Synthesis

Eco-Evolutionary Dynamics for Finite Populations and the Noise-Induced Reversal of Selection

Ananda Shikhara Bhat^{1,2,*} and Vishwesha Guttal²

1. Department of Biology, Indian Institute of Science Education and Research, Pune, Maharashtra 411008, India; 2. Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, Karnataka 560012, India

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ABSTRACT: Theoretical studies from diverse areas of population biology have shown that demographic stochasticity can substantially impact evolutionary dynamics in finite populations, including scenarios where traits that are disfavored by natural selection can nevertheless increase in frequency through the course of evolution. Here, we analytically describe the eco-evolutionary dynamics of finite populations from demographic first principles. We investigate how noise-induced effects can alter the evolutionary fate of populations in which total population size may vary stochastically over time. Starting from a generic birth-death process, we derive a set of stochastic differential equations (SDEs) that describe the ecoevolutionary dynamics of a finite population of individuals bearing discrete traits. Our equations recover well-known descriptions of evolutionary dynamics, such as the replicator-mutator equation, the Price equation, and Fisher's fundamental theorem in the infinite population limit. For finite populations, our SDEs reveal how stochasticity can predictably bias evolutionary trajectories to favor certain traits, a phenomenon we call "noise-induced biasing." We show that noise-induced biasing acts through two distinct mechanisms, which we call the "direct" and "indirect" mechanisms. While the direct mechanism can be identified with classic bet-hedging theory, the indirect mechanism is a more subtle consequence of frequency- and density-dependent demographic stochasticity. Our equations reveal that noise-induced biasing may lead to evolution proceeding in a direction opposite to that predicted by natural selection in the infinite population limit. By extending and generalizing some standard equations of population genetics, we thus describe how demographic stochasticity appears alongside, and interacts with, the more well-understood forces of natural selection and neutral drift to determine the eco-evolutionary dynamics of finite populations of nonconstant size.

Keywords: eco-evolutionary dynamics, finite populations, demographic stochasticity, noise-induced selection, bet hedging, population biology.

Introduction

Eco-evolutionary population biology has a strong mathematical underpinning and can broadly be captured mathematically via a small number of equations, such as the replicator-mutator equation and the Price equation (Page and Nowak 2002; Queller 2017; Lion 2018). The Price equation partitions changes in population composition into multiple terms, each of which lends itself to a straightforward interpretation in terms of the high-level evolutionary forces of selection and mutation, thus providing a useful mathematical framework for describing how populations change over time (Frank 2012). The Price equation also leads to a number of simple yet insightful fundamental theorems of population biology and unifies several seemingly disjointed formal structures under a single theoretical banner (Queller 2017; Lion 2018; Lehtonen 2020a; Luque and Baravalle 2021). However, the replicator-mutator equation, the Price equation, and related fundamental theorems of evolutionary dynamics are usually formulated in a deterministic setting that neglects stochastic fluctuations due to finite population effects (Page and Nowak 2002; Queller 2017; Lion 2018).

Today, we increasingly recognize that incorporating the finite and stochastic nature of the real world routinely has much stronger consequences than simply "adding noise" to deterministic expectations and can cause qualitative changes in the behavior of diverse biological systems (Horsthemke and Lefever 1984; Black and McKane 2012; Boettiger 2018; Jhawar et al. 2020; Majumder et al. 2021; DeLong and Cressler 2023; Yamamichi et al. 2023;

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^{*} Corresponding author. Present affiliation: Institute of Organismic and Molecular Evolution (iomE), Johannes Gutenberg University, 55128 Mainz, Germany; Institute for Quantitative and Computational Biosciences (IQCB), Johannes Gutenberg University, 55128 Mainz, Germany; email: abhat@uni -mainz.de.

ORCIDs: Bhat, https://orcid.org/0000-0003-3533-5989; Guttal, https://orcid.org/0000-0002-2677-857X.

Wang et al. 2023). In ecology and evolution, stochastic models need not exhibit phenomena predicted by their deterministic analogues (Proulx and Day 2005; Johansson and Ripa 2006; Black and McKane 2012; Débarre and Otto 2016). They may also exhibit novel phenomena not predicted by deterministic models (Rogers and McKane 2015; Constable et al. 2016; Joshi and Guttal 2018; DeLong and Cressler 2023; Wang et al. 2023).

A striking example of such novel phenomena is the complete "reversal" of evolutionary trajectories (relative to the expectations of infinite population models) that is seen in some finite population eco-evolutionary models (Houchmandzadeh and Vallade 2012; Constable et al. 2016; McLeod and Day 2019a; Mazzolini and Grilli 2023). For example, in public goods games, the production of a costly public good is susceptible to invasion by "cheaters" who use the public good but do not produce it. Because of this, standard (deterministic) evolutionary game theory predicts that producers should eventually become extinct in well-mixed populations. However, in finite fluctuating populations, producers not only persist but also outcompete nonproducers (Constable et al. 2016; McLeod and Day 2019a). This phenomenon of evolution proceeding in the direction of the classically disfavored type that leads to the reversal of the prediction of deterministic natural selection has been dubbed "noise-induced selection" (Week et al. 2021). Noise-induced effects have been seen in several models in fields as diverse as sex chromosome evolution (Veller et al. 2017; Saunders et al. 2018), cell cycle dynamics (Wodarz et al. 2017), social evolution (Houchmandzadeh and Vallade 2012; Chotibut and Nelson 2015; Constable et al. 2016; McLeod and Day 2019a), and epidemiology (Kogan et al. 2014; Humplik et al. 2014; Parsons et al. 2018; McLeod and Day 2019b; Day et al. 2020). Despite the ubiquity of the phenomenon of qualitative noiseinduced effects on evolutionary trajectories, we currently lack a description of how classic equations of evolutionary biology, such as the replicator-mutator equation, the Price equation, and Fisher's fundamental theorem, are affected by such demographic stochasticity.

Two qualitatively different forms of stochasticity are important for eco-evolutionary dynamics—environmental stochasticity from fluctuations in environmental factors such as temperature and precipitation, and demographic stochasticity due to stochasticity in birth and death rates in finite populations (Lande 1993; Shoemaker et al. 2020). Bet-hedging theory, a branch of evolutionary ecology that aims to build general theories that capture the effects of stochasticity on eco-evolutionary dynamics (Seger and Brockmann 1987; Frank and Slatkin 1990; Starrfelt and Kokko 2012), has typically worked with both demographic and environmental stochasticity (Gillespie 1977; Seger and Brockmann 1987; Frank and Slatkin 1990; Olofsson et al. 2009; Childs et al. 2010; Starrfelt and Kokko 2012). On the other hand, models of noiseinduced effects and noise-induced selection model stochasticity as arising from the inherent probabilistic nature of birth and death of organisms and are thus concerned only with demographic stochasticity (Parsons et al. 2010; Houchmandzadeh and Vallade 2012; Constable et al. 2016; Parsons et al. 2018; McLeod and Day 2019a; Day et al. 2020). Because of this, it is often unclear a priori under what situations these noise-induced effects become important for evolutionary dynamics (Shoemaker et al. 2020; Yamamichi et al. 2023). For example, how does noiseinduced selection interact with genetic drift or natural selection? Are noise-induced selection and bet hedging essentially the same effect that has been spoken about using different terminology (Parsons et al. 2010), or are there multiple distinct phenomena at play (Wang et al. 2023)? This article focuses on demographic stochasticity to describe how finite population size can affect eco-evolutionary outcomes.

Specifically, we derive general equations for the dynamics of finite fluctuating populations evolving in continuous time starting from mechanistic first principles via a stochastic birth-death process (fig. 1). By starting from individual-level ecological rules for birth and death and systematically describing population-level dynamics, we relax the assumption of constant (effective) population size that appears in classic finite population models of evolution, such as the Wright-Fisher or Moran models (Lambert 2010; fig. 1). Such a mechanistic approach is also thought to be a more fundamental description of ecoevolutionary dynamics (Lambert 2010; Doebeli et al. 2017). The equations we derive reduce to well-known results, such as the replicator-mutator equation and the Price equation in the infinite population limit, thus illustrating consistency with the known formal structures of eco-evolutionary population dynamics (Queller 2017; Lion 2018). For finite populations, these same equations also provide a generic description and synthesis of the noise-induced effects of finite population size and their consequences for eco-evolutionary population dynamics.

Our systematic derivation provides relations between ecological quantities, such as the expected population growth rate and the variance in population growth rate. Our equations also describe how directional stochastic effects interact with more standard evolutionary forces, such as natural selection and genetic drift. Using these equations, we synthesize the connections between noiseinduced effects on population dynamics, including the Gillespie effect of bet-hedging theory (Gillespie 1977), noiseinduced effects in ecological population models (Constable et al. 2016; Parsons et al. 2018), drift-induced selection (Veller et al. 2017; Saunders et al. 2018), noise-induced selection



Figure 1: Outline of the approach we adopt in this article.

