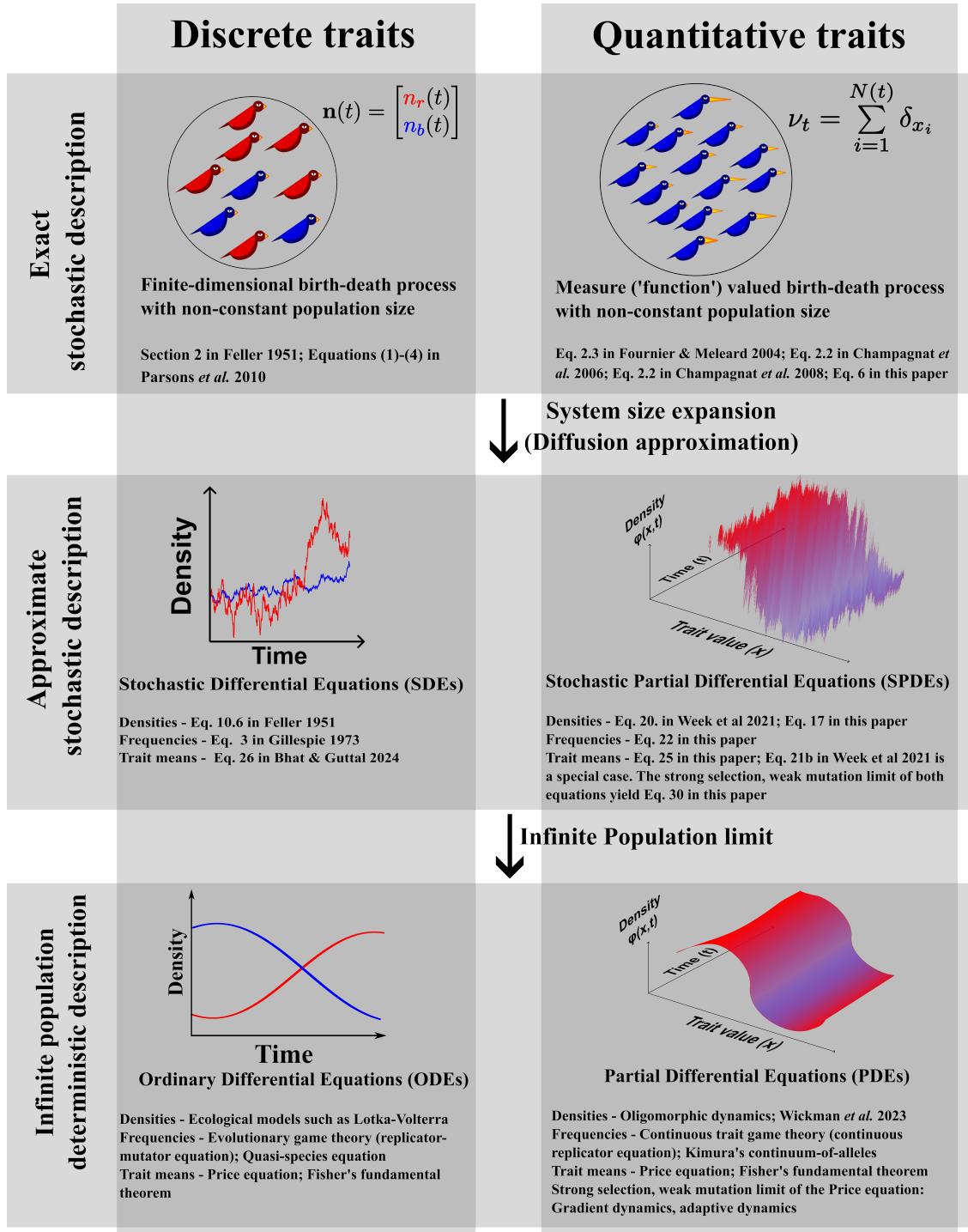
## The utility of the SPDE approach

In this paper, I have used an analytical pipeline that consists of modelling 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; Czuppon 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 techniques. I thus believe the methods I use in this paper may be more accessible to theorists familiar with statistical physics and calculus of variations on one hand, and more familiar to theorists who are acquainted with the diffusion approximation on the other. 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.



**Figure 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. Champagnat et al., 2006 discuss the rightmost panel from the measure-theoretic perspective.

## 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. Much like the Price equation, the utility of these equations thus lies not (necessarily) in their solutions for particular model systems, but instead in the clarity they provide in thinking about the various evolutionary forces operating in finite, fluctuating populations. 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) and presents an alternative perspective that complements current measure-theoretic formulations of evolutionary dynamics of quantitative traits in finite populations (Champagnat et al., 2006; Champagnat et al., 2008; Boussange and Pellissier, 2022).

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, a probability density  $P(\phi, t)$  in the usual sense (*i.e.* with respect to the Lebesgue measure) frequently does not exist in  $\geq 2$  dimensions if the system has non-trivial biological dynamics (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). Even if we were to ignore this technical point, SPDEs in  $\geq 2$  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).

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# **Supplementary Information for Bhat 2024: A stochastic field theory for the evolution of quantitative traits in finite populations**

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## S1 The Big Picture

In this document, I provide detailed derivations of the equations discussed in the main text. I use this section to provide a verbal summary of the motivation behind the calculations I carry out in subsequent sections. To study ecological dynamics, we would like an equation that describes how population densities change over time. While the functional master equation, Eq. 6, in principle describes the entire population at an exact level, in practice it is usually much too complicated to be studied directly. Much of the complication is due to the discontinuity inherent in discrete population ‘jumps’, and so an approximate continuous description is desirable. In section S2, I use an infinite-dimensional version of the system-size expansion (Gardiner, 2009) (‘diffusion approximation’ in population genetics) to derive an approximate functional Fokker-Planck equation for the stochastic dynamics of the population density field.

The basic idea of a system-size approximation originates in physics (Van Kampen, 1981, chapter 10), where it was observed that when particles (or molecules) move and interact stochastically in a container of volume  $\Omega$ , the transitions in the state of the system are in terms of changes to particle number  $n \rightarrow n \pm 1$  through the creation/annihilation of particles, but the rate of these transitions is governed by the rate at which particles meet, which is proportional to the density  $n/\Omega$  of particles per unit volume. When viewed in units of particle density  $n/\Omega$ , the system transitions in units of  $1/\Omega$  and thus looks approximately continuous if  $\Omega$  is not too small. In our biological language, birth rates, death rates, and interactions are in terms of population density, whereas the system itself is described in terms of the number of individuals. The two are related by an abstract ‘population size measure’ (Czuppon and Traulsen, 2021) that plays the role of the system size parameter  $\Omega$ . In supplementary section S2, I carry out an infinite-dimensional analog of this idea to derive a functional Fokker-Planck equation which I present as Eq. 15 in the main text. This equation is equivalent to a stochastic partial differential equation (SPDE), namely Eq. 17 in the main text.

To study evolutionary dynamics, we need to derive an equation for how trait frequencies change. When dynamics are stochastic, one cannot use the usual formulae for change of variables. Instead, we require a tool from stochastic calculus called Itô’s formula. In supplementary section S3, I use Eq. 15 along with an infinite-dimensional version of Itô’s formula (Curtain and Falb, 1970, theorem 3.8; Da Prato and Zabczyk, 2014, theorem 4.32) to derive an SPDE for the trait frequency field  $p(x, t)$  that generalizes the replicator-mutator equation to finite, fluctuating populations bearing quantitative traits. This results in Eq. 22 in the main text. In section S42, I illustrate how Eq. 22 recovers Kimura’s continuum-of-

alleles model in the infinite population limit to underscore the fact that my equation is an extension of known models in population biology.

Studying SPDEs can be complicated and the tools to analyze them are still in development. On the other hand, stochastic differential equations (SDEs) are much more well-understood. For practical applications, it may thus be better to derive an SDE to describe (at least some aspects of) the behavior of the frequency field  $p(x, t)$  via some aggregate quantity. A natural candidate is the mean trait value  $\bar{x}$  in the population, or more generally, the mean value  $\bar{f}$  of any function  $f(x|\phi)$  of the trait value  $x$  in the population  $\phi$ . In section S5, I use the equation for the trait frequency field derived in section S3 to derive an SDE for the mean value of any function  $f$  of the trait value. This equation ends up being a stochastic generalization of the celebrated Price equation, and is Eq. 25 in the main text. Fisher’s fundamental theorem, a corollary of the Price equation (Queller, 2017), is an equation for the mean fitness  $\bar{w}$  in the population and has historical significance. As an illustration of the stochastic Price equation Eq. 25, I derive a stochastic version of Fisher’s fundamental theorem in section S6. I also illustrate that the resultant SDE indeed recovers the standard version of Fisher’s fundamental theorem in the infinite population limit.

Under certain scaling limits, the Price equation (in continuous time and the standard infinite population setting) heuristically recovers Lande’s gradient equation (Page and Nowak, 2002; Lehtonen, 2018), an intuitively appealing equation describing evolution as following a gradient in fitness. Recovering the gradient equation is also of interest because it is closely related to the canonical equation of adaptive dynamics (Page and Nowak, 2002; Lion, 2018; Lehtonen, 2018), the fundamental machinery behind the enormous field of adaptive dynamics (Doebeli, 2011). In section S7, I illustrate how similar heuristic arguments can also be used in our stochastic setting to recover a stochastic version of the gradient equation (Eq. 30 in the main text). Strikingly, the stochastic gradient equation we derive does *not* predict that evolution follows a gradient for higher fitness alone, but instead also predicts a detectable effect of *noise-induced selection*, a phenomenon particular to finite populations. Nevertheless, our equation recovers the standard gradient equation in the infinite population limit.

What good is all this abstract theory? Do we gain anything that we would not already have known with the (equally if not more abstract) rigorous measure-theoretic framework of papers such as Champagnat et al. (2006)? Besides being accessible to a different audience, I believe the SPDE approach is also more suited to studying certain biological questions (while the more probabilistic approach of Champagnat et al. (2006) is better suited for others) and thus presents a useful complementary perspective on the evolution of quantitative traits in

finite populations. I illustrate this point in section S8 by using spectral methods and linear approximations to study finite-population effects on phenotypic clustering and adaptive diversification over long timescales. This section presents a general treatment of techniques that have been used to study particular ecological problems in previous studies (Rogers et al., 2012; Rogers and McKane, 2015).

