

ESTIMATING CHARACTER WEIGHTS DURING TREE SEARCH

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Abstract—A new method for weighting characters according to their homoplasy is proposed; the method is non-iterative and does not require independent estimations of weights. It is based on searching trees with maximum total fit, with character fits defined as a concave function of homoplasy. Then, when comparing trees, differences in steps occurring in characters which show more homoplasy on the trees are less influential. The reliability of the characters is estimated, during the analysis, as a logical implication of the trees being compared. The “fittest” trees imply that the characters are maximally reliable and, given character conflict, have fewer steps for the characters which fit the tree better. If other trees save steps in some characters, it will be at the expense of gaining them in characters with less homoplasy.

Introduction

Farris (1982, 1983) has shown that the most parsimonious tree is the one that best explains the data. In earlier days of cladistics, some authors (e.g. Watrous and Wheeler, 1981; Maddison et al., 1984) believed that parsimony and weighting were somehow exclusive of each other, and that parsimony analyses should be carried out using all the characters equally weighted. However, Farris (1983) discussed the relationship between parsimony and weighting, and showed that the most parsimonious cladogram is the hypothesis with greatest explanatory power, *given the weights that the characters deserve*.

It is now more widely accepted that parsimony does not preclude weighting, but some authors (e.g. Sharkey, 1989; Rodrigo, 1992) still advocate weighting as only a means to select among trees shortest under equal weights. According to this point of view, if the equally weighted data produce just one tree, there is no need to apply character weighting. Farris' argument, however, applies even when the shortest trees for the weighted data are not shortest under equal weights, or when the equally weighted data produce a single cladogram and the weighted data produce several. Then, the tree(s) obtained under equal weights could be defended only with a claim that all the characters provide equally strong evidence. But that claim of equality is rejected by almost every published cladistic analysis, where some characters show a lot of homoplasy while others are perfectly hierarchical. In conclusion, if the data are properly weighted, those results always are to be preferred, regardless of the results under equal weights. Although few authors have held this position explicitly (e.g. Kluge and Farris, 1969; Farris, 1969; Platnick et al., 1991), it is not that parsimony *does not preclude* weighting, but rather that it *requires* weighting.

After a brief review of proposed rationales for character weighting, I will propose a new method, which, like successive weighting, uses evidence on homoplasy to

estimate character reliability. The new method, however, is not iterative, does not depend on initial estimations of weights and produces trees which, given the constraints imposed by character interaction, imply the characters to be maximally reliable.

Background

Three types of arguments have been proposed to implement weighting schemes. The first requires knowledge of some properties of the characters, such as their "change rate" (Felsenstein, 1981), or the ratio of the probabilities that the character state in an ancestor is the same as the state in its descendants [Sober, 1986, based on his previous (1985) justification for parsimony in a likelihood framework]. According to this point of view, a phylogenetic hypothesis would be as good as our prior assessments of the reliability of the characters. Hence, no matter how elegant this kind of mathematical reasoning may appear on paper, it is not very useful for practicing taxonomists.

The second type of weighting scheme is based on character compatibility. It has been proposed by Penny and Hendy (1985) and Sharkey (1989), and quoted with approval by Swofford and Olsen (1990). Although this approach does not require an independent assessment of character reliability, it suffers from more serious problems. Farris et al. (at the VIII Meeting of the Society, 1989), showed that characters with fewer incompatibilities may nonetheless be more homoplastic. Therefore, a weighting scheme derived from compatibility is not based on the degree of correlation between characters and trees.

Homoplasy is the rationale for the third type of weighting scheme, coupled with the idea that characters which have a greater tendency to homoplasy are less reliable. This actually follows from the definition of homoplasy, since homoplasy for a character is discordance between the tree and the character—the character does not predict accurately the structure of the tree, nor the distribution of other characters that fit the tree well. Weighting based on homoplasy is then the only type of character weighting defensible on cladistic grounds, and it can be justified without reference to any evolutionary or statistical assumptions. It is based on the simple idea that characters which have failed repeatedly to adjust to the expectation of hierarchic correlation are more likely to fail again in the future, and so they are less likely to predict accurately the distribution of as yet unobserved characters.

A problem in implementing a weighting scheme based on homoplasy is that the homoplasy for a character cannot be calculated without reference to a tree or set of trees—for any (informative) character some of the possible trees will have homoplasy and some will not. Farris (1969) was the first author to propose a solution to this apparent dilemma, with the method of successive weighting.