(Week et al. 2021), and the effects of evolutionary noise (McLeod and Day 2019*a*, 2019*b*).

A Stochastic Birth-Death Process for Population Dynamics

We consider a well-mixed population that can contain up to *m* different types of individual entities. For example, a gene may have *m* different alleles, individuals within a species may come in one of *m* phenotypes, or a community may have *m* different species; we refer to each distinct variant of an entity as a "type." Unlike many classic stochastic formulations in evolutionary theory (Crow and Kimura 1970; Lande 1976; Kimura and Ohta 1974), we do not assume a fixed or deterministically varying (effective) population size. Instead, we allow the total population size to emerge naturally, and thus fluctuate stochastically, from the stochastic birth and death processes (fig. 1).

Description of the Process

A population consisting of up to m different kinds of entities can be completely characterized by specifying the number of individuals of each type of entity. Thus, the state of the population at a given time t is an m-dimensional vector of the form $\mathbf{n} = [n_1(t), n_2(t), \dots, n_m(t)]^T$, where $n_i(t)$ is the number of individuals of type *i*. We use $N(t) = \sum_i n_i(t)$ to denote the total population size at time *t*. Each $n_i(t)$ changes stochastically via a birth-death process, as we describe below. Since N(t) is the sum of *m* stochastically fluctuating quantities, the total population size N(t) also experiences stochastic fluctuations and is thus nonconstant in our model. We use the term "fluctuating populations" henceforth to refer to populations of nonconstant size that experience stochastic fluctuations in this manner.

We assume that the birth and death rate of each type in the population depends only on the state of the population (the vector **n**) and thus neglect any potential contributions from a temporally varying external environment. Our model unfolds in continuous time, and we assume that the probability of two or more births (or deaths) occurring at the same instant is negligible. For each type $i \in \{1, 2, ..., m\}$, we denote the birth rate and death rate by $b_i(\mathbf{n})$ and $d_i(\mathbf{n})$, respectively. We assume that the birth and death rates at the population level scale with the total population size such that $b_i(\mathbf{n})$ and $b_i(\mathbf{n})$ are of the order of N(t). Furthermore, we assume that there exists a carrying capacity or, more generally, a population size measure (Czuppon and Traulsen

2021) K > 0 that imposes a bound on population growth rate such that the growth rate of the total population size N(t) is expected to be negative whenever N(t) > K (box 1).

Given the per capita birth rates $b_i^{(ind)}(\mathbf{x})$ and per capita death rates $d_i^{(ind)}(\mathbf{x})$ of each type (box 1), we define the Malthusian fitness of the *i*th type as

$$w_i(\mathbf{x}) \coloneqq b_i^{(\text{ind})}(\mathbf{x}) - d_i^{(\text{ind})}(\mathbf{x}) \tag{1}$$

and the per capita turnover rate of the *i*th type as

$$\tau_i(\mathbf{x}) \coloneqq b_i^{(\text{ind})}(\mathbf{x}) + d_i^{(\text{ind})}(\mathbf{x}).$$
(2)

The quantity $w_i(\mathbf{x})$ describes the per capita growth rate of type *i* individuals in a population \mathbf{x} , and $\tau_i(\mathbf{x})$ describes the total rate of stochastic changes (through both births and deaths) to the density of type *i* individuals. It is notable that both w_i and τ_i depend on the state of the population as a whole (i.e., \mathbf{x}) and not just on the density of the focal type. Thus, in general both the fitness and the turnover rate in our model may be both density and frequency dependent.

Fundamental Equations of Eco-Evolutionary Dynamics

Ecological Dynamics: Changes in Population Density

Having described the key demographic processes via a generic birth and death process, we now proceed to understand how the population density vector \mathbf{x} changes over time.

Recall that the stochastic birth-death process changes in units of 1/K in density space. Thus, if *K* is large, each individual contributes a negligible amount to the population density, and the discontinuous jumps due to individuallevel births or deaths in units of 1/K can be approximated as small continuous changes in population density **x**. In section S1 of the supplemental PDF, we use a formal version of this intuitive idea via a system size expansion

Box 1: Assumptions on the birth and death rates

Scaling assumptions. Mathematically, we assume that we can find O(1) functions $b_i^{(K)}$ and $d_i^{(K)}$ such that we can write

$$b_i(\mathbf{n}) = K b_i^{(K)}(\mathbf{n}/K),$$

$$d_i(\mathbf{n}) = K d_i^{(K)}(\mathbf{n}/K).$$
(i)

We can now define a notion of population density $\mathbf{x} = \mathbf{n}/K$ by dividing the population number by the population size measure. We assume the stochastic process scales such that population densities remain well defined in the infinite population size limit $(K \rightarrow \infty)$. Thus, we consider the limit of infinite population sizes but finite population densities, the usual domain of deterministic equations of population biology, such as the Lotka-Volterra equation and logistic equation. We explain the concept of the infinite population size limit in more detail in section S1.2 of the supplemental PDF.

Functional forms and per capita rates. We assume that the birth and death rate functions have the functional form

$$b_i^{(K)}(\mathbf{x}) = x_i b_i^{(\text{ind})}(\mathbf{x}),$$

$$d_i^{(K)}(\mathbf{x}) = x_i d_i^{(\text{ind})}(\mathbf{x}),$$
(ii)

where $b_i^{(ind)}(\mathbf{x})$ and $d_i^{(ind)}(\mathbf{x})$ are nonnegative functions that respectively describe the per capita birth and death rate of type *i* individuals. In general, the birth rate of type *i* individuals may contain a component that does not depend purely multiplicatively on the current density x_i of type *i*: for example, when $x_i = 0$ (i.e., there are no type *i* individuals in the population), individuals of type *i* may still be born through mutations of other types or immigration from other sources (gene flow). We account for this possibility via an additional influx term in section S1.1 of the supplemental PDF. Since such an influx term is not majorly affected by stochasticity (sec. S2 of the supplemental PDF), we do not include it in the main text for the sake of conceptual clarity.

We emphasize that these birth and death rates can incorporate complicated interactions, but as we will see, the particular forms of these rate functions do not matter for our purposes as long as the mathematical scaling assumptions in equation (i) are met.

(Ethier and Kurtz 1986, chap. 11; Van Kampen 1981, chap. 10; Black and McKane 2012; Czuppon and Traulsen 2021) to derive a continuous description of the stochastic process for population densities. This continuous description takes the form of an Itô stochastic differential equation (SDE) that says that the density of the *i*th type changes according to

$$dx_i = x_i w_i(\mathbf{x}) dt + \sqrt{\frac{x_i \tau_i(\mathbf{x})}{K}} dW_t^{(i)}, \qquad (3)$$

where each $W_t^{(i)}$ is a one-dimensional Wiener process (standard Brownian motion). Informally, $dW_t^{(i)}$ can be thought of as a normally distributed random variable with mean 0 and variance dt.

The first and second terms on the right-hand side (RHS) of equation (3) respectively provide the so-called infinitesimal mean and infinitesimal variance of the stochastic process $x_i(t)$ that satisfies equation (3) (Karlin and Taylor 1981; Czuppon and Traulsen 2021). Informally, the infinitesimal mean and variance can be understood as follows: if we imagine that the population density of type *i* changes from x_i to $x_i + dx_i$ over a very small (infinitesimal) time interval dt, we can (informally) view dx_i as a random variable. In that case, the expected density change $\mathbb{E}[dx_i]$ and the variance in the change $\mathbb{V}[dx_i]$ are respectively given by

$$\mathbb{E}[dx_i] = x_i w_i(\mathbf{x}), \tag{4a}$$

$$\mathbb{V}[dx_i] = \frac{x_i \tau_i(\mathbf{x})}{K}.$$
 (4b)

Thus, the Malthusian fitness w_i controls the expected change in population density, whereas the turnover rate τ_i (which is also a measure of the total number of events experienced by type *i* in a given time interval) controls the variance in the change in population density.

Equation (3) describes the ecological population dynamics. To study the evolutionary dynamics of finite populations, we need to move from population densities to trait frequencies by defining some statistical quantities to describe how traits are distributed in the population (box 2). We will see that this seemingly innocuous observation has important consequences when population size is nonconstant.

Box 2: Statistical measures for population-level quantities

Given any state $\mathbf{x}(t)$ that describes our population at time *t*, let us first define the total (scaled) population size $(N_{\kappa}(t))$ and the frequency $p_i(t)$ of each type *i* in the population at time *t* as

$$N_{K}(t) := \sum_{i=1}^{m} x_{i}(t) = \frac{N(t)}{K},$$

$$p_{i}(t) := \frac{n_{i}(t)}{N(t)} = \frac{x_{i}(t)}{N_{K}(t)}.$$
(iii)

Here, $N_{K}(t)$ is an $\mathcal{O}(1)$ quantity, since the total population size $N(t) = KN_{K}(t)$ is $\mathcal{O}(K)$.

