



## A white noise approach to evolutionary ecology

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### ARTICLE INFO

#### Article history:

Received 3 August 2020

Revised 5 January 2021

Accepted 25 February 2021

Available online 6 March 2021

#### Keywords:

Quantitative genetics

Demographic stochasticity

Noise-induced selection

Measure-valued branching processes

SPDE

### ABSTRACT

Although the evolutionary response to random genetic drift is classically modelled as a sampling process for populations with fixed abundance, the abundances of populations in the wild fluctuate over time. Furthermore, since wild populations exhibit demographic stochasticity and since random genetic drift is in part due to demographic stochasticity, theoretical approaches are needed to understand the role of demographic stochasticity in eco-evolutionary dynamics. Here we close this gap for quantitative characters evolving in continuously reproducing populations by providing a framework to track the stochastic dynamics of abundance density across phenotypic space using stochastic partial differential equations. In the process we develop a set of heuristics to operationalize the powerful, but abstract theory of white noise and diffusion-limits of individual-based models. Applying these heuristics, we obtain stochastic ordinary differential equations that generalize classical expressions of ecological quantitative genetics. In particular, by supplying growth rate and reproductive variance as functions of abundance densities and trait values, these equations track population size, mean trait and additive genetic variance responding to mutation, demographic stochasticity, random genetic drift, deterministic selection and noise-induced selection. We demonstrate the utility of our approach by formulating a model of diffuse coevolution mediated by exploitative competition for a continuum of resources. In addition to trait and abundance distributions, this model predicts interaction networks defined by niche-overlap, competition coefficients, or selection gradients. Using a high-richness approximation, we find linear selection gradients and competition coefficients are uncorrelated, but magnitudes of linear selection gradients and quadratic selection gradients are both positively correlated with competition coefficients. Hence, competing species that strongly affect each other's abundance tend to also impose selection on one another, but the directionality is not predicted. This approach contributes to the development of a synthetic theory of evolutionary ecology by formalizing first principle derivations of stochastic models tracking feedbacks of biological processes and the patterns of diversity they produce.

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### 1. Introduction

Current mathematical approaches to synthesize the dynamics of abundance and evolution in populations have capitalized on the fact that biological fitness plays a key role in determining both sets of dynamics. In particular, while covariance of fitness and genotype is the basis of evolution by natural selection, the mean fitness across all individuals in a population determines the growth, stasis or decline of abundance. Although this connection has been established in the contexts of population genetics (Crow and Kimura, 1970; Roughgarden, 1979), evolutionary game theory (Hofbauer and Sigmund, 1998; Lion, 2018; Nowak, 2006), quantitative genetics (Doebeli, 1996; Lande, 1982; Lion, 2018)

and a unifying framework for these three distinct approaches to evolutionary theory (Champagnat et al., 2006), there remains a gap in incorporating the intrinsically random nature of abundance into the evolution of continuous traits. Specifically, in theoretical quantitative genetics the derivation of a population's response to random genetic drift is derived in discrete time under the assumption of constant effective population size using arguments based on properties of random samples (Lande, 1976). Though this approach conveniently mimics the formalism provided by the Wright-Fisher model of population genetics, real population sizes fluctuate over time. Furthermore, since these fluctuations are themselves stochastic, it seems natural to derive expressions for the evolutionary response to demographic stochasticity and consider how the results relate to characterizations of random genetic drift. This can be done in continuous time for population genetic models without too much technical overhead, assuming a finite

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number of alleles (Gomulkiewicz et al., 2017; Lande et al., 2009; Parsons et al., 2010). However, for populations with a continuum of types, such as a quantitative trait, finding a formal approach to derive the evolutionary response to demographic stochasticity has remained a vexing mathematical challenge. In this paper we close this gap by combining the calculus of white noise with results on rescaled limits of measure-valued branching processes (MVBP) and stochastic partial differential equations (SPDE).

Our goals in this paper are twofold: 1) Our first goal is to establish a novel synthetic framework to study theoretical evolutionary ecology that simultaneously tracks the dynamics of abundance and distribution of a quantitative character in response to selection, mutation and demographic stochasticity. This approach is based on a SPDE driven by space–time white noise which is found as the diffusion-limit of a MVBP. We refer to this SPDE model as the Stochastic Asexual Gaussian allelic model with Abundance dynamics (SAGA). SAGA can be viewed as a generalization of the classical infinitesimal model with Gaussian mutations that accounts for stochastic abundance dynamics. Although SAGA itself tracks the density of abundance across trait-space without explicitly tracking the evolution of phenotypic moments, many investigations of eco-evolutionary dynamics are concerned with the dynamics of population size, mean trait and trait variance. We therefore apply heuristics based on the calculus of space–time white noise to compute stochastic ordinary differential equations (SDE) tracking the dynamics of these three quantities. Investigators then only need to apply specific models of fitness to these SDE to obtain eco-evolutionary models. 2) Our second goal is to communicate some useful properties of space–time white noise, MVBP and SPDE to a wide audience of mathematical evolutionary ecologists. With these goals in mind we will not provide a rigorous treatment of any of these mathematically rich topics. Instead, we introduce a set of heuristics that only require the basic concepts of Riemann integration, partial differentiation and some exposure to Brownian motion and SDE. A concise introduction to SDE and Brownian motion has been provided by Evans (2014).

Since MVBP are abstract mathematical objects and their rigorous study requires elaborate mathematical machinery, the use of MVBP in mainstream theoretical evolutionary ecology has been limited. However, they provide natural models of biological populations by capturing various mechanistic details. In particular, MVBP generalize classical birth–death processes, such as the Galton-Watson process (Kimmel and Axelrod, 2015; Dawson, 1993), to model populations of discrete individuals that carry some value in a given type-space. Selection can then be modelled by associating these values with average reproductive output and mutation can be incorporated using a model that determines the distribution of offspring values given their parental value. For population genetic models the type-space is the discrete set of possible alleles individuals can carry. In quantitative genetic models tracking the evolution of  $d$ -dimensional phenotypes, this type-space is typically set to the Euclidean space  $\mathbb{R}^d$ . By starting with branching processes we can implement mechanistic models of biological fitness that account for the phenotype of the focal individual along with the phenotypes and number of all other individuals in a population or community. By taking a rescaled limit, we can then use these detailed individual-based models to derive population-level models tracking the dynamics of population abundance and phenotypic distribution driven by selection, mutation and demographic stochasticity. Hence, rescaled limits of MVBP provide a means to derive mathematically tractable, yet biologically mechanistic models of eco-evolutionary dynamics.

For univariate traits (i.e.,  $d = 1$ ) Konno and Shiga (1988), Reimers (1989), Li (1998) and Champagnat et al. (2006) have shown that rescaled limits for a large class of MVBP converge to

solutions of SPDE. Although cases in which  $d \geq 1$  can be treated using the so-called martingale problem formulation (Dawson, 1993), the SPDE formulation provides a more intuitive description of the biological processes involved. We therefore focus on the case  $d = 1$  here. This allows us to introduce a concrete set of heuristics for deriving SDE tracking the dynamics of abundance, phenotypic mean and phenotypic variance to a wide audience of mathematical evolutionary ecologists. Following our approach to simplify notation and develop heuristics for calculations, future work can possibly use the martingale formulation to extend the results presented here for  $d > 1$  and even for infinite-dimensional traits (Dawson, 1993; Stinchcombe, 2012). Rigorous introductions to SPDE and rescaled limits of MVBP have been respectively provided by Da Prato and Zabczyk (2014) and Etheridge (2000).

In this paper we begin in Section 2 by introducing the basic framework of our approach. We first outline the essential ideas behind deriving evolutionary dynamics from abundance dynamics using a deterministic partial differential equation (PDE). We then review rescaled limits of MVBP and their associated SPDE. In SM Section 3.3, we introduce an approach to compute SDE tracking the dynamics of abundance, phenotypic mean and phenotypic variance. This approach requires performing calculations with respect to space–time white noise processes and we provide heuristics for doing so in SM Section 2.1. In Section 2.2 of the main text, we list these SDE and discuss their consequences for general phenotypic distributions. We then simplify their expressions by assuming normally distributed phenotypes. For added biological relevance, we then incorporate models of inheritance and development following classical quantitative genetics (treated in SM Section 4). To demonstrate how our framework can be used to formulate a synthetic theory of evolutionary ecology, in Section 3 we derive a model of diffuse coevolution for a set of  $S$  species competing along a resource continuum. The basic approach follows classical niche theory to develop biological fitness as a function of niche parameters and niche locations of other individuals in the community. We then use this model to derive formulas for selection gradients and competition coefficients. Finally, we investigate the relationship between selection gradients and competition coefficients using a high-richness (large  $S$ ) approximation.

## 2. The Framework

At the core of our approach is a model of stochastic abundance dynamics for a structured population in continuous time and phenotypic space. From this stochastic equation we derive a system of SDE for the dynamics of total abundance, mean trait and additive genetic variance of a population. In particular, our approach develops a quantitative genetic theory of evolutionary ecology. A popular alternative to quantitative genetics is the theory of adaptive dynamics (Dieckmann and Law, 1996; Metz et al., 1996). As demonstrated by Page and Nowak (2002) and Champagnat et al. (2006), the canonical equation of adaptive dynamics can be derived from the replicator-mutator equation, which in turn can be derived from models of abundance dynamics, revealing a synthesis of mathematical approaches to theoretical evolutionary ecology. In this section we briefly outline derivations of the replicator-mutator equation and trait dynamics from abundance dynamics in the deterministic case. We then extend these formulas along with related results to the case of random reproductive output (i.e., demographic stochasticity).