Finally, sections S9 and S10 provide simple examples to illustrate how the entire analytic pipeline can be put to use. More specifically, I start with a simple Lotka-Volterra style resource competition model at the individual (‘microscopic’) level and show how the ‘mesoscopic’ behavior yields SPDEs for the population densities and trait frequencies. In the infinite population (‘macroscopic’) limit, these equations recover the quantitative logistic equation in the population density case, and a standard model from adaptive dynamics in the gradient equation case. In the Fisher-KPP case, I show that starting from an individual-based birth-death process, the ‘mesoscopic’ limit is *not* the SPDE usually referred to as the ‘stochastic Fisher-KPP equation’ (Doering et al., 2003; Barton et al., 2013) but instead the SPDE expected by Champagnat et al. (2006). The purpose of this section is once again to illustrate how well-known models can be recovered from ‘microscopic’ first principles in our framework.

## S2 A functional system-size expansion to obtain the equation for the population density field

I begin with the master equation, Eq. 6:

$$\frac{\partial P}{\partial t}(\nu, t) = \int_{\mathcal{T}} [(\mathcal{E}_x^- - 1)b(x|\nu)P(\nu, t) + (\mathcal{E}_x^+ - 1)d(x|\nu)P(\nu, t)] dx \quad (S1)$$

As mentioned in the main text, I introduce the population density field  $\phi$  via the transformation

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

and assume we can find  $\mathcal{O}(1)$  functions  $b_K$  and  $d_K$  such that the original birth and death rate functions  $b$  and  $d$  can be rewritten as:

$$\begin{aligned} b(x|\nu) &= K b_K(x|\nu/K) = K b_K(x|\phi) \\ d(x|\nu) &= K d(x|\nu/K) = K d_K(x|\phi) \end{aligned} \quad (S2)$$

where  $b_K$  and  $d_K$  are  $\mathcal{O}(1)$ . In terms of these new variables, Eq. S1 becomes:

$$\frac{\partial P}{\partial t}(\phi, t) = K \int_{\mathcal{T}} [(\Delta_x^- - 1)b_K(x|\phi)P(\phi, t) + (\Delta_x^+ - 1)d_K(x|\phi)P(\phi, t)] dx \quad (\text{S3})$$

where I have introduced new step operators  $\Delta_x^\pm$  that satisfy:

$$\Delta_x^\pm[F(y, \phi)] = F\left(y, \phi \pm \frac{1}{K}\delta_x\right)$$

We can now conduct a system-size expansion by using a functional analog of a Taylor expansion of the step operators. Below, I suppress the  $t$  dependence of  $\phi$  for notational conciseness. Recall that the functional version of the Taylor expansion of a functional  $F[\rho]$  about a function  $\rho_0$  defined on a domain  $\Omega \subseteq \mathbb{R}$  is given by:

$$F[\rho_0 + \rho] = F[\rho_0] + \int_{\Omega} \rho(x) \frac{\delta F}{\delta \rho_0(x)} dx + \frac{1}{2!} \int_{\Omega} \int_{\Omega} \rho(x) \rho(y) \frac{\delta^2 F}{\delta \rho_0(x) \delta \rho_0(y)} dx dy + \dots$$

Since  $\Delta_x^\pm[F[\phi]] = F[\phi \pm \delta_x/K]$ , we can Taylor expand the RHS to see that our step operators obey

$$\Delta_x^\pm[F[\phi]] = F[\phi] \pm \frac{1}{K} \int_{\mathcal{T}} \frac{\delta F}{\delta \phi(y)} \delta_x dy + \frac{1}{2K^2} \int_{\mathcal{T}} \int_{\mathcal{T}} \frac{\delta^2 F}{\delta \phi(y) \delta \phi(z)} \delta_x dy \delta_x dz + \dots \quad (\text{S4})$$

$$= F[\phi] \pm \frac{1}{K} \frac{\delta F}{\delta \phi(x)} + \frac{1}{2K^2} \frac{\delta^2 F}{\delta \phi(x)^2} + \dots \quad (\text{S5})$$

We will now neglect all higher order terms. Mathematically, this is justified by Pawula’s theorem (Pawula, 1967). Biologically, neglecting all higher order terms amounts to saying that the stochastic field  $\phi$  is entirely described by its first two moments and thus can be thought of as a Gaussian approximation (Black and McKane, 2012). Neglecting the higher order terms, we can now substitute Eq. S5 with  $F = b_K(x|\phi)P(\phi, t)$  and  $F = d_K(x|\phi)P(\phi, t)$  into Eq. S3 to obtain:

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

Rearranging these terms, we obtain a ‘functional Fokker-Planck equation’:

$$\boxed{\frac{\partial P}{\partial t}(\phi, t) = \int_{\mathcal{T}} \left[ -\frac{\delta}{\delta\phi(x)} \{ \mathcal{A}^-(x|\phi)P(\phi, t) \} + \frac{1}{2K} \frac{\delta^2}{\delta\phi(x)^2} \{ \mathcal{A}^+(x|\phi)P(\phi, t) \} \right] dx} \quad (\text{S6})$$

where

$$\mathcal{A}^\pm(x|\phi) = b_K(x|\phi) \pm d_K(x|\phi) = \frac{1}{K} (b(x|\nu) \pm d(x|\nu))$$

Equation S6 yields Eq. 15 in the main text upon substituting the functional forms of birth and death rates given in Eq. 8.

### S3 Deriving stochastic trait frequency dynamics via a heuristic Itô formula

In this section, I derive an SPDE for the trait frequency field. I will do this by assuming an ‘intuitive’ infinite-dimensional Itô formula holds for SPDEs. The formula in question is described below.

Let  $\mathcal{T} \subset \mathbb{R}$ , and let  $\mathcal{M}(\mathcal{T})$  be a suitable space of functions from  $\mathcal{T}$  to  $\mathbb{R}$ . Let  $\mathcal{F}[\phi, x] : \mathcal{M}(\mathcal{T}) \times \mathcal{T} \rightarrow \mathbb{R}$  and  $\mathcal{G}[\phi, x, y] : \mathcal{M}(\mathcal{T}) \times \mathcal{T} \times \mathcal{T} \rightarrow \mathbb{R}$  be two functionals. Consider the spacetime stochastic process  $\phi(x, t)$  obtained as the solution to the SPDE

$$\frac{\partial \phi}{\partial t}(x, t) = \mathcal{F}[\phi, x] + \int_{\mathcal{T}} \mathcal{G}[\phi, x, y] \dot{W}(y, t) dy \quad (\text{S7})$$

Let  $\mathcal{H} : \mathcal{M}(\mathcal{T}) \rightarrow \mathbb{R}$  be any ‘nice’ functional. Then, I assume that  $\mathcal{H}[\phi]$  satisfies the integral

equation

$$\begin{aligned}
 \mathcal{H}[\phi(\cdot, t)] &= \mathcal{H}[\phi(\cdot, 0)] + \int_0^t \int_{\mathcal{T}} \mathcal{F}[\phi(\cdot, s), x] \frac{\delta \mathcal{H}}{\delta \phi(x, s)} dx ds \\
 &\quad + \frac{1}{2} \left( \int_0^t \int_{\mathcal{T}} \int_{\mathcal{T}} \frac{\delta^2 \mathcal{H}}{\delta \phi(x, s) \delta \phi(y, s)} \left( \int_{\mathcal{T}} \mathcal{G}[\phi(\cdot, s), x, z] \mathcal{G}[\phi(\cdot, s), y, z] dz \right) dx dy ds \right) \\
 &\quad + \int_0^t \int_{\mathcal{T}} \int_{\mathcal{T}} \mathcal{G}[\phi(\cdot, s), x, y] \frac{\delta \mathcal{H}}{\delta \phi(x, s)} \dot{W}(y, s) dx dy ds
 \end{aligned} \tag{S8}$$

Here, I have used the notation  $\phi(\cdot, s)$  to refer to the entire density field  $\phi$  at time  $s$ , to be distinguished from  $\phi(x, s)$ , the particular value of the density field at the trait value  $x$  at time  $s$ . In other words,  $\phi(\cdot, s)$  is a function (element of  $\mathcal{M}(\mathcal{T})$ ) whereas  $\phi(x, s)$  is a real number.

In SDE/SPDE notation, equation Eq. S8 can be written in the form of an (infinite-dimensional) Itô formula as:

$$\begin{aligned}
 d\mathcal{H}[\phi(\cdot, t)] &= \left[ \int_{\mathcal{T}} \mathcal{F}[\phi(\cdot, t), x] \frac{\delta \mathcal{H}}{\delta \phi(x, t)} dx + \frac{1}{2} \int_{\mathcal{T}} \int_{\mathcal{T}} \frac{\delta^2 \mathcal{H}}{\delta \phi(x, t) \delta \phi(y, t)} \left( \int_{\mathcal{T}} \mathcal{G}[\phi(\cdot, t), x, z] \mathcal{G}[\phi(\cdot, t), y, z] dz \right) dx dy \right] dt \\
 &\quad + \int_{\mathcal{T}} \int_{\mathcal{T}} \mathcal{G}[\phi(\cdot, t), x, y] \frac{\delta \mathcal{H}}{\delta \phi(x, t)} \dot{W}(y, t) dx dy
 \end{aligned} \tag{S9}$$

Note that equation Eq. S9 is precisely the expression we would intuitively expect to obtain if we informally “take  $n \rightarrow \infty$ ” in the  $n$ -dimensional Itô formula for finite  $n$  (Øksendal, 1998; Gardiner, 2009). Such an Itô formula is rigorously known to hold in various special cases when the domain  $\mathcal{T}$ , the function space  $\mathcal{M}(\mathcal{T})$ , and the functionals (operators)  $\mathcal{F}, \mathcal{G}, \mathcal{H}$  all satisfy certain technical assumptions (Curtain and Falb, 1970, theorem 3.8; Dawson, 1975, theorem 4.12; Da Prato and Zabczyk, 2014, theorem 4.32; Week et al., 2021, section SM2). I will make no attempt to characterize whether our system satisfies these technical assumptions and will simply assume that equation Eq. S9 holds for our purposes.

