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STOCHASTIC ECO-EVOLUTIONARY DYNAMICS OF MULTIVARIATE TRAITS

A Framework for Modeling Population Processes Illustrated by the Study of Drifting **G**-Matrices

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Abstract

I derive a novel stochastic equation for the evolution of the additive genetic variance-covariance matrix **G** in response to mutation, selection, drift, and fluctuating population size. Common wisdom holds that **G** should respond to drift only as a scaled reduction. In contrast, I find that drift causes drastic and predictable shifts in the orientation of **G** by driving genetic correlations to their extremes. Biologically, this is a consequence of linkage build-up introduced by drift. I compare these theoretical results to empirical observations based on experiments conducted by Phillips et. al. (2001). Additionally, to derive the model of **G**-matrix evolution, I developed a novel synthetic framework for modelling ecological and evolutionary dynamics of populations carrying multivariate traits. By striking a balance between genetic detail and analytical tractability, and by minimizing requisite technical background, this framework is optimized for deriving new models across a wide range of topics in population biology. Foundations of the framework are formalized by the theory of measure-valued processes, but application of the framework only requires multivariate calculus, and heuristics are presented in the main text for making additional calculations involving stochastic processes. Collectively, this work establishes a powerful framework enabling efficient formal analysis of integrated population processes across evolution and ecology, and its potential for making new discoveries is illustrated by novel findings on fundamental aspects of **G**-matrix evolution.

Key words: Evolutionary Ecology; Quantitative Genetics; Drift; **G**-Matrices; Martingale Problems

1. Introduction

A fundamental principle of evolutionary biology is that random genetic drift erodes heritable variation at a rate inversely proportional to effective population size. At the level of allele frequencies, models for the distribution of genetic variation responding to drift are well-known (Kimura, 1964, 1968; Ewens, 2004; Hill and Robertson, 1966). In contrast, at the level of quantitative characters, models of additive genetic variation responding to drift focus on the average outcome using deterministic models (Latter, 1970; Bulmer, 1972; Lande, 1976, 1980; Chakraborty and Nei, 1982; Turelli and Barton, 1994; Lynch and Hill, 1986; Bürger, 2000; Barton and Turelli, 2004; Débarre and Otto, 2016; Walsh and Lynch, 2018). Empirical work has supported theoretical predictions for the average response of additive genetic variation to drift (Phillips et al., 2001; McGuigan et al., 2005; Whitlock et al., 2002), but has also emphasized the need to predict the distribution of outcomes (Phillips et al., 2001; Whitlock, 1995) especially for multivariate traits and genetic covariances (Phillips and McGuigan, 2006; Mallard et al., 2023a).

In the setting of multivariate traits, a common summary statistic for genetic architecture is the **G**-matrix. This matrix has the additive genetic variance (i.e., the heritable component) of each trait on the associated diagonal entry. Off-diagonal entries quantify genetic covariances between traits which may be maintained by pleiotropic loci and linkage between loci affecting different traits. The standard view is that drift produces a proportional decrease in **G** (Phillips and McGuigan, 2006; Cano et al., 2004; McGuigan, 2006; Chapuis et al., 2008; Dugand et al., 2021; Mallard et al., 2023a), and thus independent populations that have diverged due to drift should have proportional **G**-matrices (Roff, 2000; Steppan et al., 2002; Aguirre et al., 2013). However, this insight rests on results from a deterministic model for the response of **G**-matrices to drift (Lande, 1979) and a model that assumes recombination happens sufficiently fast to break-up linkage produced by selection (Lande, 1980). Hence, there is a need to develop theoretical predictions for the stochastic evolution of **G**-matrices driven solely by drift, and especially for the effect of drift on genetic covariances (Mallard et al., 2023a,b).

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The reason for this gap in evolutionary theory stems, in part, from the lack of formal approaches to place tractable models of **G**-matrix evolution on a concrete mathematical foundation. In this paper, I aim to make first steps in this direction by leveraging the powerful theory of measure-valued processes, while also keeping the presentation as accessible as possible. Furthermore, taking this approach to formally derive **G**-matrix dynamics revealed a much broader framework for modelling a wide-range of population processes. In particular, given the growing appreciation for the interplay between ecological and evolutionary processes (Reznick, 2015; Hendry, 2017; Kuosmanen et al., 2022), this framework makes an important contribution by enabling the formal interfacing of **G**-matrix evolution with models of eco-evolutionary feedbacks (e.g., Patel et al., 2018). I therefore focus this paper on presenting the framework in its full generality, and return to the study of **G**-matrix evolution as an example to illustrate its utility.

In its full generality, this framework offers tools to model the integrated ecological and evolutionary dynamics of populations with multivariate traits that respond to mutation, selection (including frequency and abundance dependence), demographic stochasticity, and consequential random genetic drift. In particular, this framework can be used to obtain generalizations of many classical models in evolution and ecology, such as such as Lotka-Volterra dynamics (Huang et al., 2015; Akjouj et al., 2024), coevolution (Gilman et al., 2012; Débarre et al., 2014), and evolutionary rescue (Klausmeier et al., 2020; Xu et al., 2023). Further details on how to apply this framework to arrive at known models are given in the discussion section.

To apply this framework, the most important biological details relevant to a modeler are the mechanisms mediating fitness. In contrast, details involving the genetic architecture of traits are abstracted in a way that captures basic biological principles while optimizing analytical tractability. For instance, asexual, clonal reproduction is assumed and mutation is modeled following the approaches of Kimura (1965) and Débarre and Otto (2016) by assuming offspring traits are distributed around their parental traits. Abstract approaches similar to this have been successful for obtaining valuable analytical insights into genetic variation maintained by mutation-selection balance (Kimura, 1965; Lande, 1975; Turelli, 1984, 1986) and by mutation-drift balance (Lande, 1976, 1979; Barton, 1989; Débarre and Otto, 2016). Hence, by optimizing a trade-off between genetic detail and analytical tractability, this framework provides an accessible approach for obtaining and communicating a wide array of novel theoretical insights.

To establish this framework, I build on the work of Week et al. (2021), which presented a stochastic differential equation framework focused on modelling the simultaneous dynamics of abundances, 1-dimensional mean traits, and 1-dimensional trait variances responding to mutation, selection, demographic stochasticity, and random genetic drift. This 1-dimensional framework was based on the development of heuristics (i.e., methods for performing exact calculations without formal justification) for working with stochastic partial differential equations (spde). However, for multivariate traits, the spde approach breaks down (Dawson, 1993; Etheridge, 2000; Perkins, 2002). To overcome this challenge, and establish a rigorous analytical framework for deriving population processes, I take an approach based on so-called *martingale problems* (Dawson, 1993; Stroock and Varadhan, 1997; Rogers and Williams, 2000). Mathematical aspects of this approach are provided in supplement section 2. In the main text, I focus on the resulting dynamical equations and heuristics for performing calculations with minimal technical background.

1.1. Overview

I begin by outlining the derivation of the deterministic version of the framework without making any assumptions on the shape of trait distributions, which is summarized by a system of ordinary differential equations. This leads to expressions of selection in terms of covariances with fitness, which I refer to collectively as the Deterministic Covariance version (or *DC* for short). By assuming traits follow multivariate normal distributions, covariances with fitness are replaced by multivariate gradients of fitness with respect to mean traits and trait variances, and I refer to the resulting system of differential equations as the Deterministic Gradient version (or *DG* for short). To simplify presentation of the deterministic version of the framework, I assume traits are perfectly heritable. However, because this work is motivated by understanding the consequences of drift for **G**-matrix evolution, I briefly describe an approach to model imperfect heritability after introducing *DC* and *DG*. This model of imperfect heritability is adopted while introducing the stochastic extensions of the framework.

The stochastic extensions of the framework include the effects of demographic stochasticity (i.e., random reproductive output) and random genetic drift (which occurs here as a consequence of demographic stochasticity). I introduce two stochastic extensions. Both build on *DG* by assuming multivariate normal trait distributions and by expressing selection in terms of fitness gradients. The first form expresses dynamics in terms of Brownian motions as drivers of stochasticity (referred to as the Brownian Motion Gradient version, or *BG* for short), which is particularly useful for numerical analysis. The second form expresses dynamics in terms of a more general underlying martingale process (referred to as the Martingale Gradient version, or *MG* for short), and I use this form to introduce heuristics for deriving analytical models. To demonstrate these heuristics, I derive a stochastic equation for the evolution of additive genetic correlations between trait values. To bring this paper full-circle, I then discuss how this exercise provides novel insights into the evolutionary response of **G**-matrices to random genetic drift and compare these theoretical results with observations obtained from experiments (Phillips et al., 2001; McGuigan et al., 2005; Whitlock et al., 2002).

Section 1 of the supplement translates discrete time models of classical quantitative genetics into the current continuous time context. Mathematical details to justify this framework are communicated in supplement section 2. Using this justification, section 3 of the supplement presents detailed calculations for the derivation of the stochastic equations presented in the main text. Supplement section 4 describes numerical implementations of this framework.

2. The Framework

The framework tracks the dynamics of the density of abundance across trait space for clonally reproducing populations. To model d-dimensional traits, I assume trait space is the entire Euclidean space $\mathbb{R}^d$. Given the d-dimensional trait $\mathbf{z} = (z_1, \ldots, z_d)^\top$ (with $^\top$ denoting matrix transposition so $\mathbf{z}$ is a column vector), I write $\nu(\mathbf{z})$ for the density of abundance at $\mathbf{z}$, and I also refer to this as the abundance density of the population. Then the total abundance of the population is given by $n = \int_{\mathbb{R}^d} \nu(\mathbf{z})\, d\mathbf{z}$. The frequency of trait value $\mathbf{z}$ is then $p(\mathbf{z}) = \nu(\mathbf{z})/n$, and this is also referred to both as the relative abundance of $\mathbf{z}$ and as the trait distribution. Using $p(\mathbf{z})$, the mean trait vector is given by $\bar{\mathbf{z}} = \int_{\mathbb{R}^d} \mathbf{z}\, p(\mathbf{z})\, d\mathbf{z}$, and the trait covariance matrix is $\mathbf{P} = \int_{\mathbb{R}^d} (\mathbf{z}-\bar{\mathbf{z}})(\mathbf{z}-\bar{\mathbf{z}})^\top p(\mathbf{z})\, d\mathbf{z}$, with P_{ij} being the covariance between z_i and z_j. The chosen notation facilitates comparison with classical multivariate quantitative genetic models (Lande, 1980; Lande and Arnold, 1983; Jones et al., 2003; Arnold et al., 2008).