### 2.1. Deterministic dynamics

*Finite Number of Types.* We start by considering the dynamics of an asexually reproducing population in a homogeneous

environment. For simplicity, we first assume individuals are haploid and carry one of  $K$  alleles. Each allele corresponds to a growth rate, allowing us to model the abundance dynamics of alleles in continuous-time. We then introduce an analogous model for a quantitative trait. Under these assumptions, the evolution of allele frequencies due to natural selection can be derived. This, and a few related approaches, have been provided by Crow and Kimura (1970). Mutation can be included using a matrix of transition rates. Specifically, denoting  $v_i$  the abundance of individuals with allele  $i$ ,  $m_i$  the growth rate of allele  $i$  (called the Malthusian parameter in Crow and Kimura, 1970),  $\mu_{ji}$  the mutation rate from allele  $j$  to allele  $i$  and assuming selection and mutation are decoupled (Bürger, 2000), we have

$$\frac{dv_i}{dt} = m_i v_i + \sum_{j=1}^K (v_j \mu_{ji} - v_i \mu_{ij}). \quad (1)$$

Starting from this model, we get the total abundance of the population as  $N(t) = \sum_i v_i(t)$ , the frequency of allele  $i$  as  $p_i(t) = v_i(t)/N(t)$  and the mean Malthusian fitness of the population as  $\bar{m}(t) = \sum_i m_i p_i(t)$ . Note we have used the abbreviation  $\sum_i = \sum_{i=1}^K$  to simplify inline notation. Observing  $\sum_{ij} \mu_{ji} v_j(t) = \sum_{ij} \mu_{ij} v_i(t)$ , we use linearity of differentiation to derive the dynamics of abundance as

$$\frac{dN}{dt} = \sum_{i=1}^K m_i v_i + \sum_{ij=1}^K (v_j \mu_{ji} - v_i \mu_{ij}) = \bar{m}N. \quad (2)$$

To derive the dynamics of the allele frequencies  $p_1(t), \dots, p_K(t)$ , we use the quotient rule of elementary calculus to find

$$\frac{dp_i}{dt} = (m_i - \bar{m})p_i + \sum_{j=1}^K (p_j \mu_{ji} - p_i \mu_{ij}). \quad (3)$$

Two important observations of these equations include: (i) The time-dependent mean Malthusian fitness  $\bar{m}(t)$  is equivalent to the population growth rate and thus determines the abundance dynamics of the entire population. (ii) Selection for allele  $i$  occurs when  $m_i > \bar{m}$  and selection against allele  $i$  occurs when  $m_i < \bar{m}$ . Hence, as mentioned in the introduction, fitness plays a key role in determining both abundance dynamics and evolution.

Eq. (3) is known in the field of evolutionary game theory as a replicator-mutator equation (Nowak, 2006). Instead of being explicitly focused on alleles, the replicator-mutator equation describes the fluctuations of relative abundances of various types in a population in terms of replication and annihilation rates of each type and hence can be used to model dynamical systems outside of evolutionary biology (Nowak, 2006).

*Continuum of Types.* Inspired by Eqs. (1)–(3), we derive an analog of the replicator-mutator equation for a continuum of types (that is, for a quantitative trait). In particular, we model a continuously reproducing population with trait values  $x \in \mathbb{R}$  and an abundance density  $v(x, t)$  that represents the amount of individuals in the population with trait value  $x$  at time  $t$ . Hence, the abundance density satisfies  $N(t) = \int v(x, t) dx$  and  $p(x, t) = v(x, t)/N(t)$  is the relative density of trait  $x$  which we also refer to as the phenotypic distribution. The mean trait and trait variance are then given respectively by  $\bar{x}(t) = \int xp(x, t) dx$  and  $\sigma^2(t) = \int (\bar{x}(t) - x)^2 p(x, t) dx$ . Note we have used the abbreviation  $\int = \int_{-\infty}^{+\infty}$  to simplify inline notation.

In analogy with the growth rates  $m_i$  for Eq. (1) we write  $m(v, x)$  as the growth rate associated with trait value  $x$  which depends on the abundance density  $v$ . We assume mutation is captured by diffusion with coefficient  $\mu/2$ . Hence, we model the demographic dynamics of a population and the dynamics of a quantitative character simultaneously by the PDE

$$\frac{\partial}{\partial t} v(x, t) = m(v, x)v(x, t) + \frac{\mu}{2} \frac{\partial^2}{\partial x^2} v(x, t). \quad (4)$$

Eq. (4) qualifies both as a semilinear evolution equation and also a scalar reaction–diffusion equation. Although the general theory of such equations is quite rich, it is also quite difficult (Evans, 2010; Zheng, 2004). Hence, to stay within the realms of technical tractability and biological plausibility, we require a set of mathematical assumptions which we list in SM Section 1.1. These assumptions guarantee solutions to Eq. (4) exist for all finite time  $t > 0$  and, hence, let us investigate the ecological and evolutionary dynamics of biological populations.

Eq. (4) can be seen as an analog of Eq. (1) for a continuum of types. By assuming mutation acts via diffusion, the effect of mutation causes the abundance density  $v(x, t)$  to flatten out across phenotypic space. In fact, if the growth rate is constant across  $x$ , then this model of mutation will cause  $v(x, t)$  to converge to a flat line in  $x$  as  $t \rightarrow \infty$ . Interpreting the trait value  $x$  as location in geographic space, Eq. (4) becomes a well-studied model of spatially distributed population dynamics (Cantrell and Cosner, 2004).

Although clearly an idealized representation of biological reality, this model is sufficiently general to capture a large class of dynamics including density dependent growth and frequency dependent selection. As an example, logistic growth combined with stabilizing selection can be captured using the growth rate

$$m(v, x) = R - \frac{a}{2}(\theta - x)^2 - c \int_{-\infty}^{+\infty} v(y, t) dy = R - \frac{a}{2}(\theta - x)^2 - cN(t), \quad (5)$$

where  $a > 0$  the is strength of abiotic stabilizing selection around the phenotypic optimum  $\theta$ ,  $c > 0$  is the strength of intraspecific competition and we refer to  $R$  as the innate growth rate (see Section 3.3 below). In the language of population ecology,  $r = R - a(\theta - x)^2/2$  is the intrinsic growth rate of the population (Chesson, 2000). This model assumes competitive interactions cause the same reduction in fitness regardless of trait value.

The growth rate in equation (5) has a few convenient properties. First, the effect of competition induces a local carrying capacity on the population, leading to a finite equilibrium abundance over bounded subsets of phenotypic (or geographic) space. Second, abiotic selection prevents the abundance density from diffusing too far from the abiotic optimum. In particular, when  $R > \sqrt{a\mu}/2 > 0$ ,  $\bar{x}(0)$  is finite,  $\sigma^2(0)$  is non-negative and finite and  $N(0)$  is positive and finite, this leads to a locally asymptotically stable equilibrium given by

$$\hat{N} = \frac{1}{c} \left( R - \frac{1}{2} \sqrt{a\mu} \right), \quad (6a)$$

$$\hat{x} = \theta, \quad (6b)$$

$$\hat{\sigma}^2 = \sqrt{\frac{\mu}{a}}. \quad (6c)$$

We demonstrate this result in SM Section 1.2. The equilibrium phenotypic variance predicted by this model coincides with a classic quantitative genetic result predicted by modelling the combined effects of Gaussian stabilizing selection and the Gaussian allelic model of mutation (Bürger, 2000; Johnson and Barton, 2005; Lande, 1975; Walsh and Lynch, 2018).

To derive a replicator-mutator equation from Eq. (4), we employ integration-by-parts and the chain rule from calculus. In particular, assuming  $N(t) < +\infty$  for all  $t > 0$ , we can pass the time derivative into the integral to obtain  $\frac{d}{dt} N = \int \frac{\partial}{\partial t} v(x, t) dx$ . The partial derivative  $\frac{\partial}{\partial t} v(x, t)$  can be replaced by the right-hand-side of equation (4). The resulting spatial derivative representing mutation is removed

using integration-by-parts. The dynamics of  $p(x, t)$  can then be obtained by applying the chain rule to  $\frac{\partial}{\partial t} p(x, t) = \frac{\partial}{\partial t} [v(x, t)/N(t)]$ . Writing

$$\bar{m}(t) = \int_{-\infty}^{+\infty} m(v, x) p(x, t) dx \tag{7}$$

for the population growth rate, we find

$$\frac{dN}{dt} = \bar{m}N, \tag{8a}$$

$$\frac{\partial}{\partial t} p(x, t) = p(x, t)(m(v, x) - \bar{m}(t)) + \frac{\mu}{2} \frac{\partial^2}{\partial x^2} p(x, t). \tag{8b}$$

Eq. (8b) closely resembles Kimura’s continuum-of-alleles model (Kimura, 1965; Bürger, 2000). The primary difference being that our model utilizes diffusion instead of convolution with an arbitrary mutation kernel. However, our model of mutation can be derived as an approximation to Kimura’s model, which has been referred to as the Gaussian allelic approximation in reference to the distribution of mutational effects on trait values at each locus in a genome (Lande, 1975; Bürger, 1986, 2000; Johnson and Barton, 2005), the infinitesimal genetics approximation in reference to modelling continuous traits as being encoded by an infinite number of loci each having infinitesimal effect (Fisher, 1919; Barton et al., 2017) and the Gaussian descendants approximation in reference to offspring trait values being normally distributed around their parental values (Bulmer, 1971; Turelli, 2017).