To derive an expression for the trait frequency field at time  $t$ , let us define for each  $x \in \mathcal{T}$  a functional

$$\mathcal{H}_x[\rho] = \frac{\rho(x)}{\int_{\mathcal{T}} \rho(u) du}$$

Note that when applied on the population density field  $\phi$ ,  $\mathcal{H}_x$  returns the value of the trait frequency field at the point  $x$ . Now, let  $\phi$  denote the population density field, given by the solution to the SPDE described by Eq. S6 (the SPDE is Eq. 17 in the main text). Comparing terms with Eq. S7, we can identify

$$\mathcal{F}[\phi, x] = \phi(x, t)w(x|\phi) + \mu Q(x|\phi) \quad (\text{S10})$$

$$\mathcal{G}[\phi, x, y] = \frac{1}{\sqrt{K}} [(\phi(x, t)\tau(x|\phi) + \mu Q(x|\phi)) (\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi))]^{1/4} \delta_{x,y} \quad (\text{S11})$$

where  $\delta_{x,y}$  is the (generalized) Kronecker delta, defined as

$$\delta_{x,y} := \begin{cases} 1 & x = y \\ 0 & x \neq y \end{cases}$$

Thus, by our Itô formula Eq. S9,  $\mathcal{H}_x[\phi]$  (and hence the trait frequency field at point  $x$ ) satisfies

$$\begin{aligned} d\mathcal{H}_x[\phi] = & \left[ \int_{\mathcal{T}} \{\phi(y, t)w(y|\phi) + \mu Q(y|\phi)\} \frac{\delta \mathcal{H}_x}{\delta \phi(y, t)} dy \right. \\ & + \frac{1}{2K} \left( \int_{\mathcal{T}} [\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)] \frac{\delta^2 \mathcal{H}_x}{\delta \phi(y, t)^2} dy \right) \Big] dt \\ & + \frac{1}{\sqrt{K}} \int_{\mathcal{T}} \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \frac{\delta \mathcal{H}_x}{\delta \phi(y, t)} \dot{W}(y, t) dy \end{aligned} \quad (\text{S12})$$

We will evaluate the RHS of Eq. S12 term by term.

To begin with, let us calculate the two functional derivatives that appear on the RHS of Eq. S12. To do this, we will use the identity

$$\frac{\delta F}{\delta \rho(x)} = \lim_{\epsilon \rightarrow 0} \frac{F[\rho + \epsilon \delta_x] - F[\rho]}{\epsilon} \quad (\text{S13})$$

obtained by substituting  $\xi(x) = \delta_x$  in the definition Eq. 16 of the functional derivative. Note that the use of a delta mass as a test function is justified for our purposes because, in our cases,  $F$  will be defined on  $\mathcal{M}_K(\mathcal{T})$ , and thus, from the definition of  $\mathcal{M}_K(\mathcal{T})$ , if  $x \in \mathcal{T}$  and  $\epsilon > 0$ ,  $\rho + \epsilon \delta_x$  will be in the domain of  $F$  provided  $\rho$  is in the domain of  $F$ . For the rest of this section, I use the notational shorthand  $\int = \int_{\mathcal{T}}$  and suppress the  $t$  dependence of all fields for conciseness.

Let  $y \in \mathcal{T}$ . We can calculate the single functional derivative as

$$\frac{\delta \mathcal{H}_x}{\delta \phi(y)} = \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} [\mathcal{H}_x[\phi + \epsilon \delta_x] - \mathcal{H}_x[\phi]] \quad (\text{S14})$$

$$= \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} \left[ \frac{\phi(x) + \epsilon \delta_x}{\int \phi(u)du + \epsilon \int \delta_u du} - \frac{\phi(x)}{\int \phi(u)du} \right] \quad (\text{S15})$$

$$= \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} \left[ \frac{\epsilon (\delta_x \int \phi(u)du - \phi(x))}{[\int \phi(u)du]^2 + \epsilon \int \phi(u)du} \right] \quad (\text{S16})$$

$$= \frac{1}{\int \phi(u)du} [\delta_x - p(x)] \quad (\text{S17})$$

where I have used the notation  $p(x) = \phi(x)/\int \phi(u)du$  for the trait frequency field from the main text Eq. 12. Now, let  $z \in \mathcal{T}$ . We can rewrite the double functional derivative in equation Eq. S12 as

$$\frac{\delta^2 \mathcal{H}_x}{\delta \phi(y)^2} = \frac{\delta}{\delta \phi(y)} \left( \frac{\delta \mathcal{H}_x}{\delta \phi(y)} \right) = \frac{\delta \mathcal{H}'_x[\phi]}{\delta \phi(y)} \quad (\text{S18})$$

where, from Eq. S17, we know

$$\mathcal{H}'_x[\phi] = \frac{1}{\int \phi(u)du} \left( \delta_x - \frac{\phi(x)}{\int \phi(u)du} \right) \quad (\text{S19})$$

Using Eq. S13, we now obtain

$$\frac{\delta^2 \mathcal{H}_x}{\delta \phi(y)^2} = \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} \left[ \frac{\delta_x}{\int \phi(u)du + \epsilon \int \delta_u du} - \frac{\phi(x) + \epsilon \delta_x}{(\int \phi(u)du + \epsilon \int \delta_u du)^2} - \left( \frac{\delta_x}{\int \phi(u)du} - \frac{\phi(x)}{(\int \phi(u)du)^2} \right) \right] \quad (\text{S20})$$

$$= \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} \left[ \frac{-\epsilon \delta_x}{\int \phi(u)du + \epsilon} + \frac{(\int \phi(u)du)^2(\phi(x) + \epsilon \delta_x) + \phi(x)(\int \phi(u)du + \epsilon)^2}{(\int \phi(u)du)^2(\int \phi(u)du + \epsilon)^2} \right] \quad (\text{S21})$$

$$= \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} \left[ \frac{-\epsilon \delta_x}{\int \phi(u)du + \epsilon} + \frac{\epsilon^2 \phi(x) + 2\epsilon \phi(x) \int \phi(u)du - \epsilon \delta_x (\phi(u)du)^2}{(\int \phi(u)du)^2(\int \phi(u)du + \epsilon)^2} \right] \quad (\text{S22})$$

$$= \lim_{\epsilon \rightarrow 0} \left[ -\frac{\delta_x}{\int \phi(u)du + \epsilon} + \frac{\epsilon \phi(x) + 2\phi(x) \int \phi(u)du - \delta_x (\phi(u)du)^2}{(\int \phi(u)du)^2(\int \phi(u)du + \epsilon)^2} \right] \quad (\text{S23})$$

$$= \left[ -\frac{\delta_x}{\int \phi(u)du} + \frac{2\phi(x) \int \phi(u)du - \delta_x (\phi(u)du)^2}{(\int \phi(u)du)^4} \right] \quad (\text{S24})$$

$$= \frac{2}{(\int \phi(u)du)^2} [p(x) - \delta_x] \quad (\text{S25})$$

We can now substitute Eq. S17 and Eq. S25 into the RHS of Eq. S12 to find an equation for

the evolution of the trait frequency field. Once again, I will do this step by step for clarity. First, we evaluate the  $dt$  term.

For the first term multiplying  $dt$  in Eq. S12, we use Eq. S17 to find

$$\int_{\mathcal{T}} \{\phi(y)w(y|\phi) + \mu Q(y|\phi)\} \frac{\delta\mathcal{H}_x}{\delta\phi(y)} dy = \int \{\phi(y)w(y|\phi) + \mu Q(y|\phi)\} \frac{1}{\int \phi(u)du} [\delta_x - p(x)] dy \quad (\text{S26})$$

$$= \frac{1}{\int \phi(u)du} \left[ \phi(x)w(x|\phi) - p(x) \int \phi(y)w(y)dy + \mu \left( Q(x|\phi) - p(x) \int Q(y|\phi)dy \right) \right] \quad (\text{S27})$$

$$= \left[ p(x)w(x|\phi) - p(x) \int p(y)w(y)dy + \frac{\mu}{\int \phi(u)du} \left( Q(x|\phi) - p(x) \int Q(y|\phi)dy \right) \right] \quad (\text{S28})$$

Using the definition of mean fitness  $\bar{w}$  from Eq. 13, we see that the first term on the RHS of Eq. S12 is given by

$$\begin{aligned} & \int_{\mathcal{T}} \{\phi(y)w(y|\phi) + \mu Q(y|\phi)\} \frac{\delta\mathcal{H}_x}{\delta\phi(y)} dy \\ &= [w(x|\phi) - \bar{w}(\phi, t)]p(x, t) + \frac{\mu}{\int \phi(u)du} \left( Q(x|\phi) - p(x) \int Q(y|\phi)dy \right) \end{aligned} \quad (\text{S29})$$

For the second term (second line) on the RHS of Eq. S12, we substitute Eq. S25 to find

$$\begin{aligned} & \frac{1}{2K} \left[ \int_{\mathcal{T}} [\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)] \frac{\delta^2 \mathcal{H}_x}{\delta \phi(y, t)^2} dy \right] \\ &= \frac{1}{2K} \left[ \int [\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)] \frac{2}{(\int \phi(u) du)^2} [p(x) - \delta_x] dy \right] \end{aligned} \quad (\text{S30})$$

$$\begin{aligned} &= \frac{1}{K(\int \phi(u) du)^2} \left[ -\phi(x, t)\tau(x|\phi) + p(x) \int \tau(y|\phi)\phi(y) dy \right. \\ &\quad \left. + \mu \left( -Q(x|\phi) + p(x) \int Q(y|\phi) dy \right) \right] \end{aligned} \quad (\text{S31})$$

$$\begin{aligned} &= \frac{1}{K(\int \phi(u) du)} \left[ -p(x, t)\tau(x|\phi) + p(x) \int \tau(y|\phi)p(y) dy \right. \\ &\quad \left. + \frac{\mu}{\int \phi(u) du} \left( -Q(x|\phi) + p(x) \int Q(y|\phi) dy \right) \right] \end{aligned} \quad (\text{S32})$$

Now using the definition of mean turnover rate  $\bar{\tau}$  from Eq. 13, we see that the second term (second line) on the RHS of Eq. S12 is given by

$$\begin{aligned} & \frac{1}{2K} \left[ \int_{\mathcal{T}} [\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)] \frac{\delta^2 \mathcal{H}_x}{\delta \phi(y, t)^2} dy \right] \\ &= -\frac{1}{K \int \phi(u) du} \left[ [\tau(x|\phi) - \bar{\tau}(t)] p(x) + \frac{\mu}{\int \phi(u) du} \left( Q(x|\phi) - p(x) \int Q(y|\phi) dy \right) \right] \end{aligned} \quad (\text{S33})$$

All that remains is to calculate the spacetime white noise term in Eq. S12. We find

$$\begin{aligned} & \frac{1}{\sqrt{K}} \int_{\mathcal{T}} \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \frac{\delta \mathcal{H}_x}{\delta \phi(y, t)} \dot{W}(y, t) dy \\ &= \frac{1}{\sqrt{K}} \int \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \frac{1}{\int \phi(u) du} [\delta_x - p(x)] \dot{W}(y, t) dy \end{aligned} \quad (\text{S34})$$

and thus we see that the spacetime white noise term is given by

$$\begin{aligned} & \frac{1}{\sqrt{K}} \int_{\mathcal{T}} \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \frac{\delta \mathcal{H}_x}{\delta \phi(y, t)} \dot{W}(y, t) dy \\ &= \frac{1}{\sqrt{K} \int \phi(u) du} \left[ \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(x|\phi)} \dot{W}(x, t) - p(x) \int \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \dot{W}(y, t) dy \right] \end{aligned} \quad (\text{S35})$$

