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Paper

Multivariate Trait Evolution: Models for the Evolution of the Quantitative Genetic G-Matrix on Phylogenies.

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Abstract

Genetic covariance matrices (G-matrices) are a key focus for research and predictions from quantitative genetic evolutionary models of multiple traits. There is a consensus among quantitative geneticists that the G-matrix can evolve through "deep" time. Yet, quantitative genetic models for the evolution of the G-matrix are conspicuously lacking. In contrast, the field of macroevolution has several stochastic models for univariate traits evolving on phylogenies. However, despite much research into multivariate phylogenetic comparative methods, analytical models of how multivariate trait matrices might evolve on phylogenies have not been considered. Here we show how three analytical models for the evolution of matrices and multivariate traits on phylogenies, based on Lie group theory, Riemannian geometry and stochastic differential (diffusion) equations, can be combined to unify quantitative genetics and macroevolutionary theory in a coherent mathematical framework. The models provide a basis for understanding how G-matrices might evolve on phylogenies, and we show how to fit models to data *via* simulation using Approximate Bayesian Computation. Such models can be used to generate and test hypotheses about the evolution of genetic variances and covariances, together with the evolution of the traits themselves, and how these might vary across a phylogeny. This unification of macroevolutionary theory and quantitative genetics is an important advance in the study of phenotypes, allowing for the construction of a synthetic quantitative theory of the evolution of species and multivariate traits over "deep" time.

Keywords: quantitative genetics, macroevolution, diffusions, Lie group theory, Riemannian geometry, Bayesian

Lay Summary

We unite Quantitative Genetics, the major mathematical theory of multivariate quantitative trait microevolution, with the mathematical theory of multivariate macroevolution. To do this, we allow the key component of quantitative genetic theory, the matrix of additive genetic variances and covariances (the G-matrix) to evolve along evolutionary trees. This is an advance because the G-matrix is assumed to be constant in quantitative genetics, but it has been recognised that it evolves on macroevolutionary timescales (in "deep time"). Uniting Quantitative Genetics with macroevolutionary theory allows for a more complete mathematical description of Darwin's theory of evolution, and allows for further testing of evolutionary hypotheses.

Introduction

The field of quantitative genetics is concerned with the evolution of traits over a small number of generations (McGuigan, 2006). A fundamental focus of research for quantitative genetics is the G-matrix, defined as the matrix of additive genetic variances and covariances of traits, usually derived from breeding experiments (Walsh and Lynch, 2018; Lynch and Walsh, 1998; Arnold, 2023). The G-matrix is an approximation of the underlying genetic architecture (Hansen, 2006). Exactly how and why it evolves are topics of current research (Arnold et al., 2008; Delahaie et al., 2017; McGlothlin et al., 2022). The matrix can be used to compute the predicted evolutionary response to selection of a collection of (multivariate) traits, using the multivariate breeders' equation (Lande, 1979; Lande and Arnold, 1983):

$$\Delta\bar{Z} = GP^{-1}S,$$

where $\Delta\bar{Z}$ is a vector of responses to selection, with length d, the number of traits. G is the G-matrix, a $d \times d$ matrix of additive genetic variances and covariances. P is the phenotypic variance-covariance matrix, and S is a vector of "selection differentials" (Falconer and Mackay, 2009), also of length d. In a more compact form, the breeder's equation can be formulated as:

$$\Delta\bar{Z} = G\beta \tag{1}$$

where β is a vector of partial regression coefficients relating traits to fitness (Lande and Arnold, 1983).

In Equation 1, G is taken to be constant over the timespan of a few generations, however Equation 1 is not appropriate for longer timespans where G likely evolves (Bégin and Roff, 2004; Steppan et al., 2002; Roff, 2000; Eroukhmanoff and Svensson, 2011; Arnold et al., 2008).