To distinguish this model from previous models of phenotypic evolution we refer to PDE (4) from which (8b) was derived as the Deterministic Asexual Gaussian allelic model with Abundance dynamics (abbreviated DAGA). Later, we will extend this model to include the effects of demographic stochasticity, which we refer to as the Stochastic Asexual Gaussian allelic model with Abundance dynamics (abbreviated SAGA).

*Evolutionary Dynamics.* We now apply DAGA to derive the dynamics of mean trait  $\bar{x}$  and phenotypic variance  $\sigma^2$ . Both of these dynamics are expressible in terms of covariances with fitness. For an abundance distribution  $v(x)$  and associated phenotypic distribution  $p(x)$ , the covariance of fitness and phenotype across the population is defined by

$$\text{Cov}(m(v, x), x) = \int_{-\infty}^{+\infty} (m(v, x) - \bar{m})(x - \bar{x}) p(x) dx. \tag{9}$$

Assuming  $|\bar{x}(t)| < +\infty$  for all  $t > 0$ , we can borrow techniques used to derive  $N(t)$  to find the dynamics of the mean trait  $\bar{x}$  as

$$\frac{d\bar{x}}{dt} = \text{Cov}(m(v, x), x). \tag{10}$$

Eq. (10) is a continuous time analog of the well known Robertson-Price equation without transmission bias (Robertson, 1966; Price, 1970; Frank, 2012; Queller, 2017; Lion, 2018). Whether or not the covariance of fitness and phenotype creates change in  $\bar{x}$  to maximize mean fitness  $\bar{m}$  depends on the degree to which selection is frequency dependent (Lande, 1976). Since this change is driven by a covariance with respect to phenotypic diversity, the response in mean trait to selection is mediated by the phenotypic variance. In particular, since this model ignores the complexity of genetic architecture, when  $\sigma^2 = 0$ ,  $\bar{x}$  will not respond to selection. However, when epistasis and linkage disequilibrium are present,  $\bar{x}$  may evolve even when  $\sigma^2 = 0$  and  $\text{Cov}(m, x) = 0$  (Bulmer, 1980; Gimelfarb, 1989; Bürger, 2000).

From a statistical perspective, if we think of  $(x - \bar{x})^2$  as a square error, we can calculate the covariance of fitness and square error via

$$\text{Cov}(m(v, x), (x - \bar{x})^2) = \int_{-\infty}^{+\infty} (m(v, x) - \bar{m})((x - \bar{x})^2 - \sigma^2) p(x) dx. \tag{11}$$

Then, following the approach taken to calculate the evolution of  $\bar{x}$ , we obtain the dynamics of phenotypic variation as

$$\frac{d\sigma^2}{dt} = \mu + \text{Cov}(m(v, x), (x - \bar{x})^2). \tag{12}$$

In the absence of mutation, Eq. (12) mirrors the result derived by Lion (2018) for discrete phenotypes. In analogy to the dynamics of the mean trait, we see that the response in  $\sigma^2$  to selection can be expressed as a covariance of fitness and square error. Just as for the evolution of  $\bar{x}$ , this covariance also creates change in  $\sigma^2$  that can either increase or decrease mean fitness  $\bar{m}$ , depending on whether or not selection is frequency dependent. The effect of selection on phenotypic variance can be positive or negative depending on whether selection is stabilizing or disruptive.

### 2.2. Extending DAGA to demographic stochasticity

In SM Section 3.4, we extend these results to include the effects of demographic stochasticity. The idea is to add an appropriate noise term to DAGA. Hence, we wish to study stochastic partial differential equations (SPDE) that provide natural generalizations of DAGA. Fortunately, rigorous first principle derivations of such SPDE have been provided by Li (1998) and Champagnat et al. (2006). The noise terms driving these SPDE are space-time white noise processes, denoted  $\dot{W}(x, t)$ , which are random processes uncorrelated in both space and time. In SM Section 2.1, we provide a set of heuristics for performing calculations with respect to space-time white noise including methods to derive SDE from SPDE in analogy to our derivations of ordinary differential equations (ODE) from PDE above. Since our aim is to present this material to a wide audience of mathematical evolutionary ecologists, our treatment of space-time white noise and stochastic integration deviates from standard definitions to remove the need for a detailed technical treatment. However, in SM Section 2.2, we show our heuristics are consistent with the rigorous infinite-dimensional stochastic calculus presented by Da Prato and Zabczyk (2014). Using our simplified approach, the reader will only need some elementary probability and an intuitive understanding of SDE, including Brownian motion, in addition to the notions of Riemann integration and partial differentiation already employed.

### 2.3. From branching processes to SPDE

To understand how SPDE can be derived from biological first principles and how population-level models can be derived from individual-based models, we provide a brief informal discussion of measure-valued branching processes (MVBP) (which serve as individual-based models) and their diffusion-limits (which serve as population-level models). In particular, denoting  $\delta_x$  the unit-mass representing an individual with trait value  $x$ , a population consisting of individuals with trait values  $x_1, \dots, x_{n(t)}$  can be represented by

$$X_t = \sum_{i=1}^{n(t)} \delta_{x_i}. \tag{13}$$

We assume the individuals are fixed in trait-space throughout their lifetime. Hence, in between branching events  $x_1, \dots, x_{n(t)}$  are constant. We also assume an individual born with trait value  $x$  at time  $t$  is assigned an exponentially distributed lifetime with rate  $\rho(X_t, x) > 0$ . We refer to  $\rho(X_t, x)$  as the branching rate and assume continuity with respect to  $X_t$  (in the weak topology of finite

measures, see Etheridge, 2000) and twice differentiability with respect to  $x$ . For simplicity, we assume the species is semelparous so that parents are replaced with a random number of offspring at branching events. Hence, population size  $n(t)$  changes at branching events. When an individual is born it is assigned probabilities of producing different numbers of offspring. In particular, an individual born at time  $t$  with trait value  $x$  will be given the probability  $f_j(X_t, x)$  of producing  $j$  offspring. However, offspring are not produced until the individual branches. This assumption is made for the sake of notational simplicity since if, for example, probabilities of offspring numbers were assigned at branching we would need to track when the individual was born and when it branches. Since either choice leads to the same diffusion-limit, we continue without loss of generality. Thus, an individual with trait  $x$  born at time  $t$  will have expectation and variance in reproductive output given respectively by

$$w(X_t, x) = \sum_{j=0}^{\infty} j f_j(X_t, x), \tag{14a}$$

$$v^2(X_t, x) = \sum_{j=0}^{\infty} (j - w(X_t, x))^2 f_j(X_t, x). \tag{14b}$$

We assume both  $w(X_t, x)$  and  $v^2(X_t, x)$  are continuous in  $X_t$  and twice differentiable in  $x$ .

There is often an intimate relationship between  $w(X_t, x)$  and  $v^2(X_t, x)$  and this observation is particularly important for understanding the relationship between deterministic selection and noise-induced selection. For example, if for each fixed  $X_t$  and  $x$  the number of offspring follow a Poisson distribution, then  $v^2(X_t, x) = w(X_t, x)$ . Alternatively, researchers may wish to work with birth and death rates. In this case we set  $f_0(X_t, x) + f_2(X_t, x) = 1$  so that the only possible offspring numbers are zero, corresponding to death, and two, corresponding to birth. Then an individual born at time  $t$  has birth and death rates given respectively by

$$b(X_t, x) = \rho(X_t, x) f_2(X_t, x), \tag{15a}$$

$$d(X_t, x) = \rho(X_t, x) f_0(X_t, x). \tag{15b}$$

Furthermore, under the birth–death approach we compute

$$v^2(X_t, x) = 2w(X_t, x) - w^2(X_t, x). \tag{16}$$

Other examples can be easily calculated, but we restrict our attention to these two distributions of offspring numbers for the sake of simplicity. We refer to the Poisson case as the Poisson model of demographic stochasticity and the birth–death case as the birth–death model of demographic stochasticity.

We assume offspring trait values are normally distributed around parental trait values with variance  $\mu$  (i.e., the Gaussian allelic model). This assumption implies the Gaussian descendants approximation coined by Turelli (2017).

To derive a population-level model from this individual-based model, we start with the initial population  $X_0$  and increase the population size to  $kn(0)$  for some positive integer  $k$ . We also rescale individual contribution to abundance by  $N_0/kn(0)$  for some positive real number  $N_0$ . In particular, this is done by replacing  $\delta_{x_i}$  in expression (13) with  $N_0 \delta_{x_i}/kn(0)$ . Hence, in the limit  $k \rightarrow \infty$  the total initial abundance remains  $N_0$  even though the population of discrete individuals becomes replaced by a set of infinitesimal individuals. We write  $X_t^{(k)}$  as the  $k$ -th stage of rescaling of the population process  $X_t$  and, when it exists,  $\mathcal{X}_t = \lim_{k \rightarrow \infty} X_t^{(k)}$  as the diffusion limit. The branching rate is rescaled by  $\rho(X_t, x) \rightarrow k\rho(X_t^{(k)}, x)$  so that branching of the infinitesimal individuals occurs instantaneously in the limit  $k \rightarrow \infty$ . We also rescale mutation by  $\mu \rightarrow \mu/k$  and expected reproductive output by  $w(X_t, x) \rightarrow w^{1/k}(X_t^{(k)}, x)$ . This last component of our rescaling is the key step our framework utilizes in computing population-level models from individual-based models. In particular, assuming  $w(X_t, x)$  is bounded above in both  $X_t$  and  $x$ , Méléard and Roelly (1992, 1993) have shown the continuous time growth rate associated with trait value  $x$  at time  $t$  can be calculated as

$$m(\mathcal{X}_t, x) = \rho(\mathcal{X}_t, x) \lim_{k \rightarrow \infty} k \left( w^{1/k}(X_t^{(k)}, x) - 1 \right). \tag{17}$$

Assuming the either the Poisson or birth–death models of demographic stochasticity, this rescaling implies the variance component of reproduction in the diffusion-limit becomes  $V(\mathcal{X}_t, x) = \rho(\mathcal{X}_t, x)$ , which we refer to as the reproductive variance. For concreteness, both of these calculations are performed for the initial conditions  $X_0^{(k)}$  following the approach to rescaling outlined above.

