The how and why of branch support and partitioned branch support, with a new index to assess partition incongruence

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Accepted 19 January 2006

Abstract

An introduction and step-by-step guide to the calculation of branch support (BS) and partitioned branch support (PBS) is provided, along with a new summary measure of conflict among data partitions, the partition congruence index (PCI). Patterns of PCI vs. BS are compared for two data matrices from butterflies. PCI is a close mirror of BS unless BY is relatively low and there is a lot of conflict among data partitions, in which case PCI becomes negative. Some theoretical concerns relating to PBS are noted.


There are a lot of phylogenetic trees around these days. Everything from cladograms to directly optimized alignments to phenograms based on distance algorithms are presented as “phylogenies” of this or that taxon. A question that most systematists would like to answer, at least in a heuristic way, is, “How good is my tree?” (e.g., Wenzel, 1997). Two aspects of clade quality that are frequently mentioned are support and stability. Support for a given branch in a tree is a measure of the net amount of evidence that favors the appearance of that branch in a most-parsimonious topology. Stability is the persistence of a given branch in the face of the addition, deletion or reweighting of characters, taxa, or both from the data matrix (Judd, 1998). Both of these attributes have proven to be particularly tricky to measure in a direct manner, due to the complexity of character interactions in homoplastic data (Goloboff and Farris, 2001). Nevertheless, having some measure of the stability of and support for particular groups in an inferred topology serves as a means to discern groups that are plausible from those that are dubious, and can act as a guide to the generation of additional data to refine and improve the hypothesis.

There are numerous methods to infer the plausibility of particular branches in a phylogenetic tree, and the pros and cons of many of these have been discussed at length in the literature (e.g., Kluge and Wolf, 1993; Davis, 1995; Sanderson, 1995). The purpose of this paper is to provide an accessible review of branch support (BS) and partitioned BS (PBS), including a simple worked example based on a contrived data matrix. Towards the end of the paper, a new index of congruence among data partitions is discussed and illustrated with contrived and empirical data sets.

Branch support

An increasingly popular way to measure the support for individual branches of a cladogram is BS, also referred to as Bremer support and sometimes as the “decay index” (Bremer, 1988, 1994; Donoghue et al., 1992). BS is a statistical parameter of a particular data set, rather than being an estimate based on pseudoreplicated subsamples of the data (like bootstrapping and jackknifing), and thus is not dependent on the data.
matching a particular assumed distribution\(^1\). Another useful quality of BS is that it never hits a maximum value (such as 100%), and continues to increase as character support for a particular branch in the tree accumulates.

When it was first developed by Bremer (1988), BS was determined by discovering the most parsimonious tree(s) for a given data set, and then examining sets of trees of increasing length (referred to as the “tree decay” method). If there are multiple equally parsimonious trees of length \(L\), then the branches that collapse in a strict consensus tree have \(BS = 0\). Branches that were resolved in the strict consensus of the \(L\) trees but collapse in the strict consensus of the \((L + 1)\) trees have a \(BS\) of 1. Branches present in the \((L + 1)\) and \(L + 2\) consensus that collapse in the \((L\) and \(L + 1)\) and \(L + 2\) consensus have a \(BS\) of 2 and so on. The tree decay approach is relatively fast, as it can determine BS for multiple branches at the same time. It works well for small, well-resolved data sets, but large data matrices with a lot of homoplastic characters (such as DNA data) tend to produce many thousands of equally parsimonious trees after \(L + 2\) or so, and it becomes increasingly difficult to perform adequate searches to ensure that all equally parsimonious trees have been discovered. It is thus quite easy to overestimate the BS for a given branch using the tree decay approach.

Another way to infer BS is by the employment of anticonstraint trees. An anticonstraint tree is a specification to the search algorithm to find the most parsimonious tree(s) that do not contain a particular clade. The difference between the length of the most parsimonious tree(s) and the length of the most parsimonious tree(s) not containing clade X is the BS for clade X. Using the anticonstraint approach requires branches to be assessed one at a time, which is more time consuming, but it does not get overwhelmed as easily as tree decay by accumulation of multiple equally parsimonious trees. Like the tree decay approach, it is possible to underestimate BS values using anticons toms if searches are not performed exhaustively. For large, homoplastic data sets, it is important to perform anticonstraint searches with comparable rigor with the original search for the MP tree(s). There are several computer programs available (Sorenson, 1999; Eriksson, 2001) that automate this process to some degree.