Note that the frequency vector is subject to the constraint $\sum_i p_i = 1$, and we thus only need to study the system using the *m* variables $[p_1, p_2, ..., p_{m-1}, N_K]$. We are often interested in tracking the effects of evolution on quantities described at a population level. To facilitate this, let *f* be any quantity that can be defined at the type level, such as phenotype or fitness, with a (possibly time-dependent) value $f_i \in \mathbb{R}$ for the *i*th type. Recall that we defined *m* discrete types in the population on the basis that individuals within each type can be approximated as identical. Now, the statistical mean value of such a quantity in the population $[p_1, p_2, ..., p_{m-1}]$, which we denote by \overline{f} , is given by

$$\bar{f}(t) \coloneqq \sum_{i=1}^{m} f_i p_i, \tag{iv}$$

while the statistical covariance of two such quantities f and g in the population is given by

$$\operatorname{Cov}(f,g) \coloneqq fg - f\overline{g}.\tag{v}$$

Last, the statistical variance of a quantity f in the population is given by $\sigma_f^2 \coloneqq \text{Cov}(f, f)$. It is important to recognize that these statistical quantities are distinct from and independent of the probabilistic expectation, variance, and covariance obtained by integrating over realizations in the underlying probability space. We will denote this latter expectation and variance by $\mathbb{E}[\cdot]$ and $\mathbb{V}[\cdot]$, respectively, for clarity.

Replicator Equation for Finite Fluctuating Populations

We now use Itô calculus to derive equations for the evolutionary dynamics of trait frequencies from equation (3), our SDE for population densities. Letting $\bar{w} = \sum_i w_i p_i$ and $\bar{\tau} = \sum_i \tau_i p_i$ be the average population fitness and the average population turnover respectively, we show in section S2 of the supplemental PDF that p_i , the frequency of the *i*th type in population $\mathbf{x}(t)$, changes according to the following equation (also see Parsons et al. 2010, eq. [7]; Kuosmanen et al. 2022, eq. [1]):

$$dp_{i}(t) = \left[\underbrace{(w_{i}(\mathbf{p}, N_{K}) - \bar{w})p_{i}}_{\text{natural selection}} - \underbrace{\frac{1}{KN_{K}(t)}(\tau_{i}(\mathbf{p}, N_{K}) - \bar{\tau})p_{i}}_{\text{noise-induced selection}}\right]dt$$

$$+ \underbrace{\frac{1}{\sqrt{KN_{K}(t)}}dW_{p}^{(i)}}_{\text{stochastic fluctuations}},$$
(5)
$$(5)$$

where $W_p^{(i)}$ is a stochastic integral term given by

$$dW_{p}^{(i)} := \sqrt{p_{i}(1-p_{i})^{2}\tau_{i} + p_{i}^{2}\left(\sum_{j\neq i}\tau_{j}p_{j}\right)dW_{t}^{(i)}} \quad (6)$$

and each $W_t^{(i)}$ is a one-dimensional Wiener process. An analogous equation has also been derived for stochastic SIR systems (Parsons et al. 2018, eq. [2.5]). The first term of equation (5) represents the effect of natural selection for increased (Malthusian) fitness. Equation (5), when derived with mutation terms (eq. [S29]), recovers the replicator-mutator equation (eq. [6] in Lion 2018) in the infinite population ($K \rightarrow \infty$) limit (see sec. S7 of the supplemental PDF), and without mutation it recovers the standard replicator equation.

Importantly, finite populations experience a directional force dependent on $\tau_i(\mathbf{x})$, the per capita turnover rate of type *i*, that cannot be captured in infinite population models but appears in the second term on the RHS of equation (5) (Parsons and Quince 2007; Parsons et al. 2010; Week et al. 2021; Kuosmanen et al. 2022; Bhat 2024). This term shows that the effect of differential turnover rates is mathematically similar to that of differential fitness, but it acts in the opposite direction—a higher relative τ_i leads to a decrease in frequency (notice the minus sign before the second term on the RHS of eq. [5]). For this reason, the effect has been termed "noise-induced selection" (Week et al. 2021), although similar ideas have been known under the names "bet hedging" and "Gillespie effect" in the evolutionary ecology literature (Gillespie 1974, 1977; Frank

and Slatkin 1990; Starrfelt and Kokko 2012; Veller et al. 2017; see box 4). The same effect has also been noticed in the epidemiology literature (Kogan et al. 2014; Parsons et al. 2018; Day et al. 2020). Noise-induced selection can be heuristically understood as a stochastic selection for reduced variance in changes in population density (box 3).

Finally, the last term describes the effects of stochastic fluctuations due to the finite size of the population and shows the $1/\sqrt{KN_K}$ scaling that is typical of demographic stochasticity. Although this last term vanishes upon taking probabilistic expectations (and is hence nondirectional in the short term), it may bias trait frequency distributions by affecting the amount of time spent in different states, as we illustrate in the next section.

To complete the description of the system, we also require an equation for the total scaled population size $N_{\kappa} = \sum_{i} x_{i}$. Upon noting that $dN_{\kappa} = \sum_{i} dx_{i}$, using equation (3) for dx_{i} , and dividing both sides by N_{κ} we find

$$\frac{1}{N_{\kappa}}dN_{\kappa} = \bar{w}(t)dt + \sqrt{\frac{\bar{\tau}(t)}{KN_{\kappa}(t)}}dW_{t}^{N_{\kappa}}, \qquad (7)$$

where $W_t^{N_k}$ is a one-dimensional Wiener process and we have used the representation of noise terms presented in section S5 of the supplemental PDF. Thus, fitness affects only the infinitesimal mean, and turnover rate affects only the infinitesimal variance of the total population size. Note that the left-hand side of equation (7) is simply the rate of change of log(N_k), that is, the rate of change of the (scaled) population size N_k when viewed on a logarithmic scale.

A Special Case: Two Interacting Types. To illustrate the way stochasticity affects evolutionary dynamics in finite fluctuating populations, we consider the simple case of two interacting types (i.e., m = 2). Letting $p = p_1$ be the frequency of type 1 individuals in the population, we see from equation (5) that our two-type population obeys the equations

$$dp = \left[(w_1 - w_2)p(1-p) - \frac{1}{KN_K}(\tau_1 - \tau_2)p(1-p) \right] dt$$

$$+ \frac{1}{\sqrt{KN_K}} \sqrt{p(1-p)[\tau_1 + (\tau_2 - \tau_1)p]} dW_t,$$
(8a)

$$\frac{1}{N_{\kappa}}dN_{\kappa} = \bar{w}(t)dt + \sqrt{\frac{\bar{\tau}(t)}{KN_{\kappa}(t)}}dW_{t}^{N_{\kappa}},$$
(8b)

where W_t and $W_t^{N_{\kappa}}$ are one-dimensional Wiener processes.

We can now identify the (frequency-dependent) selection coefficient $s(p, N_K) := w_1(p, N_K) - w_2(p, N_K)$ from classic population genetics. The selection coefficient quantifies the direction and strength of natural selection in the system—a positive (negative) value of *s* indicates that

Box 3: A heuristic explanation of noise-induced selection

One key mechanism through which demographic stochasticity can affect evolutionary dynamics is by biasing evolutionary trajectories toward types with lower turnover rates, even if these types have the same (or even lower) fitness than other types in the population. Here, we explain this mechanism via an intuitive argument that has the same flavor as arguments seen in the bet-hedging literature (Gillespie 1977; Frank and Slatkin 1990; Starrfelt and Kokko 2012).

To illustrate the idea via an example, imagine a system consisting of two types of individuals, 1 and 2, that have equal fitness but unequal turnover rates; without loss of generality, assume $\tau_1 > \tau_2$. Let us further assume that both types have the same density x_0 . From equation (4), we see that, in our example, although the two types of individuals have the same expected change in population density, type 1 individuals have a greater variance in the changes in density than type 2 individuals.

Since evolution is defined as changes in trait frequencies, we transform variables from population density to trait frequency to see how differential variance affects evolutionary trajectories. This is done via the transformation

$$p_i = \frac{x_i}{x_i + \sum_{j \neq i} x_j} \quad \text{for any fixed } i \in \{0, 1, 2, \dots, m\}.$$
(vi)

Observe now that frequency (p_i) is a concave function of density x_i (eq. [vi]). Due to concavity, equivalent changes in density do not correspond to equivalent changes in frequency. Instead, a result mathematically known as Jensen's inequality and diagrammatically represented in box figure 1 applies.

An increase in density leads to a relatively smaller increase in frequency, whereas an equivalent decrease in density leads to a larger decrease in frequency. This implies that stochastic reductions in density have a higher cost (decrease in frequency) than the benefit (increase in frequency) conferred by a numerically equivalent increase in density (box fig. 1). Thus, variance in the density process leads to a net cost in frequency space, and all else being equal, a greater variance comes with a greater cost. Types with lower turnover rates (corresponding to lower infinitesimal variance in eq. [3]) are thus favored.