We note that, just as for the individual-based model, deterministic and noise-induced selection in the diffusion-limit are interwoven via the branching rate  $\rho(\mathcal{X}_t, x)$ . Furthermore, under the birth–death model of demographic stochasticity we have

$$m(\mathcal{X}_t, x) = b(\mathcal{X}_t, x) - d(\mathcal{X}_t, x), \tag{18a}$$

$$V(\mathcal{X}_t, x) = b(\mathcal{X}_t, x) + d(\mathcal{X}_t, x). \tag{18b}$$

For details on these calculations, see SM Section 3.1. In SM Section 3.2 we describe an approach to simulating the rescaled processes  $X_t^{(k)}$  and illustrate their dynamics for  $k = 1, 5$  and  $10$ .

In the diffusion-limit  $\lim_{k \rightarrow \infty} X_t^{(k)}$  the particle picture of the individual-based model is replaced by a mass  $\mathcal{X}_t$  distributed across  $\mathbb{R}$ . Given appropriate conditions on  $w(X_t, x)$  and  $v^2(X_t, x)$  (Konno and Shiga, 1988; Reimers, 1989; Li, 1998), the mass  $\mathcal{X}_t$  can be described by a density  $v(x, t)$  continuous in both  $x$  and  $t$  such that

$$\mathcal{X}_t(D) = \int_D v(x, t) dx, \tag{19}$$

for subsets  $D \subset \mathbb{R}$ . When the diffusion-limit  $\mathcal{X}_t$  exists and admits a density  $v(x, t)$ , we write  $m(v, x)$  and  $V(v, x)$  in place of  $m(\mathcal{X}_t, x)$  and  $V(\mathcal{X}_t, x)$ .

In general, diffusion-limits of individual-based models return so-called superprocesses which track the evolution of abundance and phenotypic (or geographic) distribution (Etheridge, 2000). Although the superprocess approach can handle very general assumptions including multivariate phenotypes and non-Gaussian mutation, its technical prerequisites are far beyond the scope of this paper. Fortunately, under our above assumptions, Li (1998) formally proved the density  $v(x, t)$  can be described by the following SPDE which generalizes DAGA,

$$\begin{aligned} \frac{\partial}{\partial t} v(x, t) &= m(v, x)v(x, t) + \frac{\mu}{2} \frac{\partial^2}{\partial x^2} v(x, t) \\ &+ \sqrt{V(v, x)v(x, t)} \dot{W}(x, t). \end{aligned} \tag{20}$$

In particular, we can apply the white noise heuristics developed in SM Section 2.1 to this SPDE to derive SDE tracking the total abundance, mean trait and trait variance. We refer to this SPDE as the Stochastic Asexual Gaussian allelic model with Abundance dynamics (SAGA). Unfortunately, one of the assumptions used to show  $v(x, t)$  satisfies SAGA is boundedness of the growth rate  $m(v, x)$  above and below across all possible combinations of  $v(x, t)$  and  $x$ . However, classical models of resource competition use growth rates that decrease towards  $-\infty$  as total abundance diverges towards  $+\infty$ . Thus, solutions to SAGA may not exist for all growth rates of interest. Hence, we proceed informally

following calculations inspired by SAGA. Future work is needed to determine the general conditions on  $m(v, x)$  for which SAGA admits a solution. Alternatively, one may be able to take the superprocess approach to justify our calculations. For examples of superprocess models of competition, see Dawson (1978), Etheridge (2004) and Evans and Perkins (1994).

#### 2.4. From SPDE to SDE

The simplicity of SAGA allows us to use the white noise heuristics developed in SM Section 2.1 to compute a set of SDE that generalize Eqs. (8a), (10) and (12) to include the effects of demographic stochasticity (see SM Sections 3.3 and 3.4). In particular, we find

$$\frac{dN}{dt} = \bar{m}N + \sqrt{\bar{V}N} \frac{dW_N}{dt}, \quad (21a)$$

$$\begin{aligned} \frac{d\bar{x}}{dt} &= \text{Cov}(m, x) - \frac{1}{N} \text{Cov}(V, x) \\ &+ \sqrt{\frac{1}{N} (\text{Cov}(V, (x - \bar{x})^2) + \bar{V}\sigma^2)} \frac{dW_{\bar{x}}}{dt}, \end{aligned} \quad (21b)$$

$$\begin{aligned} \frac{d\sigma^2}{dt} &= \mu + \text{Cov}(m, (x - \bar{x})^2) \\ &- \frac{1}{N} (2\text{Cov}(V, (x - \bar{x})^2) + \bar{V}\sigma^2) \\ &+ \sqrt{\frac{1}{N} [\text{Cov}(V, [(x - \bar{x})^2 - \sigma^2]^2) + \bar{V}((x - \bar{x})^4 - \sigma^4)]} \frac{dW_{\sigma^2}}{dt}, \end{aligned} \quad (21c)$$

where  $W_N$ ,  $W_{\bar{x}}$  and  $W_{\sigma^2}$  are standard Brownian motions and barred expressions such as  $\overline{(x - \bar{x})^4}$  are averaged quantities with respect to the phenotypic distribution  $p(x, t)$ . Intuitively, one can interpret Eqs. (21) as if they are ordinary differential equations, but this is not technically rigorous since Brownian motion is nowhere differentiable with respect to time. In SM Section 3.5 we show that when  $V(v, x)$  does not depend on  $x$ ,  $W_N$  is independent of both  $W_{\bar{x}}$  and  $W_{\sigma^2}$ , but  $W_{\bar{x}}$  and  $W_{\sigma^2}$  may covary depending on the shape of the phenotypic distribution  $p(x, t)$ . However, when the phenotypic distribution is Gaussian and  $V(v, x)$  does not depend on  $x$ ,  $W_{\bar{x}}$  and  $W_{\sigma^2}$  will also be independent.

Many well known results follow directly from expressions (21). Firstly, assuming no variance in reproductive output so that  $V = 0$  recovers the deterministic dynamics derived in Section 2.1. Alternatively, one can take  $N \rightarrow \infty$  to recover the deterministic dynamics for  $\bar{x}$  and  $\sigma^2$ , which also shows the effect of demographic stochasticity on evolutionary dynamics diminish when population size becomes sufficiently large. Characteristically, we find the effect of demographic stochasticity on per-capita growth rate diminishes with increased population size. To see this, divide each side of equation (21) by  $N$ . Furthermore, one can apply Itô's formula to  $\ln N$  to find increased abundance leads to smoother log-scale abundance dynamics. From the third term in the deterministic component of expression (21c) we see also the characteristic effect of random genetic drift eroding heritable variation when  $V(v, x)$  is independent of trait value. However, this expression also shows when the covariance of reproductive variance and  $(x - \bar{x})^2$  is sufficiently negative, the component of random genetic drift due to demographic stochasticity will actually increase heritable variation. Finally, the second term of equation (21b) and third term of (21c) show that adaptation is not only mediated by a covariance between expected reproductive output and trait values, but also from a covariance between the variance around this expectation and trait values. Hence, this stochastic extension allows the mod-

elling of noise-induced selection. We include this here only for the sake of completeness. In particular, our model of diffuse coevolution below assumes constant reproductive variance across trait values and abundance densities within each species.

These expressions can be used to investigate the dynamics of the mean and variance for a very general set of phenotypic distributions. However, conditions for the existence of solutions to (21) are at least as restrictive as those for SAGA. Since, as mentioned above, the most general form of these conditions are not known, we do not formally show existence of solutions to (21). However, our results for DAGA and theorem 2.3 of Evans and Perkins (1994) suggest that if  $m(v, x)$  and  $V(v, x)$  are bounded above, then  $N(t)$ ,  $\bar{x}(t)$  and  $\sigma^2(t)$  should remain finite for finite time.

In the next subsection we sidestep the issue of existence by assuming normally distributed trait values, known as the Gaussian population assumption (Turelli, 2017). In particular, assuming normally distributed trait values implies the existence of a mean  $\bar{x}$  and variance  $\sigma^2$ . This assumption also significantly simplifies the expressions of equations (21), transforming them into powerful tools for computing eco-evolutionary models. Hence, although the Gaussian population assumption is very restrictive as a model of phenotypic diversity and, except for very special cases of growth rates, is not formally justified, its exceedingly convenient properties make it an important initial approximation.