Successive Weighting and Self-consistency

Farris (1969) proposed an iterative procedure, successive weighting, in which the weights implied by the most parsimonious tree(s) for one set of weights are used in a reanalysis of the data. The procedure is repeated until a stable solution is achieved. Farris originally suggested using compatibility to estimate initial weights, but successive weighting is generally done using the trees obtained under equal

weights as the starting point. Carpenter (1988) and Guyer and Savage (1986) were among the first authors to apply the method in empirical studies, but after its implementation in Hennig86 (Farris, 1988) and PAUP (Swofford, 1990) it became much more widely used.

As successive weighting is currently implemented, the final stable solution depends on the initial set of weights. This is not a new finding; Farris himself (1969: 380–382) considered the problem of a starting point as crucial. In some sense, however, the essence of successive weighting seems contained more in its “stopping” point. Farris proposed to stop the iterations when the weights no longer change, i.e. when the weights implied by a tree lead to a preference for the same tree. This is a criterion of self-consistency. A tree which is shortest under the weights it implies is a tree which resolves character conflict in favor of the characters which, on the tree itself, have less homoplasy, and is therefore *self-consistent*. If the tree is not shortest under the weights it implies, the tree is self-contradictory: it resolves character conflict in favor of exactly those characters the tree is telling us not to trust.

Note that self-consistency is better defined with respect to one tree at a time. Successive weighting is generally done on a pooled set of trees (in Hennig86, the best fit among all the trees is used for every character; in PAUP, the average or the worst fit can be used optionally). But that a set of trees is stable under successive weighting does not imply that every one of the trees in the set is self-consistent. That would be a paradoxical situation, because those trees which would not be shortest under the weights they imply themselves could only be defended by preferring the other trees.

The criterion of self-consistency is then better implemented examining each tree separately, and it does not, in principle, require iterations: any tree which is not self-consistent should be rejected. From a limited examination of data sets, I found that it is often the case that, when a tree implies weights that lead us to prefer another tree, that other tree is closer to being self-consistent. This facilitates finding some self-consistent trees, but it does not guarantee finding *all* the possible self-consistent trees. If there is significant incongruence, there may be many self-consistent trees for a data set. I suggest that self-consistency is not all there is to cladistic analysis, and that some of the self-consistent trees may be more “reasonable” than others. Some of those trees, of course, could result from using particular sets of weights as a starting point, but then defending the trees would require defending the initial weighting schemes.

Alternatively, one may prefer to choose among self-consistent trees without reference to the starting point(s) that might lead to them, but this again leads to the choice among different weighting schemes. As an example, consider the initial results in my analysis of mygalomorph spider relationships (Goloboff, 1993). I found that a parsimony analysis with equally weighted characters produced self-consistent trees in which some groups proposed by previous taxonomists did not appear as monophyletic, but the trees in which those groups were monophyletic were also self-consistent. Both kinds of trees were “shortest” under different (and reasonable) weighting schemes. The tree lengths are not comparable for different weights, and so the choice between the two kinds of trees would require instead comparing the weighting schemes that imply, and are implied by, each kind.

Traditionally, trees are compared on the basis of how many steps they require for the data. But the above discussion suggests that trees could be compared on the basis of weights. It is in this sense that self-consistency is a necessary but not a sufficient condition: a tree may be self-consistent just by implying that many characters can be almost completely disregarded. It seems obvious that trees which imply higher weights "fit" the data better. It will be seen on further analysis that (when character weights are considered as a function of the proper shape), the trees of highest weight always resolve character conflict self-consistently.

Self-consistency and Maximization of Fit

The idea behind successive weighting or examination of self-consistency is that the trees themselves should tell us how reliable the characters are; extra steps in highly homoplastic characters should count less. So far, this has been implemented through the use of a weighting function to find a new set of weights used to reanalyze the data. The weights are not modified when searching most parsimonious trees for the given set of weights. I will call those "prior" weights, since they are assigned before an actual search starts and are not modified until it is completed.

Although parsimony is generally presented as a minimization, my points are best illustrated in terms of maximizations. I have suggested above that the trees which imply higher weights are to be preferred. The "weight" of a character is a function of its fit to a tree, and so I will refer to the quantity to be maximized as the "total fit". The fit for each character would be measured as a function of its homoplasy and the total fit of the tree would be the sum of the fits of the characters. Among all possible trees, the tree with highest total fit would be chosen. Obviously, some heuristic strategy (such as branch swapping), must be used to find the fittest tree(s) for large numbers of taxa.