Thus, using Eq. S29, Eq. S33, and Eq. S35 in Eq. S12, we see that the trait frequency

field obeys the SPDE

$$\frac{\partial p}{\partial t}(x, t) = \underbrace{\mathcal{S}_w[x|\phi]}_{\text{Classical selection-mutation}} - \underbrace{\frac{1}{KN_K(t)}\mathcal{S}_\tau[x|\phi]}_{\text{Noise-induced selection-mutation}} + \underbrace{\frac{1}{\sqrt{KN_K(t)}}\dot{W}_p(x, t)}_{\text{Undirected stochastic fluctuations}} \quad (\text{S36})$$

where  $N_K = \int \phi(u)du$  is the scaled total population size,

$$\mathcal{S}_f[x|\phi] = \underbrace{(f[x|\phi] - \bar{f}(t))p(x, t)}_{\text{Selection for higher values of } f} + \underbrace{\frac{\mu}{N_K(t)} \left( Q(x|\phi) - p(x) \int_{\mathcal{T}} Q(y|\phi) dy \right)}_{\text{Mutation biases/transmission biases}} \quad (\text{S37})$$

represents selection-mutation balance for  $f$ , and

$$\dot{W}_p(x, t) := \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(x|\phi)} \dot{W}(x, t) - p(x) \int_{\mathcal{T}} \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \dot{W}(y, t) dy \quad (\text{S38})$$

Eq. S36 is precisely Eq. 22 in the main text.

## S4 Recovering Kimura’s continuum-of-alleles model from the continuous replicator-mutator equation

In this section, I recover Kimura’s continuum of alleles model from equation Eq. 24, the continuous replicator-mutator equation<sup>1</sup>, when mutation is modelled via convolution with a non-negative function that integrates to unity. To see this, let  $Q(y|\phi) = (m * \phi)(y, t)$ , where  $m : \mathbb{R} \rightarrow [0, \infty)$  is the ‘mutation kernel’, which by definition is non-negative and normalized such that  $\int_{\mathbb{R}} m(x)dx = 1$ . Here,  $*$  denotes convolution, defined for any two real functions  $F$  and  $G$  as

$$(F * G)(x) = \int_{\mathbb{R}} F(x - y)G(y)dy \quad (\text{S39})$$

Let us further recall that I assume (in the main text) that the population density process scales such that in the infinite population limit,  $N_K(\cdot) = \int_{\mathcal{T}} \phi(x, \cdot)dx = 1$ . Thus, both  $m$  and  $\phi(\cdot, t)$  are  $L^1(\mathbb{R})$  functions. We can now use the general result that for any two  $L^1(\mathbb{R})$

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<sup>1</sup>obtained as the infinite population ( $K \rightarrow \infty$ ) limit of Eq. S36

functions  $F$  and  $G$ , the convolution  $F * G$  satisfies:

$$\int_{\mathbb{R}} (F * G)(x) dx = \left( \int_{\mathbb{R}} F(x) dx \right) \left( \int_{\mathbb{R}} G(x) dx \right) \quad (\text{S40})$$

This general result is an easy consequence of the Fubini-Tonnelli theorem.

Using this result, the rightmost integral in Eq. 24 is

$$\int_{\mathbb{R}} Q(y|\phi) dy = \int_{\mathbb{R}} (m * \phi)(y) dy = \int_{\mathbb{R}} \phi(y, t) dy \int_{\mathbb{R}} m(y) dy \quad (\text{S41})$$

Now, by definition of  $N_K$ , we have  $\int_{\mathbb{R}} \phi(y, t) dy = N_K$ . Further, since  $m$  is a kernel, it satisfies  $\int_{\mathbb{R}} m(y) dy = 1$ . Equation Eq. S41 therefore becomes  $\int_{\mathbb{R}} Q(y|\phi) dy = N_K(t)$ . Substituting this in Eq. 24, we have

$$\frac{\partial p}{\partial t}(x, t) = [w(x|\phi) - \bar{w}(t)] p(x, t) + \frac{\mu}{N_K(t)} \left[ \int_{\mathbb{R}} m(x-z) \phi(z, t) dz - p(x, t) N_K(t) \right]$$

Substituting our definition  $p(z, t) = \phi(z, t)/N_K(t)$  now yields

$$\frac{\partial p}{\partial t}(x, t) = [w(x|\phi) - \bar{w}(t)] p(x, t) + \mu \left[ \int_{\mathbb{R}} m(x-z) p(z, t) dz - p(x, t) \right] \quad (\text{S42})$$

which is Kimura’s continuum of alleles model (Kimura, 1965; Crow and Kimura, 1970).

## S5 Deriving an equation for the mean value of any type-level quantity

In this section, I use the equation for the trait frequency field Eq. S36 to derive an SDE for how the statistical mean value of any type level quantity changes in the population. I use the shorthand  $\int = \int_{\mathcal{T}}$

Let  $f(x|\phi)$  be any type-level quantity with statistical mean  $\bar{f}(t)$ . I allow for the possibility of  $f$  varying through time even when  $\phi$  is constant, to allow for the possibility of phenotypic plasticity and eco-evolutionary feedbacks. Assuming derivatives and integrals commute, we can calculate the rate of change of the mean value as

$$\frac{d\bar{f}}{dt} = \int \frac{d}{dt} f(x|\phi) p(x,t) dx = \int f(x|\phi) \frac{\partial p}{\partial t} dx + \int p(x,t) \frac{\partial f}{\partial t} dx \quad (\text{S43})$$

We can now substitute the equation for  $\partial p/\partial t$  from equation Eq. S36 to calculate the first term on the RHS of Eq. S43. We can thus write

$$\int f(x|\phi) \frac{\partial p}{\partial t} dx = \int f(x|\phi) \left( \mathcal{S}_w[x|\phi] - \frac{1}{KN_K(t)} \mathcal{S}_\tau[x|\phi] + \frac{1}{\sqrt{KN_K(t)}} \dot{W}_p(x,t) \right) dx \quad (\text{S44})$$

Given any type-level quantity  $g(x|\phi)$ , the selection-mutation operator for  $g$  obeys

$$\begin{aligned} \int f(x|\phi) \mathcal{S}_g[x|\phi] dx &= \int f(x|\phi) (g(x|\phi) - \bar{g}(t)) p(x,t) dx \\ &\quad + \frac{\mu}{N_K(t)} \left( \int f(x|\phi) \left( Q(x|\phi) - p(x,t) \int Q(y|\phi) dy \right) dx \right) \quad (\text{S45}) \\ &= \int f(x|\phi) g(x|\phi) p(x,t) dx - \left( \int f(x|\phi) dx \right) \bar{g}(t) \\ &\quad + \frac{\mu}{N_K(t)} \left( \int f(x|\phi) Q(x|\phi) dx - \int f(x|\phi) p(x,t) dx \int Q(y|\phi) dy \right) \quad (\text{S46}) \end{aligned}$$

$$= \bar{f}\bar{g} - \bar{f}\bar{g} + \frac{\mu}{N_K} \left( \int f(x|\phi) Q(x|\phi) dx - \bar{f} \int Q(y|\phi) dy \right) \quad (\text{S47})$$

Now using the definition of covariance from Eq. 14, we thus see that we have the relation

$$\int f(x|\phi) \mathcal{S}_g[x|\phi] dx = \text{Cov}(g, f) + \frac{\mu}{N_K} \left( \int f(x|\phi) Q(x|\phi) dx - \bar{f} \int Q(y|\phi) dy \right) \quad (\text{S48})$$

Using Eq. S48 in Eq. S44 for  $g = w$  and  $g = \tau$ , we obtain

$$\begin{aligned} \int f(x|\phi) \frac{\partial p}{\partial t} dx &= \text{Cov}(w, f) - \frac{1}{KN_K} \text{Cov}(\tau, f) + \frac{\mu}{N_K} \left( 1 - \frac{1}{KN_K} \right) \left( \int f(x|\phi) Q(x|\phi) dx - \bar{f} \int Q(y|\phi) dy \right) \\ &\quad + \frac{1}{\sqrt{KN_K(t)}} \int f(x|\phi) \dot{W}_p(x,t) dx \quad (\text{S49}) \end{aligned}$$

All that remains now is to calculate the stochastic integral term in Eq. S49. Using Eq. 23,

we find

$$\begin{aligned} & \int f(x|\phi) \dot{W}_p(x, t) dx \\ &= \int f(x|\phi) \left[ \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(y|\phi)} \dot{W}(x, t) - p(x) \int \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \dot{W}(y, t) dy \right] dx \end{aligned} \quad (\text{S50})$$

$$= \int f(x|\phi) \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(y|\phi)} \dot{W}(x, t) dx - \bar{f}(t) \int \sqrt{\phi(y, t)\tau(y|\phi) + \mu Q(y|\phi)} \dot{W}(y, t) dy \quad (\text{S51})$$

Since  $x$  and  $y$  are both dummy variables that are being integrated over the entire space, we can therefore equivalently write Eq. S51 as

$$\int f(x|\phi) \dot{W}_p(x, t) dx = \int (f(x|\phi) - \bar{f}(t)) \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(y|\phi)} \dot{W}(x, t) dx \quad (\text{S52})$$

Note that the spacetime white noise in Eq. S52 is being integrated over the entire domain of the space variable, and thus the resultant stochastic term is a stochastic integral with respect to a Brownian motion. In other words, the mean value  $\bar{f}$  obeys a one-dimensional SDE. Defining

$$M_{\bar{f}}(p, N_K) = \frac{\mu}{N_K} \left( 1 - \frac{1}{KN_K} \right) \left( \int f(x|\phi) Q(x|\phi) dx - \bar{f} \int Q(y|\phi) dy \right) \quad (\text{S53})$$

$$\frac{dW_{\bar{f}}}{dt} = \int (f(x|\phi) - \bar{f}(t)) \sqrt{\phi(x, t)\tau(x|\phi) + \mu Q(y|\phi)} \dot{W}(x, t) dx \quad (\text{S54})$$

and substituting Eq. S49 into Eq. S43, we thus obtain

$$\frac{d\bar{f}}{dt} = \text{Cov}(w, f) - \frac{1}{KN_K} \text{Cov}(\tau, f) + M_{\bar{f}}(p, N_K) + \overline{\left( \frac{\partial f}{\partial t} \right)} + \frac{1}{\sqrt{KN_K}} \frac{dW_{\bar{f}}}{dt} \quad (\text{S55})$$

which is equation Eq. 25 in the main text.