#### 2.5. Particular results assuming a Gaussian phenotypic distribution

By assuming normally distributed trait values, expressions (21) transform into efficient tools for deriving the dynamics of populations given fitness functions  $m(v, x)$ ,  $V(v, x)$ . Gaussian phenotypic distributions can be formally obtained through Gaussian, exponential or weak selection approximations together with a simplified model of mutation, genotype-phenotype mapping and asexual reproduction or random mating (Bürger, 2000; Lande, 1980; Turelli, 2017, 1986, 1984). Hence, given appropriate assumptions on selection, mutation and reproduction, the abundance density  $v(x, t)$  can be approximated as a Gaussian curve in  $x$ . In SM Section 5.5, we briefly explore the consequences of relaxing the Gaussian population assumption in the context of resource competition. In general, we find the Gaussian population assumption provides a reasonable approximation over short time periods. However, over longer time periods populations restricted to normally distributed trait values exhibited trait variances orders of magnitude lower in comparison to letting the trait distribution evolve freely. Allowing for these restrictions, we assume

$$v(x, t) = \frac{N(t)}{\sqrt{2\pi\sigma^2(t)}} \exp\left(-\frac{(x - \bar{x}(t))^2}{2\sigma^2(t)}\right). \quad (22)$$

Under this assumption, covariances with fitness can be written in terms of fitness gradients (see SM Section 3.6). In particular, setting  $\partial_x = \frac{\partial}{\partial x}$  and  $\partial_{\sigma^2} = \frac{\partial}{\partial \sigma^2}$ , trait dynamics under the Gaussian population assumption can then be rewritten as

$$\begin{aligned} \frac{d\bar{x}}{dt} &= \sigma^2 (\partial_{\bar{x}} \bar{m} - \overline{\partial_{\bar{x}} \bar{m}} + \overline{\partial_{\bar{x}} V} - \partial_{\bar{x}} \bar{V}) \\ &+ \sqrt{\frac{\sigma^2}{N} [2\sigma^2 (\partial_{\sigma^2} \bar{V} - \overline{\partial_{\sigma^2} \bar{V}}) + \bar{V}]} \frac{dW_{\bar{x}}}{dt}, \end{aligned} \quad (23a)$$

$$\begin{aligned} \frac{d\sigma^2}{dt} &= \mu + 2\sigma^4 (\partial_{\sigma^2} \bar{m} - \overline{\partial_{\sigma^2} \bar{m}}) - \frac{\sigma^2}{N} [4\sigma^2 (\partial_{\sigma^2} \bar{V} - \overline{\partial_{\sigma^2} \bar{V}}) + \bar{V}] \\ &+ \sigma^2 \sqrt{\frac{2}{N} [2\sigma^4 (\partial_{\sigma^2}^2 \bar{V} - 2\partial_{\sigma^2} \overline{\partial_{\sigma^2} \bar{V}} + \overline{\partial_{\sigma^2}^2 \bar{V}}) + 4\sigma^2 (\partial_{\sigma^2} \bar{V} - \overline{\partial_{\sigma^2} \bar{V}}) + \bar{V}]} \frac{dW_{\sigma^2}}{dt}. \end{aligned} \quad (23b)$$

From Section 2.3 we know that when selection is due to variation in expected offspring numbers and not variation in rates of death and reproduction, the deterministic and stochastic components of fitness are decoupled and the effects of noise-induced selection disappear. In particular, this case implies  $\partial_x V = \partial_x \bar{V} = 0$  and  $\partial_{\sigma^2} V = \partial_{\sigma^2} \bar{V} = 0$ , greatly simplifying the above expressions. Equations (23) allow us to derive the response in trait mean and variance by taking derivatives of fitness, a much more straightforward operation than calculating a covariance for general phenotypic distributions. Note that in the above expressions, the partial derivatives of  $\bar{m}$  and  $\bar{V}$  represent frequency independent selection and the averaged partial derivatives of  $m$  and  $V$  represent frequency dependent selection. This relationship has already been pointed out by Lande (1976) for the evolution of the mean trait in discrete time without noise-induced selection, but here we see an analogous relationship holds in continuous time with noise-induced selection and also for the evolution of trait variance. In particular, focusing on mean trait evolution, when reproductive variance is frequency independent so that  $\partial_x \bar{V} = 0$ , we see noise-induced selection selects for trait values that minimize  $V(v, x)$ . Hence, in general there may be conflicts between deterministic selection and noise-induced selection. Indeed, previous work has shown evolutionary responses to noise-induced selection can reverse the expectations of deterministic theory (Parsons et al., 2010; Constable et al., 2016).

In SM Section 4 we generalize this result to the case when traits are imperfectly inherited. In this case, the phenotypic variance  $\sigma^2$  is replaced by a genetic variance  $G$ . This genetic variance represents the component of  $\sigma^2$  explained by additive effects among genetic loci encoding for the focal phenotype (Bulmer, 1971; Roughgarden, 1979; Walsh and Lynch, 2018). It is therefore fitting that  $G$  is referred to as the additive genetic variance. Following classical quantitative genetic assumptions we find

$$\frac{dx}{dt} = G(\partial_x \bar{m} - \overline{\partial_x m} + \partial_x \bar{V} - \overline{\partial_x V}) + \sqrt{\frac{G}{N} [2G(\partial_c \bar{V} - \overline{\partial_c V}) + \bar{V}]} \frac{dW_{\bar{x}}}{dt}, \quad (24a)$$

$$\frac{dG}{dt} = \mu + 2G^2(\partial_c \bar{m} - \overline{\partial_c m}) - \frac{G}{N} [4G(\partial_c \bar{V} - \overline{\partial_c V}) + \bar{V}] + G\sqrt{\frac{2}{N} [2G^2(\partial_c^2 \bar{V} - 2\partial_c \overline{\partial_c V} + \overline{\partial_c^2 V}) + 4G(\partial_c \bar{V} - \overline{\partial_c V}) + \bar{V}]} \frac{dW_G}{dt}. \quad (24b)$$

From expressions (24) we see that, under our simple treatment of inheritance, focusing on additive genetic variance  $G$  instead of the variance in expressed traits  $\sigma^2$  makes no structural changes to the basic equations describing the dynamics of populations. Instead we see the role played by the variance of expressed traits  $\sigma^2$  is now being played by  $G$ , except for the effects on growth rate  $m(v, x)$  since fitness here is determined by expressed traits. Under our approach, the two variances are related by  $\sigma^2 = G + E$ , where  $E$  is the environmental variance (Walsh and Lynch, 2018). As a special case of our framework, we can further assume that  $G$  and  $N$  are constant across time and set  $V(v, x) \equiv 1$  to obtain a continuous time analog of the random genetic drift model introduced by Lande (1976). In the next section, we make use of the above expressions to develop a model of diffuse coevolution in a guild of  $S$  species competing along a resource continuum.

### 3. A model of diffuse coevolution

In this section we demonstrate the use of our framework by developing a model of diffuse coevolution across a guild of  $S$  spe-

cies whose interactions are mediated by resource competition along a single niche axis. Because our approach treats abundance dynamics and evolutionary dynamics simultaneously, this model allows us to investigate the relationship between selection gradients and competition coefficients, which we carry out in Section 3.3. For the sake of mathematical tractability, we assume Gaussian populations so that individual niche locations are normally distributed within each species.

#### 3.1. Formulation

General formulas for the dynamics of phenotypic distributions and abundances have been derived above. Thus, the only task remaining is the formulation of growth rates and reproductive variances as functions of trait values. For the sake of simplicity, we ignore noise-induced selection by assuming constant reproductive variances  $V(v, x) \equiv V > 0$  and focus our attention on developing growth rates as functions of abundance densities and trait values. Our approach mirrors closely the theory developed by MacArthur and Levins (1967), Levins (1968) and MacArthur (1972, 1970, 1969). The most significant difference, aside from allowing evolution to occur, is our treatment of resource availability. In particular, we assume resources are replenished rapidly enough to ignore the dynamics of their availability. In SM Section 5 we provide motivation for this population-level model from an individual-based model.

For species  $i$  we inherit the above notation for trait value, distribution, average, variance, abundance, etc., except with an  $i$  in the subscript. Real world examples of niche axes include the size of seeds consumed by competing finch species and the date of activity in a season for pollinators competing for floral resources. For mathematical convenience, we model the axis of resources by the real line  $\mathbb{R}$ . The trait value  $x$  will denote the location along the niche axis (i.e.,  $x \in \mathbb{R}$ ),  $\bar{x}_i$  the mean niche location of species  $i$  and  $G_i$  the additive genetic variance of niche locations for species  $i$ .