Box Figure 1: Diagrammatic representation of the consequences of demographic stochasticity when total population size can vary. The gray curve represents the transformation from population densities to trait frequencies via equation (vi). The ellipses are representations of possible changes in population composition for two types with the same fitness and same initial density but different variances (yellow > blue). The center of the ellipse represents the infinitesimal mean of the density process, the major axis captures the infinitesimal variance, and the colored region is thus representative of all possible changes given that an event (birth or death) has occurred. Reductions in density have a stronger effect on frequency than increases in density, and due to this the expected frequency (centers of ellipses on the *y*-axis) after an event has occurred is less than the initial frequency p_0 even if the expected density (centers of ellipses on the *x*-axis) coincides with the initial density x_0 . Types with a larger variance in the density process (yellow ellipse in the figure) experience a greater reduction in expected frequency relative to types with a lower variance (blue ellipse). Similar figures, with the *x*- and *y*-axes being absolute fitness and relative fitness, respectively, appear in expositions of bet hedging (e.g., Frank and Slatkin 1990; Starrfelt and Kokko 2012). In our figure, the axes are population density and trait frequency, respectively.

Box 3 (Continued)

The argument we provide here is particular to populations of nonconstant size. To see this, assume that the total (scaled) population size $\sum_i x_i$ is a constant N > 0. The transformation in equation (vi) then becomes

$$p_i = \frac{x_i}{x_i + \sum_{j \neq i} x_j} = \frac{x_i}{N}$$
(vii)

and is now simply a linear rescaling of x_i . The asymmetry between increases in density and decreases in density thus disappears. In other words, the mechanism that we identified above no longer operates for constant populations.

type 1 individuals are favored (disfavored) by natural selection.

Equation (8a) also motivates the definition of an analogous noise-induced selection coefficient $\kappa(p, N_K) := \tau_2(p, N_K) - \tau_1(p, N_K)$ to quantify the direction and strength of noise-induced selection. If type 1 has a lower turnover rate, $\kappa(p, N_K) > 0$, and thus type 1 is favored by noise-induced selection.

With this notation, equation (8a) becomes

$$dp = p(1-p) \left[s(p, N_{\kappa}) + \frac{\kappa(p, N_{\kappa})}{KN_{\kappa}} \right] dt + \frac{1}{\sqrt{KN_{\kappa}}} \sqrt{p(1-p)(\tau_1 + p\kappa(p, N_{\kappa}))} dW_t,$$
(9)

where we see that the selection coefficient $s(p, N_K)$ affects the infinitesimal mean (*dt* term) of equation (9) and the noise-induced selection coefficient $\kappa(p, N_K)$ affects both the infinitesimal mean and the infinitesimal variance. Note that fitness only enters into the population dynamics via the selection coefficient *s*, whereas turnover also appears via τ_1 in the second term on the RHS of equation (9). In other words, only the relative fitness or the difference $w_1 - w_2$, but not the absolute value of the fitness w_b , matters for the deterministic dynamics. In contrast, the functional form and absolute value of the per capita turnover rate does affect the stochastic dynamics of the system via the second term on the RHS of equation (9).

Demographic stochasticity can also affect population dynamics through the second term on the RHS of equation (9) due to turnover-dependent stochastic effects (McLeod and Day 2019*a*). To study these effects, we will examine the speed density *m* (Karlin and Taylor 1981; Czuppon and Traulsen 2021) of the stochastic process described by equation (9). As we explain in section S6 of the supplemental PDF, the speed density $m(p_0)$ at the point p_0 is a measure of the amount of time the population spends in the "immediate neighborhood" of the state p_0 (formally, it is proportional to the amount of time spent in the interval $(p - \epsilon, p + \epsilon)$ in the limit $\epsilon \rightarrow 0$; see Karlin and Taylor 1981, chap. 15, remark 3.2). When a stationary distribution or quasi-stationary distribution (Collet et al. 2013) exists, it is proportional to the speed density (Karlin and Taylor 1981, chap. 15, eq. [5.34], along with chap. 15, eq. [3.10]; Collet et al. 2013, theorem 6.4), and the speed density thus describes the trait frequency distribution at (quasi) stationarity in such cases. In section S6 of the supplemental PDF, we show (eq. [S83]) that the speed density m(p) obeys the equation

$$\frac{dm}{dp} = m(p) \left[\underbrace{\frac{2p-1}{p(1-p)}}_{\text{antisymmetric}} + \underbrace{2\frac{E(p)}{V(p)}}_{\text{Same sign as}} - \underbrace{\frac{1}{V(p)}\frac{dV}{dp}}_{\text{From second term RHS of eq. (9)}} \right],$$
(10)

where

$$E(p, N_{\kappa}) = s(p, N_{\kappa}) + \frac{1}{KN_{\kappa}}\kappa(p, N_{\kappa}), \qquad (11a)$$

$$V(p,N_{\kappa}) = \frac{1}{KN_{\kappa}} (\tau_1(p,N_{\kappa}) + p\kappa(p,N_{\kappa})).$$
(11b)

The sign of dm/dp tells us whether the system spends more time in states in which type 1 is overrepresented (positive meaning that type 1 is favored), and the points at which dm/dp = 0 tell us about the states that are most likely/least likely to be observed before fixation/extinction has taken place (McLeod and Day 2019a; Majumder et al. 2021). The first term on the RHS of equation (10) is antisymmetric about p = 0.5. In other words, if we change p to (1 - p) (track type 2 instead of type 1), the term retains the same magnitude but has the opposite sign. Thus, the term does not contribute to directional effects and can be ignored for our purposes. Biologically, the term is smallest at p = 0.5 and symmetrically larger as one moves toward the boundaries, and thus it can be thought of as capturing the effect of neutral genetic drift in pushing trait frequency *p* to the boundaries of [0, 1].

The second term of equation (10) represents the balance between classical selection and noise-induced selection.

Box 4: Two distinct nonneutral effects of demographic stochasticity

Demographic stochasticity can cause certain types to be systematically overrepresented in the population relative to infinite population expectations, even if the fitness of these focal types is the same as (or lower than) the fitness of other types in the population. Since such biases in the trait distribution are induced purely by stochasticity and do not appear in deterministic models, we call this phenomenon "noise-induced biasing." Our equations reveal that noise-induced biasing can occur through two distinct mechanisms. In this box, we provide a summary of the connections and delineations between the two mechanisms.

- 1. The direct mechanism selects for reduced variance in changes in population density (Gillespie 1974, 1977). This mechanism appears in the deterministic term (dt term) of the replicator equation (eq. [5]) and is detectable as a systematic deviation of the expected trajectory $\mathbb{E}[dp/dt]$ from the infinite population prediction (Parsons et al. 2010, 2018). The direct mechanism can be identified with the Gillespie effect from the bet-hedging literature (Gillespie 1974) and is obtained as a balance between natural selection for increased ecological growth rate and a stochastic selection for reduced variance in changes in population densities (see box 3). Since the direct mechanism looks mathematically very similar to the force of natural selection (compare the first and second terms on the RHS of eq. [5]), it has also been called "noise-induced selection" in the literature (Week et al. 2021). Noise-induced selection in this sense is thus a version of classical evolutionary bet hedging (Frank and Slatkin 1990; Starrfelt and Kokko 2012) in an explicitly demographic, dynamical context. Note that unlike in bet-hedging models, w and τ (and thus *s* and κ) are derived from the underlying demographic processes.
- 2. The indirect mechanism appears as an apparent selection for reduced variance in changes in trait frequency (McLeod and Day 2019*a*). The effects of demographic stochasticity, in this case, appear in the stochastic term (*dW* term) of the replicator equation (eq. [5]) and affect the time spent at various configurations and thus, indirectly, the probability of observing a polymorphic population in a particular configuration ($p_1, p_2, ..., p_{m-1}, N_K$). The indirect mechanism results from frequency dependence in the variance of changes in trait frequencies and can be thought of as analogous to frequency-dependent viscosity; populations tend to accumulate in those configurations that lead to slower changes in population composition, and we are thus more likely to observe the population in those configurations that make the rate of change of the population slower. The strength of indirect noise-induced biasing varies inversely with (the square root of) population size, and the direction of the effect depends on the frequency dependence of the per capita turnover rates τ_i .

Unlike natural selection, the balance between noise-induced biasing (through either mechanism) and genetic drift in the absence of natural selection does not depend on the total population size. Instead, it is determined by the details of the demographic processes occurring in the population. If different types have different turnover rates, the direct mechanism (noise-induced selection) operates, and if some types are associated with lower variance in the change in trait frequencies, the indirect mechanism operates. Note that this observation means that noiseinduced biasing, via both direct and indirect mechanisms, need not operate or be a significant force in small populations, depending on demographic details.