In the following section (2.1) I describe how to obtain the deterministic version of the framework using multivariate calculus. I do this in two parts. The first part (*DC*) makes no assumption on the shape of $p(\mathbf{z})$. The second part (*DG*) assumes $p(\mathbf{z})$ is the density of a multivariate normal distribution. I continue to make this assumption in section 2.2 where I introduce the stochastic extension of this framework.

2.1. Deterministic Dynamics

2.1.1. The Deterministic Covariance Version (DC)

To establish a flexible, but tractable framework to model the dynamics of n, $\bar{\mathbf{z}}$, and $\mathbf{P}$, I generalize the deterministic model used by Week et al. (2021), referred to there as the Deterministic Asexual Gaussian Allelic model (DAGA), to the multivariate setting. Specifically, DAGA focuses on dynamics due to just mutation and selection for asexually reproducing populations. Mutation is modeled as the variance μ of a normal distribution determining offspring traits centered on their parental traits, and selection results from the covariance of fitness and phenotype.

In the multivariate trait setting, mutation is modeled as a $d \times d$ covariance matrix $\boldsymbol{\mu}$, with the off-diagonal entries contributing to trait covariances. This setup fits within the conceptual framework that has been popular for theoretical and empirical studies of **G**-matrix evolution, with $\boldsymbol{\mu}$ taking the place of the **M**-matrix (Jones et al., 2007; Arnold et al., 2008; Mallard et al., 2023a). Fitness is quantified by a rate $m(\nu, \mathbf{z})$, which is the growth rate for the sub-population of individuals with trait value $\mathbf{z}$ in a population summarized by ν. The dependency of m on ν and $\mathbf{z}$ allows for the modelling of interwoven ecological and evolutionary dynamics. We will also refer to $m(\nu, \mathbf{z})$ as a *fitness function*, and this function may also depend on environmental parameters such as the trait values of individuals in interacting species. However, I omit notation accounting for such possibilities to simplify the frameworks presentation. Putting these components together, the multivariate generalization of DAGA is given by the partial differential equation

$$\dot{\nu}(\mathbf{z}) = m(\nu, \mathbf{z})\, \nu(\mathbf{z}) + \tfrac{1}{2} \nabla^\top \boldsymbol{\mu} \nabla\, \nu(\mathbf{z}), \tag{1}$$

where $\dot{\nu}(\mathbf{z})$ is the instantaneous rate of change of $\nu(\mathbf{z})$ over time, the symbol $\nabla = (\partial/\partial z_1, \ldots, \partial/\partial z_d)^\top$ is the gradient operator with respect to the d-dimensional trait $\mathbf{z}$, and

$$\tfrac{1}{2} \nabla^\top \boldsymbol{\mu} \nabla = \tfrac{1}{2} \sum_{i,j=1}^{d} \mu_{ij} \frac{\partial}{\partial z_i} \frac{\partial}{\partial z_j} \tag{2}$$

is the mutation operator. If $\mu_{ij} = 0$ when $i \neq j$ and $\mu_{ii} = \mu_{jj}$ is constant across all ij, then the above mutation operator becomes proportional to the Laplacian operator on $\mathbb{R}^d$, which causes symmetric diffusion of the abundance density. Hence, unequal entries imply that mutation results in asymmetric diffusion across trait space so that some traits mutate faster than others. Additionally, if $\mu_{ij} \neq 0$ when $i \neq j$, mutation contributes to covariance between traits z_i and z_j. This model of mutation can be obtained from a diffusion limit of an individual-based model that assumes independence of reproduction and mutation in which the phenotypic effect size of mutation is small (Méléard and Roelly, 1993). A model where mutation and reproduction interact has been studied by Wickman et al. (2023).

Mathematically, assuming n is finite allows us to write $\dot{n} = \int_{\mathbb{R}^d} \dot{\nu}(\mathbf{z})\, d\mathbf{z}$. We can then apply integration-by-parts to obtain

$$\dot{n} = \bar{m}\, n, \tag{3}$$

where $\bar{m}(\nu) = \int_{\mathbb{R}^d} m(\nu, \mathbf{z})\, p(\mathbf{z})\, d\mathbf{z}$ is mean fitness. Biologically, n should be very large since drift is being ignored. However, this approach can still be useful for gaining insights when n is small, which occurs for example with Lotka-Volterra models (Akjouj et al., 2024).

Dynamics of the mean trait vector are obtained by applying the quotient rule and integration-by-parts to $\dot{\bar{\mathbf{z}}} = \int_{\mathbb{R}^d} \mathbf{z}\, \dot{p}(\mathbf{z})\, d\mathbf{z}$, which provides

$$\dot{\bar{\mathbf{z}}} = \mathrm{Cov}(m, \mathbf{z}), \tag{4}$$

where $\mathrm{Cov}(m, \mathbf{z})$ is a d-dimensional vector with i-th entry given by

$$\mathrm{Cov}(m, z_i) = \int_{\mathbb{R}^d} (\, m(\nu, \mathbf{z}) - \bar{m}(\nu)\,)\, (z_i - \bar{z}_i)\, p(\mathbf{z})\, d\mathbf{z}, \tag{5}$$

where $\bar{z}_i$ is the i-th entry of $\bar{\mathbf{z}}$.

The same techniques can also be applied to obtain $\dot{\mathbf{P}}$ as

$$\dot{\mathbf{P}} = \boldsymbol{\mu} + \mathrm{Cov}(m, (\mathbf{z}-\bar{\mathbf{z}})(\mathbf{z}-\bar{\mathbf{z}})^\top), \tag{6}$$

where $\mathrm{Cov}(m, (\mathbf{z}-\bar{\mathbf{z}})(\mathbf{z}-\bar{\mathbf{z}})^\top)$ is a $d \times d$ matrix with ij-th entry given by $\mathrm{Cov}(m, (z_i - \bar{z}_i)(z_j - \bar{z}_j))$.

This version of the framework is especially flexible because it makes no assumptions on the trait distribution. In this form, the framework can then be used to study the dynamics of populations with non-trivial higher moments, such as skewed distributions. However, this flexibility of accommodating general trait distributions comes at the cost of a limited range of fitness functions that are amenable to study. This consequence is due to i) the challenge of calculating covariances between arbitrary fitness functions and phenotypic moments, and ii) moment-closing issues that often arise during these calculations (Barton and Turelli, 1987; Gilpin and Feldman, 2019; Guerand et al., 2023). In spite of this limitation, a family of biologically important fitness functions are tractable to study using *DC*. These function take the form

$$m(\nu, \mathbf{z}) = r + \mathbf{b}^\top \mathbf{z} - \tfrac{1}{2} (\boldsymbol{\theta} - \mathbf{z})^\top \boldsymbol{\Psi}\, (\boldsymbol{\theta} - \mathbf{z}) - c\, n, \tag{7}$$

where $\mathbf{b} = (b_1, \ldots, b_d)^\top$ confers directional selection (positive or negative for trait z_i depending on the sign of b_i), and $\boldsymbol{\Psi}$ is a matrix that mediates stabilizing or disruptive selection around the multivariate optimum $\boldsymbol{\theta}$ (classically, $\boldsymbol{\Psi}$ is denoted $\boldsymbol{\omega}^{-1}$ in quantitative genetic theory e.g., Lande, 1979; Jones et al., 2012). Additionally, the parameter $c \geq 0$ is the strength of competition, which here acts globally between individuals regardless of trait, and r is the growth rate in the absence of selection and competition (i.e., when $\mathbf{b}, \boldsymbol{\Psi}$, and c are all zero). It is possible to generalize this family so that competition is non-global, but this requires additional technical details as the fitness function becomes operator-valued (which is treated, for example, by Volpert, 2014; and by Etheridge et al., 2024). Supplementary material section 1 connects these fitness functions to those known from classical discrete time quantitative genetic models.

Combining equations (3), (4), and (6) with equation (7) provides

$$\dot{n} = \Big(r + \mathbf{b}^\top \bar{\mathbf{z}} - \tfrac{1}{2}(\boldsymbol{\theta} - \bar{\mathbf{z}})^\top \boldsymbol{\Psi}\,(\boldsymbol{\theta} - \bar{\mathbf{z}}) - \tfrac{1}{2}\mathrm{tr}(\boldsymbol{\Psi}\,\mathbf{P}) - c\,n\Big)\,n, \quad (8a)$$

$$\dot{\bar{\mathbf{z}}} = \mathbf{P}\,\mathbf{b} + \mathbf{P}\,\boldsymbol{\Psi}\,(\boldsymbol{\theta} - \bar{\mathbf{z}}) + \mathbf{K} : \boldsymbol{\Psi}, \quad (8b)$$

$$\dot{\mathbf{P}} = \boldsymbol{\mu} - \mathbf{P}\,\boldsymbol{\Psi}\,\mathbf{P} + \mathbf{K}\cdot\boldsymbol{\Psi}(\boldsymbol{\theta} - \bar{\mathbf{z}}) - \mathbf{K}\cdot\mathbf{b}, \quad (8c)$$

where $\mathbf{K}$ is the third-order skew tensor of $\mathbf{z}$ defined by $K_{ijk} = \mathbb{E}[(z_i - \bar{z}_i)(z_j - \bar{z}_j)(z_k - \bar{z}_k)]$. Products with $\mathbf{K}$ are given by $(\mathbf{K} : \boldsymbol{\Psi})_i = \sum_{jk} K_{jki}\Psi_{jk}$, $(\mathbf{K}\cdot\boldsymbol{\Psi})_{ij} = \sum_k K_{ijk}\Psi_{kj}$, and $(\mathbf{K}\cdot\mathbf{b})_{ij} = \sum_k K_{ijk}b_k$.