The field of macroevolution also deals with the evolution of traits, but over "deep" time, that is, over millions of years and across many speciation events. Quantitative macroevolutionary studies typically assume that evolution occurs according to some stochastic process, most often a diffusion (but see Landis et al., 2012; Bartoszek, 2017; Duchen et al., 2017; Landis and Schraiber, 2017). The stochastic differential equation (SDE) for an Itô diffusion process has the general form (Øksendal, 2010):

$$dZ_t = b(Z_t, t)dt + \sigma(Z_t, t)dW_t,$$

where $b(\cdot)$ and $\sigma(\cdot)$ are the "drift" and "diffusion" functions of a (univariate) trait Z at time t. W_t is a Wiener process, that is, Brownian motion (BM) at time t. This formulation is very general and many diffusion models have been proposed for macroevolutionary problems (Blomberg et al., 2020). Univariate models have been the focus of most macroevolutionary research, with some exceptions (Butler and King, 2004; Arnold et al., 2008; Bartoszek et al., 2012; Adams and Collyer, 2019; Clavel et al., 2015). Pure Brownian motion is the simplest and most used diffusion model in macroevolutionary studies, though BM should be treated carefully in the multivariate case because the process is transient for dimensions $d > 2$ (Blomberg et al., 2020).

In some circumstances, the matrix of phenotypic covariances (P) can be used instead of G (Roff, 1995; Cheverud, 1988; Sodini et al., 2018). This substitution may be necessary if considering fossil taxa or non-model organisms. The methods described below can be used on *any* covariance matrices. However we restrict our attention to the G-matrix as that is of the most theoretical importance.

Models of Evolution

Without loss of generality, consider two traits evolving according to their own SDE where $b_1(\cdot), \sigma_1(\cdot)$ and $b_2(\cdot), \sigma_2(\cdot)$ are the drift and diffusion functions for trait 1 and trait 2, respectively. A system of *correlated* SDEs can be expressed as:

$$dZ_{t,1} = b_1(Z_{t,1}, t)dt + \sigma_1(Z_{t,1}, t)dW_{t,1} \tag{2}$$

$$dZ_{t,2} = b_2(Z_{t,2}, t)dt + \sigma_2(Z_{t,2}, t)dW_{t,2} \tag{3}$$

$$\rho_t dt = dW_{t,1}dW_{t,2} \tag{4}$$

where ρ_t is the additive genetic correlation between Wiener processes W_1 and W_2 at time t. Parameter ρ_t can be derived from the G-matrix as

$$\rho_t = \Sigma^{-1}G_t\Sigma^{-1}, \text{ where} \tag{5}$$

$$\Sigma = diag(G_t)^{1/2} \tag{6}$$

We wish to include the evolution of ρ_t by studying the evolution of the G-matrix at each time, G_t. To do so, we must be careful that our evolutionary model ensures that, like all covariance matrices, G remains symmetric, real and positive-semidefinite. This requires that all eigenvalues of G should be non-negative. We use Lie group theory to enforce these restrictions (Belinfante et al., 1966; Iserles et al., 2000; Stillwell, 2008). Lie group theory is well-known in physics, where it is used to study symmetry relations in physical theories (Das and Okubo, 2014). However, there have been few applications of Lie group theory in biology (but see House, 2012; Shang, 2012, 2013). Recent advances in the application of Lie group theory to the evolution of covariance matrices according to SDEs show that in order to evolve matrices with the above properties (which form a Lie group), it is much easier to evolve matrices on the corresponding Lie algebra, which is the tangent space to the matrix Lie group at the identity (Muniz et al., 2022b,a, 2023). Matrices can be transferred onto the Lie algebra using the matrix logarithmic map (Bui, 2022; Bui et al., 2023). The results on this Lie algebra can then be transferred back to the matrix Lie group (which forms a Riemannian manifold; Petersen, 2006; Bhatia, 2015) by using the matrix exponential map $\exp(X) = \Sigma_{k=0}^{\infty}\frac{1}{k!}X^k$ (Hall, 2015; Bui, 2022; Bui et al., 2023). In particular, if Ω_t is a skew-symmetric matrix solution to the following SDE:

$$d\Omega_t = aA_t dt + bB_t dW_t, \ \Omega_0 = 0_{d\times d} \tag{7}$$

where a and b are constants to be estimated, A_t and B_t are time-dependent skew-symmetric matrices, and W_t is a scalar Wiener process, then