Since both *s* and κ are $\mathcal{O}(1)$ functions, natural selection will tend to dominate E(p) when the total population size KN_K is large. Additionally, if *s* and κ are of similar magnitude (i.e., the strength of natural selection is comparable to the strength of the Gillespie effect), natural selection will still dominate the sign of E(p), since the total population size KN_K must be greater than 1. However, noise-induced selection can qualitatively affect evolutionary dynamics if differences in Malthusian fitnesses are close to zero (i.e., natural selection is weak, $|s| \ll 1$) or if total population size KN_K is small (Parsons et al. 2010, 2018). We also show this explicitly using an example in box 5.

Equation (10) also tells us that noise-induced selection (explained heuristically in box 3) is not the only way in which demographic stochasticity can bias trait distributions. Instead, the speed density is also profoundly affected by the noise terms in equation (9), as captured by the last term on the RHS of equation (10). In particular, even when the first term on the RHS of equation (9) vanishes or acts in the same direction as classical selection,

Box 5: An example: noise-induced biasing with two competing types

Consider a population comprised of two competing types of individuals (denoted 1 and 2). For pedagogical clarity, we assume that the birth and death rates of type 1 are simply shifted from those of type 2 by constants ϵ_b and ϵ_d respectively; that is,

$$b_1^{(\text{ind})}(p, N_K) = b_2^{(\text{ind})}(p, N_K) + \epsilon_b \text{ and } d_1^{(\text{ind})}(p, N_K) = d_2^{(\text{ind})}(p, N_K) + \epsilon_d.$$
 (viii)

We provide potential biological interpretations of this model in terms of either ecological rate modulators (Fronhofer et al. 2023) or competing pathogen strains (Parsons et al. 2018) in section S10 of the supplemental PDF. Using the definitions of the selection coefficient (*s*) and noise-induced selection coefficient (κ), we find

$$\kappa(p, N_K) = \epsilon_b - \epsilon_d \text{ and } \kappa(p, N_K) = -[\epsilon_b + \epsilon_d].$$
 (ix)

Equation (ix) shows that all else being equal, reducing the death rate leads to a more favorable evolutionary outcome than increasing the birth rate by the same amount (also see McLeod and Day 2019*a*; Raatz and Traulsen 2023). We now explain the subtle ways in which demographic stochasticity biases evolutionary dynamics.

Noise-induced biasing in the absence of natural selection. Let us assume that $\epsilon_b = \epsilon_d = \epsilon$. This corresponds to a faster pace of life in type 1 relative to type 2. From equation (ix), we see that $s(p, N_K) = 0$, and thus the two types have equal fitness. In the absence of natural selection, a given initial frequency remains unchanged over time in infinitely large populations. In finite populations experiencing only neutral genetic drift, we expect the probability of fixation of a type to be proportional to its initial frequency. The effects of noise-induced biasing through the direct mechanism (noise-induced selection) can be observed by looking at the change in the expected frequency $\mathbb{E}[p]$, which from equation (9) follows:

$$\frac{d}{dt}\mathbb{E}[p] = \mathbb{E}\left[\frac{\kappa(p, N_{\kappa})}{N_{\kappa}}p(1-p)\right] = -\frac{2\epsilon}{KN_{\kappa}}\mathbb{E}[p(1-p)].$$
(x)

Since the RHS of equation (x) is always negative for $p \in (0, 1)$, we can infer that the proportion of type 1 individuals is expected to decrease to zero from any initial frequency. Note that unlike for neutral drift, it is always type 2 that is expected to fix. This result is a manifestation of noise-induced selection—all else being equal, a faster pace of life comes with a greater variance in the change of population density within a given time interval, since there are simply more stochastic birth/death events taking place, and types with a slower pace of life (type 2) are thus favored (Parsons and Quince 2007; Parsons et al. 2010; Wodarz et al. 2017).

To illustrate the indirect mechanism of noise-induced biasing, we need to assume a functional form for the turnover rates τ_i . In section S10 of the supplemental PDF, we obtain an exact expression for the speed density when $\tau_1 = bp + c$ and $\tau_2 = bp + c - 2\epsilon$ for suitable constants b and c. The parameter c can be viewed as an intrinsic turnover rate, and b can be viewed as a frequency-dependent component that may be either positive or negative. Box figure 2 plots the speed density for various parameter values, illustrating both the direct (box fig. 2A) and the indirect (box fig. 2B) mechanisms of noise-induced biasing. Note that the direct and indirect mechanisms may operate either in isolation or simultaneously and may either supplement (red curve in box fig. 2A) and green curve in box fig. 2B) or oppose (red curves in box fig. 2) each other.

Noise-induced biasing in the presence of natural selection. Assume now that $\epsilon_b > \epsilon_d > 0$. In this case, s > 0, and thus natural selection favors type 1 individuals. As before, there are two ways in which demographic stochasticity can bias evolutionary dynamics toward certain types. Noise-induced selection could drive the expected trajectory toward fixation of type 2 despite type 1 being favored by natural selection. In section S10 of the supplemental PDF, we show that this can happen if and only if

$$(KN_K - 1)s(p, N_K) = (KN_K - 1)(\epsilon_b - \epsilon_d) < 2\epsilon_d.$$
(xi)

Thus, noise-induced selection can reverse the predictions of natural selection when $s(p, N_K)(KN_K - 1)$ is sufficiently small—that is, when natural selection is weak ($s(p, N_K)$ is small), populations are small (KN_K is small), or both. Since the strength and direction of the indirect mechanism depend on the functional form of τ_i , we do not explicitly study it here. However, we provide some preliminary observations in section S10 of the supplemental PDF.



cient $\kappa = -2\epsilon$ is large relative to the intrinsic turnover rate *c*, the direct mechanism of noise-induced biasing operates. Parameters are chosen such that $V(p) = \tau_1 + p\kappa = (b - 2\epsilon)p + c$ is not frequency dependent (blue: $\epsilon = 0.5$, b = 1, c = 10; red: $\epsilon = 0.5$, b = 1, c = 0.5). *B*, The speed density can also be biased if V(p) is frequency dependent. This indirect mechanism of noise-induced biasing favors the type that reduces V(p). Parameters in this panel are chosen such that $|\kappa|$ is small relative to *c* and thus the strength of the fast mechanism is negligible (blue: $\epsilon = 0.025$, b = 0.05, c = 10; green: $\epsilon = 0.025$, b = 50, c = 10; red: $\epsilon = 0.025$, b = -8.5, c = 10.

populations may still spend much more time in states where a certain type is overrepresented, in particular possibly reversing the prediction of infinite population models, if dV/dp is nonzero. For example, the system may spend much more time in configurations where type 1 individuals are overrepresented even if $s + \kappa/KN_K < 0$ (meaning that the first term on the RHS of eq. [9] favors type 2 individuals) as long as dV/dp is sufficiently negative (McLeod and Day 2019a). Thus, one type is "favored" through this effect in the sense that we are more likely to observe the population in states where the focal type is overrepresented, an effect that has been ascribed to evolutionary noise (McLeod and Day 2019a, 2019b). As an aside, note that (1/V)(dV/dp) could also equivalently be written as the derivative of log(V) with respect to p and thus represents the strength and direction of the frequency dependence of $\log(V)$. Since $\mathbb{V}[dp] = p(1 - p)$ p)V(p) from equation (9), log(V) can be interpreted as being proportional to the logarithm of the variance in the changes in the trait frequency dp. This term thus captures the contributions of stochastic fluctuations (or noise) in the trait frequency changes dp and can be interpreted as selecting for reduced variance in the change in trait frequencies dp, whereas noise-induced selection is a selection for reduced variance in the change in population densities

(box 3). Both of these effects can bias the distribution of types observed in finite populations, and we therefore collectively refer to the two effects as "noise-induced biasing." Since noise-induced selection is directly visible as a deviation in the expected change in frequency $\mathbb{E}[dp]$, we call it the "direct" mechanism. Since the term looks mathematically similar to the action of natural selection (compare the first and second terms on the RHS of eq. [5] or [9]), we also use the phrase "noise-induced selection" for the direct mechanism (following Week et al. 2021). In contrast, noise-induced biasing via frequency dependence of *V* is a more subtle mechanism that affects the distribution of types indirectly by biasing the time spent in different states, and we thus refer to this effect as the "indirect" mechanism of noise-induced biasing (box 4).

Remarkably, when natural selection does not operate (s = 0), there are situations where the speed density, and thus the stationary distribution when it exists, does not depend on the total population size. In particular, if τ_1 and κ are such that the ratio τ_1/κ is independent of the total population size KN_κ , then so is the speed density. Intuitively, this is because both noise-induced biasing and drift arise from the stochasticity associated with finite populations. More precisely, when s = 0, the total population size KN_κ affects the dynamics only through a prefactor

of $1/KN_{\kappa}$ that occurs in both E(p) and V(p). It therefore disappears in the ratio E/V. Thus, unlike the classic results regarding natural selection-drift balance, the total population size does not affect the relative strengths of noiseinduced biasing and genetic drift—instead, it is the details of the demographic processes, as captured by κ and V, that determine which effect dominates. A similar observation has been made in life history theory (Shpak 2005).