Equations (8) demonstrate that, for fitness functions taking the form of (7), the dynamics of abundance, mean trait, and trait covariance matrix depend on higher phenotypic moments. In fact, a complete description requires an infinite number of equations. However, by combining equation (7) with multivariate DAGA (i.e., with equation (1)), we can use linear stability analysis to show that, when $\boldsymbol{\Psi}$ is positive definite, $\nu(\mathbf{z})$ has an asymptotically stable equilibrium proportional to the density of a multivariate normal distribution with covariance matrix $\hat{\mathbf{P}} = \sqrt{\boldsymbol{\mu}\boldsymbol{\Psi}^{-1}}$ (with matrix square roots defined using eigenvalue decomposition: $\mathbf{M} = \mathbf{U}\boldsymbol{\Lambda}\mathbf{U}^{-1}$ implies $\sqrt{\mathbf{M}} = \mathbf{U}\sqrt{\boldsymbol{\Lambda}}\mathbf{U}^{-1}$), equilibrium mean vector

$$\hat{\bar{\mathbf{z}}} = \boldsymbol{\Psi}^{-1}\mathbf{b} + \boldsymbol{\theta}, \quad (9)$$

and total abundance

$$\hat{n} = \frac{1}{c}\Big(r + \mathbf{b}^\top\boldsymbol{\theta} + \tfrac{1}{2}\mathbf{b}^\top\boldsymbol{\Psi}^{-1}\mathbf{b} - \tfrac{1}{2}\mathrm{tr}\big(\sqrt{\boldsymbol{\mu}\boldsymbol{\Psi}}\big)\Big). \quad (10)$$

The mutation-selection balance of phenotypic variance $\hat{\mathbf{P}}$ is a multivariate generalization of the univariate classical result obtained from multi-locus models (e.g., Bulmer, 1972) and continuum-of-alleles models (e.g., Bürger, 1986). Further work is needed to extend these results for more general fitness functions and higher phenotypic moments, which are already known to have important evolutionary consequences (Débarre et al., 2015). A new approach to study the dynamics of higher moments for univariate traits was recently introduced by Gilpin and Feldman (2019).

2.1.2. The Deterministic Gradient Version (DG)

As noted above, deriving population dynamics from arbitrary fitness functions can be challenging in the more general framework based on covariances between fitness and phenotype. To overcome this we can make the useful simplifying assumption that traits follow a multivariate normal distribution. While deviations from normality can have consequences for ecological and evolutionary processes (Turelli, 1988; Débarre et al., 2015), normality has been an important initial assumption for studying a wide range of topics such as reaction-norm evolution (Lande, 2014), coevolving mutualistic networks (Nuismer et al., 2018), and niche construction (Fogarty and Wade, 2022). Furthermore, normality is a well-established approximation that holds under many genetic and selective scenarios (Turelli and Barton, 1994). Then, as a first pass, I assume traits are multivariate normally distributed for the rest of this paper.

In the context of this framework, the assumption of multivariate normality is particularly useful because it allows us to rewrite covariances between fitness and phenotype as gradients of fitness functions with respect to moments of the trait distribution. Such gradients can be analytically calculated for a broad range of fitness functions. The calculations to obtain these expressions begin with the definitions of covariances between fitness and phenotype, and then apply properties of the multivariate Gaussian function and integration-by-parts. As a result, the deterministic *DG* version of the framework is given by

$$\dot{n} = \bar{m}\,n, \quad (11a)$$

$$\dot{\bar{\mathbf{z}}} = \mathbf{P}\,(\nabla_{\bar{\mathbf{z}}}\,\bar{m} - \overline{\nabla_{\bar{\mathbf{z}}}\,m}), \quad (11b)$$

$$\dot{\mathbf{P}} = \boldsymbol{\mu} + 2\,\mathbf{P}\,(\nabla_{\mathbf{P}}\,\bar{m} - \overline{\nabla_{\mathbf{P}}\,m})\,\mathbf{P}, \quad (11c)$$

where $\nabla_{\bar{\mathbf{z}}}\,\bar{m}$ and $\overline{\nabla_{\bar{\mathbf{z}}}\,m}$ are d-dimensional vectors that respectively capture the effects of frequency independent and frequency dependent selection on mean trait evolution. More precisely, writing $\partial_i = \partial/\partial\bar{z}_i$ as the partial derivative operator with respect to the i-th mean trait, the i-th entry of $\nabla_{\bar{\mathbf{z}}}\,\bar{m}$ and $\overline{\nabla_{\bar{\mathbf{z}}}\ m}$ are respectively given by $\partial_i\,\bar{m}$ and $\overline{\nabla_{\bar{\mathbf{z}}}\ m}$ is $\overline{\partial_i\,m} = \int_{\mathbb{R}^d} p(\mathbf{z})\,[\,\partial_i\,m(\nu,\mathbf{z})\,]\,d\mathbf{z}$. Similarly, $\nabla_{\mathbf{P}}\,\bar{m}$ and $\overline{\nabla_{\mathbf{P}}\,m}$ are $d \times d$ matrices that respectively quantify the dependence of fitness on trait variances and covariances. Writing $\partial_{ij} = \partial/\partial P_{ij}$ as the partial derivative operator with respect to the covariance between trait components i and j, the ij-th entries of $\nabla_{\mathbf{P}}\,\bar{m}$ and $\overline{\nabla_{\mathbf{P}}\,m}$ are respectively given by $\partial_{ij}\,\bar{m}$ and $\overline{\partial_{ij}\,m} = \int_{\mathbb{R}^d} p(\mathbf{z})\,[\,\partial_{ij}\,m(\nu,\mathbf{z})\,]\,d\mathbf{z}$.

Mean trait and trait covariance dynamics can be expressed in index form as

$$\dot{\bar{z}}_i = \sum_{j=1}^{d} P_{ij}\,(\partial_j\,\bar{m} - \overline{\partial_j\,m}), \quad (12a)$$

$$\dot{P}_{ij} = \mu_{ij} + 2\sum_{k,l=1}^{d} P_{ik}\,(\partial_{kl}\,\bar{m} - \overline{\partial_{kl}\,m})\,P_{lj}. \quad (12b)$$

Inclusion of the terms $\overline{\nabla_{\bar{\mathbf{z}}}\,m}$ and $\overline{\nabla_{\mathbf{P}}\,m}$ in equations (11b) and (11c) make it clear that this framework accounts for frequency-dependent selection. This is similar to the form of frequency-dependent selection that appears in classical quantitative genetics (see eqn. (9) of Lande, 1976). Additionally, the approach outlined here can make a useful alternative to model frequency-dependent selection complementing adaptive dynamic and evolutionary game theoretic methods (Dieckmann and Law, 1996; Hofbauer and Sigmund, 1998; Traulsen et al., 2005).

An important caveat of both *DC* and *DG* versions of the framework taking the form presented above is that they rely on perfect heritability of trait values. However, traits are in general not perfectly heritable, and this is of fundamental importance in evolutionary biology. I therefore address this additional complexity in the following sub-subsection. I note here that extending *DC* and *DG* to include imperfect heritability results in nearly identical equations, the important difference is that average growth rates must additionally be averaged over a phenotypic noise term. I state this explicitly for the *DG* version below.

2.1.3. Imperfect Inheritance

Following classical quantitative genetics, imperfect inheritance of trait values can be accounted for by assuming traits decompose into a genetic component and a noise component: $z_i = g_i + e_i$ (Lynch et al., 1998). The noise component e_i is assumed to be independent for each trait and each individual, and thus not heritable. In contrast, the genetic component (g_i) follows the same Gaussian mutation model describe above. In particular, focusing on a d-dimensional trait, given that $\mathbf{g} = (g_1, \dots, g_d)$ is the vector of genetic components for the trait of a parent, an offspring will have a genetic component vector that is multivariate normally distributed with mean $\mathbf{g}$ and covariance matrix $\boldsymbol{\mu}$. Assuming the noise component is identically distributed for all individuals with mean zero and covariance matrix $\mathbf{E}$, and denoting $\gamma(\mathbf{g})$ the density of abundance at genetic value $\mathbf{g}$, and $\varepsilon(\mathbf{e})$ the frequency of noise terms, the abundance density of trait values is given by $\nu(\mathbf{z}) = \int_{\mathbb{R}^d} \varepsilon(\mathbf{e})\gamma(\mathbf{z}-\mathbf{e})d\mathbf{e}$. This preserves total abundance so that $n = \int_{\mathbb{R}^d} \nu(\mathbf{z})d\mathbf{z} = \int_{\mathbb{R}^d} \gamma(\mathbf{g})d\mathbf{g}$. These assumptions also imply that the growth rate for the sub-population of individuals carrying genetic value $\mathbf{g}$ is given by $m_*(\gamma, \mathbf{g}) = \int_{\mathbb{R}^d} \varepsilon(\mathbf{e}) m(\nu, \mathbf{g}+\mathbf{e})d\mathbf{e}$. Furthermore, the fitness function for trait values $m(\nu, \mathbf{z})$ and the fitness function for genetic values $m_*(\gamma, \mathbf{g})$ have the same mean value across the population

$$\begin{aligned}\bar{m}_* &= \frac{1}{n}\int_{\mathbb{R}^d} m_*(\gamma, \mathbf{g})\,\gamma(\mathbf{g})\,d\mathbf{g}\\ &= \frac{1}{n}\int_{\mathbb{R}^d}\int_{\mathbb{R}^d} m(\nu, \mathbf{z})\,\varepsilon(\mathbf{e})\,\gamma(\mathbf{z}-\mathbf{e})\,d\mathbf{e}\,d\mathbf{z}\\ &= \frac{1}{n}\int_{\mathbb{R}^d} m(\nu, \mathbf{z})\,\nu(\mathbf{z})\,d\mathbf{z} = \bar{m}. \qquad (13)\end{aligned}$$

The dynamics of γ are given in analogy to $\dot{\nu}$ as

$$\dot{\gamma}(\mathbf{g}) = m_*(\gamma, \mathbf{g})\,\gamma(\mathbf{g}) + \tfrac{1}{2}\nabla^{\top}\boldsymbol{\mu}\nabla\,\gamma(\mathbf{g}). \qquad (14)$$

The frequency of $\mathbf{g}$ in the population is given by $\varrho(\mathbf{g}) = \gamma(\mathbf{g})/n$. In combination with the model for phenotypic noise, the mean trait vector is calculated as $\bar{\mathbf{z}} = \bar{\mathbf{g}}$ and the trait covariance matrix is $\mathbf{P} = \mathbf{G} + \mathbf{E}$. To simplify calculating fitness, and to accommodate the assumption of multivariate normal traits, I assume $\varepsilon(\mathbf{e})$ is the density of a multivariate normal distribution (with mean zero and covariance matrix $\mathbf{E}$).

