

A final review of Brower & Garzón-Orduña

I'd suggested in my previous review that the authors had some basis for publication if they shortened their piece to discuss data they argued had been transposed, properly tested the effects of that transposition on the signal of reticulation using the same or improved methods as those used by the authors themselves, and completely cut out the pro-parsimony, anti-probabilistic ranting about support which will have zero effect anyway on our community. They do not do that, and in fact they double down on their views, and have not as far as I see conceded a single point from my review. Therefore there seems no further basis for this reviewer recommending publication. It is my opinion against theirs. They appear to have fought bravely for a pyrrhic victory. So be it. I'll voice my opinion and leave the rest to the editors.

Regarding the following:

Reticulating genealogical hypotheses (tokogenies) are not hierarchical and so are not "phylogenetic" in the sense of Hennig. Even if you are willing to accept reticulation in your "phylogenetic" system, the null hypothesis or weight of evidence or whatever you want to call it is still that there is a single, one-many hierarchical "species tree" to which individual characters or gene trees may or may not conform. You can't even detect "reticulation" unless you have a priori a tree on which characters reticulate.

Unfortunately for these authors, I don't agree with their last point, because it is conceivable that one might be able to detect the difference between a fishing net of inheritance and a bifurcating tree; and a number of people are now working on it. With regard to the first point, there are many authors from the 1950s and 1960s that I disagree with, so selecting a single statement from Hennig as Gospel is hardly likely to sway me or the general readership of this journal to recruitment to the authors' cause. I also disagree with their middle sentence, that we should accept the null hypothesis unless we happen to be able to disprove it; this is the "P value fallacy" of null hypothesis testing – see Wikipedia. (Of course, the authors would deny "P values" because they are probability-based measures, but it's the general sentiment that a null hypothesis is proved provided that the alternative suggested by the data is not convincingly disproved that I'm talking about here).

Parsimony has been investigated statistically, and found wanting, especially in cases where there's a lot of homoplasy as is both expected and known for DNA data, where saturation with only four possible character states at each site is a real problem, especially as transitions are very frequent and usually much more common than transversions. Bremer support for the most parsimonious tree, being just a list of characters, gives no measure of RELATIVE support, because it doesn't include probability. The authors' counter-argument that Bremer support is more powerful because it doesn't have a maximum at 100% is absurd, and only a micro-minority of people today would find a non-probabilistic measure of statistical support convincing.

Of course, minority opinions are not always wrong, and I'm all for Systematic Biology having a plurality of views. But just as I think a paper that denies evolution should be given short shrift in this journal, a paper that ignores evidence, both theoretical and via simulation, that parsimony methods perform poorly when a lot of the data is evolving non-parsimoniously on purely a priori and philosophical grounds, must also be rejected from this journal. See below:

We realize that the rationale for the model-based approaches that *Syst. Biol.* has championed over the past two decades is founded upon the supposed limitations of "maximum parsimony," but while the methods have become highly sophisticated, the statistical premise by which they are justified is defective (Sober, 2015; Brower, 2016). We only raise this philosophical point here because we do not feel it is a fair or legitimate criticism to belittle parsimony methods as "unreliable." That is simply naive.

So two people, one of them Brower himself (in a book chapter unavailable to me in my library), the other, Eliot Sober, a philosopher who wrote a philosophical book (a person who understands too little of the statistics or the biology to be regarded as an expert on phylogenetics or hybridization), apparently agree with a central thesis of this manuscript that Bayesian and likelihood-based methods are "highly sophisticated, but the statistical premise by which they are justified is defective." In their rebuttal, the authors cite as authorities to back up their point of view a total of 16 papers, of which 12 are authored or coauthored by Brower himself.

By that kind of reasoning, a meteorology journal should publish anti-climate-change articles, and geology journals should publish flat earth articles. On parsimony, the evidence is in: if the data are well behaved, it performs ok, though gives no measure of probabilistic support. If homoplasy is a problem in the data, as is likely, it often gives misleading results. On this basis Systematic Biology should not publish this manuscript. Methods have not been perfected yet, especially phylogenetic methods to analyse species trees, but we do already understand the needs in this area. Parsimony of the concatenated data is likely not a good option, even if there has been no actual introgression between species.

But in any case, these authors cannot be expected to be interested in obtaining an approximation to the species' true evolutionary relationships (apparently they also agree that this is not the aim of phylogenetics); instead they argue fervently that the most parsimonious hierarchical tree is what they want even if that's not what happened during evolution.

But even ignoring the diatribes against "model-based approaches," I found it very odd that the authors feel that their parsimony-based argument disproves the arguments of the original paper by Kozak et al based on completely different methods. It seems to me you cannot disprove an argument about chalk with cheese.

If the authors had bothered to do the NeighborNet analysis on corrected data or something like this, or maybe even improved on it with another related method to detect reticulation, it might

at least have suggested that the conclusions about reticulation were suspect – and the original authors could have responded in kind. Many cladists including even Hennig have long recognized that hybridization would cause problems for methods that purely assume bifurcation. In Hennig's case, he felt that hybridization, while a potential threat, was such a minor problem in nature that we could effectively ignore it (Hennig 1966 p. 207-8). Warren Wagner, a card-carrying cladist who after all developed the Wagner Parsimony algorithm, on the other hand felt the need based on his extensive research experience with ferns to argue for proper treatment of hybrids and hybridization, in a paper he called "reticulistics" (Wagner, W.H. 1983. Reticulistics: the recognition of hybrids and their role in cladistics and classification, Pages 63-79 in N.I. Platnick, and V.A. Funk, eds. Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society. New York, Columbia University Press). And recent results, especially with animal genomes, show that we now know better, and we are going to have to do reticulistics even with animal genetic data.

The current authors instead chose to use methods never intended to reveal reticulate signal (a parsimony analysis to reveal a single hierarchical tree) and so of course they haven't found evidence for reticulate signal claimed by Kozak et al. Hardly convincing stuff. If they're not interested in evolution (pattern cladistics, as they admit in the response to the reviewer, an approach I very much doubt Hennig himself would have supported), and are only interested in finding, and using methods to find bifurcating trees, it's hardly likely that they're going to find that evolution is reticulate. It's always going to be a very biased analysis from the get-go.

That's probably enough, now.