Farris (1969) discussed three types of functions of the homoplasy (linear, concave and convex; Fig. 1).

If fits are considered as a linear function of the homoplasy, the tree with highest fit is a shortest tree. The fit f for character i might be defined as $f_i = k - s_i$ (where $k = \text{constant}$, and $s = \text{steps}$), or $g_i - s_i$ ($g = \text{number of steps of the character on its worst-fitting tree}$; Farris, 1989).¹ For those functions the difference in fit for an individual character having s_1 steps on one tree and s_2 on another is $(s_1 - s_2)$. The implication of this can be shown in an example. Suppose that character 1 has 1 step on tree X and 2 steps on tree Y, and that character 2 has 15 steps on tree X and 14 on Y. The same difference in number of steps always implies the same difference of fit, regardless of whether that difference occurs in characters with much or little homoplasy [Fig. 1(a)]. Trees X and Y are then considered as equivalent under a linear function, even if tree Y would save extra steps in a poor character at the expense of sacrificing them in a good one.

Parsimony analysis has been traditionally approached in this way. If fit is measured as a linear function of the homoplasy, the reliability of the characters is fixed beforehand, and character conflict is resolved according to those prior

¹ Note that although the (unit) retention index ($r = g - s / g - m$; Farris, 1989) is a linear function of the homoplasy for a given character, the tree with the highest $\sum r_i$ may not be a shortest tree, because r has different slopes for characters in which $g - m$ (the informative variation; Farris, 1991) is different. This would give higher "weight" to characters with less informative variation.

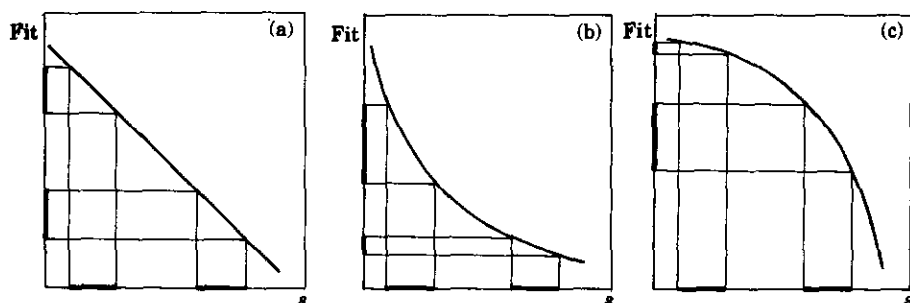


Fig. 1. The effect of considering the fit as a linear (a), concave (b) or convex (c) function of the homoplasy. The same step difference is equally important regardless of the homoplasy for (a), less important if there is more homoplasy for (b) and more important if there is more homoplasy for (c). See text for discussion.

weights. If the characters had been assigned different prior weights, this would result in different slopes; the "heavier" the character, the steeper the line of fit vs steps.

Ideally, however, one would want a measure of parsimony sensitive to differences in the homoplasy that the characters have on the trees being compared, such as characters 1 and 2 on the trees X and Y. Although at first this may sound complex, it is easily done just by considering the fit as a concave function of the homoplasy. A well-known function of that type is the (unit) consistency index, c , of Kluge and Farris (1969). Then, the fittest tree would be the one for which the average c is maximum. Measuring fit with a concave function like c , the curve of fit vs. steps would be steeper (i.e. the character is "heavier") for fewer extra steps. Figure 1(b) shows that the same differences in numbers of steps are less important if occurring between trees with more steps. Table 1 shows the differences in fit for a given difference in number of steps and different numbers of extra steps. In general, if c is used as measure of fit and two trees have s_1 and s_2 steps for a character, the difference in fit will be proportional to $(s_1 - s_2)/(s_1 \times s_2)$. Going back to trees X and Y in the example above, tree Y represents a *decrease* in fit, over tree X, of $(2 - 1/2 \times 1) = 0.5$, for character 1, and an *increase* of $(15 - 14/14 \times 15) = 0.005$, for character 2. Choosing tree Y instead of X, in others words, we loose much more than we gain.

Note that a "fittest" tree involves (implicitly) such a pairwise comparison with all the other trees, and therefore will be preferable to all of them. The fittest tree is the

Table 1

Difference in fit between two trees, one requiring H extra steps and the other requiring different numbers of additional extra steps, for a binary character using c as measure of fit. The values are scaled so that there is one unit of difference between 0 and 1 extra steps.