Under these assumptions the expression for abundance dynamics does not change, but the mean trait dynamics can be calculated as

$$\dot{\bar{\mathbf{z}}} = \mathbf{G}\,(\nabla_{\bar{\mathbf{z}}}\,\bar{m} - \overline{\nabla_{\bar{\mathbf{z}}}\,m}), \qquad (15)$$

and $\mathbf{G}$-matrix dynamics are given by

$$\dot{\mathbf{G}} = \boldsymbol{\mu} + 2\,\mathbf{G}\,(\nabla_{\mathbf{G}}\,\bar{m} - \overline{\nabla_{\mathbf{G}}\,m})\,\mathbf{G}. \qquad (16)$$

I apply this model of imperfect inheritance while describing the stochastic extensions of the framework below. Further details about how imperfect inheritance is interfaced with the formal details of the stochastic extension are provided in the supplement section 3.

2.2. Stochastic Dynamics

In this section, I present an extension of the framework to the case where demographic stochasticity induces random genetic drift. This extension comes in two variants, and both build on the deterministic DG version of the framework above.

The first variant, called BG, expresses stochastic dynamics with respect to Brownian motion processes, as is standard for stochastic differential equations (Øksendal, 2003; Evans, 2012). BG is particularly useful for numerical applications, and can be implemented using the Euler-Maruyama algorithm (Bayram et al., 2018). I illustrate this during a brief study of genetic correlations evolving in response to random genetic drift. Further information is provided in supplement 4. Implementations of this approach using the DifferentialEquations.jl package in Julia (Rackauckas and Nie, 2017), and a manual implementation are provided at the github repository github.com/bobweek/multi-mtgl.

The second variant, called MG, is useful for deriving the dynamics of more specific quantities. This use-case is illustrated below to formally obtain a stochastic differential equation tracking the evolution of genetic correlations in response to random genetic drift. To do so, I introduce a powerful set of novel heuristics (i.e., methods for performing exact calculations without formal justification) that can be used to derive an array of models from this variant of the framework. These heuristics are obtained by examining a so-called martingale process underlying this entire framework, which is also the namesake of MG. Mathematical details are provided in section 2 of the supplement.

Both stochastic extensions of the framework include an additional variable v, which is associated with the variance of lifetime reproductive output of individuals (Week et al., 2021). Previous work has shown that a novel form of selection can emerge when v depends on trait value, referred to as *noise-induced selection*, and for which evolutionary responses behave radically different from classical deterministic selection (Constable et al., 2016; Parsons et al., 2010; Kuosmanen et al., 2022; Bhat and Guttal, 2025). However, accounting for noise-induced selection leads to significantly more complex expressions for the evolution of mean trait vector and trait covariance matrix (e.g., see Week et al., 2021, for the univariate case). Furthermore, the importance of noise-induced selection has not been empirically established. Then, as a first pass, I keep the expressions relatively simple by assuming v is constant across trait values.

2.2.1. The Brownian Motion Gradient Version (BG)

Accounting for the effects of demographic stochasticity, the abundance dynamics can now be expressed as the following stochastic differential equation

$$dn = \bar{m}\,n\,dt + \sqrt{v\,n}\,dB_n, \qquad (17)$$

where the noise process B_n is a standard Brownian motion (i.e., $B_n(t)$ has variance equal to t and $B_n(0) = 0$). Assuming multivariate normality, and the above model of imperfect inheritance, the mean trait dynamics are given by

$$d\bar{\mathbf{z}} = \mathbf{G}\,(\nabla_{\bar{\mathbf{z}}}\,\bar{m} - \overline{\nabla_{\bar{\mathbf{z}}}\,m})\,dt + \sqrt{\frac{v}{n}\,\mathbf{G}}\;d\mathbf{B}_{\bar{\mathbf{z}}}, \qquad (18)$$

with $\mathbf{B}_{\bar{\mathbf{z}}}$ a d-dimensional vector of independent standard Brownian motions. Equation (18) provides a continuous-time extension to the framework of multivariate evolution introduced by Lande (1979). Alternatively, the stochastic dynamics of mean traits can be expressed using index notation as

$$d\bar{z}_i = \sum_{j=1}^{d} G_{ij}\,(\partial_j\,\bar{m} + \overline{\partial_j\,m})\,dt + \sqrt{\frac{v}{n}\,G_{ii}}\;dB_{\bar{z}_i}, \qquad (19)$$

where $\partial_i = \partial/\partial\bar{z}_i$ and, for each i, $B_{\bar{z}_i}$ is a standard Brownian motion and non-independence for each ij is encoded by the heuristic $dB_{\bar{z}_i}\, dB_{\bar{z}_j} = \rho_{ij}\, dt$, with $\rho_{ij} = G_{ij}/\sqrt{G_{ii}\, G_{jj}}$ the genetic correlation between traits i and j. This heuristic is particularly useful when applying Itô's formula (the stochastic analog of the chain rule, see Øksendal, 2003; Evans, 2012) to derive dynamics for functions of mean trait values. This approach may be used, for example, to track the dynamics of interaction coefficients for coevolving species as a multivariate generalization of the approach taken by Week and Nuismer (2021).

In equation (18) the correlated effects of genetic drift on mean trait evolution are encoded by the product $\sqrt{\mathbf{G}}d\mathbf{B}_{\bar{\mathbf{z}}}$. In contrast, for equation (19), these correlated effects are encoded directly by the non-independence of the Brownian motions $B_{\bar{z}_1}, \ldots, B_{\bar{z}_d}$. In particular, the i-th entry of $d\mathbf{B}_{\bar{\mathbf{z}}}$ is not equal to $dB_{\bar{z}_i}$ because $(d\mathbf{B}_{\bar{\mathbf{z}}})_i\, (d\mathbf{B}_{\bar{\mathbf{z}}})_j = \delta_{ij}\, dt$, where $\delta_{ij} = 1$ when $i = j$ and zero otherwise. These heuristics work in the absence of multivariate normality, but the deterministic component of $d\bar{\mathbf{z}}$ expressed above does depend on multivariate normality.

The application of the multivariate normal approximation to the stochastic dynamics of the $\mathbf{G}$-matrix leads to the matrix equation

$$d\mathbf{G} = \left(\boldsymbol{\mu} + 2\,\mathbf{G}\,(\nabla_{\mathbf{G}}\,\bar{m} - \overline{\nabla_{\mathbf{G}}\, m})\,\mathbf{G} - \frac{v}{n}\,\mathbf{G}\right)\, dt + \sqrt{\frac{v}{n}\,\boldsymbol{\Gamma}} : d\mathbf{B}_{\mathbf{G}}, \tag{20}$$

where $\boldsymbol{\Gamma}$ is a fourth-order tensor describing the covariance structure for the response of $\mathbf{G}$ to drift. Defining products of fourth-order tensors $\mathbf{X}$ and $\mathbf{Y}$ by $(\mathbf{X} : \mathbf{Y})_{ijkl} = \sum_{mn} \mathbf{X}_{ijmn}\mathbf{Y}_{mnkl}$, we can write $\boldsymbol{\Gamma} = \sqrt{\boldsymbol{\Gamma}} : \sqrt{\boldsymbol{\Gamma}}$. Furthermore, we have $\sqrt{\boldsymbol{\Gamma}}_{ijkl} = \left(\sqrt{\mathbf{G}}_{ik}\sqrt{\mathbf{G}}_{jl} + \sqrt{\mathbf{G}}_{il}\sqrt{\mathbf{G}}_{jk}\right)/\sqrt{2}$, and $\sqrt{\mathbf{G}}_{ij}$ is the ij-th entry of $\sqrt{\mathbf{G}}$ which is *not* equal to $\sqrt{G_{ij}}$. Matrix square roots are defined using the eigenvalue decomposition (given $\mathbf{G} = \mathbf{U}\boldsymbol{\Lambda}\mathbf{U}^{-1}$ then $\sqrt{\mathbf{G}} = \mathbf{U}\sqrt{\boldsymbol{\Lambda}}\mathbf{U}^{-1}$).

The product $\sqrt{\boldsymbol{\Gamma}} : d\mathbf{B}_{\mathbf{G}}$ returns a $d \times d$ matrix with ij-th entry $(\sqrt{\boldsymbol{\Gamma}} : d\mathbf{B}_{\mathbf{G}})_{ij} = \sum_{kl} \sqrt{\boldsymbol{\Gamma}}_{ijkl}\, (d\mathbf{B}_{\mathbf{G}})_{kl}$. The $d \times d$ matrix-valued Brownian motion $\mathbf{B}_{\mathbf{G}}$ has independent standard Brownian motions along its diagonal entries. The off-diagonal entries are standard Brownian motions scaled by one-half (i.e., the variance of $(\mathbf{B}_{\mathbf{G}})_{ij}(t)$ is $t/2$ when $i \neq j$), and symmetric entries are equivalent so that $(\mathbf{B}_{\mathbf{G}})_{ij} = (\mathbf{B}_{\mathbf{G}})_{ji}$. The covariance structure of $\mathbf{B}_{\mathbf{G}}$ is summarized by the heuristic

$$(d\mathbf{B}_{\mathbf{G}})_{ij}\, (d\mathbf{B}_{\mathbf{G}})_{kl} = \frac{\delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk}}{2}\, dt. \tag{21}$$

Scaling the off-diagonals by one-half ensures variances and covariances are correctly propagated while calculating the stochastic consequences of drift for $\mathbf{G}$-matrix dynamics. Further information on symmetric normal matrices can be found in Gupta and Nagar (2018), particularly theorem 2.5.1.

Unlike the expression for the stochastic component of $d\bar{\mathbf{z}}$, the stochastic component for $d\mathbf{G}$ does depend on the assumption of a multivariate normal trait distribution.

