

# Phylogenetic mixed model

## Current model description

For each of  $n$  species, we assumed data were generated from the following sampling distribution:

$$y_j \sim \mathcal{N}(\mu_j, \sigma_e^2) \quad (1)$$

where:

$$\mu_j = \alpha_j + \beta_j X \quad (2)$$

Predictor  $X$  is continuous (in this case, year), and its effects on the phenology of species  $j$  are determined by parameter  $\beta_j$  representing response over time. We assumed each trait, including the specific-level intercept  $\alpha_j$ , evolved independently following a Brownian motion model of evolution. Thus, species traits are elements of the following normal random vectors:

$$\boldsymbol{\alpha} = \{\alpha_1, \dots, \alpha_n\}^T \text{ such that } \boldsymbol{\alpha} \sim \mathcal{N}(\mu_{\alpha}, \boldsymbol{\Sigma}_{\alpha}) \quad (3)$$

$$\boldsymbol{\beta} = \{\beta_1, \dots, \beta_n\}^T \text{ such that } \boldsymbol{\beta} \sim \mathcal{N}(\mu_{\beta}, \boldsymbol{\Sigma}_{\beta}) \quad (4)$$

where the means of the multivariate normal distributions are root trait values (i.e., trait values prior to evolving across a phylogenetic tree) and  $\boldsymbol{\Sigma}_i$  are  $n \times n$  phylogenetic variance-covariance matrices of the form:

$$\begin{bmatrix} \sigma_i^2 & \lambda_i \times \sigma_i^2 \times \rho_{12} & \dots & \lambda_i \times \sigma_i^2 \times \rho_{1n} \\ \lambda_i \times \sigma_i^2 \times \rho_{21} & \sigma_i^2 & \dots & \lambda_i \times \sigma_i^2 \times \rho_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \lambda_i \times \sigma_i^2 \times \rho_{n1} & \lambda_i \times \sigma_i^2 \times \rho_{n2} & \dots & \sigma_i^2 \end{bmatrix} \quad (5)$$

where  $\sigma_i^2$  is the variance of the Brownian motion model of evolution and thus represents the rate of evolution across a tree for trait  $i$  (assumed to be constant along all branches). Parameter  $\lambda_i$  is Pagel's  $D$ , which scales the covariance and therefore is a measure of the “phylogenetic signal” within trait  $i$  (note: because estimates can be partitioned into phylogenetic and nonphylogenetic components in this model,  $0 \leq \lambda \leq 1$ ; see Freckleton et al. 2002 Am Nat). Finally,  $\rho_{xy}$  is the phylogenetic correlation between species  $x$  and  $y$ , or the fraction of the tree shared by the two species.

The above specification is exactly equivalent to writing equation 2 in terms of root trait values and residuals, such that:

$$\mu_j = \mu_\alpha + \mu_{\beta_1} X_1 + \mu_{\beta_2} X_2 + \mu_{\beta_3} X_3 + e_{\alpha_j} + e_{\beta_1,j} + e_{\beta_2,j} + e_{\beta_3,j} \quad (6)$$

where the residual error terms (e.g.,  $e_{\alpha_j}$ ) are elements of normal random vectors from multivariate normal distributions centered on 0 with the same phylogenetic variance-covariance matrices as in equation 5.

## Lizzie's basic model and code description

Let's start with the basic PMM (phylogenetic mixed model)

As I understand it:

$$y = \alpha + \beta x + a + e \quad (7)$$

$$a \sim \text{normal}(0, \sigma_P^2 \Sigma) \quad (8)$$

$$e \sim \text{normal}(0, \sigma_R^2 I) \quad (9)$$

... where  $\alpha$  and  $\beta$ , respectively, are the intercept and the slope for the co-factor  $x$ ,  $a$  is the phylogenetic random effect, and  $e$  is the residual error.  $\Sigma$  is a phylogenetic correlation matrix,  $I$  stands for the relevant identity matrix. (The above from Chapter 11: General Quantitative Genetic Methods for Comparative Biology, by Villemereuil & Nakagawa, though seems similar to Housworth.)

What we would like to do is have the phylogenetic effect structure the species-level slopes (while also allowing partial pooling on the species given uneven data, that is, for some species we might have 3 observations, each at a different  $x$  value, and for other species, we have 30 observations).

We think we have this running in `ubermini_2.R` (simulation code) and `ubermini_2.stan`.

In the Stan code,  $\beta$  is:

```
b_force ~ multi_normal(rep_vector(b_z, n_sp),  
lambda_vcv(Vphy, lam_interceptsb, sigma_interceptsb))
```

So the `b_z` represents the root trait value, and all the action happens in the second part of the function, which calls `lambda_vcv`, which is defined at the top of the Stan code. This function sets up two matrices (both the size of the VCV in your data): (1) a matrix of your VCV with  $\lambda$  on the off-diagonals only (`local_vcv`) and (2) a matrix with  $\sigma$  on the diagonal (`sigma_mat`) and then returns the product `sigma_mat * lambda_mat * sigma_mat`. So that, when you put the  $\beta$  code above with the `lambda_vcv` function you get:

$$\beta \sim MVN(\mu, \Phi\Sigma)$$
$$\Phi\Sigma = \begin{bmatrix} \sigma_\beta^2 & \lambda\sigma_\beta^2 & \lambda\sigma_\beta^2 \\ \lambda\sigma_\beta^2 & \sigma_\beta^2 & \lambda\sigma_\beta^2 \\ \lambda\sigma_\beta^2 & \lambda\sigma_\beta^2 & \sigma_\beta^2 \end{bmatrix}$$