Step difference	Extra steps (H)						
	0	1	2	3	4	5	6
$H+1$	1.00	0.33	0.16	0.10	0.06	0.04	0.03
$H+2$	1.33	0.50	0.26	0.16	0.11	0.08	0.06
$H+3$	1.50	0.60	0.33	0.21	0.15	0.11	0.08
$H+4$	1.60	0.66	0.38	0.25	0.17	0.13	0.10
$H+5$	1.66	0.71	0.41	0.27	0.20	0.15	0.11
$H+6$	1.71	0.75	0.44	0.30	0.22	0.16	0.13

one which, in the face of character conflict, implies fewer steps for those characters which fit the tree better. If other trees save steps in some characters, it will be at the expense of gaining steps in other characters with less homoplasy. Concave functions of the homoplasy provide a more refined way to compare the relative parsimony of trees. When comparing trees during a search, the characters will be "weighted" differently for different pairwise comparisons, according to the different implications on character reliability of the trees being compared (with relative weights determined by the ratio of the fit slopes, not by the ratio of the fits themselves). This is one important difference from successive weighting, where the trees would be compared according to the implications on character reliability of a tree found in a previous analysis, not necessarily their own.

The ensemble consistency index does not equal the average unit: consistency index (Farris, 1969); if c is used as measure of fit, the fittest tree is the one that maximizes $\sum c_i = \sum (m_i/s_i)$, while the shortest tree is the one that maximizes $C = \sum m_i / \sum s_i$. Therefore, the shortest tree may not be the fittest.

Finally, convex functions of homoplasy as measures of fit imply the absurdity that the same difference in number of steps is more important when there is more homoplasy [Fig. 1(c)]. Conflict between characters would be resolved in favor of those with more homoplasy. Farris (1969) preferred concave functions of the homoplasy as estimators of reliability, on the grounds of the treatment of mediocre characters. In the context of the present argument, linear and convex functions of the homoplasy can be rejected because the evidence on homoplasy provided by the trees being compared is either ignored or misinterpreted.

"Heaviest" Trees

Character weights in a parsimony analysis are often considered as an independent parameter. Under that point of view, it may be admissible to assign most of the characters a low weight. But any such weighting scheme is inadmissible from a cladistic perspective.

In contrast, the trees with maximum fit can be seen as the trees which imply the characters to have (on average) as high a weight as possible. Cladistic analysis seeks the best explanation of the data. Explanation consists of not dismissing evidence (Farris, 1982, 1983); that is, of treating evidence as *non-dismissable*. In consequence, the best explanation does not require that the data be weighted prior to the analysis, but rather is the one which confers the highest weight on the data. Searching for "heaviest" trees, therefore, is in direct agreement with cladistic ideas, and provides what self-consistency alone did not. The problem is, then, how to estimate weights as a function of the homoplasy. Farris (1969) proposed using concave functions of the homoplasy to estimate weights, and under those functions the heaviest trees not only imply that the characters are maximally reliable, but also resolve conflict among characters according to the homoplasy the characters show on them.

Shortest trees, of course, would also be "heaviest" if weights are considered as a linear function of the homoplasy. Defending shortest trees would then require defending the notion that weights decrease linearly with extra steps. That is, the idea that characters worsen more and more with the addition of more and more additional extra steps. It seems more reasonable to think that adding one step to a perfectly hierarchical character worsens it more than adding one step to a

character with, say, 50 extra steps. Obviously, Farris (1969) also preferred the latter interpretation, since he defended concave functions of the homoplasy.

Fitting Functions

It is evident that, just as the issue on weighting cannot be ignored by simply assigning equal weights to all the characters, the issue of fitting functions cannot be ignored. The function to be maximized may actually determine which tree is chosen if there is significant incongruence. Then it has to be decided how strongly homoplasy should decrease our confidence in the characters.

Farris (1969) argued that homoplastic characters should be strongly down-weighted. Farris (1988) implemented as weighting function, in Hennig86, the unit rescaled consistency index (rc) (Farris, 1989), which is stronger than c and has a lowest bound of 0. In the present context, however, rc should not be used. Because $rc = r \times c$, choosing the tree with highest $\sum rc_i$ would make less influential not only those characters with more homoplasy, but also those *with more informative variation*. When using rc to assign *prior* weights and search a shortest tree, the problem would be the opposite (Goloboff, 1991): for similar numbers of extra steps, characters with more informative variation would be given higher weights.