Using index notation, the expression (20) simplifies to a $d(d+1)/2$-dimensional system of equations summarized by

$$\begin{aligned} dG_{ij} = \left(\mu_{ij} + 2\sum_{kl} G_{ik}\,(\partial_{kl}\,\bar{m} - \overline{\partial_{kl}\, m})\, G_{lj} - \frac{v}{n}\, G_{ij}\right)\, dt \\ + \sqrt{\frac{v}{n}}\sqrt{G_{ii}\, G_{jj} + G_{ij}^2}\, dB_{G_{ij}}, \end{aligned} \tag{22}$$

for $1 \leq i \leq j \leq d$ where $\partial_{ij} = \partial/\partial G_{ij}$ and for each ij we have $B_{G_{ij}}$ is a standard Brownian motion with $B_{G_{ij}} = B_{G_{ji}}$. Importantly, note that $dB_{G_{ij}}$ is *not* the ij-th entry of $d\mathbf{B}_{\mathbf{G}}$. This is made clear by the heuristic

$$dB_{G_{ij}}\, dB_{G_{kl}} = \frac{G_{ik}\, G_{jl} + G_{il}\, G_{jk}}{\sqrt{(G_{ii}\, G_{jj} + G_{ij}^2)\, (G_{kk}\, G_{ll} + G_{kl}^2)}}\, dt. \tag{23}$$

Finally, the noise process driving abundance in general does not covary with the noise processes driving mean traits and trait covariances (i.e., $dB_n\, dB_{\bar{z}_i} = dB_n\, dB_{G_{kl}} = 0$), and, under the assumption of multivariate normality, the same holds for trait means and trait covariances (i.e., $dB_{\bar{z}_i}\, dB_{G_{kl}} = 0$). This agrees with the off-diagonal entries in equation (8b) of Barton (1989), but my results for the diagonal entries disagree. See supplement section 3 for more details.

The vector-matrix expression of *BG* (equations (18) and (20)) is particularly well-suited for numerical exploration of models because the covariance structure of the noise processes associated with random genetic drift are written explicitly in terms of sums involving the entries of the matrix square root $\sqrt{\mathbf{G}}$. Hence, this version of the framework is easily interfaced with a common algorithm to numerically integrate systems of stochastic differential equations, the Euler-Maruyama method (Bayram et al., 2018). The numerical benefits of the *BG* version of the framework are highlighted in section 3 below to study $\mathbf{G}$-matrix evolution.

The expression of *BG* in index notation (equations 19 and 22), while arguably more complex in appearance, are useful for deriving analytical results, and especially when applying Itô's formula (a stochastic generalization of the chain-rule from calculus, see section 2.2 of the supplement) to derive the dynamics of a quantity depending on $\bar{\mathbf{z}}$ and/or $\mathbf{G}$ (such as the dynamics of growth rate, $d\bar{m}$, for instance). However, there are limitations with this application of *BG*, particularly for dealing with sums of stochastic differentials such as $U = a\, dB_{G_{ij}} + b\, dB_{G_{kl}}$. If the Brownian motions $B_{G_{ij}}$ and $B_{G_{kl}}$ were independent, then we can write $U = \sqrt{a^2 + b^2}dB$ with B being another standard Brownian motion. Because $B_{G_{ij}}$ and $B_{G_{kl}}$ are not independent, which is captured by equation (23) above, it is not obvious how to properly express U in terms of a, b and a single standard Brownian motion B.

To overcome these challenges, and also to simplify typical calculations, it is useful to rewrite the stochastic components of equations (19) and (22) in terms of an underlying stochastic process $\mathcal{M}$. Because $\mathcal{M}$ satisfies a martingale property (roughly, this means $\mathbb{E}[\,\mathcal{M}(t+s) \mid \mathcal{M}(t)\,] = \mathcal{M}(t)$ for all $s > 0$), I refer to this version of the framework as the Martingale Gradient version (or *MG* for short). In the following sub-section, I present this version of the framework in a way that minimizes technical pre-requisites, while maintaining the same scope as equations (19) and (22) above. Additionally, heuristics are offered for making calculations, and these are demonstrated by deriving a stochastic differential equation for the correlation between two traits driven purely by random genetic drift.

2.2.2. The Martingale Gradient Version (MG)

In supplement section 2, I show that this framework is justified based on a martingale process $\mathcal{M}$. Brownian motion is a special case of a martingale process, and stochastic equations are often expressed in terms of a Brownian stochastic differential dB. However, in this framework, stochastic equations can also be expressed in terms of the stochastic differential with respect to $\mathcal{M}$, denoted by $d\mathcal{M}$. This establishes a powerful approach for deriving fundamental insights into evolutionary processes. Further mathematical details are provided in supplement sections 2 and 3, but here I focus on pragmatic aspects regarding calculations that involve $d\mathcal{M}$.

I begin by artificially defining symbols related to $d\mathcal{M}$ in terms of the Brownian motions that appear in equations (17), (18), and (20), and use these definitions to express the framework in terms of $d\mathcal{M}$. This is done purely for the sake of motivating the material that follows. After this, I introduce some properties of $d\mathcal{M}$ and show how these can be used to recover the Brownian motions initially used in the artificial definitions mentioned above. I then provide general heuristics for working with $d\mathcal{M}$ and illustrate these heuristics by deriving the response of trait correlations to random genetic drift.

For now, define the symbols $d\mathcal{M}(1), d\mathcal{M}(g_i - \bar{g}_i)$ and $d\mathcal{M}\big((g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij}\big)$ as follows:

$$d\mathcal{M}(1) := \sqrt{v\,n}\, dB_n, \tag{24a}$$

$$d\mathcal{M}(g_i - \bar{g}_i) := \sqrt{v\,n\,G_{ii}}\, dB_{\bar{z}_i}, \tag{24b}$$

$$d\mathcal{M}\big((g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij}\big) := \sqrt{v\,n}\,\sqrt{G_{ii}\,G_{jj} + G_{ij}^2}\, dB_{G_{ij}}. \tag{24c}$$

Using this notation, the MG version of the framework can be written as

$$dn = \bar{m}\,n\,dt + d\mathcal{M}(1), \tag{25a}$$

$$d\bar{z}_i = \sum_{j=1}^{d} G_{ij}\,(\partial_j\,\bar{m} + \overline{\partial_j\,m})\,dt + \frac{1}{n}\,d\mathcal{M}(g_i - \bar{g}_i), \tag{25b}$$

$$\begin{aligned} dG_{ij} = {} & \left(\mu_{ij} + 2\sum_{kl} G_{ik}\,(\partial_{kl}\,\bar{m} - \overline{\partial_{kl}\,m})\,G_{lj} - \frac{v}{n}G_{ij}\right) dt \\ & + \frac{1}{n}d\mathcal{M}\big((g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij}\big), \end{aligned} \tag{25c}$$

where recall that $\partial_i = \partial/\partial\bar{z}_i$ and $\partial_{ij} = \partial/\partial G_{ij}$.

The covariance structure of the system is maintained through heuristics for computing products of the above stochastic differentials $d\mathcal{M}(x)$. To understand these heuristics, I introduce some useful notation for keeping track of averages across the distribution of traits in the population. Specifically, for functions $x(\mathbf{g})$ and $y(\mathbf{g})$, I define the symbols $\|\,x\,\|$ and $\langle\, x,\, y\,\rangle$ as follows:

$$\|\,x\,\| = \sqrt{v\,n}\sqrt{\overline{x^2}} = \sqrt{v\,n}\sqrt{\int_{\mathbb{R}^d} x^2(\mathbf{g})\,\varrho(\mathbf{g})\,d\mathbf{g}}, \tag{26a}$$

$$\langle\, x,\, y\,\rangle = v\,n\,\overline{x\,y} = v\,n\int_{\mathbb{R}^d} x(\mathbf{g})\,y(\mathbf{g})\,\varrho(\mathbf{g})\,d\mathbf{g}, \tag{26b}$$

where $\varrho(\mathbf{g}) = \gamma(\mathbf{g})/n$ is the distribution of additive genetic values $\mathbf{g}$ in the population (assumed to be multivariate normal). To provide a few examples, one can calculate $\|1\| = \sqrt{v\,n}\sqrt{\int 1^2\,\varrho(\mathbf{g})\,d\mathbf{g}} = \sqrt{v\,n}$ along with

$$\|g_i - \bar{g}_i\| = \sqrt{v\,n}\sqrt{\int_{\mathbb{R}^d} (g_i - \bar{g}_i)^2\,\varrho(\mathbf{g})\,d\mathbf{g}} = \sqrt{v\,n\,G_{ii}}, \tag{27a}$$

$$\langle\, g_i - \bar{g}_i,\, g_j - \bar{g}_j\,\rangle = v\,n\int_{\mathbb{R}^d} (g_i - \bar{g}_i)\,(g_j - \bar{g}_j)\,\varrho(\mathbf{g})\,d\mathbf{g} = v\,n\,G_{ij}. \tag{27b}$$

The martingale process $\mathcal{M}$ mentioned above can be thought of as a mapping that associates functions with stochastic processes. This idea is made precise in section 2 of the supplement. What is relevant here is that, by setting $\hat{x}(\mathbf{g}) = x(\mathbf{g})\,/\,\|\,x\,\|$, the stochastic differential $d\mathcal{M}(\hat{x})$ is formally equivalent to the stochastic differential of a standard Brownian motion (such as dB_n, for example). Furthermore, from supplement section 2.2 we have the *scaling property*:

$$\frac{d\mathcal{M}(x)}{\|\,x\,\|} = d\mathcal{M}\left(\frac{x}{\|\,x\,\|}\right). \tag{28}$$

Using this heuristic, we can calculate

$$d\mathcal{M}(1) = \|1\|\,d\mathcal{M}\left(\frac{1}{\|1\|}\right) = \sqrt{v\,n}\,d\mathcal{M}(\hat{1}), \tag{29a}$$

$$d\mathcal{M}(g_i - \bar{g}_i) = \|g_i - \bar{g}_i\|\,d\mathcal{M}\left(\frac{(g_i - \bar{g}_i)}{\|g_i - \bar{g}_i\|}\right) = \sqrt{v\,n\,G_{ii}}\,d\mathcal{M}(\widehat{g_i - \bar{g}_i}). \tag{29b}$$

Comparing with equations (17) and (18), these calculations highlight the fact that $dB_n = d\mathcal{M}(\hat{1})$ and $dB_{\bar{z}_i} = d\mathcal{M}(\widehat{g_i - \bar{g}_i})$. A similar equality holds for $dB_{G_{ij}}$, but for the sake of brevity this expression is omitted.

