Review of a Manuscript by Revell for PeerJ

This paper provides a very readable account of a new phylogenetic comparative model that allows for evolutionary rate changes along a phylogeny. It is a little unclear to me precisely what this model is, as no equations describing the model have been presented, although likelihood equations are described. However, it looks very much like the normal Stochastic α, β, ρ (SABR) model that is well-known in the financial statistical literature. The SABR model is described by a system of diffusion equations thus:

$$\begin{aligned} dx_t &= \sigma_t (x_t)^\beta dW_t \\ d\sigma_t &= \sigma_{BM} \sigma_t dZ_t \\ dW_t dZ_t &= \rho dt \end{aligned}$$

In the present context, $\beta = 0$ and $\rho = 0$, implying ordinary Brownian motion for the trait x_t with rate σ_t and geometric Brownian motion for σ_t, with rate parameter σ_{BM}, assumed to be constant. In the financial literature, σ_{BM} is known as the volatility of volatility (or volvol, usually given the symbol α). The $\rho = 0$ condition forces the Brownian motions Z_t and W_t to be uncorrelated. This simplifies the model considerably. An aspect of the present model not captured by the SABR model is that each branch (edge) has its own σ_t which does *not* change over the length of the branch. σ_t changes only at nodes (speciation events). I don't understand why this should be so. What is so special about σ_t that it changes at nodes but is constant elsewhere? Why not let σ_t evolve everywhere according to its own (geometric) Brownian motion? This would reduce the number of parameters in the model, and focus would then shift to estimating the volvol (σ_{BM}). This truly SABR model has been well-studied in the literature and estimation methods ("calibration" in the finance literature) are available (e.g. Fatone et al., 2013, 2014; Floc'h and Kennedy, 2014; Zhai and Cao, 2014), including the case where data are sparse ("illiquid markets", West, 2005), which is almost always the case with phylogenetic comparative data without a good fossil record.

A more general SABR model might also be of interest to readers, such as one where $\rho \neq 0$ and/or $\beta \neq 0$. Whatever the case, it seems to me that there exists a good opportunity to steal models and methods from the financial literature and apply them to biological evolution. The present SABR-like model seems that these sorts of models might be productive, for theoretical studies if not for fitting to real data sets.

The problem with all these comparative methods is usually the lack of fossil data. Time and again when we have a good fossil record, we find that conclusions based on just having tip data are wrong, often severely so. This must be true because the tip data hold very little information about the true underlying dynamics of evolution (Blomberg et al., 2020). Pretending that fossils are not crucial for analysing real data sets using comparative methods is very misleading. The present paper does nothing to allay these concerns. The author suggests that the new methods that have been presented might best be used for exploratory analyses (line 72) does not fill me with hope. Given a method, you can guarantee that someone will use it for something for which it wasn't designed.

The use of penalised likelihood to fit the model, with a smoothing parameter (λ) is reasonable. It is clear that with so many parameters (the σ_n^2's) that it is not possible to estimate them all with the usual likelihood methods. A grid search for the best λ, where "best" is determined by cross-validation, seems to me to be a pretty good solution. Alternatively, if we let σ_t^2 to vary as in the SABR model, we may have a better chance of estimating σ_{BM}. Certainly there are methods in the financial literature which might do the job, as mentioned above. One other criticism I have is that although there is an extensive literature on cross validation, only Sanderson (2002) and Smith and O'Meara (2012) have been cited. These are hardly go-to papers for understanding cross validation. A reference to the statistical literature would be useful, e.g. Efron and Gong (1983), which provides a good general introduction and has been cited more than 2200 times.

As mentioned at the beginning, this is a very readable account of a quite complicated modelling study. But it is almost too readable. It reads to me like a talk or seminar speech. The tone doesn't seem to have the right scientific *gravitas*. I don't know what the PeerJ editors like in terms of prose style, but I think I should raise this as a minor point.

I am happy to be identified as a reviewer:

Simone Blomberg.

References

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