The consistency index would not be affected by differences in informative variation across characters, but choosing the tree with highest $\sum c_i$ would make multistate characters less influential. The (complement of the) consistency index measures the fraction of total change on the tree which is homoplastic (Farris, 1989). One step represents a smaller fraction of the total change on the tree if the character has more states. Other things being equal, if a binary and a multistate character are in conflict, one extra step would lower less the consistency index for the multistate. For similar numbers of extra steps, the binary character would then be more influential than the multistate. Although some authors have proposed that multistate characters should be downweighted, Farris (1990) convincingly argued against that practice. To avoid such differential weighting, a modification of the consistency index, such as $1/(s + 1 - m)$, can be used to measure fit. Because that formula takes into account only the number of extra steps, it would eliminate the influence of additional states.

Farris (1969) discussed functions to assign *prior* weights, and although he suggested that c might not be strong enough in the context, its modification may be even too strong when used as fitting function. As can be seen in Table 1, the cost of adding a step to a (binary) character with only two extra steps is only 16% of the cost of adding a step to a perfectly hierarchical character, so that the second character would have a weight about six times higher than the first. The above function can be modified to be less steep by adding a constant of concavity, k . Then, $f_i = (k+1)/(s_i + k + 1 - m_i)$. For $k = 0$ the function downweights as strongly as c , but for higher values of k the function weights less drastically against characters with homoplasy. For $k = 4$, the cost of adding one step to a character with two extra steps is 54% of the cost of adding one step to a perfectly hierarchical character. The degree of concavity that should be preferred, and whether the same concavity should be used for different numbers of taxa, remains to be investigated.

Another important point is that of scaling the weights or fits. In the successive weighter of Hennig86, for example, (prior) weights are scaled between 0 and 10,

i.e. to one significant digit. That coarse-grained scale acknowledges the fact that the estimation of weights from trees is approximate, so that only relatively important difference in homoplasy will cause a difference in weight. Further, even when highly homoplastic characters have a small difference in steps in the trees to be compared, this difference will be reflected in the total measure of optimality, as steps times prior weight. If the weights or fits themselves are what is to be maximized, however, the situation may change. Suppose that the fits for each character are calculated, rounded to be integers between 0 and 10, and the total fit for the tree is calculated from those numbers. A possible consequence is that, for a given character, trees differing by small numbers of steps could be taken to have the same fit, even if there is no character conflict in the differing parts of the trees. Consider as example two trees, differing only in the resolution of a monophyletic group of three of their taxa, such that (AB)C requires 10 extra steps for a character, (AC)B requires 11 and no other character has different numbers of steps between the two trees. Using the above function with $k = 4$, the fit for (AB)C would be 0.3333, and the fit for (AC)B would be 0.3125; rescaled between 0 and 10 and rounded to the nearest integer, both trees would have a fit of 3 for the character, and would be taken as equivalent. However, that would be unjustified: although (AB)C is certainly not *much* better than (AC)B, weak support is certainly better than no support at all, and (AB)C should be preferred. Therefore, fitting functions should be finely grained, to two or three significant digits.

Conclusion

Several authors have suggested that cladistic analysis depends crucially on the weights assigned to the characters. That notion is well exemplified by Sober (1986): "parsimony is not a device that tells biologists how to weight characters; rather, parsimony requires that the characters already should be weighted". It is ironic that Sober's (1986) intent was, if anything, to defend parsimony, but his approach actually has the opposite effect. It lends support to people like Saether (1988) or Wilkinson (1991), who think that because there is no way to estimate the weights prior to the analysis, cladistic results are no more than sand castles. Sober, Saether and Wilkinson ignored Farris' (1969) ideas on how to estimate character reliability, or their possible implications. The point of view of those authors, therefore, has no real basis. There is no necessity to estimate the weights prior to the analysis, because the reliability of the characters is a logical implication of the trees being examined. More than depending on prior estimations of weights, parsimony provides a means for weighting characters. Those trees which imply the characters to be more reliable explain the data better.

An MS-DOS program available from the author, Pee-Wee, implements the approach described here. It reads Hennig86 data files and searches for trees which imply higher total fits (calculated according to the above formula). The computational cost of searching fittest trees is roughly the same as that of searching shortest trees, but the number of fittest trees is usually smaller, so that fewer trees have to be swapped. Then, run times for Pee-Wee may often be as short as run times for Hennig86—even when Hennig86 is about five times more efficient in terms of speed for calculations—and considerably shorter than for PAUP. If programmed as efficiently as Hennig86, searches for fittest trees could be even faster.

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