Informally speaking, this scaling property allows us to "factor out" the standard deviation from the noise process driving the dynamics of a univariate function of the population (such as n, $\bar{z}_i$, or G_{ij}), and to replace that noise process with the product of the resulting standard deviation with a standard Brownian motion. This is the crucial step for obtaining equations (17), (19), and (22) from the underlying martingale process $\mathcal{M}$, as detailed in supplement section 3 where these heuristics are applied to derive MG and BG.

Just as $B_{\bar{z}_i}$ and $B_{\bar{z}_j}$ have a covariance encoded by the heuristic $dB_{\bar{z}_i}\,dB_{\bar{z}_j} = \big(G_{ij}\,/\sqrt{G_{ii}\,G_{jj}}\big)\,dt$, the processes $\mathcal{M}(x)$ and $\mathcal{M}(y)$ will also covary following a more general heuristic. More precisely, for functions x, y, we have the *multiplicative property*:

$$d\mathcal{M}(x)\,d\mathcal{M}(y) = \langle\, x,\, y\,\rangle\,dt, \tag{30}$$

where $\langle\, x,\, x\,\rangle = \|\,x\,\|^2$. In addition, we have $dt^2 = 0$ and $dt\,d\mathcal{M}(x) = d\mathcal{M}(x)\,dt = 0$ for any function x, which are common heuristics in standard approaches to stochastic differential equations (Øksendal, 2003; Evans, 2012).

Finally, we also have the *additive property*: $d\mathcal{M}(a\,x + b\,y) = a\,d\mathcal{M}(x) + b\,d\mathcal{M}(y)$, for functions x, y and constants a, b. This property is particularly useful for computing the correct stochastic term for an equation resulting from the application of Itô's formula, as illustrated below.

With these heuristics, it is straightforward to work with the MG version of the framework presented by equations (25) to rigorously obtain the dynamics of quantities related to the population. For instance, these heuristics may be used to formally derive a stochastic differential equation for the evolution of genetic correlations in response to drift. Indeed, I do this now.

3. Genetic Correlations and **G**-matrix Dynamics

In the following sub-section I illustrate how to apply the above framework to obtain new models of evolutionary phenomena. Specifically, I apply the heuristics introduced in the MG version of the framework to derive the dynamics of genetic correlations responding only to random genetic drift. Using this derivation, I then provide biological insights into the consequences of drift for genetic correlations in a clonally reproducing populations. In section 3.2, I then discuss the significance of these results in the context of empirical research on **G**-matrix dynamics.

3.1. Consequences of Drift for Trait Correlations

The additive genetic correlation between traits z_i and z_j is given by $\rho_{ij} = G_{ij} / \sqrt{G_{ii}\, G_{jj}}$. For this sub-section, I focus on the single correlation between z_i and z_j, and simply write this as ρ. To focus on the effects of random genetic drift, and for the sake of simplicity, I ignore mutation, selection, and abundance dynamics in this analysis.

Because we have the stochastic equations for dG_{ij}, dG_{ii}, and dG_{jj} (equation 25c), and because ρ can be thought of as a function $\rho(G_{ij}, G_{ii}, G_{jj}) = G_{ij} / \sqrt{G_{ii}\, G_{jj}}$, we can apply Itô's formula, which, in this context, states the following stochastic analog of the chain-rule: $d\rho = K + L$, with $K = (\partial_{ij}\rho)\, dG_{ij} + (\partial_{ii}\rho)\, dG_{ii} + (\partial_{jj}\rho)\, dG_{jj}$ and

$$\begin{aligned} L = \tfrac{1}{2} \Big[\, &(\partial^2_{ij}\rho)\, (dG_{ij})^2 + (\partial^2_{ii}\rho)\, (dG_{ii})^2 + (\partial^2_{jj}\rho)\, (dG_{jj})^2 \, \Big] \\ &+ (\partial_{ij}\, \partial_{ii}\rho)\, (dG_{ij})\, (dG_{ii}) + (\partial_{ij}\, \partial_{jj}\rho)\, (dG_{ij})\, (dG_{jj}) \\ &+ (\partial_{ii}\, \partial_{jj}\rho)\, (dG_{ii})\, (dG_{jj}), \qquad (31) \end{aligned}$$

where $\partial_{ij}\rho$ is the partial derivative of ρ with respect to G_{ij}.

With this formula in hand, all that is left is to carry out calculations based on the heuristics from the *MG* version of the framework. First off, we can directly compute the *deterministic* component of the sum K and find that this cancels to zero. This part of the calculation does not require the heuristics for $d\mathcal{M}$ introduced above. However, by leveraging the additive property of $d\mathcal{M}$, the *stochastic* component of K can be rewritten as

$$\begin{aligned} &\tfrac{1}{n}(\partial_{ij}\rho)\, d\mathcal{M}\big((g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij}\big) \\ &\quad + \tfrac{1}{n}(\partial_{ii}\rho)\, d\mathcal{M}\big((g_i - \bar{g}_i)(g_i - \bar{g}_i) - G_{ii}\big) \\ &\quad + \tfrac{1}{n}(\partial_{jj}\rho)\, d\mathcal{M}\big((g_j - \bar{g}_j)(g_j - \bar{g}_j) - G_{jj}\big) \\ &= \tfrac{1}{n}\, d\mathcal{M}\Big((\partial_{ij}\rho)\big((g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij}\big) \\ &\quad + (\partial_{ii}\rho)\big((g_i - \bar{g}_i)(g_i - \bar{g}_i) - G_{ii}\big) \\ &\quad + (\partial_{jj}\rho)\big((g_j - \bar{g}_j)(g_j - \bar{g}_j) - G_{jj}\big)\Big). \qquad (32) \end{aligned}$$

Writing the argument to $d\mathcal{M}$ on the right-hand-side of equation (32) as H_{ij}, the stochastic component of K becomes

$$\tfrac{1}{n}\|H_{ij}\| d\mathcal{M}(\hat{H}_{ij}), \qquad (33)$$

where $\hat{H}_{ij} = H_{ij}/\|H_{ij}\|$. Calculation of $\|H_{ij}\|$ only requires computation of the first order derivatives $\partial_{ij}\rho$, $\partial_{ii}\rho$, $\partial_{jj}\rho$ and the fact from multivariate normal distributions that

$$\begin{aligned} &\int_{\mathbb{R}^d} (g_i - \bar{g}_i)(g_j - \bar{g}_j)(g_k - \bar{g}_k)(g_l - \bar{g}_l)\varrho(g) dg \\ &\qquad = G_{ij}G_{kl} + G_{ik}G_{jl} + G_{il}G_{jk}. \qquad (34) \end{aligned}$$

Working through these calculations provides

$$K = \sqrt{\frac{v}{n}}(1 - \rho^2) dB_\rho, \qquad (35)$$

where $dB_\rho = d\mathcal{M}(\hat{H}_{ij})$ is a scalar-valued standard Brownian motion.

To compute L, I first rewrite the product $(dG_{ij})\,(dG_{kl})$ using the notation introduced in the *MG* version of the framework above, which provides

$$\begin{aligned} (dG_{ij})\,(dG_{kl}) = \tfrac{1}{n^2}\, &d\mathcal{M}\big[\, (g_i - \bar{g}_i)(g_j - \bar{g}_j) - G_{ij} \,\big] \\ &\times d\mathcal{M}\big[\, (g_k - \bar{g}_k)(g_l - \bar{g}_l) - G_{kl} \,\big]. \qquad (33) \end{aligned}$$

Applying the heuristics for $d\mathcal{M}$, the product simplifies to

$$\begin{aligned} (dG_{ij})\,(dG_{kl}) = \tfrac{1}{n^2}\big[\, &\langle\, (g_i - \bar{g}_i)(g_j - \bar{g}_j),\, (g_k - \bar{g}_k)(g_l - \bar{g}_l) \,\rangle \\ &- v\, n\, G_{ij}\, G_{kl} \,\big]\, dt, \qquad (34) \end{aligned}$$

where I made use of $\langle\, (g_i - \bar{g}_i)(g_j - \bar{g}_j),\, G_{kl} \,\rangle = v\, n\, G_{ij}\, G_{kl}$. Again applying property (34) from above, I obtain the further simplification $(dG_{ij})\,(dG_{kl}) = \frac{v}{n}(G_{ik}G_{jl} + G_{il}G_{jk})$. Interfacing this result with derivatives of f, I arrive at

$$L = -\frac{1}{2}\frac{v}{n}\,\rho\,(1 - \rho^2)\, dt. \qquad (36)$$

Hence, by applying the *MG* version of the framework, I find that trait correlations driven entirely by drift follow the ordinary stochastic differential equation

$$d\rho = -\frac{1}{2}\frac{v}{n}\rho(1 - \rho^2)dt + \sqrt{\frac{v}{n}}(1 - \rho^2)dB_\rho. \qquad (37)$$

Equation (37) shows that the effect of drift is mediated by the ratio of the variance of lifetime reproductive output v (typically set to $v = 1$ in classical quantitative genetic models such as Lande, 1976) to the effective population size n. Additionally, one can check that (because mutation and selection are absent) $\rho = \pm 1$ are stationary points. Furthermore, leveraging the fact that equation (37) defines a one-dimensional diffusion, we can in principle solve for its stationary distribution $\hat{q}(\rho)$ (Karlin and Taylor, 1981; Etheridge, 2010). However, in attempt to do so we arrive at the non-integrable function:

$$\hat{q}(\rho) \propto \frac{1}{(1 - \rho^2)^{3/2}}. \qquad (38)$$

The lack of a formal stationary distribution creates a challenge for understanding the limiting behavior of genetic correlations evolving solely in response to drift. This can be partially overcome by again leveraging the theory of one-dimensional diffusions to demonstrate that the boundaries ± 1 are both attracting and unattainable (Karlin and Taylor, 1981). That is, genetic correlations tend towards their extremes, but never fix at ± 1. This is visualized in Figure 1 by plotting the distribution $q(\rho)$ of genetic correlations as numerical solutions to the forwards Kolmogorov (i.e., Fokker-Planck) equation associated with (37). Biologically, $|\rho|$ increases because drift randomly samples finite numbers of individuals, thereby causing spurious correlations among the additive genetic values these individuals carry. Further biological implications are discussed in the following section.