*The Fitness Function.* Assuming the effects due to competitive interactions and abiotic stabilizing selection on the expected reproductive output of individuals accumulate multiplicatively, we find in SM Section 5 an expression for the expected reproductive output (i.e., absolute fitness) of individuals in each species as functions of their niche location along with the state of the entire community. Applying equation (17), we arrive at an expression for the growth rate associated with niche location  $x$  in species  $i$  as a function of  $x$  and the state of the entire community. Following this, we assume normally distributed niche locations within each species to find the following explicit expression of the growth rate associated with trait value  $x$  for species  $i$ :

$$m_i(v, x) = R_i - \frac{a_i}{2} (\theta_i - x)^2 - \sum_{j=1}^S c_{ij} N_j(t) U_i U_j \sqrt{\frac{\bar{b}_{ij}(t)}{2\pi}} e^{-\frac{b_{ij}(t)}{2} (x - \bar{x}_j(t))^2}, \quad (25)$$

where now growth rate depends on  $\mathbf{v} = (v_1, \dots, v_S)$ , the  $S$ -tuple of trait distributions describing the community of competing species. We refer to  $R_i$  as the innate growth rate of species  $i$  to distinguish it from the classical intrinsic growth rate  $r_i$  considered in the field of population ecology. The parameter  $a_i$  is the strength of abiotic stabilizing selection for species  $i$  around the optimal resource  $\theta_i$  and  $c_{ij}$  is the impact of resource competition with species  $j$  on species  $i$ . We denote the total niche usage of individuals in species  $i$  by  $U_i$ . The quantity  $\bar{b}_{ij}(t)$  determines the sensitivity of competition between species  $i$  and  $j$  to differences in their niche use. Denoting  $\lambda_i$  the variance of niche use for individuals of species  $i$  (which we will call the niche breadth), the quantity  $\bar{b}_{ij}(t)$  decomposes as

$$\tilde{b}_{ij}(t) = 1/(\lambda_i + \lambda_j + E_j + G_j(t)). \quad (26)$$

Again applying our assumption of normally distributed niche centers, we find the population growth rate of species  $i$ , defined by  $\bar{m}_i(t) = \int m_i(\mathbf{v}, \mathbf{x}) p_i(\mathbf{x}, t) dx$ , can be explicitly expressed as

$$\bar{m}_i(t) = R_i - \frac{a_i}{2} \left( (\theta_i - \bar{x}_i(t))^2 + G_i(t) + E_i \right) - \sum_{j=1}^S c_{ij} N_j(t) U_i U_j \sqrt{\frac{b_{ij}(t)}{2\pi}} e^{-\frac{b_{ij}(t)}{2} (\bar{x}_i(t) - \bar{x}_j(t))^2}. \quad (27)$$

Similar to  $\tilde{b}_{ij}(t)$ , the quantity  $b_{ij}(t)$  determine the sensitivity of competitive effects on species  $i$  to differences in niche locations between species  $i$  and  $j$ . Specifically,  $b_{ij}$  decomposes as:

$$b_{ij}(t) = 1/(\lambda_i + \lambda_j + E_i + E_j + G_i(t) + G_j(t)). \quad (28)$$

Further details on the biological motivation and calculation of growth rates can be found in [SM Section 5](#).

### 3.2. The Model

In [SM Section 5](#) we combine Eqs. (21a), (24), (25) and (27) to find

$$\frac{dN_i}{dt} = \left\{ R_i - \frac{a_i}{2} \left( (\theta_i - \bar{x}_i)^2 + G_i + E_i \right) - \sum_{j=1}^S c_{ij} N_j U_i U_j \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2} \right\} N_i + \sqrt{V_i N_i} \frac{dW_{N_i}}{dt}, \quad (29a)$$

$$\frac{d\bar{x}_i}{dt} = a_i G_i (\theta_i - \bar{x}_i) - G_i \left( \sum_{j=1}^S c_{ij} N_j U_i U_j b_{ij} (\bar{x}_j - \bar{x}_i) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2} \right) + \sqrt{V_i \frac{G_i}{N_i}} \frac{dW_{\bar{x}_i}}{dt}, \quad (29b)$$

$$\frac{dG_i}{dt} = \mu_i + G_i^2 \left( \sum_{j \neq i} c_{ij} N_j U_i U_j b_{ij} (1 - b_{ij} (\bar{x}_i - \bar{x}_j)^2) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2} + \frac{c_{ii} N_i U_i^2 b_{ii}}{2} \sqrt{\frac{b_{ii}}{2\pi}} - a_i \right) - V_i \frac{G_i}{N_i} + G_i \sqrt{\frac{2V_i}{N_i}} \frac{dW_{G_i}}{dt}. \quad (29c)$$

Together, Eqs. (29) provide a synthetic model capturing the dynamics of abundance and evolution from common biological mechanisms.

**Model Behavior.** Despite the convoluted appearance of system (29), there are some nice features that reflect biological reasoning. For example, the dynamics of abundance generalize Lotka-Volterra dynamics. In particular, the effect of competition with species  $j$  on the fitness of species  $i$  grows linearly with  $N_j$ . However, as biotic selection pushes  $\bar{x}_i$  away from  $\bar{x}_j$ , the effect of competition with species  $j$  on the fitness of species  $i$  rapidly diminishes due to the Gaussian weights capturing a reduction in niche overlap. These Gaussian weights have been usefully employed to capture interaction preference in recent investigations of coevolution in mutualistic networks ([de Andreazzi et al., 2019](#); [Medeiros et al., 2018](#); [Guimarães et al., 2017](#)). The divergence of  $\bar{x}_i$  and  $\bar{x}_j$  due to competition is referred to in the community ecology literature as character displacement ([Brown and Wilson, 1956](#)). We also see that the fitness of species  $i$  drops quadratically with the difference between  $\bar{x}_i$  and the abiotic optimum  $\theta_i$ . Hence, abiotic selection acts to pull  $\bar{x}_i$  towards  $\theta_i$ .

The response in mean trait  $\bar{x}_i$  to natural selection is proportional to the amount of heritable variation in the population, represented by the additive genetic variance  $G_i$ . However, we have that  $G_i$  is itself a dynamic quantity. Under our model, abiotic stabilizing selection erodes heritable variation at a rate that is independent of both  $N_i$  and  $\bar{x}_i$ . The effect of competition on  $G_i$  is more complicated. When  $b_{ij} (\bar{x}_i - \bar{x}_j)^2 < 1$ , competition with species  $j$  acts as diversifying selection which tends to increase the amount of heritable variation. However, when  $b_{ij} (\bar{x}_i - \bar{x}_j)^2 > 1$ , competition with species  $j$  acts as directional selection and reduces  $G_i$ . In the following subsections we demonstrate the behavior of system (29) by plotting numerical solutions and investigate implications for the relationship between the strength of ecological interactions and selection.

**Community Dynamics.** For the sake of illustration we numerically integrated system (29) for a richness of  $S = 100$  species. We assumed homogeneous model parameters across species in the community as summarized by [Table 1](#). We repeated numerical integration under the two scenarios of weak and moderate competition. For the scenario of weak competition we set  $c = 10^{-8}$  and for the scenario of moderate competition we set  $c = 10^{-6}$ . With these two sets of model parameters, we simulated our model for  $10^5$  units of time. For both scenarios, we drew initial mean traits from a normal distribution centered on zero with unit variance, initial trait variances  $\sigma_i^2(0)$  and initial abundances  $N_i(0)$  from log-normal distributions such that  $\mathbb{E}[\ln \sigma_i^2(0)] = 4$ ,  $\mathbb{V}[\ln \sigma_i^2(0)] = 1/2$ ,  $\mathbb{E}[\ln N_i(0)] = 15$  and  $\mathbb{V}[\ln N_i(0)] = 1$ . To avoid numerical issues, we replaced  $N_i$  with  $N_i + 1$  when  $N_i$  appears in the denominator. Numerical integration was conducted in Julia using the `DifferentialEquations.jl` package ([Rackauckas and Nie, 2017](#)).

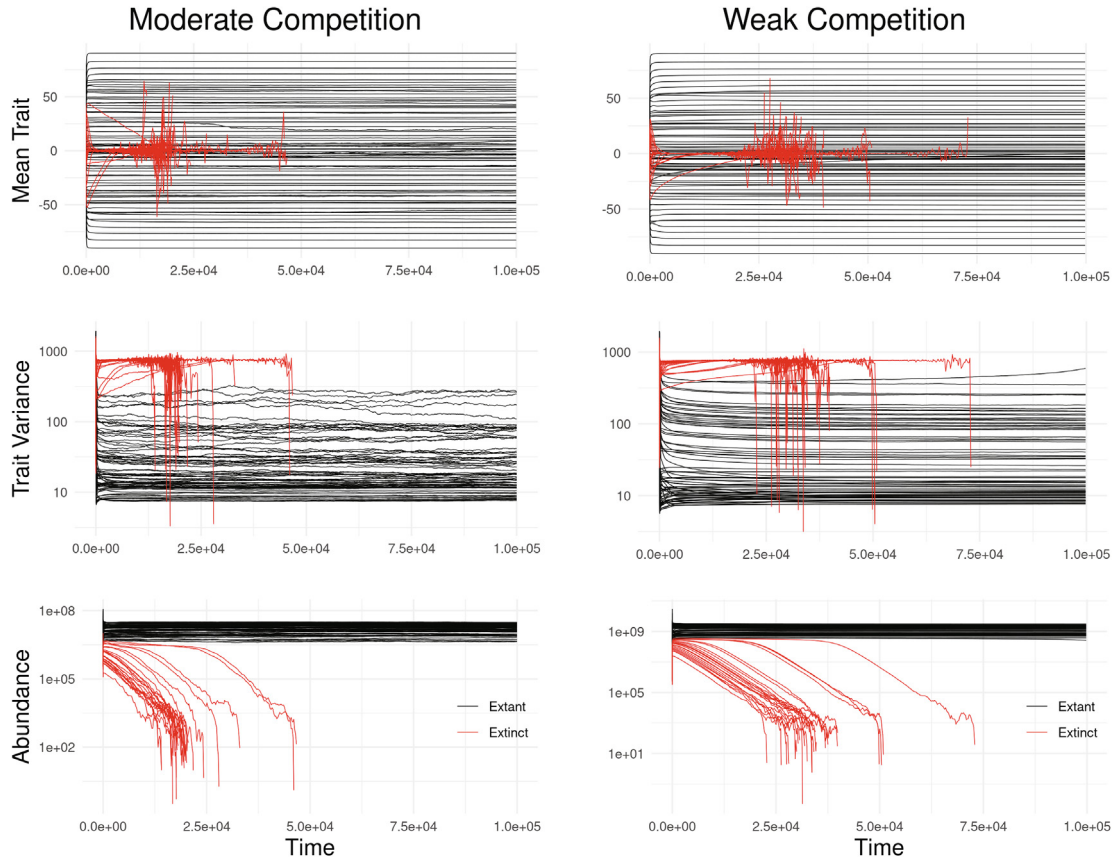
Temporal dynamics for each scenario are provided in [Fig. 1](#). This figure suggests weaker competition leads to smoother dynamics and increased abundances for the species that persist. Considering expression (29a) we note that, all else equal, relaxed competition allows for larger growth rates which promote greater abundances. From (29a) we also see the per-capita effects of demographic stochasticity diminish with abundance. Inspecting expressions (29b) and (29c), we see that larger abundances also erode the effects of demographic stochasticity on the evolution of mean trait and additive genetic variance. These effects were already noted in [Section 2.2](#), and thus are not a consequence of our model of coevolution per se.