Price Equation for Finite Fluctuating Populations

Having described how the frequencies of types change over time, we now examine the behavior of the statistical population mean \overline{f} of any type-level quantity f (e.g., phenotype, fitness). Classically, the evolution of the statistical mean of a trait in a population is described by the Price equation and related formalisms, such as the breeder's equation (Page and Nowak 2002; Queller 2017; Lehtonen 2018; Lion 2018). Our formalism naturally allows us to extend these results to a stochastic, dynamic setting to describe how mean values change over time in finite fluctuating populations. We find that \overline{f} satisfies the SDE (see sec. S3 of the supplemental PDF)

$$d\bar{f} = \underbrace{\operatorname{Cov}(w,f)dt}_{\substack{\text{classical}\\ \text{solaction}}} - \underbrace{\frac{1}{KN_{K}(t)}\operatorname{Cov}(\tau,f)dt}_{\substack{\text{noise-induced selection}\\ (\text{direct mechanism})}} + \underbrace{\overline{\left(\frac{\partial f}{\partial t}\right)}dt}_{\substack{\text{effects of changes}\\ \text{in trait values } f_{i}}} + \underbrace{\frac{1}{\sqrt{KN_{K}(t)}}dW_{\bar{f}}}_{\text{fluctuations}}, \qquad (12)$$

where

$$dW_{\bar{f}} \coloneqq \left(\sqrt{\operatorname{Cov}\left(\tau, \left(f - \bar{f}\right)^2\right) + \bar{\tau}\sigma_f^2}\right) dW_t \qquad (13)$$

is a stochastic integral term describing undirected stochastic fluctuations (see eq. [S67] in sec. S5 of the supplemental PDF). Here, we use W_i to denote a generic Wiener process whose relation to the Wiener processes in equation (5) can be studied using a relation discussed in section S5 of the supplemental PDF. Equation (12) has previously been derived in the epidemiology literature (Day et al. 2020, eq. [5.2]; see sec. S8 in the supplemental PDF), and a quantitative trait version of the equation has also been derived using more sophisticated mathematical techniques (Week et al. 2021, eq. [21b]; Bhat 2024, eq. [25]).

Equation (12) recovers the Price equation (eq. [11] in Lion 2018) in the infinite population $(K \rightarrow \infty)$ limit (see

sec. S7 of the supplemental PDF). Each term in equation (12) lends itself to a simple biological interpretation. The first term, Cov(w, f), is well understood in the classical Price equation and represents the effect of natural selection. If the trait and the fitness are positively correlated, the mean trait value in the population increases due to the effect of selection. The second term, $Cov(\tau, f)/KN_K(t)$, is the effect of noise-induced selection in finite fluctuating populations. Biologically, the $Cov(\tau, f)$ term (with negative sign) describes a biasing effect due to differential turnover rates between different types; if the trait is positively correlated with turnover rate, this term causes the mean trait value to decrease.

The third term of equation (12) is relevant whenever f_i can vary over time. Such variation over short ("ecological") timescales could potentially occur through a changing environment, phenotypic/behavioral plasticity, or any manner of other ecological phenomena that change f_i over time. As we will see in the next section, this term is also responsible for what Fisher called "environmental deterioration" in Fisher's fundamental theorem (Price 1972; Frank and Slatkin 1992).

Finally, the last term of equation (12) describes the role of stochastic fluctuations. Recall that the square of this term corresponds to the infinitesimal variance of the change in the mean value $d\bar{f}$ of the quantity f in the population. The expression $(f_i - \bar{f})^2$ is a measure of the distance of f_i from the population mean \overline{f} . The Cov $(\tau, (f - \overline{f})^2)$ term thus tells us that if turnover τ_i of the *i*th type covaries positively with the distance of f_i from the population mean (i.e., individuals with more extreme f have higher turnover rates), the population experiences a greater variance in df(i.e., the change in the mean value of f) over infinitesimal time intervals. The $\overline{\tau}\sigma^2$ term tells us that even if τ and f do not covary, there is still some variance in $d\bar{f}$, given now by the product of the mean turnover rate $\bar{\tau}$ with the standing variation σ_f^2 in the quantity f. As we shall see in the next section, this is a manifestation of neutral genetic/ecological drift. Just as in the replicator equation, stochastic fluctuations through dW_f^- can profoundly affect the time spent at different values of f (and the stationary distribution, when it exists) via the indirect mechanism of noiseinduced biasing if the term inside the square root of equation (13) depends on f. Note that unlike for the replicator equation, the SDE in equation (12) is one-dimensional regardless of the number of traits (m), and thus the stationary distribution of the mean value f can always be studied the way we studied equation (9).

Fisher's Fundamental Theorem for Finite Fluctuating Populations

Two particularly interesting implications of equation (12) are realized upon considering the time evolution of mean

fitness and mean turnover rate. First, upon substituting f = w in equation (12) and taking expectations over the underlying probability space, we obtain

$$\mathbb{E}\left[\frac{d\bar{w}}{dt}\right] = \underbrace{\mathbb{E}[\sigma_{w}^{2}]}_{\text{Fisher's}} - \underbrace{\mathbb{E}\left[\frac{\sigma_{b}^{2}(\text{ind}) - \sigma_{d}^{2}(\text{ind})}{KN_{K}(t)}\right]}_{\text{noise-induced}} + \underbrace{\mathbb{E}\left[\frac{\partial w}{\partial t}\right]}_{\text{eco-evolutionary}}$$

$$(14)$$

The first term, σ_w^2 , is the subject of Fisher's fundamental theorem (Frank and Slatkin 1992; Kokko 2021) and says that in infinite populations, the rate of change of mean fitness in the population is proportional only to the standing variation in fitness σ_w^2 if fitness at the type level (w_i) does not change over time. The second term of equation (14) is a manifestation of noise-induced selection acting and is particular to finite populations (note that the indirect mechanism does not operate because we are only looking at expectation values). Finally, the last term arises whenever w_i can vary over time and represents the effect that Fisher called the "deterioration of the environment" (Price 1972; Frank and Slatkin 1992). In short, this last term captures feedback effects on the fitness w_i of the *i*th species over short (ecological) timescales (Mylius and Diekmann 1995; Kokko 2021), and we refer the interested reader to Kokko (2021) for a more detailed treatment. Equation (14) recovers the standard version of Fisher's fundamental theorem in the infinite population $(K \rightarrow \infty)$ limit (see sec. S7 of the supplemental PDF).

The Demographic Origins of Fitness Differences Induce Quantitative Corrections to Fisher's Fundamental Theorem in Finite Populations. Since $w = b^{(ind)} - d^{(ind)}$ by definition, equation (14) can alternatively be written as

$$\mathbb{E}\left[\frac{d\bar{w}}{dt}\right] = \underbrace{\mathbb{E}\left[\left(1 - \frac{1}{KN_{K}}\right)\sigma_{b^{(\mathrm{ind})}}^{2}\right]}_{\text{changes in mean fitness}} + \underbrace{\mathbb{E}\left[\left(1 + \frac{1}{KN_{K}}\right)\sigma_{d^{(\mathrm{ind})}}^{2}\right]}_{\text{changes in mean fitness}}_{\text{due to variation}} + \underbrace{\mathbb{E}\left[\frac{\partial w}{\partial t}\right]}_{\text{eco-evolutionary}}_{\text{feedbacks to fitness}}$$

(15)

Equation (15) redescribes variation in fitness in terms of the more fundamental processes of birth and death. Equation (15) also tells us that variation in death rates leads to a slightly greater rate of increase in mean fitness than an equivalent variation in birth rates. For example, if individuals differ in birth rates alone (i.e., $\sigma_{d^{(ind)}}^2 = 0$, $\sigma_w^2 = \sigma_{\mu(ind)}^2$), equation (15) predicts that the rate of mean fitness in the absence of eco-evolutionary effects is given by $\mathbb{E}[(1 - 1/KN_K)\sigma_w^2]$. On the other hand, if individuals instead differ in death rates alone (i.e., $\sigma_{\mu^{(ind)}}^2 = 0$, $\sigma_{w}^2 =$ $\sigma^2_{d^{(\mathrm{ind})}}$), the rate of change of mean fitness in the absence of eco-evolutionary effects is given by $\mathbb{E}[(1 + 1/KN_K)\sigma_w^2]$, which is a slightly faster rate of change. Note, however, that these are only minor quantitative corrections to Fisher's fundamental theorem, and the two cases exhibit the same qualitative behavior.