$$G_t = \exp(\Omega_t) \cdot G_0 \cdot \exp(-\Omega_t), \tag{8}$$

where $\mathbf{G}_0$ is the G-matrix at the root of the tree. Variable $\mathbf{G}_t$ will have the same (non-negative) eigenvalues as $\mathbf{G}_0$, and hence this is termed an "isospectral" model (Muniz et al., 2022a). Equations 2 to 8 together form a model of multivariate trait evolution, with the G-matrix evolving on the matrix Lie group. As well as the evolution of G, we can also simulate the vector of traits (Z), using univariate SDE models, one for each trait. Hence, we can model both G and the mean trait values across species. Since the traits follow their own evolutionary model constrained by the G-matrix,

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as the G-matrix evolves, the traits can be made to evolve along the phylogeny using consecutive updates of the G-matrix at each time step t.

The main assumptions of the model are that for all species, and traits Z, the G-matrix and the phylogeny are known without error. However, more complicated extensions can be easily envisaged, for example accounting for various model uncertainties by drawing samples from prior distributions of matrices, traits, or trees.

An Ornstein-Uhlenbeck model for Covariance Matrices

One of the most popular univariate trait evolutionary models is the Ornstein-Uhlenbeck process (OU; Bartoszek et al., 2012; Hansen, 1997; Hansen and Martins, 1996) (but see Cooper et al., 2015; Cornuault, 2022; Ho and Ané, 2014) which describes a process that is "mean-reverting:" as the process moves away from its central tendancy (μ), it gets "pulled" back towards the central tendency with a "force" α. Stochasticity is introduced with the addition of white noise to the system. Hence, the SDE for the OU process can be written as:

$$dZ_t = \alpha(\mu - Z_t)dt + \sigma dW_t,$$

where σ is usually interpreted as the rate of evolution. Parameter α is interpreted as the strength of stabilising selection on trait Z, but if the process starts outside its (Gaussian) stationary distribution, directional selection can be observed as the process returns to equilibrium around μ. There are several univariate models that have OU-like reversion behaviour, and they have different stationary distributions, but we do not consider them here although we recognise that these models may prove to be valuable extensions (Blomberg et al., 2020).

The success of the OU process in modelling aspects of trait evolution on the adaptive landscape (Arnold et al., 2001; Svensson and Calsbeek, 2013; Bartoszek et al., 2012; Clavel et al., 2015), and the existence of models of covariance evolution as described here, suggest that it may be interesting to derive an OU-type model for covariance matrices. A matrix version of the OU process is:

$$d\mathbf{G}_t = \alpha_{\mathbf{G}} \mathrm{Log}_{\mathbf{G}_t}(\mu_{\mathbf{G}})dt + \sigma_{\mathbf{G}} d\mathbf{W_t},$$

where $\mathbf{G}_t$ is the covariance matrix at time t, $\alpha_{\mathbf{G}}$ is a $d^* \times d^*$ dimensional real matrix of reversion parameters, where $d^* = \frac{d(d+1)}{2}$, $\mu_{\mathbf{G}}$ is the long-term mean covariance matrix, and $\sigma_{\mathbf{G}}$ is a $d^* \times d^*$ matrix of diffusion parameters. $\mathbf{W}_t$ is a $d^* \times d^*$-dimensional multivariate Brownian motion. $\mathrm{Log}_{\mathbf{G}_t}(\mu_{\mathbf{G}})$ is the logarithmic map from $\mathbf{G}_t$ evaluated at $\mu_{\mathbf{G}}$. To implement this model, we use the same general approach as for the isospectral model. Instead of modelling on the covariance Lie group manifold (it is a convex cone; Hill and Waters, 1987), we model the evolution of the covariance matrix on the tangent space to the manifold. If the tangent is taken at the identity value for the manifold, then the manifold is a Lie group and the tangent space is a Lie algebra, as before. However, the tangent does not have to be taken at the identity, and the starting values for the covariance matrix evolution can be mapped to the tangent space from any point on the manifold using the logarithmic map (defined as the inverse of the exponential map) with an appropriate metric (Bui, 2022; Bui et al., 2023). Here we use the Fisher-Rao Affine Invariant metric (Rao, 1945), where the distance δ between two covariance matrices P and Q on the manifold is:

