

# DPM Simulation

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## 2.3. Synthetic example

In order to demonstrate that our formal model is able to accurately recover true coevolutionary dynamics, we use a simple synthetic example.

Consider an ancestral species with two continuous traits,  $X$  and  $Y$ . We simulate the coevolution of these traits over time, allowing traits to have autoregressive effects (*i.e.*, change in a trait influences itself in the future), coevolutionary effects (*i.e.*, change in a trait influences the other trait in the future), and stochastic drift. In this particular simulation, we specify that changes in  $X$  influence future changes in  $Y$ , but not vice versa.

The data generating model is as follows:

$$\begin{aligned} Y_t &= 0.90 \cdot Y_{t-1} + 0.85 \cdot X_{t-1} + \epsilon_X \\ X_t &= 0.90 \cdot X_{t-1} + \epsilon_Y \\ \epsilon_X, \epsilon_Y &\sim \mathcal{N}(0, 0.05) \end{aligned}$$

We allow this coevolutionary process to play out over discrete timesteps. In each timestep, there is a small probability ( $p = 0.05$ ) of a speciation event, where the parent species splits into two child species. Coevolutionary dynamics then continue independently on each separate phylogenetic branch. We continue this process of evolution and speciation until we have a sufficient sample size of species. We then fit our statistical model using the resulting phylogenetic tree and the “contemporary” values of  $X$  and  $Y$  from the final timestep.

Note that this data generating process is a basic autoregressive model and, as such, is not identical to the statistical model. Despite this misspecification, we find that, when fitted to data from 100 species, the statistical model converges normally and is able to accurately recover the true coevolutionary dynamics.

By plugging the fitted model parameters into Equation 3 above, we are able to calculate  $\Delta\theta_z$ , the change in the equilibrium value of each trait resulting from an absolute deviation increase in the other trait. Figure 1 visualises the resulting posterior distributions of  $\Delta\theta_z$  for  $X \rightarrow Y$  and  $Y \rightarrow X$ . We can see that the posterior distribution for  $X \rightarrow Y$  is positive (median posterior value = 5.67, 95% CI [1.55 28.27]) suggesting that an absolute deviation increase in  $X$  results in an increase in the equilibrium value of  $Y$ . However, the posterior distribution for  $Y \rightarrow X$  includes zero (median posterior value = 0.77, 95% CI [-3.98 6.59]) suggesting that an absolute deviation increase in  $Y$  does not change the equilibrium value of  $X$ . This result accurately reflects the data generating process.

We can further visualise the influence of  $X$  on  $Y$  by plotting a phase plane of the evolutionary dynamics implied by the model. Figure 2 depicts the expected change in  $X$  and  $Y$  depending on their current states. Both variables have been standardised as z-scores for easier interpretation. The solid lines in the figure represent nullclines where  $X$  (blue) and  $Y$  (red) are at equilibrium, depending on the state of the other.

The phase plane shows that changes in the value of  $X$  have large effects on the direction of selection on  $Y$ . When  $X$  is low, there is strong negative selection on  $Y$ . When  $X$  is high, there is strong positive selection on

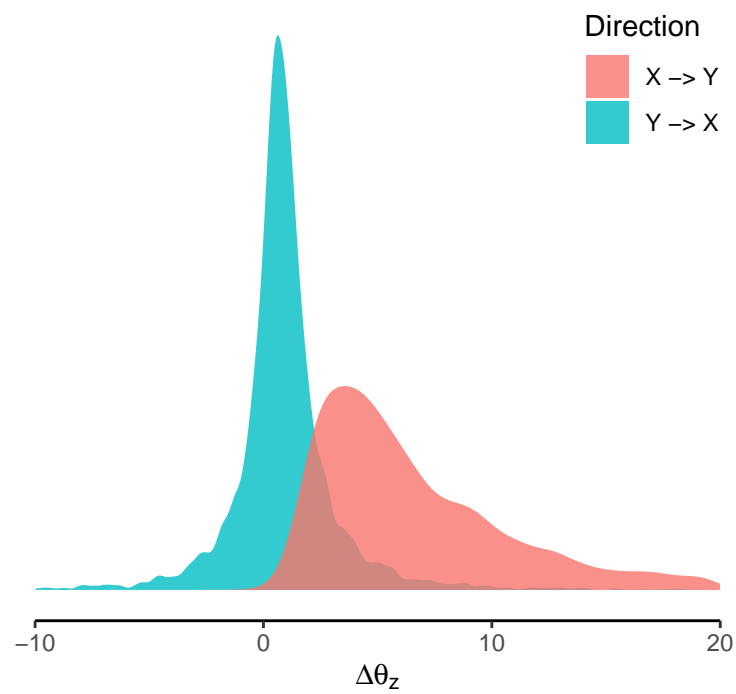


Figure 1: Posterior distributions for  $\Delta\theta_z$  for both directions of coevolution.  $\Delta\theta_z$  represents the expected z-score change in the equilibrium value of each trait resulting from an absolute deviation increase in the other trait.