In both scenarios, a significant fraction of the community became extinct before our numerical integration ended (24 species in both scenarios). However, extinction happens slower under the scenario of weak competition than under moderate competition. From inspecting the initial conditions ([SM Fig. S2](#)), we see the species that go extinct first tend to be the ones with lower initial abundances and lower initial trait variances. Interestingly, the trait variances of the less abundant species tend to increase above the

**Table 1**  
Values of model parameters used for numerical integration.

Parameter	Description	Value
$S$	species richness	100
$R$	innate growth rate, see <a href="#">Section 3.3</a>	10.0
$\theta$	abiotic optimum	0.0
$a$	strength of abiotic selection	0.002
$c$	sensitivity to competition	$\{10^{-8}, 10^{-6}\}$
$\lambda$	niche breadth	1.0
$U$	total niche use	1.0
$E$	environmental variance	0.0
$\mu$	mutation rate	5.0
$V$	reproductive variance	1.0





**Fig. 1.** Temporal dynamics of mean trait (top), additive genetic variance (middle) and abundance (bottom) for the scenarios of moderate competition (left) and weak competition (right). Black lines represent species that persisted to the end of numerical integration. Red lines represent species that became extinct at some time before the numerical integration ended.

others. Eq. (28) shows that selection due to competition tends to decrease with increased trait variance. In response, the mean traits of these species tend to evolve towards the abiotic optima before their abundances decrease so far that random genetic drift begins to dominate. Random genetic drift then causes extreme fluctuations in the mean trait and dramatically reduces the trait variance just before extinction.

Although Fig. 1 suggests interesting patterns in the dynamics of abundance and trait evolution, a more formal investigation is needed to better understand the relationship between them. In the following subsection we take a step in this direction by approximating correlations between competition coefficients and components of selection gradients induced by interspecific interactions.

### 3.3. The relation between the strength of ecological interactions and selection

Here we investigate the relationship between competition coefficients, which measure the effect of ecological interactions on abundance dynamics, with selection gradients, which measure the magnitude and direction of selection on mean trait and trait variance. We start by considering the expressions of absolute competition coefficients implied by Eqs. (29). However, it turns out absolute competition coefficients display some unfortunate behaviour with respect to our model. We therefore introduce a slightly modified form of absolute competition coefficients. We then provide formula for the components of linear and quadratic selection coefficients corresponding to the effects of interspecific interactions. Lastly, we use a high-richness (large  $S$ ) approximation to determine correlations between competition coefficients and

selection gradients across the community. Associated calculations are provided in SM Section 6.3.

**Competition coefficients.** Relating our treatment of resource competition to theoretical community ecology, the absolute competition coefficient  $\tilde{\alpha}_{ij}$ , which measures the effect of species  $j$  on the growth rate of species  $i$  (sensu Chesson, 2000), becomes a dynamical quantity that can be written as

$$\tilde{\alpha}_{ij}(t) = \frac{c_{ij}U_iU_j}{r_i(t)} \sqrt{\frac{b_{ij}(t)}{2\pi}} \exp\left(-\frac{b_{ij}(t)}{2}(\bar{x}_i(t) - \bar{x}_j(t))^2\right), \quad (30)$$

where

$$r_i(t) = R_i - \frac{a_i}{2} \left( (\bar{x}_i(t) - \theta_i)^2 + G_i(t) + E_i \right), \quad (31)$$

is the intrinsic growth rate of species  $i$ . Then,  $dN_i(t)$  can be expressed as

$$\frac{dN_i}{dt} = r_i \left( 1 - \sum_{j=1}^S \tilde{\alpha}_{ij}N_j \right) N_i + \sqrt{V_iN_i} \frac{dW_{N_i}}{dt}. \quad (32)$$

Following our model, the classically defined absolute competition coefficient for species  $i$  is parameterized with the intrinsic growth rate of species  $i$  appearing in the denominator. In turn, these intrinsic growth rates depend on the balance between the innate growth rate  $R_i$  and the effect of abiotic stabilizing selection. However, this balance further depends on mean trait and additive genetic variance, which evolve freely. This leads to the potential for the signage of  $r_i$  to switch between positive and negative which implies the potential for infinite absolute competition coefficients. Furthermore, we see these competition coefficients are influenced by abiotic stabilizing selection instead of solely capturing the

effects of inter/intraspecific interactions. Hence, we find it necessary to introduce a modification of the absolute competition coefficient  $\tilde{\alpha}_{ij}$  that avoids these caveats. In particular, we define

$$\alpha_{ij} = r_i \tilde{\alpha}_{ij} = c_{ij} U_i U_j \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2}(\bar{x}_i - \bar{x}_j)^2}. \quad (33)$$

We call  $\alpha_{ij}$  the *specific* competition coefficient mediating the effects of species  $j$  on the growth rate of species  $i$ . Under this parameterization, the abundance dynamics of species  $i$  is now expressed as

$$\frac{dN_i}{dt} = \left( r_i - \sum_{j=1}^S \alpha_{ij} N_j \right) N_i + \sqrt{V_i N_i} \frac{dW_{N_i}}{dt}. \quad (34)$$

**Selection Gradients.** Linear and quadratic selection gradients have been defined by Lande and Arnold (1983). While the linear selection gradient  $\beta$  measures the effect of selection on mean trait evolution, the quadratic selection gradient  $\gamma$  measures the effect of selection on additive genetic or phenotypic variance. Since these quantities are classically defined with respect to discrete-time models of trait evolution, we provide the analogous definitions for continuous-time models in SM Section 6.1. Following our model of diffuse coevolution, we then show these selection gradients can be additively partitioned into components due to interactions with each species and abiotic stabilizing selection. In particular, we find the components of linear and quadratic selection gradients for species  $i$  induced by species  $j$  are given respectively by

$$\beta_{ij} = c_{ij} U_i U_j N_j b_{ij} (\bar{x}_i - \bar{x}_j) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2}(\bar{x}_i - \bar{x}_j)^2}, \quad (35a)$$

$$\gamma_{ij} = c_{ij} U_i U_j N_j b_{ij} \left( 1 - b_{ij} (\bar{x}_i - \bar{x}_j)^2 \right) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2}(\bar{x}_i - \bar{x}_j)^2}, \quad i \neq j, \quad (35b)$$

$$\gamma_{ii} = \frac{c_{ii} N_i U_i^2 b_{ii}}{2} \sqrt{\frac{b_{ii}}{2\pi}}, \quad i = j. \quad (35c)$$

With these expressions, the dynamics of mean trait and additive genetic variance simplify to

$$\frac{d\bar{x}_i}{dt} = G_i \left( a_i (\theta_i - \bar{x}_i) + \sum_{j=1}^S \beta_{ij} \right) + \sqrt{V_i \frac{G_i}{N_i}} \frac{dW_{\bar{x}_i}}{dt}, \quad (36a)$$

$$\frac{dG_i}{dt} = \mu_i + G_i^2 \left( -a_i + \sum_{j=1}^S \gamma_{ij} \right) - V_i \frac{G_i}{N_i} + G_i \sqrt{\frac{2V_i}{N_i}} \frac{dW_{G_i}}{dt}. \quad (36b)$$

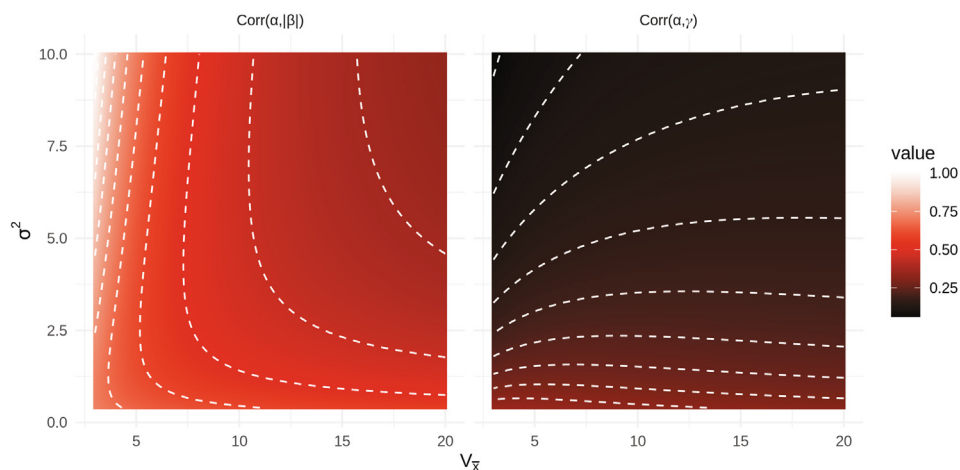
**High-Richness Approximation.** We now make use of the expressions derived for competition coefficients and selection gradients to investigate their relationship. As a first pass, we assume the niche-breadths  $\lambda_i$  and intraspecific variances  $\sigma_i^2$  are equivalent across species so that the sensitivity parameters  $b_{ij} = 1 / (\lambda_i + \lambda_j + \sigma_i^2 + \sigma_j^2) = b$  are constant across interacting pairs of species. We also assume abundances  $N_i$ , niche-use parameters  $U_i$ , strengths of competition  $c_{ij}$  and mean traits  $\bar{x}_i$  are distributed independently of each other with respective means and variances denoted by  $\bar{N}$ ,  $V_N$ ,  $\bar{U}$ ,  $V_U$ ,  $\bar{c}$ ,  $V_c$ ,  $\bar{\lambda}$ ,  $V_\lambda$ . We further assume that richness  $S$  is large and the distribution of mean trait values is approximately normal.

