

Phylogenetic Models

Achaz von Hardenberg

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Back to the Rhinogradis: Phylogenetic Structural Equation Models with **because**

One of the core features of **because** is the ability to fit phylogenetic structural equation models (PSEMs), allowing researchers to account for shared evolutionary history among species when analysing trait relationships.

Once again we will use the Rhinogradis dataset and tree previously analysed in Gonzalez-Voyer and von Hardenberg, (2014) and in von Hardenberg and Gonzalez-Voyer (2025). Let's start by loading the necessary packages and data:

```
library(because)
library(ape)

data(rhino.dat)
data(rhino.tree)
```

While in previous implementations it was necessary to compute the variance-covariance matrix from the tree and pass it to JAGS, **because** handles this internally. You only need to provide the phylogenetic tree (class **phylo**) via the **structure** argument. Also, **because** automatically matches the species names in the data and tree: you only need to ensure that the species names in the data frame column specified by **species** match the tip labels in the tree and provide the name of the species column to the **because()** function through the **id_col** argument. Also, you do not need to rescale the total tree length to 1 (needed for a correct estimation of Pagel's lambda parameter), as **because** will handle this internally.

So, let's specify the structural equations of the best model (sem8) as fitted by von Hardenberg and Gonzalez-Voyer (2025):

```
sem8_eq <- list(
  LS ~ BM,
  NL ~ BM + RS,
  DD ~ NL
)
```

Now we can fit the model with **because()** including the phylogenetic tree with the **structure** argument. Also, as this is a more complex model than in the previous examples, to speed up the model fitting we will run 3 chains in parallel using the **parallel = TRUE** and **n.cores = 3** arguments. Also we will request the WAIC information criterion to be computed by setting **WAIC = TRUE**:

```
fit_sem8 <- because(
  equations = sem8_eq,
  data = rhino.dat,
  structure = rhino.tree,
  id_col = "SP",
  WAIC = TRUE,
  parallel = TRUE,
  n.cores = 3
)
```

)

```
summary(fit_sem8)
```

```
summary(fit_sem8)
```

	Mean	SD	Naive SE	Time-series SE	2.5%	50%	97.5%
alphaDD	0.581	0.276	0.005	0.007	0.036	0.582	1.146
alphaLS	0.344	0.416	0.008	0.016	-0.490	0.346	1.138
alphaNL	-0.055	0.339	0.006	0.015	-0.731	-0.054	0.601
beta_DD_NL	0.536	0.074	0.001	0.001	0.390	0.538	0.682
beta_LS_BM	0.472	0.085	0.002	0.002	0.309	0.470	0.641
beta_NL_BM	0.470	0.068	0.001	0.001	0.336	0.471	0.604
beta_NL_RS	0.597	0.068	0.001	0.001	0.461	0.596	0.728
lambdaDD	0.462	0.130	0.002	0.003	0.218	0.462	0.717
lambdaLS	0.696	0.107	0.002	0.003	0.459	0.709	0.862
lambdaNL	0.719	0.086	0.002	0.002	0.533	0.727	0.863
sigma_DD_phylo	0.803	0.174	0.003	0.003	0.503	0.790	1.178
sigma_DD_res	0.856	0.088	0.002	0.002	0.694	0.852	1.041
sigma_LS_phylo	1.253	0.204	0.004	0.005	0.865	1.246	1.675
sigma_LS_res	0.804	0.104	0.002	0.002	0.615	0.802	1.013
sigma_NL_phylo	1.026	0.145	0.003	0.004	0.766	1.013	1.338
sigma_NL_res	0.626	0.075	0.001	0.002	0.490	0.622	0.783

	Rhat	n.eff
alphaDD	1.000	1408
alphaLS	1.003	639
alphaNL	1.000	553
beta_DD_NL	1.000	3088
beta_LS_BM	1.001	2178
beta_NL_BM	1.000	2255
beta_NL_RS	1.001	2801
lambdaDD	1.002	2136
lambdaLS	1.000	1595
lambdaNL	1.001	1788
sigma_DD_phylo	1.002	2741
sigma_DD_res	1.000	2712
sigma_LS_phylo	1.000	1612
sigma_LS_res	1.001	2103
sigma_NL_phylo	1.001	1600
sigma_NL_res	1.001	2427

DIC:

Mean deviance: 670

penalty 133.7

Penalized deviance: 803.6

WAIC:

WAIC with Standard Errors

N = 300 observations, 3000 MCMC samples

	Estimate	SE
elpd_waic	-395.1	9.9
p_waic	93.7	5.1
waic	790.2	19.8

The output shows that the posterior parameters are consistent with those we obtained coding the model directly in JAGS (von Hardenberg and Gonzalez-Voyer, 2025; the code is available in the supplementary materials of the paper).