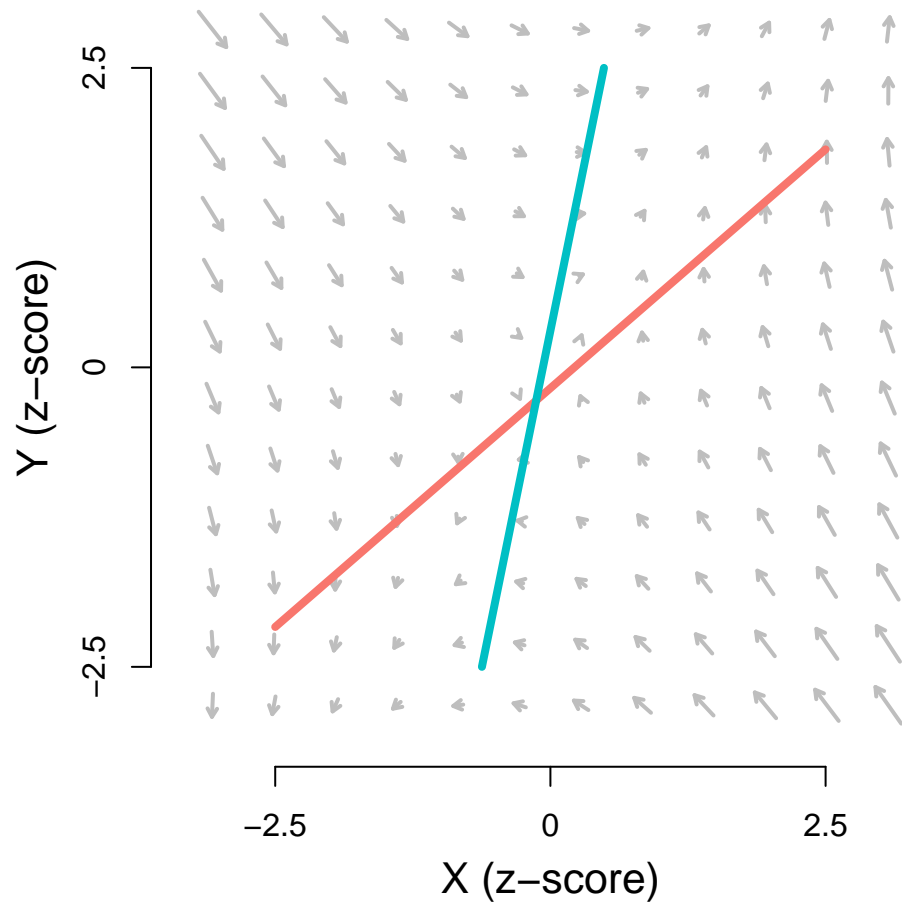


Figure 2: Phase plane showing the expected changes in  $X$  and  $Y$  depending on the state of the other trait. Arrows represent the direction and strength of selection in trait space. Solid lines represent nullclines where  $X$  (blue) and  $Y$  (red) are at equilibrium depending on the state of the other.

Table 1: The proportion of models in which the 95% credible interval for  $\Delta\theta_z$  is greater than zero for three different sample sizes. 100 simulations were run for each sample size. Four models did not converge ( $\hat{R}$  values  $> 1.1$ ) and were not included in these proportions.

Direction	n = 20	n = 50	n = 100
X $\rightarrow$ Y	0.35	0.83	1.00
Y $\rightarrow$ X	0.00	0.09	0.18

Y. The nullclines also show that changes in  $X$  have a large effect on the equilibrium value for  $Y$ . However, changes in the value of  $Y$  do not have the same effect on the direction of selection on  $X$  or the equilibrium value of  $X$ .

To determine whether this pattern of results generalises beyond a single simulation run, we iterated the above simulation 100 times for three different sample sizes: 20, 50, and 100 species. Table 1 shows the proportion of models where the posterior  $\Delta\theta_z$  values have 95% credible intervals excluding zero. The results show that the model is relatively underpowered to detect the causal effect of  $X$  on  $Y$  when there are only 20 species, but it is able to detect this causal effect with sufficient power when the sample size is 50 or 100.

## 2.4.2. Evolution of social complexity across human societies

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Sheehan et al. (2023) studied the coevolution of religious and political authority in 97 Austronesian societies. Religious and political authority were both coded as four-level ordinal variables: absent, sub-local authority, local authority, and supra-local authority. Mapping these variables onto a phylogeny of Austronesian languages revealed that both religious and political authority had high phylogenetic signals, suggesting that a DPM could reasonably be used to assess the coevolution of these variables over the past 5000 years. Instead of binarising the two ordinal variables to use Pagel’s discrete method, as previous work had done (Sheehan et al. 2018; Watts et al. 2016), the authors explicitly modelled both variables as ordinal in the DPM. The model revealed that both religious and political authority coevolved reciprocally over time. In other words, increases in religious authority led to strong positive selection on political authority and, likewise, increases in political authority led to strong positive selection on religious authority. This is akin to “runaway selection” where both traits enter a positive feedback loop and increase concomitantly. This coevolutionary relationship makes sense in light of Austronesian ethnographies, which describe how both forms of authority are tightly interdependent and have often historically served to legitimise one another (*e.g.*, Goodenough 2002).

## References

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