$$\delta = \left|\left|\mathrm{Log}(P^{-1/2}QP^{-1/2})\right|\right| \tag{9}$$

where $||\cdot||$ is the Frobenius matrix norm and Log is the matrix logarithm. Results can then be transferred back from the tangent space using the Fisher-Rao metric, the tangent point and the matrix exponential map.

Brownian Motion of Covariance Matrices

Since the Brownian Motion model (BM) is just an OU model with $\alpha = 0$, we can fit a matrix BM using the same computational methods as for the OU model. It has been pointed out that G-matrices cannot evolve by Brownian Motion (L. Revell, pers. comm., cited in McGlothlin et al., 2018). This is because covariance matrices are constrained to be positive-semidefinite, so if the elements of the matrix are allowed to evolve by BM in ordinary $\mathbb{R}^d$ then the matrices will "wander" off the manifold and the resulting matrices will not be positive-semidefinite (see Fig. 2 and Fig. 3 of Marjanovic et al. (2015) for a graphical representation of this phenomenon). This is avoided by allowing the log-mapped matrices to evolve on the manifold tangent space, and transforming the resultant matrices back to the manifold of covariance matrices using the exponential map and the Fisher-Rao metric.

Methods

We implemented the above models in the computer language, Julia (Bezanson et al., 2017). Julia is an ideal choice for analysing models of this type, as there are excellent facilities for solving differential equations (Rackauckas and Nie, 2017b), including SDEs (Rackauckas and Nie, 2017a), as well as packages for computations on manifolds (Congedo, 2024), linear algebra and using phylogenies (Reeve et al., 2023). Julia is fast, and is an open-source solution for technical and scientific computing. As a motivating example, we analysed the evolution of eight traits and G-matrices for seven species of *Anolis* lizards, using data from McGlothlin et al. (2022). We used simulation to test our models' ability to recover the "true" value, using a simulated phylogeny with 50 tips (leaves).

For many SDE models, transition densities and thus model likelihood functions are either intractable or unknown. For this reason, researchers have generally resorted to approximations of the likelihood, e.g. the Euler approximation (Iacus, 2008; Blomberg et al., 2020), although if the OU process is considered, the transition density (and hence the likelihood) is Gaussian and the usual maximum likelihood and Bayesian approaches can be used. Another approach, taken here, is to give up on likelihood inference altogether and use Approximate Bayesian Computation (ABC; Beaumont, 2010; Csilléry et al., 2010; Lintusaari et al., 2017; Toni et al., 2009). We use ABC here, even though we are demonstrating the theory with the multivariate OU process for which the transition density is known, because we wish to keep the analytical methods general so more complicated models with unknown transition densities may be used in the future (Blomberg et al., 2020). Another reason is that the evolutionary process is simpler to visualise when modelling traits and matrices on a phylogeny, compared to matrix equations involving the inverse of matrices and Kronecker products.

A simple ABC algorithm involves four steps: 1. Draw parameter values from a prior distribution. 2. Use these parameters to simulate data. 3. Compare the simulated data to the real data. 4. If the simulated and real data are sufficiently similar, the current parameter values (particles) are accepted into the posterior distributions for the parameters. This process is repeated a large number of times, to build up posterior distributions for all the model parameters. The approach has had some success in constructing phylogenetic comparative methods (e.g. Bartoszek and Liò, 2019; Beaumont, 2010; Haba and Kutsukake, 2019; Jhwueng, 2020). We used the Julia package `GpABC.jl` to implement ABC for our matrix simulation models (Tankhilevich et al., 2020).