## S6 A stochastic version of Fisher’s fundamental theorem

In this section, I derive a stochastic version of Fisher’s fundamental theorem for finite, fluctuating populations and show that it indeed recovers Fisher’s fundamental theorem in

the infinite population limit. Let us first substitute  $f(x|\phi) = w(x|\phi)$  and  $\mu = 0$  into Eq. S55. Note that since  $\mu = 0$ , the mutation term  $M_{\bar{w}}$  vanishes. Thus, Eq. S55 becomes

$$\frac{d\bar{w}}{dt} = \sigma_w^2 - \frac{1}{KN_K(t)} \text{Cov}(\tau, w) + \overline{\left( \frac{\partial w}{\partial t} \right)} + \frac{1}{\sqrt{KN_K(t)}} \frac{dW_{\bar{w}}}{dt} \quad (\text{S56})$$

where

$$\frac{dW_{\bar{w}}}{dt} = \int_{\mathcal{T}} (w(x|\phi) - \bar{w}(t)) \sqrt{\phi(x,t)\tau(x|\phi)} \dot{W}(x,t) dx \quad (\text{S57})$$

Now, since the covariance operator is bilinear, we can write

$$\text{Cov}(\tau, w) = \text{Cov}(b^{(\text{ind})} + d^{(\text{ind})}, b^{(\text{ind})} - d^{(\text{ind})}) \quad (\text{S58})$$

$$= \text{Cov}(b^{(\text{ind})}, b^{(\text{ind})}) - \text{Cov}(b^{(\text{ind})}, d^{(\text{ind})}) + \text{Cov}(d^{(\text{ind})}, b^{(\text{ind})}) - \text{Cov}(d^{(\text{ind})}, d^{(\text{ind})}) \quad (\text{S59})$$

$$= \sigma_{b^{(\text{ind})}}^2 - \sigma_{d^{(\text{ind})}}^2 \quad (\text{S60})$$

Let us now take probabilistic expectations  $\mathbb{E}[\cdot]$  over the underlying probability space in Eq. S56. Upon doing this,  $dW_{\bar{w}}/dt$  vanishes (by definition of white noise) and we therefore obtain

$$\mathbb{E} \left[ \frac{d\bar{w}}{dt} \right] = \underbrace{\mathbb{E} [\sigma_w^2]}_{\text{Fisher's fundamental theorem}} - \underbrace{\mathbb{E} \left[ \frac{\sigma_{b^{(\text{ind})}}^2 - \sigma_{d^{(\text{ind})}}^2}{KN_K(t)} \right]}_{\text{Noise-induced selection}} + \underbrace{\mathbb{E} \left[ \overline{\frac{\partial w}{\partial t}} \right]}_{\text{Eco-evolutionary feedbacks to fitness}} \quad (\text{S61})$$

where we have used the relation Eq. S60. This equation is a version of Fisher’s fundamental theorem for finite, fluctuating populations. The first term on the RHS is the standard version of Fisher’s fundamental theorem, the last term is present whenever we have eco-evolutionary feedbacks to fitness (Frank and Slatkin, 1992; Kokko, 2021), and the middle term represents the effects of noise-induced selection. Note that in finite populations, mean fitness can change directionally even when there is no standing variation in fitness ( $\sigma_w^2 = 0$ ) as long as  $\sigma_{b^{(\text{ind})}}^2 \neq \sigma_{d^{(\text{ind})}}^2$ . Equation S61 has been independently derived for discrete traits in a recent preprint focused on life-history evolution (Kuosmanen et al., 2022).

## The infinite population limit

In the infinite population limit ( $K \rightarrow \infty$ ), the expectations in equation Eq. S61 become superfluous (since the process is now deterministic), and we thus obtain

$$\frac{d\bar{w}}{dt} = \sigma_w^2 + \overline{\frac{\partial w}{\partial t}} \quad (\text{S62})$$

which is Fisher’s fundamental theorem in the presence of ecological changes to fitness (Frank and Slatkin, 1992; Kokko, 2021).

## S7 Deriving a stochastic version of gradient dynamics

In this section, I derive an equation of gradient dynamics for finite, fluctuating equations. I begin by once more listing my assumptions. I assume

- Rare mutations, *i.e.*  $\mu$  is infinitesimally small.
- Small mutational effects with ‘almost faithful’ reproduction, meaning  $Q(x|\phi)$  is infinitesimally small.
- Strong selection, meaning that variants with low relative fitness are immediately eliminated from the population and the population remains sharply peaked around a small number of trait values. Mathematically, this means that if we begin with a monomorphic population  $\phi(x, 0) = N_K(0)\delta_{y_0}$  for some constants  $N_K(0) > 0$  and  $y_0 \in \mathcal{T}$ , the population remains sufficiently well clustered for some time  $t > 0$  that we can continue to approximate the distribution  $\phi(x, t)$  as a Dirac Delta mass  $N_K(t)\delta_{y(t)}$  that is moving across the trait space according to a trajectory dictated by a function  $y(t)$  (to be found). Note that we are not assuming that the population is exactly given by a delta mass, only that it is sufficiently sharply peaked that it can be approximated as one (*i.e.* ‘almost’ every individual has trait value  $y$ ).

I will call these together the strong-selection-weak-mutation (SSWM) assumption. Let  $\int = \int_{\mathcal{T}}$  for notational convenience. Under SSWM, we wish to obtain an equation for  $y(t)$ . Note first that we have:

$$p(x, t) = \frac{\phi(x, t)}{N_K(t)} = \frac{N_K(t)\delta_{y(t)}}{N_K(t)} = \delta_y(t) \quad (\text{S63})$$

Further, for any type level quantity  $f(x|\phi)$ , we have

$$\bar{f}(t) = \int f(x|\phi)p(x, t)dx = \int f(x|N_K\delta_{y(t)})\delta_{y(t)}dx = f(y(t)|N_K\delta_{y(t)}) \quad (\text{S64})$$

We can now substitute  $f(x|\phi) = x$  into our stochastic Price equation (Eq. S55) and, by virtue of our SSWM assumptions, neglect all terms of the form  $\mu Q(x|\phi)$ . Upon doing this and using the expressions for  $\bar{x}$  and  $p(x, t)$  from above, we obtain

$$\frac{dy}{dt} = \text{Cov}(w, x) - \frac{1}{KN_K(t)} \text{Cov}(\tau, x) + \frac{1}{\sqrt{K}N_K} \frac{dW_y}{dt} \quad (\text{S65})$$

where

$$\frac{dW_y}{dt} = \int_{\tau} (x - y(t)) \sqrt{\tau(x|N_K(t)\delta_y(t))} \dot{W}(x, t) dx \quad (\text{S66})$$

Let  $f(x|\phi)$  be any type-level quantity. We can calculate the statistical covariance of  $f$  with  $x$  under SSWM as

$$\text{Cov}(f, x) = \int (f(x|\phi) - \bar{f})(x - \bar{x}) p(x, t) dx \quad (\text{S67})$$

$$= \int (f(x|N_K\delta_{y(t)}) - f(y(t)|N_K\delta_{y(t)}))(x - y(t)) p(x, t) dx \quad (\text{S68})$$

Now, since under SSWM the population at time  $t$  is sharply peaked around  $y(t)$ , we only need to worry about the value of  $f(x|N_K\delta_{y(t)})$  at trait values that are (infinitesimally) close to  $y(t)$ . We can thus Taylor expand  $f$  as:

$$f(x|N_K\delta_{y(t)}) = f(y(t)|N_K\delta_{y(t)}) + (x - y) \left. \frac{\partial f}{\partial z} (z|N_K\delta_{y(t)}) \right|_{z=y} + \dots \quad (\text{S69})$$

and neglect all higher order terms. Using the relation Eq. S69 in Eq. S68, we obtain

$$\text{Cov}(f, x) = \int (x - y)^2 \left. \frac{\partial f}{\partial z} (z|N_K\delta_{y(t)}) \right|_{z=y} p(x, t) dx \quad (\text{S70})$$

$$= \int (x - y)^2 p(x, t) dx \left. \frac{\partial f}{\partial z} (z|N_K\delta_{y(t)}) \right|_{z=y} \quad (\text{S71})$$

$$= \int (x - \bar{x})^2 p(x, t) dx \left. \frac{\partial f}{\partial z} (z|N_K\delta_{y(t)}) \right|_{z=y} \quad (\text{S72})$$

$$\Rightarrow \text{Cov}(f, x) = \sigma_x^2(t) \left. \frac{\partial f}{\partial z} (z|N_K\delta_{y(t)}) \right|_{z=y} \quad (\text{S73})$$

Finally, using Eq. S73 in Eq. S65 with  $f = w$  and  $f = \tau$  yields

$$\frac{dy}{dt} = \sigma_x^2(t) \frac{\partial}{\partial z} \left[ w(z|N_K\delta_{y(t)}) - \frac{1}{KN_K(t)} \tau(z|N_K\delta_{y(t)}) \right] \Big|_{z=y(t)} + \frac{1}{\sqrt{K}N_K} \frac{dW_y}{dt} \quad (\text{S74})$$

which is equation 30 in the main text. Note that strictly speaking, if  $\phi(x, t) = N_K \delta_{y(t)}$  exactly, then  $\sigma_x^2 \equiv 0$ . This just reflects our assumption that mutations are vanishingly rare and mutants are sampled from infinitesimally close to the resident value, *i.e.* that the population evolves in very small mutational steps. Thus, for our equation to make sense, the limits  $\mu \rightarrow 0$ ,  $Q(x|\phi) \rightarrow 0$ , and  $\phi(x, t) \rightarrow \delta_{y(t)} N_K(t)$  must be taken simultaneously such that  $\sigma_x^2(t) \not\rightarrow 0$ , a standard assumption in such heuristic derivations of gradient dynamics (Dieckmann and Law, 1996; Lehtonen, 2018). More detailed mathematical arguments are required to ensure that this limit ‘makes sense’. Such convergence has been proved rigorously for the standard gradient equation using sophisticated mathematical tools grounded in martingale theory (Champagnat et al., 2006).

## S8 Detecting phenotypic clustering and speciation using spectral methods

In this section, I present a general analytical technique to study phenotypic clustering using the Fourier transform. To do this in full generality, we first require an approximation known as the weak noise approximation.