The random effects formulation of `because`

If you are familiar with the output obtained from that model, you may however have noticed that besides Pagel’s λ parameters for each response variable, with `because()` we also get estimates of the standard deviations of the phylogenetic and residual components (`sigma_[RESP]_phylo` and `sigma_[RESP]_res`, respectively). These are estimated because `because` uses an optimised random effect formulation to improve MCMC and significantly reduce runtime. While standard phylogenetic models must invert the covariance matrix at every iteration (as λ changes), the random effect approach is mathematically equivalent but computationally more efficient. `because` decomposes the response into three additive components:

$$y_i = \mu_i + u_i + \epsilon_i$$

where:

- μ_i is the fixed effect (structural equation mean)
- u_i is the phylogenetic random effect: $\mathbf{u} \sim \mathcal{N}(\mathbf{0}, \sigma_u^2 \mathbf{V})$
- ϵ_i is the residual error: $\epsilon \sim \mathcal{N}(\mathbf{0}, \sigma_e^2 \mathbf{I})$

This allows us to pre-compute the inverse phylogenetic variance-covariance matrix (\mathbf{V}^{-1}) only once and pass it to JAGS as fixed data. JAGS simply scales this fixed precision matrix by $1/\sigma$, avoiding costly repeated inversions.

Consequently, λ is derived from the posterior variance components as:

$$\lambda = \frac{\sigma_{phylo}^2}{\sigma_{phylo}^2 + \sigma_{res}^2}$$

This is the approach also used in other packages such as `MCMCg1mm` (Hadfield, 2010) and `brms` (Bürkner, 2017).

Improved WAIC calculation

In `because` we also improved the WAIC calculation. The WAIC is now computed directly from the pointwise log-likelihoods monitored during model fitting, rather than approximating it from the deviance as done previously. This approach, besides providing more accurate estimates of the WAIC than the deviance-based approximation provided by JAGS, also allows us to compute the standard errors for WAIC (following the method suggested by Vehtari et al. 2017) allowing for more reliable model comparisons.

Testing conditional independencies with d-separation

Let’s now test the conditional independencies implied by the model (We will set `WAIC = FALSE` here to speed up the computation, as we do not need to compare models):

```
test_sem8_dsep <- because(
  equations = sem8_eq,
  data = rhino.dat,
  structure = rhino.tree,
  id_col = "SP",
  dsep = TRUE,
  WAIC = FALSE,
  parallel = TRUE,
  n.cores = 3
)
```

d-separation Tests

=====

Test: RS _||_ BM | {}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_RS_BM	-0.029	-0.238	0.177	Yes	0.78	1.002	2177

Test: RS _||_ DD | {NL}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_RS_DD	-0.117	-0.33	0.107	Yes	0.301	1	2563

Test: RS _||_ LS | {BM}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_RS_LS	-0.019	-0.248	0.22	Yes	0.873	1	2423

Test: BM _||_ DD | {NL}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_BM_DD	0.117	-0.111	0.342	Yes	0.322	1	1824

Test: NL _||_ LS | {RS,BM}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_NL_LS	0.013	-0.151	0.177	Yes	0.86	1	2134

Test: DD _||_ LS | {NL,BM}

Parameter	Estimate	LowerCI	UpperCI	Indep	P	Rhat	n.eff
beta_DD_LS	-0.063	-0.245	0.114	Yes	0.495	1.002	2693

Legend:

Indep: 'Yes' = Conditionally Independent, 'No' = Dependent (based on 95% CI)

P: Bayesian probability that the posterior distribution overlaps with zero

As expected, all conditional independencies are supported, indicating that the the hypothesised causal structure is consistent with the data.

Accounting for variability in traits in PhyBaSE models

In von Hardenberg and Gonzalez-Voyer (2025), we showed how PhyBaSE models can be specified to account for measurement error or intraspecific variability in the traits. These models can also be fitted with `because()`. In the case of repeated measures per species, it is sufficient to provide the data frame with all measurements (i.e. multiple rows per species) and specify the `id_col` argument to indicate the species identifier column. `because()` will automatically format the data to create a response matrix with species in rows and replicates in columns, padding with NAs as necessary. As an example, we will use the same simulated data as in von Hardenberg and Gonzalez-Voyer (2025):

##References Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413-1432.