Central to the application of ABC to any problem is the question of how to measure the "similarity" of simulated data to observed data. There are many ways to describe the similarity of matrices (reviewed in Steppan et al., 2002). Here we use the Fisher-Rao Affine Invariant metric of the distance between two covariance matrices on the manifold (Equation 9). We recognise that other metrics could be useful for determining the similarities of simulated matrix and trait data to observed data (e.g. Phillips and Arnold, 1999). Some methods may be able to better describe the way that matrices differ, e.g. in their patterns of eigenvalues and eigenvectors. However we chose to keep the analysis relatively simple and as a demonstration, rather than provide more precise measures of matrix similarity.

For the trait values, we used the root mean squared error (RMSE) between the simulated trait data and the observed trait data, averaged over each trait $x_{i,j}$ for the ith trait and the jth species:

$$RMSE = \sqrt{\frac{1}{dN}\sum_{i=1}^{d}\sum_{j=1}^{N}(x_{ij,sim} - x_{ij,obs})^2}$$

where d is the number of traits, and N is the number of species. *sim* and *obs* refer to the simulated values and the observed values, respectively.

Parameter Estimation

Initial trait values at the root were estimated as the grand mean for each trait. The value of the G-matrix at the root was set to be the "ancestral" G-matrix, as per McGlothlin et al. (2022). For each model, we ran our ABC analysis 1000 times and selected the fourth smallest distance as an appropriate acceptance threshold, where the distance was the sum of the trait RMSE and the Fisher-Rao Affine Invariant metric for the covariance matrix. We then ran simulations until we had produced 1000 draws for each posterior distribution. For the OU model we used a Gamma(2, 0.25) prior for all trait α values and for the α_G value. All σ values were set to $\sqrt{2}$ for the OU model. A Gamma(2.0, 0.25) prior was used for all trait σ values and for σ_G for the BM model. A Gamma(2.0, 0.25) prior was used for the a and b parameters in the isospectral model. While the isospectral model also has time-dependent skew-symmetric matrices as parameters, these were not saved as they have no clear biological meaning.

We calibrated the skew-symmetric matrices for the isospectral model ($\mathbf{\Omega_t}$) using the "ancestral" G-matrix, derived in McGlothlin et al. (2022). We scaled the phylogeny to have a height of one. For the tree topology, (see Zheng and Wiens, 2016; McGlothlin et al., 2022). We used a step size of 0.001 time units along the tree.

For the OU model, we restricted the number of parameters to just one α_G for the G-matrix estimation, and one α for each for the trait estimations, to improve model identifiability.

Model selection

We performed Bayesian model selection for each of the three models using the same model specifications as for the parameter estimation and the method described in (Toni et al., 2009) and implemented in the `GpABC.jl` package for Julia (Tankhilevich et al., 2020). The relative posterior probability for each model was approximated by the number of draws (particles) obtained for each model. The model selection criterion was that the better model(s) have a higher number of particles. The prior used for each model was a discrete Uniform distribution of span 3, since there were three models in the comparison set.

Results

Simulations

Parameter Estimation

We simulated multivariate data (4 traits) along an artificial tree with 50 leaves, under BM and OU models for both the traits and their G-matrix. The effectiveness of parameter estimation (For BM, σ and for OU, α) was variable but in most cases the prior distributions moved towards the true values such that the posterior distributions easily covered the true values. The exception to this was where the true value was particularly high (Fig. 1). Further experiments (not shown) suggested that parameter estimation is easier if the starting value at the root is in the tails of the stationary distribution, indicating that the inclusion of fossil information is useful, particularly when fossils look unlike modern forms (Benton, 2015; Slater et al., 2012).

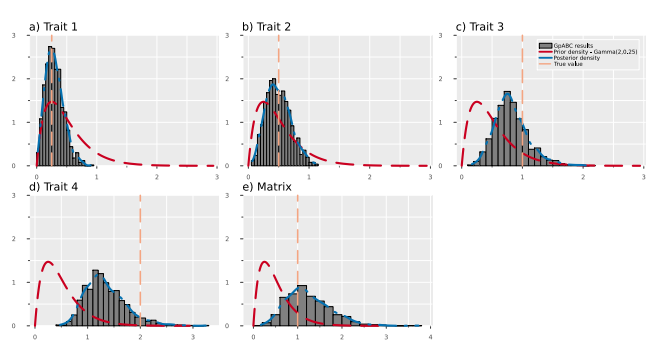

Fig. 1: Prior distributions and simulated posteriors for simulated data, 4 traits on a tree with 50 leaves. Posteriors mostly contain the true value (orange dashed line), except when the true value is large (part d) Trait 4).