### S8.1 The weak noise approximation

If stochasticity takes the form of weak fluctuations about a deterministic trajectory, we can carry out a functional analog of the ‘linear noise approximation’ or ‘weak noise approximation’ (Gardiner, 2009) to obtain a linear functional Fokker-Planck equation for the population density field. In the next section, we will use this linear approximation to illustrate how phenotypic clustering can be detected.

Assume that  $\psi(x, t)$  is the deterministic trajectory of the density field in the infinite population limit, obtained as the solution to Eq. 19. Consider a new process  $\{\zeta(\cdot, s)\}_{s \geq 0}$  which measures the fluctuations of  $\phi(x, t)$  from the deterministic trajectory  $\psi(x, t)$ . More precisely, let us introduce the new variables:

$$\begin{aligned} \zeta(x, s) &= \sqrt{K}(\phi(x, t) - \psi(x, t)) \\ s &= t \\ \tilde{P}(\zeta, s) &= \frac{1}{\sqrt{K}}P(\phi, t) \end{aligned} \tag{S75}$$

where we have introduced a new time variable  $s = t$  just to makes the substitutions/calculations

cleaner. Note that the following relations hold:

$$\frac{\delta F[\zeta]}{\delta \phi(x)} = \int_{\mathcal{T}} \frac{\delta F[\zeta]}{\delta \zeta(y)} \frac{\delta \zeta(y)}{\delta \phi(x)} dy = \sqrt{K} \frac{\delta F[\zeta]}{\delta \zeta(x)} \quad (\text{S76})$$

$$\frac{\partial}{\partial s} = \frac{\partial}{\partial t} \quad (\text{S77})$$

Furthermore, for any  $\zeta \in \mathcal{M}_K(\mathcal{T})$ , we have:

$$\begin{aligned} \frac{\partial \tilde{P}}{\partial t}(\zeta, s) &= \frac{\delta \tilde{P}}{\delta \zeta} \frac{\partial \zeta}{\partial t} + \frac{\partial \tilde{P}}{\partial s} \frac{\partial s}{\partial t} \\ &= \frac{\delta \tilde{P}}{\delta \zeta} \left( -\sqrt{K} \frac{\partial \psi}{\partial t} \right) + \frac{\partial \tilde{P}}{\partial s} \\ &= -\sqrt{K} \frac{\delta}{\delta \zeta} \{ \mathcal{A}^-(x|\psi) \tilde{P}(\zeta, s) \} + \frac{\partial \tilde{P}}{\partial s} \end{aligned} \quad (\text{S78})$$

Reformulating equation Eq. 15 in terms of the new variables Eq. S75 and using the relations Eq. S76, Eq. S77 and Eq. S78, we obtain:

$$\begin{aligned} -\sqrt{K} \frac{\delta}{\delta \zeta(x)} \{ \mathcal{A}^-(x|\psi) \tilde{P}(\zeta, s) \} + \frac{\partial \tilde{P}}{\partial s} &= \int_{\mathcal{T}} \left[ - \left( \sqrt{K} \frac{\delta}{\delta \zeta(x)} \right) \{ \mathcal{A}^- \left( x \middle| \psi + \frac{\zeta}{\sqrt{K}} \right) \tilde{P}(\zeta, s) \} \right] dx \\ &\quad + \int_{\mathcal{T}} \left[ \frac{1}{2K} \left( K \frac{\delta^2}{\delta \zeta(x)^2} \right) \{ \mathcal{A}^+ \left( x \middle| \psi + \frac{\zeta}{\sqrt{K}} \right) \tilde{P}(\zeta, s) \} \right] dx \end{aligned}$$

and rearranging gives us:

$$\begin{aligned} \frac{\partial \tilde{P}}{\partial s} &= -\sqrt{K} \int_{\mathcal{T}} \frac{\delta}{\delta \zeta(x)} \left\{ \left( \mathcal{A}^- \left( x \middle| \psi + \frac{\zeta}{\sqrt{K}} \right) - \mathcal{A}^-(x|\psi) \right) \tilde{P}(\zeta, s) \right\} dx \\ &\quad + \frac{1}{2} \int_{\mathcal{T}} \frac{\delta^2}{\delta \zeta(x)^2} \{ \mathcal{A}^+ \left( x \middle| \psi + \frac{\zeta}{\sqrt{K}} \right) \tilde{P}(\zeta, s) \} dx \end{aligned} \quad (\text{S79})$$

We will now Taylor expand our functionals about  $\psi$  (I assume that this is possible). Thus,

we have the expansions:

$$\begin{aligned}\mathcal{A}^-\left(x\left|\psi+\frac{\zeta}{\sqrt{K}}\right.\right) &= \mathcal{A}^-(x|\psi) + \frac{1}{\sqrt{K}} \int_{\tau} \zeta(y) \frac{\delta}{\delta\psi(y)} \{\mathcal{A}^-(y|\psi)\} dy + \dots \\ \mathcal{A}^+\left(x\left|\psi+\frac{\zeta}{\sqrt{K}}\right.\right) &= \mathcal{A}^+(x|\psi) + \frac{1}{\sqrt{K}} \int_{\tau} \zeta(y) \frac{\delta}{\delta\psi(y)} \{\mathcal{A}^+(y|\psi)\} dy + \dots\end{aligned}$$

I also assume that  $\tilde{P}$  can be expanded as

$$\tilde{P} = \sum_{n=0}^{\infty} \tilde{P}_n \left( \frac{1}{\sqrt{K}} \right)^n$$

substituting these expansions into equation Eq. S79, equating coefficients of powers of  $1/K$ , and truncating at the lowest order term, we have:

$$\frac{\partial \tilde{P}_0}{\partial s}(\zeta, s) = \int_{\tau} \left[ -\frac{\delta}{\delta\zeta(x)} \left\{ \int_{\tau} \zeta(y) \frac{\delta}{\delta\psi(y)} \{\mathcal{A}^-(y|\psi)\} dy \tilde{P}_0(\zeta, s) \right\} + \frac{1}{2} \mathcal{A}^+(x|\psi) \frac{\delta^2}{\delta\zeta(x)^2} \{\tilde{P}_0(\zeta, s)\} \right] dx$$

We thus arrive at the functional Fokker-Planck equation:

$$\frac{\partial \tilde{P}_0}{\partial s}(\zeta, s) = \int_{\tau} \left( -\frac{\delta}{\delta\zeta(x)} \left\{ \mathcal{D}_{\zeta}[\mathcal{A}^-](x) \tilde{P}_0(\zeta, s) \right\} + \frac{1}{2} \mathcal{A}^+(x|\psi) \frac{\delta^2}{\delta\zeta(x)^2} \{\tilde{P}_0(\zeta, s)\} \right) dx \quad (\text{S80})$$

where

$$\mathcal{D}_{\zeta}[\mathcal{A}^-](x) = \int_{\tau} \zeta(y) \frac{\delta}{\delta\psi(y)} \{\mathcal{A}^-(y|\psi)\} dy = \frac{d}{d\epsilon} \mathcal{A}^-(x|\psi + \epsilon\zeta) \Big|_{\epsilon=0}$$

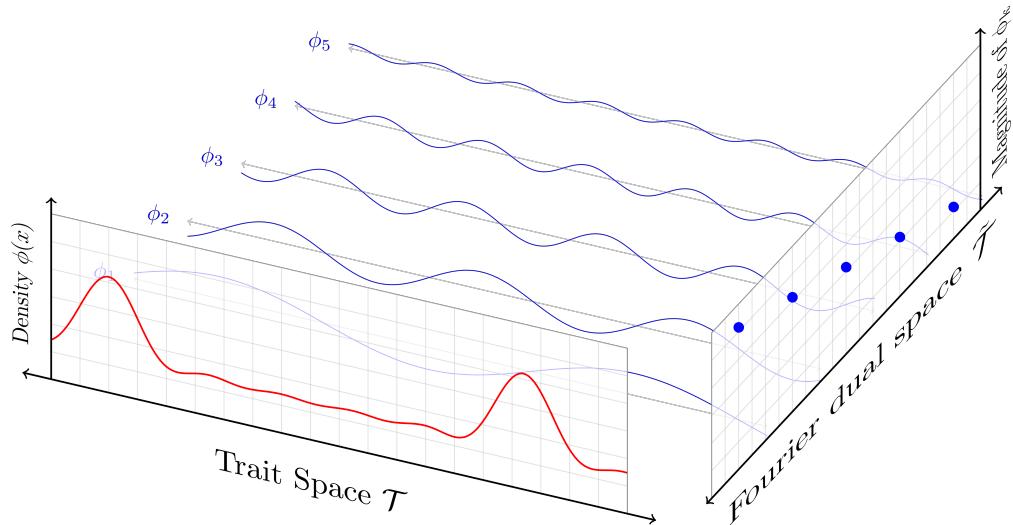
can be thought of as the functional analog of a directional derivative of  $\mathcal{A}^-(x|\psi)$  ‘in the direction of the field’  $\zeta$ . We will now use this linear approximation to study phenotypic clustering/evolutionary branching using spectral methods first introduced for various specific models by Rogers et al. (2012) and further expanded upon for some specific models of adaptive dynamics in Rogers and McKane (2015).

## S8.2 Detecting phenotypic clusters through Fourier analysis

We begin with the linear functional Fokker-Planck equation

$$\frac{\partial P}{\partial t}(\zeta, t) = \int_{\mathcal{T}} \left( -\frac{\delta}{\delta \zeta(x)} \{ \mathcal{D}_\zeta[\mathcal{A}^-](x)P(\zeta, t) \} + \frac{1}{2} \mathcal{A}^+(x|\psi) \frac{\delta^2}{\delta \zeta(x)^2} \{ P(\zeta, t) \} \right) dx \quad (\text{S81})$$

for describing stochastic fluctuations  $\zeta$  from the deterministic solution obtained by solving Eq. 19. Our goal is now to find a method to effectively detect and describe evolutionary branches (modes in trait space, corresponding to individual morphs) for this process. We will do this by measuring the autocorrelation of the field  $\phi$ , a task made easier by moving to Fourier space.



**Figure S1: Schematic description of Fourier decomposition.** Any density field  $\phi$  (shown in red) can be decomposed into a sum of infinitely many Fourier modes  $\phi_k$  (shown in blue). In the Fourier dual space, we can look at the peaks of each of these Fourier modes: The magnitude of  $\phi_k$  tells us how much it contributes to the actual function of interest  $\phi$ . The autocorrelation of  $\phi$  in the trait space can be measured using the power spectral density in the Fourier dual space.