An Analog of Fisher's Fundamental Theorem for the Mean Turnover Rate of the Population

Carrying out the same steps in deriving equation (14) with $f = \tau$ in equation (12) yields a dynamical equation for the evolution of mean turnover rates (Kuosmanen et al. 2022) and reads

$$\mathbb{E}\left[\frac{d\bar{\tau}}{dt}\right] = \underbrace{\mathbb{E}\left[\sigma_{b^{(\mathrm{ind})}}^{2} - \sigma_{d^{(\mathrm{ind})}}^{2}\right]}_{\text{natural selection}} - \underbrace{\mathbb{E}\left[\frac{\sigma_{\tau}^{2}}{KN_{K}(t)}\right]}_{\text{noise-induced selection effects}} + \underbrace{\mathbb{E}\left[\frac{\bar{\partial}\tau}{\partial t}\right]}_{\text{eco-evolutionary}}.$$
(16)

The first term captures the effect of natural selection on mean turnover rates and says that natural selection may either increase or decrease the mean turnover rate depending on the demographic details of the population. More precisely, we predict that natural selection is expected to increase the mean turnover rate in the population if (and only if) the expected variance in the birth rates is greater than the expected variance in the death rates (see also Kuosmanen et al. 2022). The second term of equation (16) represents the effect of noise-induced selection and is exactly analogous to the σ_w^2 term in Fisher's fundamental theorem. This term says that noise-induced selection always reduces mean turnover in the population, with the rate of reduction of the mean turnover rate being proportional to the standing variation in turnover rates σ_{τ}^2 . Finally, the last term on the RHS of equation (16) guantifies the effect of eco-evolutionary feedback via changes in the turnover of each type over time. In infinitely large populations $(K \rightarrow \infty)$, the second term on the RHS of equation (16) disappears; thus, the mean turnover rate $\bar{\tau}$ may either decrease or increase in infinitely large populations based on demographic details of (the variance of) birth and death rates in the population (Kuosmanen et al. 2022). In contrast, the noise-induced selection (second term) always reduces the mean turnover rate.

The Fundamental Equation for the Population Variance via a Generalization of an Equation for Variance of Type-Level Quantities

Equation (12) is a general equation for the mean value of an arbitrary type-level quantity f in the population. In many real-life situations, we are interested in not just the population mean but also the variance of a quantity in the population. In section S4 of the supplemental PDF, we show that the statistical variance of any type-level quantity f obeys

$$d\sigma_{f}^{2} = \underbrace{\operatorname{Cov}\left(w, (f - \bar{f})^{2}\right) dt}_{\text{classical selection}} - \underbrace{\frac{2}{KN_{K}}\operatorname{Cov}\left(\tau, (f - \bar{f})^{2}\right) dt}_{\text{noise-induced selection}} - \underbrace{\frac{1}{KN_{K}} \bar{\tau} \sigma_{f}^{2} dt}_{\text{genetic/ecological}} + \underbrace{2\operatorname{Cov}\left(\frac{\partial f}{\partial t}, f\right) dt}_{\text{effects of changes}} + \underbrace{\frac{1}{\sqrt{KN_{K}(t)}} dW_{\sigma_{f}^{2}}}_{\text{stochastic}},$$

$$(17)$$

where

$$dW_{\sigma_f^2} \coloneqq \sqrt{\operatorname{Cov}\left(\tau, \left(f - \bar{f}\right)^4\right) + \bar{\tau}(\sigma_f^2)^2} dW_t \qquad (18)$$

is a stochastic integral term measuring the (nondirectional) effect of stochastic fluctuations that vanishes upon taking an expectation over the probability space (see eq. [S69] in sec. S5 of the supplemental PDF). As before, we use W_t to denote a generic Wiener process—the W_t that appears in equation (17) is not necessarily the same process that appears in either equation (5) or equation (12). The stochastic dependencies between the various Wiener processes can be studied using a relation discussed in section S5 of the supplemental PDF. An infinite population ($K \rightarrow \infty$) version of equation (17) appears in Lion (2018; see sec. S7 of the supplemental PDF) as a dynamic version of earlier, dynamically insufficient equations for the change in trait variation over a single generation (e.g., see eq. [6.14] in Rice 2004).

Once again, the terms of equation (17) lend themselves to straightforward biological interpretation. The quantity $(f_i - \overline{f})^2$ is a measure of the distance of f_i from the population mean value \bar{f} , and thus covariance with $(f - \bar{f})^2$ quantifies the type of selection operating in the system: a negative correlation is indicative of stabilizing or directional selection, and a positive correlation is indicative of disruptive (i.e., diversifying) selection (Rice 2004, chap. 6; Lion 2018). An extreme case of diversifying selection for fitness occurs if the mean fitness of the population is at a local minimum but $f_i \not\equiv \overline{f}$ (i.e., the population still exhibits some variation in f). In this case, if the variation in f is associated with a variation in fitness, then $Cov(w, (f - f)^2)$ is strongly positive and the population experiences a sudden explosion in variance, causing the emergence of polymorphism in the population. If $Cov(w, (f - f)^{2})$ is still positive after the initial emergence of multiple morphs, evolution eventually leads to the emergence of stable coexisting polymorphisms in the population-this phenomenon is a slight generalization of the idea of evolutionary branching that occurs in frameworks such as adaptive dynamics (Doebeli 2011). The $Cov(\partial f / \partial t, f)$ term represents the effect of changes in *f* at the type level over time (due to plasticity, for instance).

Finally, the last term on the RHS of equation (17) describes the role of stochastic fluctuations. The square of this term is the infinitesimal (probabilistic) variance of the changes in statistical variance $d\sigma_f^2$ of f. Just like in the stochastic replicator and Price equations, this term can affect the time spent at different values of trait variance through the indirect mechanism of noise-induced biasing. Just like the stochastic Price equation, the SDE in equation (17) is always one-dimensional, and thus the stationary distribution of the variance σ_f^2 can also always be studied the way we studied equation (9).

In the case of one-dimensional quantitative traits, an infinite-dimensional version of equation (17) has recently been rigorously derived (Week et al. 2021) using measure-theoretic tools under certain additional assumptions (Week et al. 2021, eq. [21c]; see sec. S9 of the supplemental PDF). Taking expectations over the probability space in equation (17) also recovers an equation previously derived and used (Débarre and Otto 2016) in the context of evolutionary branching in finite populations as a special case (eq. [A.23] in Débarre and Otto [2016] is equivalent to our eq. [17] for their choice of functional forms upon converting their change in variance to an infinitesimal rate of change, i.e., derivative).

Loss of Trait Variation in Populations Experiencing Drift. The $\bar{\tau}\sigma_j^2$ term quantifies the loss of variation due to stochastic extinctions (i.e., demographic stochasticity) and thus represents the classic effect of neutral drift in finite populations. Our equations are agnostic to whether each type *i* is an allele, a phenotype, a morph, or a species, so the drift in question may be either genetic or ecological drift, depending on the biological context. To see why $\bar{\tau}\sigma_f^2$ quantifies the loss of trait variation, it is instructive to consider the case in which this is the only force at play. Let us imagine a population of asexual organisms in which each f_i is simply a label or mark arbitrarily assigned to individuals in the population at the start of an experiment/ observational study and subsequently passed on to offspring-for example, a neutral genetic tag in a part of the genome that experiences a negligible mutation rate. Since the labels are arbitrary and have no effect whatsoever on the biology of the organisms, each label has the same fitness $w_i \equiv w$ and per capita turnover $\tau_i \equiv \tau$, and thus $\bar{w} = w$ and $\bar{\tau} = \tau$. Note that since every type has the same fitness and turnover rate, we have $Cov(w, (f - \bar{f})^2) \equiv$ $\operatorname{Cov}(\tau, (f - \overline{f})^2) \equiv 0$. Since the labels do not change over time, we also have $Cov(\partial f / \partial t, f) = 0$. From equation (17), we see that in this case the variance changes as

$$d\sigma_f^2 = -\frac{\tau \sigma_f^2}{KN_K(t)} dt + \frac{1}{\sqrt{KN_K(t)}} dW_{\sigma_f^2}.$$
 (19)

Taking expectations, the second term on the RHS vanishes, and we see that the expected variance in the population obeys

$$\frac{d\mathbb{E}[\sigma_j^2]}{dt} = -\left(\mathbb{E}\left[\frac{\tau}{KN_K}\right]\right)\mathbb{E}[\sigma_j^2],\tag{20}$$

where we have decomposed the expectation of the product on the RHS into a product of expectations, which is admissible since the label f is completely arbitrary and thus independent of both $\bar{\tau}$ and $N_{K}(t)$. Equation (20) is a simple linear ODE and has the solution

$$\mathbb{E}[\sigma_f^2](t) = \sigma_f^2(0)e^{-\mathbb{E}[\tau/KN_\kappa]t}.$$
 (21)

This equation tells us that the expected diversity (variance) of labels in the population decreases exponentially over time. The rate of loss of diversity is $\mathbb{E}[\tau(KN_K)^{-1}]$, and thus populations with a higher turnover rate τ and/ or a lower population size KN_K lose diversity faster. This is because populations with higher τ experience more stochastic events per unit time and are thus more prone to stochastic extinction, while extinction is "easier" in smaller populations because a smaller number of deaths is sufficient to eliminate a label from the population completely. Note that which labels/individuals are lost is entirely random (since all labels are arbitrary), but nevertheless labels tend to be stochastically lost until only a single label remains in the population. Upon rescaling time as $t \rightarrow \tau t$, equation (21) recovers the continuous-time version of the loss of heterozygosity formula for finite populations from population genetics (Ewens 2004, eq. [1.5]; Crow and Kimura 1970, secs. 7.3 and 8.4).