Model Selection

For the simulated data, ABC model selection typically chose the correct model, with the exception of the Ornstein-Uhlenbeck model, where Brownian motion was favoured even though the data were generated using the OU model. (Table 1). We suspect that if the simulations start well within the OU stationary distribution, there is little information in the data with which to estimate α.

	Generation method	OU	BM	Iso
1	OU	0	246	754
2	BM	9	830	161
3	Isospectral	0	16	984

Table 1. Results from model selection for the simulated tree of 50 species and three evolutionary models. Models fitted were Ornstein-Uhlenbeck, Brownian Motion, and the isospectral model. Note that the OU model was almost never chosen, even when data were simulated using OU. When data were simulated under the isospectral model, that model performed best. Under other models, it was found more difficult to choose between BM and the isospectral model, although the isospectral model was chosen in each case.

Anolis analysis

Parameter Estimation

The estimates of the trait α parameters were not precise, and not very different from the prior distributions (Figs. 2 - 4). This is to be expected as the sample size (seven species) was very small and there is little information about the dynamics (ie. α) in data based only on extant species (Blomberg et al., 2020).

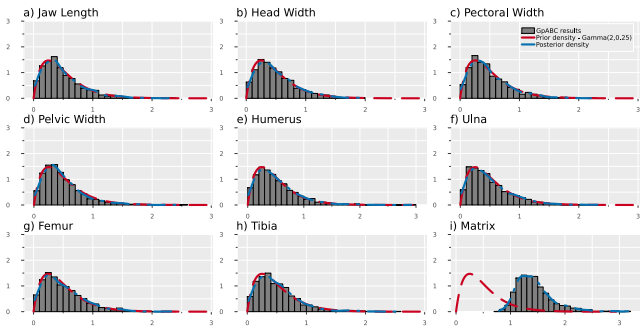

Fig. 2: Prior and posterior distributions for the estimate of parameters using an OU model for trait and G-matrix evolution based on the Anole dataset. This simulation allowed for a different α value for each trait. a-h) - distributions for the estimate of the trait's α values based on the Anole dataset. i) - distributions for the estimate of the matrix α based on the Anole dataset.

Given the lack of biological realism (using a single α for the G-matrix. We do not expect each element of the G-matrix to have the same α), we view this result as a demonstration of what is possible in this model-fitting framework, rather than a definitive answer to the question of the strength of stabilising selection on the G-matrix. We do note that such a question could not be answered except by using a quantitative macroevolutionary model for the G-matrix.

Model Selection

Model selection for the Anole data clearly favoured the isospectral model over OU and BM (Table 2). Further, OU was never selected as a favoured model. While this result may seem surprising, it should be interpreted in the context of the simulation results, where the isospectral model was also strongly favoured. Also, in the absence of fossil data, the data contain very little information about the evolutionary dynamics of the OU process such that the model cannot easily be distinguished from a BM model (Cooper et al., 2015; Ho and Ané, 2014).