Another way to view this result is by applying Itô's formula to $u = \tanh(\rho)$. Doing so returns

$$du = \frac{1}{2}\frac{v}{n}\tanh(u)dt + \sqrt{\frac{v}{n}}dB_u. \qquad (39)$$

Because $\rho = \tanh^{-1}(u)$ is a monotone increasing function of u, statements about u map directly to ρ. In particular, $u = \rho = 0$ is unstable because $\tanh(u)$ is positive for positive u, and negative for negative u. Additionally, if u is much greater than 1, then $du \approx v\, dt/2n + \sqrt{v/n}\, dB_u$ and, writing

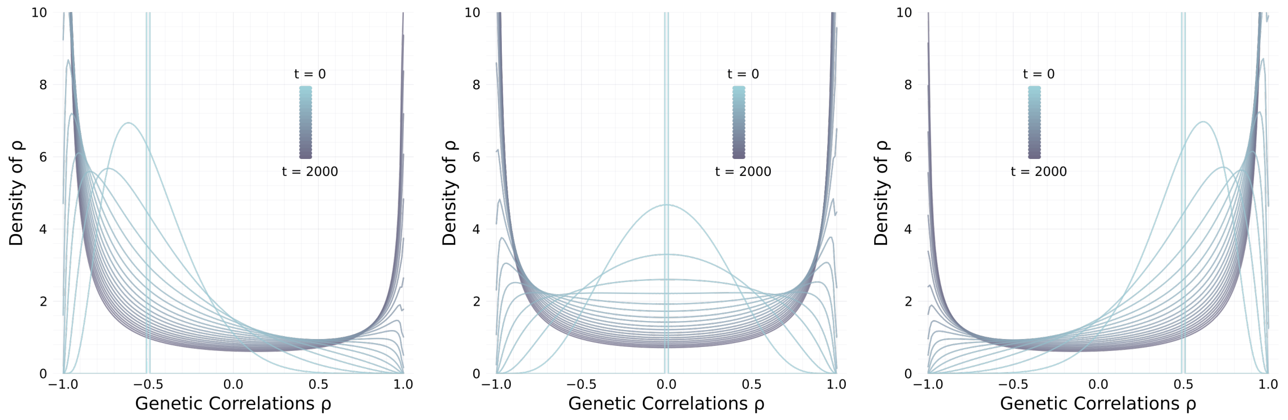

Fig. 1. The distribution of genetic correlations evolving under drift alone converges to a non-integrable stationary solution. Shown here are dynamics for initial distributions taking approximate point masses at $\rho_0 = -0.5$ (left panel), $\rho_0 = 0.0$ (middle panel), and $\rho_0 = 0.5$ (right panel). Solutions at earlier times are colored green, and later times are purple which run until $t = 2000$. The rate of drift is set to $v/n = 0.001$.

this point as u_0, we have $\mathbb{E}[u_t] \approx u_0 + v\,t/2n$. The analogous approximation holds when u is much less than -1. This agrees with the boundary classification result above that demonstrates drift has an overall tendency to drive trait correlations towards ±1. Numerical estimates for sample paths of the solution to (37), illustrated by Figure 2, support this conclusion.

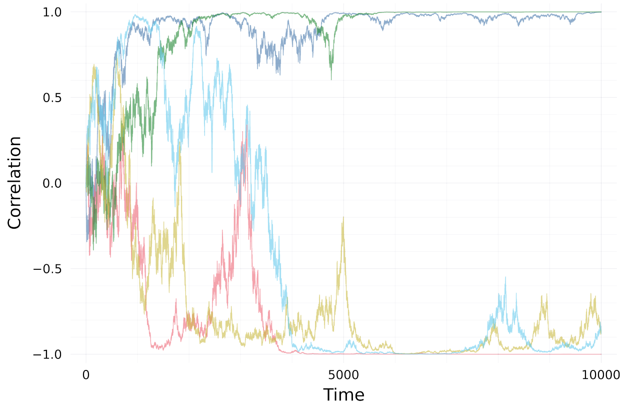

Fig. 2. Drift drives trait correlations towards ±1. Shown here are five replicates illustrating the path-behavior of trait correlations following equation (37). Each replicate is initiated with $\rho_0 = 0$ and the rate of drift is set to $v/n = 0.001$.

To confirm the heuristics return correct expressions, I also simulated the evolution of the **G**-matrix driven solely by random genetic drift for a 2-dimensional trait by applying the Euler-Maruyama method (Bayram et al., 2018) to the *BG* version of the framework. I then back-calculated the genetic correlation ρ based on the simulated time-series of **G**. Figure 1 in the supplement demonstrates this approach agrees with equation (37). Further information on the numerical implementation is given in supplement section 4, and associated code is available at the github repository github.com/bobweek/multi-mtgl.

3.2. Evolution of The G-Matrix in Response to Drift

The above result demonstrates that drift increases correlations between traits, especially for clonally reproducing populations where recombination is absent. This perspective offers an important refinement of the conventional wisdom that **G**-matrices responding to drift should merely scale in size (Lande, 1979; Phillips and McGuigan, 2006; Dugand et al., 2021; Mallard et al., 2023a). In particular, it is classically thought that the orientation of the **G**-matrix should not change due to drift on average, and hence any changes in orientation may be a sign of selection (Roff, 2000; Steppan et al., 2002; Cano et al., 2004; Chapuis et al., 2008; Aguirre et al., 2013).

This idea can be obtained from equation (20) if the stochastic component is neglected. Then, the deterministic response due to drift is described by $\dot{\mathbf{G}} = -v\,\mathbf{G}/n$, which has the solution $\mathbf{G}_t = \mathbf{G}_0 e^{-v\,t/n}$, and is a continuous-time equivalent of the result found by Lande (1979). Numerical results displayed in Figure 2 of the supplement indicate agreement with this classical scaling result. However, when stochastic outcomes are highly variable, the average response to drift may provide little information for within-population dynamics.

Taking an experimental approach, Phillips et al. (2001) established isolated populations of *Drosophila melanogaster* from a common base population and found significant variation across replicates for the response of **G** to drift. This occurs in spite of the fact that *Drosophila melanogaster* is a sexually reproducing organism, and recombination should act to break up correlations caused by linkage (discussed further below) and thereby reduce variation across replicates. Figure 3 emphasizes these variable outcomes theoretically by superimposing expected trait correlations over a collection of individual outcomes. The expected correlations are approximated by averaging over replicates, but it took a very large number of replicates (>1000) to obtain a satisfactory deterministic trend. The averages shift towards zero, but we can see individual replicates are not predicted by this trend. Hence, to gain a more accurate picture of **G**-matrix evolution, there is a need to understand the path behavior of individual outcomes.

One approach to gain insight for the trait correlation of a given replicate, as opposed to the average, is to analyze the

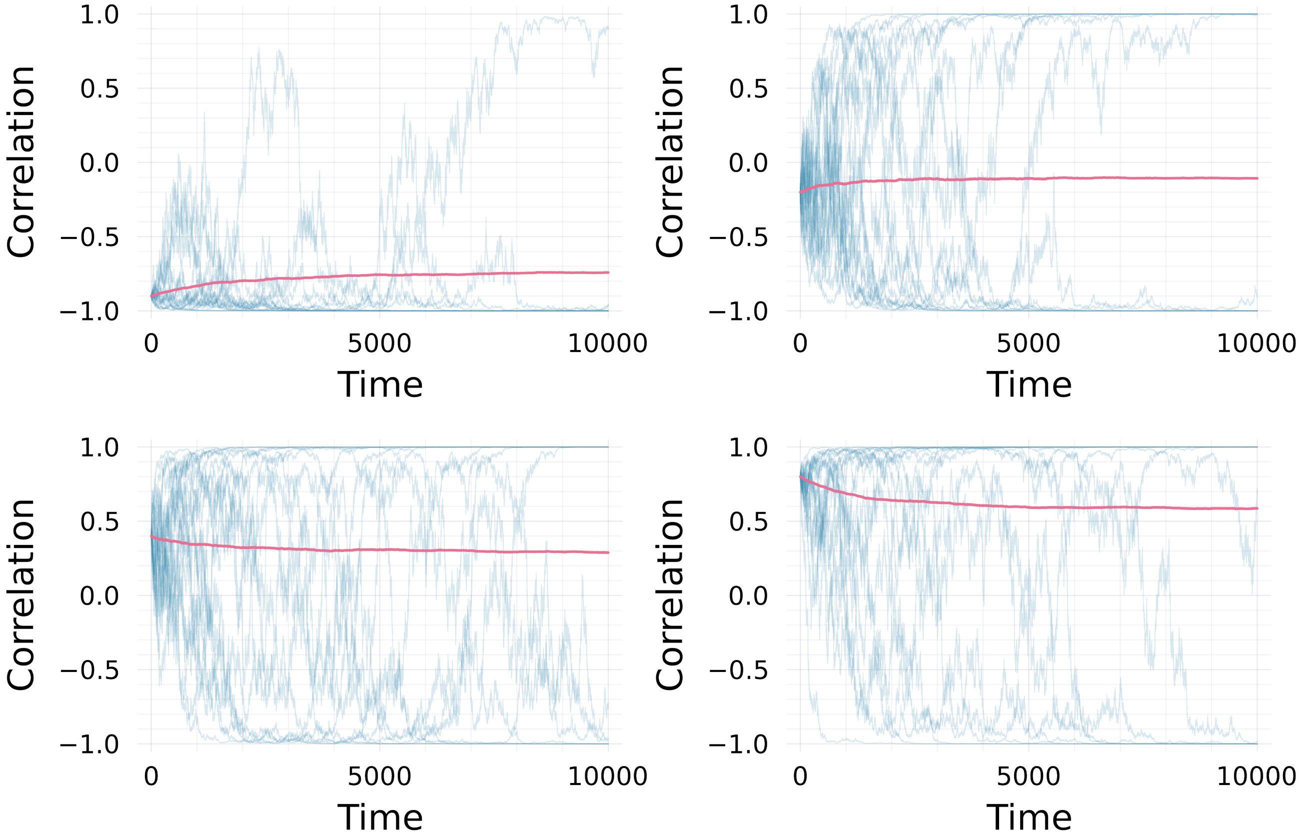

Fig. 3. Averages over replicated time-series of trait correlation do not predict within population trait correlations. Averages were computed using 3000 replicates with initial correlations $\rho_0 = -0.9$ (top-left), $\rho_0 = -0.5$ (top-right), $\rho_0 = 0.3$ (bottom-left), and $\rho_0 = 0.8$ (bottom-right). For the sake of clarity, just 20 random replicates are shown behind the average trends.

proportion of time that correlations spend near ±1 over the total time the process is running. Figure 4 plots the proportion of time that a correlation spends either in the range $0.95 < \rho < 1.0$ or in $-1.0 < \rho < -0.95$ averaged over 100 replicates with initial value $\rho_0 = 0$ and $v/n = 0.001$. This result shows that trait correlations typically aggregate near ±1 in drifting, isolated, asexual populations with no mutational input. Hence, interpreting this as a signature of drift, we can say that if trait correlations in a population exhibit significant variation away from ±1, then either the population has been drifting for only a short time relative to its effective population size, or other processes not captured by this model must be at play such as mutation and recombination. I therefore discuss mechanisms maintaining genetic correlations before concluding this section.