Discussion

The central result of our article is a set of stochastic dynamical equations for changes in trait frequencies in the population, equation (5), that generalizes the replicator equation (or, with mutations, the replicator-mutator equation-eq. [S29]) to finite populations of nonconstant size evolving in continuous time. From this, we derive a generalization of the Price equation (eq. [12]) and Fisher's fundamental theorem (eq. [14]) as well as an equation for changes in population variance of a type-level quantity (eq. [17]). Our equations reveal that demographic stochasticity alone can cause certain types to be more likely to be observed in a population, an effect we term "noiseinduced biasing." Noise-induced biasing can operate through two distinct mechanisms (box 4), one that directly affects the selection term in the replicator equation and another that acts indirectly by affecting the time spent at various states. Several theorists have called for a reformulation of eco-evolutionary dynamics starting from stochastic birth-death processes on the grounds that such a formulation is more fundamental and mechanistic (Metcalf and Pavard 2007; Lambert 2010; Doebeli et al. 2017). Our equations provide a starting point for such a reformulation by deriving some fundamental equations for the ecoevolutionary dynamics of finite, stochastically fluctuating populations.

Finite Population Effects on Eco-Evolutionary Dynamics

Our equations show that noise-induced effects can bias evolutionary outcomes through two major, qualitatively different mechanisms (box 4). The direct mechanism appears in the infinitesimal mean of our SDEs via a noiseinduced term that is inversely proportional to the population size (the second term on the RHS of eqq. [5], [12], and [17]). The direct mechanism has previously been reported in various contexts (Parsons and Quince 2007; Parsons et al. 2010; Wodarz et al. 2017; Parsons et al. 2018; Kuosmanen et al. 2022). Since the terms capturing these effects in equations (5), (12), and (17) have the same mathematical form as the effect of classic natural selection, the direct mechanism has previously been referred to as noise-induced selection (Week et al. 2021). It has also been the object of study in early models of bet hedging in finite populations (Gillespie 1974; Gillespie 1977; Shpak 2005), thus explaining why noiseinduced selection has previously been associated with the Gillespie effect for reduced variance (Parsons and Quince 2007; Parsons et al. 2010, 2018). However, note that the variance that is studied in bet-hedging models is typically variance in offspring numbers (Gillespie 1977). The variance in equation (4b) is not variance in offspring numbers

but instead variance in the (infinitesimal) ecological growth rate dx_i , a quantity that has sometimes been called "demographic variance" (Engen et al. 1998; Shpak 2007). Furthermore, unlike many classic bet-hedging articles, such as Gillespie (1974), in our framework both w_i and τ_i (and thus the mean and variance of the change in population density) are defined from first principles in terms of birth and death rates (eqq. [1], [2]).

In contrast, the indirect mechanism acts through the infinitesimal variance of our SDEs and thus does not appear in the expected change in trait frequency. This mechanism is a subtle effect of frequency-dependent demographic stochasticity and can be present even when the direct mechanism (i.e., noise-induced selection) is weak or absent (box fig. 2B). Mathematically, the indirect mechanism is revealed as a systematic bias in the speed density that causes the system to spend disproportionately more time in certain states (McLeod and Day 2019a, 2019b; see box 4). If a stationary distribution exists, the indirect mechanism will be visible in the stationary distribution but not in the expected trajectory. The indirect mechanism can be thought of as analogous to frequencydependent viscosity; populations tend to accumulate in those configurations that lead to slower changes in population composition, and we are thus more likely to observe the population in those configurations that make the rate of change of the population slower. This observation has previously been referred to as the effect of evolutionary noise on evolutionary dynamics (McLeod and Day 2019a, 2019b).

Our results suggest an intriguing requirement for neutral evolution in finite populations. In models of genetic drift, evolution is said to be neutral if the fixation probability of a type in a population is proportional to the initial frequency alone (Ewens 2004). For populations of nonconstant size, we see that neutrality in this sense is not ensured if the trait in question is neutral with respect to fitness w alone. Instead, neutral evolution also requires all trait variants to have equal turnover rates, failing which evolution will be quasi neutral and favor those types associated with lower turnover rates (Parsons and Quince 2007; Parsons et al. 2010; Kuosmanen et al. 2022). In other words, even in (finite) populations with no differential fitness among traits, there exists a directional evolutionary force that may systematically bias the course of evolution. Furthermore, the indirect mechanism of noise-induced biasing means that we may be more likely to observe the population in states in which certain types are overrepresented due to a biasing of the speed density and, when it exists, the stationary distribution (McLeod and Day 2019a, 2019b). Thus, even if all individuals in the population have equal fitness and equal turnover, types associated with lower V(p) are still favored in the sense that we are more

likely to observe the population in a configuration at which these types are overrepresented (McLeod and Day 2019*a*, 2019*b*) relative to neutral expectations, as defined above. However, it may be noted that the strength of noiseinduced biasing is likely to be small or even negligible unless the population size is sufficiently small and/or all types in the population have close to equal fitness (i.e., natural selection is weak).

In our model, noise-induced selection is particular to fluctuating populations and does not occur in models with fixed population sizes, such as the Wright-Fisher or Moran models (box 3). Taken alongside other theoretical (Lambert 2010; Parsons et al. 2010; Abu Awad and Coron 2018; Kuosmanen et al. 2022; Mazzolini and Grilli 2023) and empirical (Papkou et al. 2016; Chavhan et al. 2019) studies of evolution in fluctuating populations, this last point suggests that models that assume fixed total population size, such as Wright-Fisher and Moran, may miss out on important evolutionary phenomena that are seen only in finite populations of nonconstant size. We explain how our framework incorporates the drift-induced selection from sex chromosome evolution (Veller et al. 2017; Saunders et al. 2018) as well as some previous studies from social evolution (McLeod and Day 2019a) and epidemiology (Parsons et al. 2018; Day et al. 2020) in section S8 of the supplemental PDF. We also explain connections with some other general frameworks of eco-evolutionary dynamics (Rice 2020; Week et al. 2021; Kuosmanen et al. 2022) in section S9 of the supplemental PDF.

Concluding Remarks

A growing body of literature has begun to highlight the surprising and counterintuitive effects of demographic stochasticity in shaping evolutionary outcomes in many ecological scenarios. In this article, we derive from first principles stochastic dynamical equations for eco-evolutionary dynamics that generalize some standard equations of population biology, thus providing a conceptual synthesis of the findings of these previous studies. The terms of the equations we derive lend themselves to simple biological interpretations and recover standard equations of evolutionary theory in the infinite population limit. To the best of our knowledge, the equations we derive in this article are the first to showcase how demographic stochasticity generically alters some standard equations of population biology. The utility of the equations we derive thus lies not (necessarily) in their solutions for specific models but instead in their generality and the fact that their terms help us clearly think about the various evolutionary phenomena operating in biological populations (Queller 2017; Lehtonen 2018; Lion 2018; Luque and Baravalle 2021). The direct and indirect mechanisms of noise-induced biasing

have distinct origins, may operate either independently or together, and may push evolution in different directions (see the example in box 5). It is therefore essential that studies explicitly differentiate between these two mechanisms to identify which noise-induced effects are germane to any particular biological population (box 4). By rederiving some standard equations of population dynamics for finite populations, we provide a framework with which to approach particular finite population systems and systematically determine which evolutionary forces are important from demographic first principles.

Although we neglect environmental stochasticity in our current work, populations that experience both environmental and demographic stochasticity often exhibit surprising and counterintuitive eco-evolutionary dynamics (Gokhale and Hauert 2016; Chavhan et al. 2021). Studying the interplay of noise-induced biasing with environmental stochasticity may thus present a promising avenue for future work. Since both the strength (Hamilton 1966; Mallet et al. 2011; Lehtonen 2020b) and the direction (Chapman et al. 2003; Maklakov and Chapman 2019) of natural selection may vary in populations structured by classes such as age or sex, extending our model to include population structure could also be fruitful. On the empirical side, developing methods to disentangle different demographic stochastic effects from empirical datasets could be another interesting avenue for future work.

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Statement of Authorship

A.S.B.: conceptualization, methodology, formal analysis, investigation, writing—original draft, writing—review and editing, visualization; V.G.: conceptualization, methodology, validation, writing—review and editing, supervision.

Data and Code Availability

Code for running the simulations and reproducing the figures presented in this article is available as a GitHub re-

pository at https://github.com/tee-lab/Bhat_Guttal_2023 _finite_evolution. A citable Zenodo repository with a permanent DOI is available at https://doi.org/10.5281/zenodo .13384640.

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