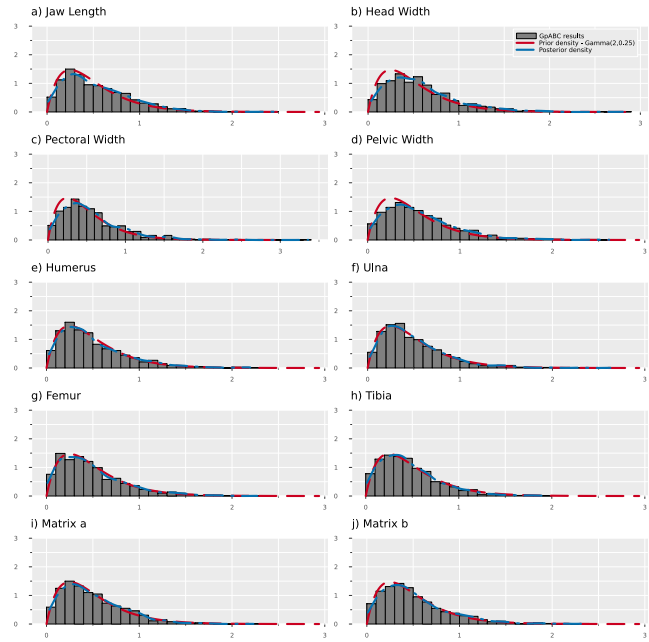

Fig. 3: Prior and posterior distributions for the estimate of parameters using an OU model for trait and an ISO model for G-matrix evolution based on the Anole dataset. This simulation allowed for a different α value for each trait. a-h) - distributions for the estimate of the trait's α values based on the Anole dataset. i-j) - distributions for the estimate of the matrix a and b parameters respectively based on the Anole dataset.

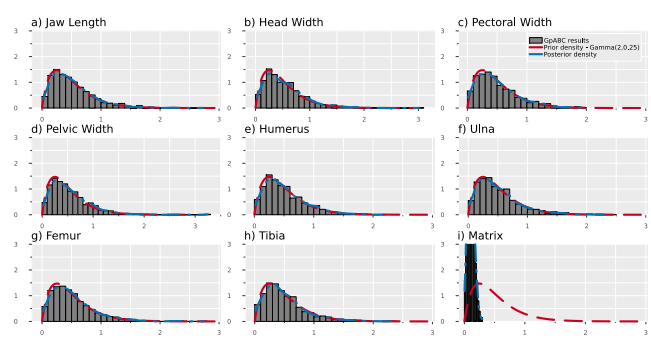

Fig. 4: Prior and posterior distributions for the estimate of parameters using an OU model for trait and a BM model for G-matrix evolution based on the Anole dataset. This simulation allowed for a different α value for each trait. a-h) - distributions for the estimate of the trait's α values based on the Anole dataset. i) - distribution for the estimate of the matrix σ parameter based on the Anole dataset.

OU	BM	Iso
0	177	823

Table 2. Model selection results comparing OU, BM and the isospectral model for 7 *Anolis* species. The isospectral model was roundly favoured, and OU was never chosen. See Discussion.

Discussion

We have shown how to effectively model the macroevolution of traits over deep time, including the information on covariance matrices (the G-matrix) to determine the correlation among traits. Further, we have been able to model the evolution of the G-matrix itself. This fills an important gap in the macroevolutionary theory for multivariate traits, as the G-matrix probably does evolve over time, as evidenced by the fact that G-matrices can be different for related taxa (e.g. the *Anolis* case, McGlothlin et al., 2018, 2022).

Central to the mathematical description of the evolution of G-matrices is our use of Lie group theory and Riemannian geometry to ensure that the evolution of G results in matrices that are symmetric, positive-semidefinite and are thus interpretable as covariance matrices. We have developed three models that can represent the evolution of covariance matrices, two based on the univariate case, BM and OU, and the isospectral model which preserves the eigenvalues of the ancestral covariance matrix. BM and the isospectral model may both serve as null models in further studies of the evolution of G-matrices on phylogenies. OU may be particularly useful in testing for selection on G-matrices, and to determine how much of G-matrix evolution is constrained, by studying the $\alpha_{\mathbf{G}}$ parameter.

Overall, we found these models difficult to fit to both simulated and real data (figs. 1 to 4). While the posterior densities of simulated model parameters usually included the true value, the densities were wide, leading to very wide credibility intervals. In addition, some posteriors looked very much like the priors, leading us to conclude that there is very little information about model parameters in datasets that do not contain fossils. Computer experiments (not shown) starting simulations from root values outside of the OU stationary distribution, which may be interpreted as an initial burst of directional selection followed by stabilising selection, appeared more promising for the estimation of the OU parameter α. Hence, it may be possible to obtain better model fits if the dataset includes traits of fossil taxa as well as extant taxa, and if optima differ in different places in the phylogeny, or if the root values are very different from the tip species values.