Under these assumptions we obtained analytical expressions for the correlations between specific competition coefficients  $\alpha_{ij}$  and selection gradients  $\beta_{ij}, \gamma_{ij}$ . These calculations are provided in SM Section 6.3. In particular, we found linear selection gradients and competition coefficients lacked a linear statistical relationship ( $\text{Corr}(\alpha, \beta) = 0$ ). However, we did find a linear relationship between the magnitudes of linear selection gradients and competition coefficients ( $\text{Corr}(\alpha, |\beta|) \neq 0$ ) and also between quadratic selection gradients and competition coefficients ( $\text{Corr}(\alpha, \gamma) \neq 0$ ). Their expressions can be found in SM Section 6.3.

To understand if correlations between competition coefficients and selection gradients tend to be positive or negative, we visualized these relationships in Fig. 2. We fixed  $\lambda$ ,  $\bar{c}$ ,  $V_c$ ,  $\bar{U}$ ,  $V_U$ ,  $\bar{N}$  and  $V_N$  and allowed the amounts of intraspecific trait variance  $\sigma^2$  and interspecific trait variance  $V_\lambda$  to vary. We found absolute values of linear selection gradients and quadratic selection gradients tend to be positively correlated with competition coefficients. Hence, if we know of competing species that strongly affect each others abundances then we can guess they also impose directional and diversifying selection on one another. However, based on this information alone, we cannot guess at the direction of selection.

#### 4. Conclusion

We have introduced a novel approach to compute eco-evolutionary models using the calculus of space-time white noise and diffusion-limits of individual-based models and coined SAGA,



**Fig. 2.** Heatmaps of the correlation between the magnitude of linear selection gradients and competition coefficients (left) and between stabilizing selection gradients and competition coefficients (right) as functions of community-wide variance of mean trait values  $V_\lambda$  and intraspecific trait variances  $\sigma^2$ . In both plots we set  $\lambda = 1.0$ ,  $\bar{c} = 10^{-7}$ ,  $V_c = 0.0$ ,  $\bar{U} = 1.0$ ,  $V_U = 0.0$ ,  $\bar{N} = 1.0 \times 10^5$ , and  $V_N = 100.0$ .

a SPDE model of phenotypic evolution that accounts for demographic stochasticity. Numerical implementations of SAGA allow the investigation of general evolving phenotypic distributions without tracking specific moments. However, since population size, trait mean and additive genetic variance are key descriptors of biological populations, we calculated from SAGA a set of SDE tracking the dynamics of these three quantities. Without assuming Gaussian trait distributions, the SDE for the mean and additive genetic variance are expressible in terms of the covariance between trait values and growth rate and the covariance between trait values and reproductive variance. However, working directly with covariances between fitness and phenotype will likely be challenging in most cases. By assuming Gaussian trait distributions, the SDE for the mean trait and additive genetic variance become expressible in terms of gradients of growth rate and reproductive variance, thereby providing efficient analytical tools for computing stochastic eco-evolutionary models. These SDE provide a continuous-time generalization of the classical approach introduced by Lande (1976) by allowing stochastic dynamics of abundance and trait variance and incorporating noise-induced selection.

To illustrate the relevance of our approach to studies of evolutionary ecology, we combined our SDE with classical competition theory to derive a model of diffuse coevolution. We then used this model to investigate the relationship between standardized selection gradients and competition coefficients. We found absolute values of linear selection gradients and raw values of quadratic selection gradients are positively correlated with competition coefficients. In the process, we derived expressions for competition coefficients and components of selection gradients due to pairwise interactions as functions of niche-use parameters (niche breadth, total use and mean and variance of niche location), strength of competitive interactions and abundance.

Although the framework outlined here holds great potential for developing a synthetic theory of coevolving ecological communities, there are two technical gaps in the mathematical foundations of our approach. Firstly, we were unable to derive formal conditions under which trait means and variances remain finite for finite time. However, a result due to Evans and Perkins (1994) shows that the diffusion-limit for a pair of interacting individual-based processes following our simple niche-based treatment of competition exists when growth rates, as functions of trait values and abundances, are bounded above. This result can be easily extended to finite sets of competing species and therefore formally establishes the existence of abundances as diffusion processes. Further work is needed to determine the conditions under which trait means and variances exist as diffusion processes. The models studied here provide likely sufficient conditions. In particular, since diffusive mutation does not lead to “heavy-tailed” phenotypic distributions, we expect the mean trait and trait variance to remain finite so long as total abundance is positive, given finite initial values for trait mean and variance. That is, since we have not included any processes that would cause blow-up either in mean trait or trait variance, we expect solutions of the SDE (21) to exist for all finite time  $t$  such that  $N(t) > 0$  when  $|\bar{x}(0)|, \sigma^2(0) < +\infty$ . This assumption appears especially well-founded under quadratic stabilizing selection. Since fitness indefinitely decreases as individual trait value becomes indefinitely large (see Eq. (27)), the diversifying effects of mutation and competition will eventually be overwhelmed by stabilizing selection. Hence quadratic stabilizing selection prevents the abundance densities of populations from venturing indefinitely far from their phenotypic optima.

Secondly, although SDE calculated under the assumption of normally distributed phenotypes provide particularly useful formula by replacing covariances between fitness and phenotype with gradients of growth rate and reproductive variance, this assumption is

mathematically rigorous only under deterministic dynamics and when the growth rate is a linear or concave-down quadratic function of trait value. However, following our model based on classical competition theory, we found the associated growth rate is highly non-linear which implies trait distributions may evolve to become non-normal. While this extreme non-linearity is mathematically inconvenient, it also captures important biological details (such as the decay of competition with niche divergence) and thus allows for a more realistic model of community dynamics. In spite of this inconsistency in our model formulation, we found resulting dynamics under the assumption of normally distributed trait values retained well-founded biological intuition. In addition, a brief numerical exploration suggests the Gaussian population assumption may hold when population sizes and trait variances are sufficiently large and when the strength of intraspecific competition is equal to the strength of interspecific competition for each species (see SM Section 5.5). Furthermore, previous work in the field of theoretical quantitative genetics has demonstrated the assumption of normally distributed trait values is robust to fitness functions that select for non-normal trait distributions when inheritance is given a more realistic treatment and when populations reproduce sexually (Turelli and Barton, 1994; Barton et al., 2017). However, since the maintenance of heritable variation in sexually reproducing populations is still poorly understood (Bürger, 2020), it is commonplace to assume the additive genetic variance  $G$  is constant across time. Hence, future work is needed to extend our approach to account for sexual reproduction, more realistic models of inheritance and to investigate the community-level consequences of non-normally distributed trait values.

Overall, this work demonstrates that connecting contemporary theoretical approaches of evolutionary ecology with some fundamental results in the theory of measure-valued branching processes and their diffusion-limits allows for the development of a flexible approach to synthesizing the dynamics of abundance and distribution of quantitative characters. In particular, Eqs. (21a) and (24) provide a fundamental set of equations for deriving stochastic eco-evolutionary models involving quantitative traits. However, these equations require an expression for growth rates and reproductive variances associated with each trait value. Conveniently, Eq. (17) provides a means to derive such expressions from individual-based models. Taken together, these results provide a means to derive analytically tractable dynamics from mechanistic formulations of fitness as a function of phenotype. The motivation for our model of diffuse coevolution, located in SM Section 5, demonstrates how to derive eco-evolutionary models involving a set of interacting species from biological first principles. Hence, this work provides a novel set of mathematical tools and a tutorial for their use in theoretical studies of evolutionary ecology, paving the way for future work that provides a holistic theoretical treatment of coevolving ecological communities.

#### CRediT authorship contribution statement

**Bob Week:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Scott L. Nuismer:** Writing - review & editing, Supervision, Funding acquisition. **Luke J. Harmon:** Writing - review & editing. **Stephen M. Krone:** Validation, Writing - review & editing, Supervision.

#### Declaration of Competing Interest

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

## Acknowledgements

We thank three anonymous reviewers for their supportive and insightful comments. Funding was provided by National Science Foundation [Grant No. DEB-1450653].

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jtbi.2021.110660>.

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