Pleiotropic loci and genetic linkage are two mechanisms that maintain genetic correlations (Lande, 1980). In this framework, pleiotropic mutations would arise from non-zero off-diagonals of the mutation matrix $\boldsymbol{\mu}$. In contrast, drift facilitates chance correlations of additive genetic values between traits across individuals. Hence, this second mode of genetic correlation accumulation is directly analogous to the build-up of linkage by drift (Hill and Robertson, 1966; Ohta and Kimura, 1969; Lucek and Willi, 2021). For sexually reproducing populations, it is expected that genetic correlations should be maintained by pleiotropic loci as recombination breaks up linkage (Lande, 1980; Jones et al., 2003; Phillips and McGuigan, 2006). However, the results in this section suggest that, because drift drives correlations towards ±1, and recombination drives them towards zero, these two forces should interact to maintain genetic linkage in agreement with classical population genetic theory (Ohta and Kimura, 1969).

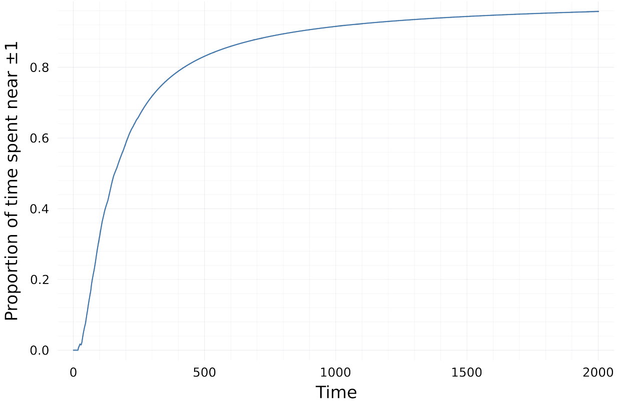

Fig. 4. Trait correlations (ρ) within populations rapidly evolve towards ±1 under random genetic drift, as show here by the proportion of time that $|\rho| > 0.95$ averaged over 10 replicates, given $\rho_0 = 0$ and $v/n = 0.001$.

An extension of this framework that formally integrates sexual reproduction would be useful for making quantitative predictions for genetic correlations maintained at drift-recombination balance. However, as is, the above analysis shows that conventional perspectives on **G**-matrix evolution deserve closer examination.

4. Discussion

The classical quantitative genetic approach has stressed the importance of considering the genetic architecture of traits for understanding evolutionary processes, and has placed particular emphasis on the use of multi-locus models (Bulmer, 1972; Chakraborty and Nei, 1982; Slatkin, 1987; Turelli and Barton, 1994; Barton and Turelli, 2004; Barton et al., 2017; Walsh and Lynch, 2018). The advantage of this approach is its clear connection with explicit genetic details. However, its primary challenge is the manipulation of complex expressions that emerge at such level of detail. To overcome this, and establish a flexible tool for modelling the integrated ecological and evolutionary dynamics of populations carrying multivariate traits, I struck a balance between incorporating genetic detail and analytical tractability. As a consequence, this framework has potential for wide-spread use across topics in evolution, ecology, and population biology.

A central feature of this framework is that a wide range of classical models can be obtained by choosing an appropriate fitness function m. For example, stochastic Lotka-Volterra dynamics for a community of species is obtained from this framework by applying the growth rate $m_i = r_i + \sum_j \alpha_{ij} n_j$ for species i, with n_j being the abundance of species j and α_{ij} the interaction coefficient. This provides an approach to derive an analytical alternative to the simulation model of stochastic Lotka-Volterra dynamics studied by Huang et al. (2015). In addition, by making the interaction coefficients α_{ij} dependent on multivariate trait values $\mathbf{z}_i$, $\mathbf{z}_j$, models integrating coevolution with abundance feedbacks can be obtained similar to those studied by Gokhale et al. (2013), Cortez and Weitz (2014), and Patel et al. (2018). As a special case, continuous time analogs of multivariate coevolution models are obtained by focusing on two species with fixed (or infinite) abundances, and assuming $\alpha_{ij}(\mathbf{z}_i, \mathbf{z}_j)$ depends on the Euclidean distance between $\mathbf{z}_i$ and $\mathbf{z}_j$ (Gilman et al., 2012; Débarre et al., 2014). Klausmeier et al. (2020) studied models of evolutionary rescue with univariate traits using growth rates of the forms $m(z,t) = r - \psi(\theta(t) - z)^2/2$ and $m(z,t) = r + r_0 e^{-\psi(\theta(t)-z)^2/2}$, where $\theta(t)$ is a dynamic phenotypic optimum and ψ is the strength of stabilizing selection. Applying multivariate generalizations of these growth rates to the above framework leads to extensions of an evolutionary rescue model involving demographic stochasticity studied by Xu et al. (2023). Additionally, Jones et al. (2012) also studied a model of phenotypic adaptation to a dynamic optimum, but in the context of **G**-matrix evolution. This framework can then be used as a bridge between research topics such as evolutionary rescue and **G**-matrix evolution. This list provides a small set of examples for how this framework can be used to derive new models across a broad range of topics in ecology, evolution, and population biology.

Further work is needed to extend this framework in several directions. For instance, it is possible to incorporate sexual reproduction and recombination by assuming each trait value, instead of being encoded by a single genetic value g_i, is encoded by the sum of two genetic values $g_i + g_i'$ that result from convex combinations of the parental values. How to formalize this using measure-valued processes is not obvious. In another direction, environmental stochasticity (i.e., stochastic growth rates) can be formally incorporated in a measure-valued context following the work of Mytnik (1996). Extending the framework in this direction may yield important additional insights complementing the work of Lande (2007; 2008), who studied the consequences of environmental stochasticity for long-run population growth rates. An extension in this direction may also be useful for studies investigating the consequences of environmental stochasticity on **G**-matrix evolution (e.g., Engen and Sæther, 2024). Lastly, I point to a possible extension that accounts for the the evolution of the mutation matrix $\boldsymbol{\mu}$. Doing so enables derivation of analytical and simulation models for the evolution of evolvability similar to that studied by Jones et al. (2007), and may yield more precise quantitative predictions amenable to experimental study (Mallard et al., 2023a).

The application of this framework to study **G**-matrix evolution uncovered a more nuanced picture for the role of drift than what conventional wisdom suggests (Phillips and McGuigan, 2006). In particular, although drift indeed scales **G**-matrices when averaged over many replicated populations, it also drives trait correlations towards their extremes within populations. This agrees with the result that the expected eigenvalues of **G** differ from the eigenvalues of the expectation of **G** under drift (Griswold et al., 2007). In addition, the impact of drift on genetic correlations can be understood as a reduction in the effective dimensionality of **G**-matrices (Hine and Blows, 2006), reflecting an extension of the principle that drift erodes heritable variation. That is, because drift drives pairwise correlations to ±1, the distribution of multivariate traits in a population that has been evolving solely under drift may be well approximated after projecting onto a lower-dimensional trait space. Conceptually, this is similar to dimensionality reduction techniques such as principal components analysis (Kirkpatrick and Meyer, 2004). Importantly, this effect of drift on trait correlations calls into question comparative quantitative genetic methods utilizing **G**-matrices to detect selection in diverged populations (Roff, 2000; Steppan et al., 2002; Phillips and McGuigan, 2006; Cano et al., 2004; McGuigan, 2006; Chapuis et al., 2008; Aguirre et al., 2013; Dugand et al., 2021; Mallard et al., 2023a). These findings have broad implications for evolutionary biology, highlighting the need for revised theoretical perspectives and further empirical validation.

The study of genetic correlations and **G**-matrix dynamics using this framework can be extended by studying equation (20) with mutation and selection. In the special case of one-dimensional traits, stabilizing selection, and no abundance dynamics, the theory of one-dimensional diffusions (Etheridge, 2010) can be used to show that the stationary distribution of additive genetic variance follows a generalized inverse Gaussian distribution (Jorgensen, 2012). This suggests the stationary distribution of **G** may follow a matrix-variate generalization, such as the matrix generalized inverse Gaussian (MGIG) distribution (Fazayeli and Banerjee, 2016). Proposed distributions may be checked by evaluating the forwards Kolmogorov equation associated with equation (20) at equilibrium assuming a solution that follows the density of the proposal. Identification of the stationary distribution for (20) may then be used to study the distribution of genetic correlations maintained by interactions between mutation, selection, and random genetic drift.

In summary, this work introduces a versatile framework for modeling the stochastic eco-evolutionary dynamics of multivariate traits, providing a unifying approach that integrates mutation, selection, demographic stochasticity, and drift. By balancing mathematical rigor with accessibility, this framework enables the derivation of new models across a broad spectrum of population biology, making it a valuable tool for both theoretical and applied researchers. With its broad applicability, the framework presented here offers a foundation for future studies investigating the dynamics of populations in both theoretical and empirical contexts.

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