Similar difficulties were observed with the model selection results. The isospectral model was preferred over the OU model for which the simulated data were generated under OU (table 1) and the isospectral model was also strongly preferred in the Anole example (table 2). We suspect that these are general difficulties related to the limited amount of data (for the Anoles) and the limited amount of information present in tip data for the estimation of model parameters. Perhaps future work might show how to better fit these models. That there are several software packages that use the OU model (e.g. Bartoszek et al., 2012; Clavel et al., 2015; Ingram and Mahler, 2013) and for that model it is possible to write down the transition densities (they are Gaussian) and hence maximum likelihood inference can be used. However for models that are only slightly more complicated so that the transition densities are unknown, other methods need to be used (Blomberg et al., 2020).

The relationship between macroevolution and microevolution has long been a topic of speculation (Serrelli and Gontier, 2015), with some researchers convinced that macroevolution is in some fundamental way different from microevolution (e.g. Gould, 1985). Alternatively, others claim that macroevolution is just microevolution "writ large" (Hendry and Kinnison, 2001; Reznick and Ricklefs, 2009). It is clear now that statistical genetics and phylogenetics have very deep common roots (Schraiber et al., 2024). The time is ripe for a synthetic mathematical theory that unites macroevolutionary theory in terms of stochastic processes of trait evolution acting cross many generations and speciation events, and microevolutionary theory, the theory of phenotypic evolution on small timescales, in the form of evolutionary quantitative genetics (Rolland et al., 2023). The models proposed here are a step in that direction. These models could be extended in various ways, e.g. the model parameters might be allowed to vary over time, producing models that allowed for different selection regimes (α), different optimal trait values (μ) different values of σ (Beaulieu et al., 2012; Ingram and Mahler, 2013; Beaulieu and O'Meara, 2023; Revell, 2021), the use of non-Gaussian OU-like models (Blomberg et al., 2020), the application of "early burst" models of adaptive radiations (Gavrilets and Losos, 2009), or even the importance of phenotypic plasticity in macroevolution (de Souza Silva et al., 2023). Diffusion models provide a rich framework for studying macroevolution, and there are many possibilities open to answer questions using a wide variety of models. The models presented here can form the basis for further studies. This new modelling paradigm will allow the testing of new hypotheses of trait variation, including hypotheses about the evolution of phenotypic integration (Pigliucci, 2003; Eble et al., 2004; Caetano and Harmon, 2017) and the coevolution of the strength of the association among groups of traits (Steppan, 2004).

We suggest that there is another useful application of these stochastic process models: They provide us with a way to think about quantitative trait evolution. Even if these models prove difficult to fit to trait data, which is often the case (Cooper et al., 2015; Cornuault, 2022; Ho and Ané, 2014), they nevertheless have heuristic value. They allow us to draw a picture of the evolution of traits that is elegant, instructive, rigorous, and is a concise mathematical treatment of the known subject matter. In this sense, the statistical approach to trait evolution offered here is similar to the use of the Wright-Fisher model in population genetics (Fisher, 1930; Wright, 1931). It is unlikely that the Wright-Fisher model (and its extensions) is "true" in every respect (or at all), but nevertheless the heuristic value of the model in explaining the influences of drift, migration, mutation and selection of alleles in populations is profound. While our models are necessarily wrong, we believe they may be useful (Box, 1976). We think that statistical models can have a value of their own, beyond the usual role as serving as an adjunct to the testing of hypotheses about parameters (Sokal, 1965). They can reveal the processes of trait evolution.

Competing interests

The authors declare that they have no competing interests.

Data and code availability

All original Julia code is available at: `https://github.com/simone66b/JMMenura`. The *Anolis* data come from McGlothlin et al. (2022).

Author contributions

S.P.B conceived the study, wrote code, and prepared the manuscript. M.M. and M.N.B. contributed to theory and approved the manuscript. C.J. wrote code, ran analyses and contributed to writing the manuscript.

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