A convenient theorem due to Weiner and Khinchin relates the autocorrelation of a probability distribution to its power spectral density via Fourier transformation. I will thus restrict myself to cases in which we can express our focal function  $\phi$  in terms of the Fourier basis  $\{e^{ikx}\}_{k \in \mathbb{Z}}$  (Figure S1). For example, if  $\mathcal{T}$  is an interval, this can be done by imposing ‘periodic boundary conditions’ (*i.e.* extending all functions from  $\mathcal{T}$  to  $\mathbb{R}$  in a way that they appear periodic with period given by the length of the interval  $\mathcal{T}$ ). If  $\mathcal{D}_\zeta[\mathcal{A}^-]$  is a

translation-invariant linear operator, then  $\exp(ikx)$  acts as an eigenfunction, significantly simplifying the calculations. I therefore assume that  $\mathcal{D}_\zeta[\mathcal{A}^-]$  takes the form:

$$\mathcal{D}_\zeta[\mathcal{A}^-](x, t) = L[\zeta(x, t)]$$

for a translation-invariant linear operator  $L$  that only depends on  $x$  and  $t$ . This is not as restrictive as it initially sounds. For example, both the Laplacian operator and the convolution operator are linear and translation invariant. The presence of phenotypic clustering and polymorphisms can be analyzed by examining the power spectrum of  $P(\zeta, t)$  over the trait space, which is precisely what we will do.

Let the Fourier basis representations  $\zeta$ , and  $\mathcal{A}^+(x|\psi)$  be given by:

$$\begin{aligned}\zeta(x, t) &= \sum_{k=-\infty}^{\infty} e^{ikx} \zeta_k(t) \quad ; \quad \zeta_k(t) = \int_{\mathcal{T}} \zeta(x, t) e^{-ikx} dx \\ \mathcal{A}^+(x|\psi) &= \sum_{k=-\infty}^{\infty} e^{ikx} A_k(t) \quad ; \quad A_k(t) = \int_{\mathcal{T}} \mathcal{A}^+(x|\psi) e^{-ikx} dx\end{aligned}\tag{S82}$$

In this case, the functional derivative operator obeys:

$$\frac{\delta}{\delta \zeta(x)} = \sum_{k=-\infty}^{\infty} e^{-ikx} \frac{\partial}{\partial \zeta_k}\tag{S83}$$

and since  $L$  is linear and translation-invariant, we also have the relation<sup>2</sup>:

$$L[\zeta] = \sum_{k=-\infty}^{\infty} L_k \zeta_k e^{ikx}\tag{S84}$$

where

$$L_k = e^{-ikx} L[e^{ikx}]$$

Lastly, by definition of Fourier modes, we have, for any differentiable real function  $F$  and any fixed time  $t > 0$ :

$$\frac{\partial}{\partial \zeta_j(t)} F(\zeta_i(t)) = \delta_{i,j} F'(\zeta_j(t))\tag{S85}$$

---

<sup>2</sup>This is because  $\exp(ikx)$  acts as an eigenfunction for translation invariant linear operators, and therefore, for any function  $\varphi = \sum \varphi_k \exp(ikx)$ , we have the relation  $L[\varphi] = L[\sum \varphi_k \exp(ikx)] = \sum \varphi_k L[\exp(ikx)] = \sum \varphi_k L_k \exp(ikx)$ , where  $L_k$  is the eigenvalue of  $L$  associated with the eigenfunction  $\exp(ikx)$ . It is helpful to draw the analogy with eigenvectors of matrices and view  $L_k \varphi_k$  as the projection of  $L[\varphi]$  along the  $k$ th eigenvector  $e_k = \exp(ikx)$ .

where  $\delta_{i,j}$  is the Kronecker delta, defined as

$$\delta_{i,j} = \begin{cases} 1 & i = j \\ 0 & i \neq j \end{cases}$$

Using Eq. S82, Eq. S83, and Eq. S84 in Eq. S81, we get, for the first term of the RHS:

$$\begin{aligned} & - \int_{\mathcal{T}} \frac{\delta}{\delta \zeta(x)} \{L[\zeta(x, t)]P(\zeta, t)\} dx \\ &= - \int_{\mathcal{T}} \sum_k e^{-ikx} \frac{\partial}{\partial \zeta_k} \left\{ \sum_n e^{inx} L_n \zeta_n P \right\} dx \\ &= - \int_{\mathcal{T}} \sum_k \sum_n e^{-i(k-n)x} \frac{\partial}{\partial \zeta_k} \{L_n \zeta_n P\} dx \\ &= -2\pi \sum_k L_k \frac{\partial}{\partial \zeta_k} \{\zeta_k P\} \end{aligned} \quad (\text{S86})$$

and for the second:

$$\begin{aligned} & \int_{\mathcal{T}} \sum_k e^{ikx} A_k \left( \sum_m \sum_n e^{-i(m+n)x} \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} P \right) dx \\ &= \int_{\mathcal{T}} \sum_k \sum_m \sum_n e^{i(k-m-n)x} A_k \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} \{P\} dx \\ &= 2\pi \sum_m \sum_n A_{m+n} \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} \{P\} \end{aligned} \quad (\text{S87})$$

Substituting Eq. S86 and Eq. S87 into Eq. S81, we see that the Fokker-Planck equation Eq. S81 in Fourier space reads:

$$\frac{\partial P}{\partial t} = -2\pi \sum_k L_k \frac{\partial}{\partial \zeta_k} \{\zeta_k P\} + \pi \sum_m \sum_n A_{m+n} \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} \{P\} \quad (\text{S88})$$

It is important to remember that since  $\zeta(x, t)$  is a stochastic process,  $\zeta_i$  is really a stochastic process and thus  $\zeta_i(t)$  is actually shorthand for the random variable  $(\zeta_i)_t(\omega)$ , where  $\omega$  is a sample path in the Fourier dual of our original probability space. Multiplying both sides of Eq. S88 by  $\zeta_r$  and integrating over the probability space to obtain expectation values, we

see that

$$\frac{d}{dt} \mathbb{E}[\zeta_r] = -2\pi \sum_k \int \zeta_r L_k \frac{\partial}{\partial \zeta_k} \{\zeta_k P\} d\omega + \pi \sum_m \sum_n A_{m+n} \int \zeta_r \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} (P) d\omega \quad (\text{S89})$$

We will evaluate the terms on the RHS of Eq. S89 using integration by parts. Recall that for any two functions  $u$  and  $v$  defined on a domain  $\Omega$ , the general formula for integration by parts is given by:

$$\int_{\Omega} \frac{\partial u}{\partial x_i} v d\mathbf{x} = - \int_{\Omega} u \frac{\partial v}{\partial x_i} d\mathbf{x} + \int_{\partial\Omega} uv \gamma_i dS(\mathbf{x}) \quad (\text{S90})$$

where  $\partial\Omega$  is the boundary of  $\Omega$ ,  $dS$  is the surface element of this boundary, and  $\gamma_i$  is the  $i^{\text{th}}$  component of the unit outward normal to the boundary. In our case, I assume that the probability of extreme events is negligible enough that  $P$  decays rapidly near the boundaries and we can neglect the contributions of the boundary term (second term on the RHS of Eq. S90). Thus, using integration by parts and neglecting the boundary terms on the RHS of equation Eq. S89, we obtain

$$\frac{d}{dt} \mathbb{E}[\zeta_r] = 2\pi \sum_k L_k \int \zeta_k \frac{\partial \zeta_r}{\partial \zeta_k} P d\omega + \pi \sum_m \sum_n A_{m+n} \int \frac{\partial^2 \zeta_r}{\partial \zeta_m \partial \zeta_n} P d\omega = 2\pi L_r \mathbb{E}[\zeta_r] \quad (\text{S91})$$

where we have used the relation in Eq. S85 to arrive at the final expression. Similarly, multiplying Eq. S88 by  $\zeta_r \zeta_s$ , integrating over the probability space and using integration by parts, we get:

$$\begin{aligned} \frac{d}{dt} \mathbb{E}[\zeta_r \zeta_s] &= 2\pi \sum_k L_k \int \zeta_k P \frac{\partial}{\partial \zeta_k} \{\zeta_r \zeta_s\} d\omega + \pi \sum_m \sum_n A_{m+n} \int P \frac{\partial}{\partial \zeta_m} \frac{\partial}{\partial \zeta_n} \{\zeta_r \zeta_s\} d\omega \\ &= 2\pi(L_r + L_s) \mathbb{E}[\zeta_r \zeta_s] + \pi(A_{2r} + A_{2s}) \end{aligned} \quad (\text{S92})$$

At the stationary state, the LHS must be zero by definition, and we must therefore have, for every  $r, s \in \mathbb{Z}$ :

$$\mathbb{E}[\zeta_r \zeta_s] = -\frac{A_{2r} + A_{2s}}{2(L_r + L_s)} \quad (\text{S93})$$

Recall now that the Fourier modes of any real function  $\varphi$  must satisfy  $\varphi_{-r} = \bar{\varphi}_r$ . Since  $\zeta$ ,  $A$  and  $L$  are all real, we can substitute  $s = -r$  in equation Eq. S93 to obtain the autocovariance relation:

$$\mathbb{E}[|\zeta_r|^2] = -\frac{\text{Re}(A_{2r})}{2\text{Re}(L_r)} \quad (\text{S94})$$

The presence of phenotypic clustering can be detected using the ‘spatial covariance’ of

our original process  $\phi$ , defined as (Rogers et al., 2012):

$$\Xi[x] = m(\mathcal{T}) \int_{\mathcal{T}} \mathbb{E}[\phi_\infty(x)\phi_\infty(y-x)]dy \quad (\text{S95})$$

where  $\phi_\infty$  is the stationary state distribution of  $\{\phi_t\}_t$  and  $m$  is the Lebesgue measure. We can use a spatial analogue of the Wiener-Khinchin theorem to calculate (Rogers et al., 2012; Rogers and McKane, 2015):

$$\Xi[x] = m(\mathcal{T}) \left[ \underbrace{\int_{\mathcal{T}} \psi_\infty(x)\psi_\infty(y-x)dy}_{\text{Infinite population prediction}} + \underbrace{\frac{1}{K} \sum_{r=-\infty}^{\infty} \mathbb{E}[|\zeta_r|^2]e^{irx}}_{\text{Finite population corrections}} \right] \quad (\text{S96})$$

where the expectations in the second term are for the stationary state. A flat  $\Xi[x]$  indicates that there are no clusters, and peaks indicate the presence of clusters. Notice that we generically expect stochastic fluctuations to induce some finite population corrections to the spatial covariance.

## S9 An example: Asexual resource competition

In this section, I present an example of a model of resource competition to illustrate the analytical pipeline outlined in this paper. Let us imagine a population of asexual individuals bearing some quantitative trait  $x$  taking values in  $\mathbb{R}$ . I assume the particular birth and death rate functionals

$$\begin{aligned} b(x|\nu) &= \int M(x,y)\nu(y,t)dy ; \quad M(x,y) = \exp\left(\frac{-(x-y)^2}{\sigma_m^2}\right) \\ d(x|\nu) &= \frac{\nu(x,t)}{K} \int \alpha(x,y)\nu(y,t)dy ; \quad \alpha(x,y) = \exp\left(\frac{-(x-y)^2}{\sigma_\alpha^2}\right) \end{aligned} \quad (\text{S97})$$

where the integrals are over the entire real line.

The interpretation is as follows: Individuals give birth to offspring with mutations. The effect of the mutations is parametrized by the ‘mutation kernel’  $M$ .  $M(x,y)$  represents the per-capita rate at which type  $y$  individuals give birth to type  $x$  individuals. I assume  $M$  has the functional form of a Normal distribution centered around the focal trait value and with a variance of  $\sigma_m^2$ . Thus, birth is most often with no mutation, and more extreme mutations are less likely. The death rate functional incorporates the effect of death due

to resource competition. The effects of competition are parametrized by a competition kernel  $\alpha$ . The quantity  $\alpha(x, y)$  represents the per-capita additional death rate of type  $x$  individuals due to competition with type  $y$  individuals. I have assumed that the strength of competition effects takes the form of a Normal distribution about the focal trait value, with variance  $\sigma_\alpha^2 > 0$ . Thus, individuals experience less competition from individuals who are at a greater phenotypic distance away from them in trait space. The death rate term also incorporates a carrying capacity  $K > 0$ . This functional form for the death rate can be seen as the continuous analog of the death rate term that arises in Lotka-Volterra competition ( $x_i \sum_j \alpha_{ij} x_j / K$ ).

Switching from population numbers  $\nu$  to the population density field  $\phi = \nu/K$  via the variable transformation presented in Eq. S2, we obtain the new stochastic field equations parameterized by the scaled birth and death rate functionals:

$$\begin{aligned} b(x|\phi) &= \int M(x, y)\phi(y, t)dy \\ d(x|\phi) &= \phi(x, t) \int \alpha(x, y)\phi(y, t)dy \end{aligned} \tag{S98}$$

Assuming the mutational variance  $\sigma_m^2$  is small, we can approximate the birth rate functional as

$$\int e^{-(x-y)^2/\sigma_m^2} \phi(y, t) dy = \phi(x, t) + \frac{\sigma_m^2}{2} \frac{\partial^2 \phi}{\partial x^2} + \dots \tag{S99}$$

Discarding higher order terms, we can thus write the birth and death rates presented in Eq. S98 as

$$\begin{aligned} b(x|\phi) &= \phi(x, t) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi \\ d(x|\phi) &= \phi(x, t) \int \alpha(x, y)\phi(y, t)dy \end{aligned} \tag{S100}$$

where we have used the notation  $\nabla_x^2 = \partial^2/\partial x^2$  for convenience. We can now compare terms with the definitions of fitness, turnover, and mutational effects to identify:

$$w(x|\phi) = 1 - \int \alpha(x, y)\phi(y, t)dy \tag{S101}$$

$$\tau(x|\phi) = 1 + \int \alpha(x, y)\phi(y, t)dy \tag{S102}$$

$$\mu = \sigma_m^2/2 \tag{S103}$$

$$Q(x|\phi) = \nabla_x^2 \phi \tag{S104}$$

These quantities are sufficient to derive all the general equations presented in this paper. For conciseness, I only present the resultant equations for the density field (Eq. 17) and the stochastic gradient equation (Eq. 30) below.

## S9.1 The population density field

From Eq. 17, we see that the population density field obeys the SPDE

$$\begin{aligned} \frac{\partial \phi}{\partial t}(x, t) &= \phi(x, t) \left( 1 - \int \alpha(x, y) \phi(y, t) dy \right) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi \\ &\quad + \frac{1}{\sqrt{K}} \sqrt{\phi(x, t) \left( 1 + \int \alpha(x, y) \phi(y, t) dy \right) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi} \dot{W}(x, t) \end{aligned} \quad (\text{S105})$$

Equation S105 is a stochastic version of the quantitative logistic equation that includes the effects of noise-induced selection and drift. This can be seen by examining the infinite population limit.

### *The infinite population limit*

In the infinite population limit, we see from Eq. 19 that the density field obeys the PDE

$$\frac{\partial \phi}{\partial t}(x, t) = \phi(x, t) \left( 1 - \int \alpha(x, y) \phi(y, t) dy \right) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi \quad (\text{S106})$$

Equation S106 is the so-called ‘quantitative logistic equation’ and has been used to model asexual resource competition (Doebeli, 2011).

## S9.2 The stochastic gradient equation

Let us first calculate the relevant fitness and turnover functions. From Eq. S101, we obtain:

$$w(x|N_K \delta_y) = 1 - \int \alpha(x, z) N_K \delta_y dz = 1 - N_K \alpha(x, y) \quad (\text{S107})$$

and similarly, from Eq. S102, we obtain

$$\tau(x|N_K \delta_y) = 1 + \int \alpha(x, z) N_K \delta_y dz = 1 + N_K \alpha(x, y) \quad (\text{S108})$$

Substituting Eq. S107 and Eq. S108 into Eq. S74, we thus obtain the stochastic gradient equation:

$$\frac{dy}{dt} = \sigma_x^2(t) \frac{\partial G(x; y)}{\partial x} \Big|_{x=y} + \frac{dW_y}{dt} \quad (\text{S109})$$

where

$$G(x; y) = 1 - \frac{1}{KN_K(t)} - \left( \frac{1 + KN_K(t)}{K} \right) \alpha(x, y) \quad (\text{S110})$$

and

$$\frac{dW_y}{dt} = \int (x - y(t)) \sqrt{1 + N_K(t)\alpha(x, y)} \dot{W}(x, t) dx \quad (\text{S111})$$

Equation S109 is a gradient equation that incorporates the effects of noise-induced selection and genetic drift, and thus can be used to study evolution in finite populations. The infinite population limit recovers a well-known model from adaptive dynamics, as I show below.

### *The infinite population limit*

In the infinite population limit, we see from Eq. S74 and Eq. S107 that we obtain the gradient equation

$$\frac{dy}{dt} = -\sigma_x^2(t) \frac{\partial \alpha(x, y)}{\partial x} \Big|_{x=y} \quad (\text{S112})$$

Equation S112 is the asexual model of sympatric speciation due to resource competition presented in Chapter 3 of Doebeli, 2011.

## S10 A stochastic Fisher-KPP equation from an individual-based model

Consider the birth and death rate functionals given by S97 with the competition kernel  $\alpha(x, y) = \delta_x$ . Thus, we can write

$$\begin{aligned} b(x|\nu) &= \int M(x, y)\nu(y, t)dy ; \quad M(x, y) = \exp\left(\frac{-(x-y)^2}{\sigma_m^2}\right) \\ d(x|\nu) &= \frac{\nu(x, t)}{K} \int \delta_x \nu(y, t) dy = \frac{1}{K} \nu^2(x, t) \end{aligned} \quad (\text{S113})$$

Biologically,  $\alpha(x, y) = \delta_x$  means that individuals only compete with other individuals that have the exact same phenotype as them, and can be thought of as taking the limit of infinitely narrow niche width in the competition model introduced in the previous section.

For instance, such dynamics could be a reasonable model if the trait in question is location in physical space. Using the same approximation for the birth rate as in the previous section, we arrive at the birth and death rates in density space

$$\begin{aligned} b(x|\phi) &= \phi(x, t) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi \\ d(x|\phi) &= \phi^2(x, t) \end{aligned} \quad (\text{S114})$$

and thus

$$w(x|\phi) = 1 - \phi(x, t) \quad (\text{S115})$$

$$\tau(x|\phi) = 1 + \phi(x, t) \quad (\text{S116})$$

$$\mu = \sigma_m^2 / 2 \quad (\text{S117})$$

$$Q(x|\phi) = \nabla_x^2 \phi \quad (\text{S118})$$

We can now substitute these functions into the population level equations for population densities (abundances).

## S10.1 The population density field

From Eq. 17, we see that the population density field obeys the SPDE

$$\frac{\partial \phi}{\partial t}(x, t) = \phi(1 - \phi) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi + \frac{1}{\sqrt{K}} \sqrt{\phi(1 + \phi) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi} \dot{W}(x, t) \quad (\text{S119})$$

Equation S119 is similar to a stochastic analog of the Fisher-KPP equation on  $\mathbb{R}$ , as will become clear upon taking the infinite population limit below. However, note that Eq. S119 is *not* the SPDE that is usually referred to as the ‘stochastic Fisher-KPP’ equation (Doering et al., 2003; Barton et al., 2013). The usual ‘stochastic Fisher-KPP’ equation is instead the SPDE (Doering et al., 2003; Barton et al., 2013)

$$\frac{\partial u}{\partial t}(x, t) = u(1 - u) + \frac{\sigma_m^2}{2} \nabla_x^2 u + \epsilon \sqrt{u(1 - u)} \dot{W}(x, t) \quad (\text{S120})$$

The discrepancy arises because the SPDE (S120) in fact does *not* correspond to the mesoscopic limit of a (spatially-extended/infinite dimensional) birth-death process (Doering et al., 2003) but is instead written down directly in analogy to the discrete trait Wright-Fisher

diffusion

$$dp = p(1-p)dt + \sqrt{p(1-p)}dW_t \quad (\text{S121})$$

While Eq. S120 can be connected with birth-death processes via duality (Doering et al., 2003) and can be derived as a scaling limit of either a contact process (Mueller and Tribe, 1995) or a spatial  $\Lambda$ -Fleming-Viot process (Barton et al., 2013), I show here that it does not arise as the expected mesoscopic limit of a measure-valued *birth-death* process. Instead, the mesoscopic limit I obtain is Eq.S119, which is also the equation expected from the more rigorous measure-theoretic approach to studying the processes I consider in this paper (see section 4.2 in Champagnat et al., 2006 with  $\eta = 1$ ).

### ***The infinite population limit***

In the infinite population limit, we see from Eq. 19 that the density field obeys the PDE

$$\frac{\partial \phi}{\partial t} = \phi(1-\phi) + \frac{\sigma_m^2}{2} \nabla_x^2 \phi \quad (\text{S122})$$

This is the famous Fisher-KPP equation and is widely used to model spatial evolution (Perthame and Génieys, 2007; Berestycki et al., 2009; Barton et al., 2013).

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