\(^1\)It should be noted that tree quality measures that rely on counterfactual perturbations of the data are really measures of stability not support in the sense defined above, at all: stability is the recoverability of relationships implied in the optimal tree under alternate search criteria from those used to obtain the result being tested. “Counterfactual perturbations” include differential character weighting, variable gap-change costs, and the resampling methods of bootstrap and jackknife, which randomly assign zero weights to some characters (and multiple weights to others, in the case of bootstrap).

Partitioned branch support

An important extension of BS was the discovery by Baker and DeSalle (1997; Baker et al., 1998) that when a data set is divided into partitions (e.g., multiple gene regions, or DNA versus morphology), the overall BS for a given branch is the sum of the BS derived from each of the data partitions for the most parsimonious tree(s).

Like BS, PBS is a parameter of the data matrix. The PBS value for a particular branch for a given data partition is determined by subtracting the length of the data partition on the MP tree(s) from the length of the data partition on the MP anticonstraint tree(s) for that branch. Note that the length of the most parsimonious tree for the partition analyzed separately does not enter into the calculation of PBS.

A given partition may contribute positively, be neutral, or conflict with the weight of the evidence that supports a particular branch in combined analysis. The details of PBS have been elaborated in a series of papers by Gatesy and colleagues (Gatesy et al., 1999; Gatesy and Arctander, 2000; Gatesy, 2000, 2002; see also Lee 2000; Baker et al., 2001; Lambkin et al., 2002). Lee and Huggall (2003) have proposed a significance test for PBS values.

PBS is particularly valuable because it allows exploration of partition incongruence within a “total evidence” framework (Kluge, 1989; Brower et al., 1996; DeSalle and Brower, 1997; Judd, 1998), and on a branch-by-branch basis, not simply as a unitary value for the entire tree, like the incongruence length difference (Mickevich and Farris, 1981; Farris et al., 1994) or various statistical tests that have been proposed [Thornton and DeSalle (2000) have proposed a technique for assessing the significance of incongruence among data partitions for individual branches]. The ability to localize incongruence to a single partition for a single branch has the potential to reveal both interesting evolutionary processes, such as selection on a particular gene, and also allows detection of error by the process of reciprocal illumination (Hennig, 1966).

A worked example

Consider the following simple data matrix:

\[
\begin{array}{cccccc}
1 & 1234567890 \\
X & 0000000000 \\
A & 1100001111 \\
B & 1111111000 \\
C & 0011100111 \\
\end{array}
\]

The shortest tree for this data set, which contains clade (AB), and the two shortest trees not containing clade

(AB) are shown in Fig. 1. To determine the BS for clade (AB), the length of the MP tree is determined (16 steps, in this case). Then the length of the shortest tree(s) not containing (AB) is found. In this case, there are two alternatives, both of which are 17 steps, 1 step longer than the MP tree. Thus, the BS for (AB) is 1.

Now suppose that the data matrix is split into two partitions:

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It will be immediately evident that neither of these partitions supports clade (AB): partition I supports (BC), and partition II supports (AC). However, as noted above, the calculation of PBS depends upon the length of each partition on the MP tree and on the average length of the shortest trees not containing the branch of interest (AB) from the analysis of all the data, not on the lengths of the MP trees for the partitions analyzed separately.

Figure 2 shows partition I mapped on the three cladograms from Fig. 1. The partition mapped on the MP tree (a) is eight steps, and on the other two trees (b) and (c), its length is seven and 10 steps, respectively. The average length of these two trees is 8.5 steps. Thus, the PBS for partition I is \((L(b) + L(c))/2 - L(a) = 0.5\).

Figure 3 shows partition II mapped on the three cladograms from Fig. 1. Because the partitions of the data in this example are symmetrical, it is a mirror image of Fig. 2. Again, the length of the partition on MP cladogram (a) is eight steps, and now the lengths of the other two trees are 10 and 7. Their average length is 8.5 steps, and the PBS from partition II is also 0.5. Note that \(PBS_{I} + PBS_{II} = BS\).

Partitions need not be symmetrical or of equal size (in most instances real data will not be). Here the same data matrix has been split into two partitions of unequal size:

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As in the first case, neither partition unambiguously supports the grouping (AB) that is supported by the entire matrix. Figures 4 and 5 show partitions III and IV mapped on the three cladograms (different ways of dividing up the data have no effect on the trees: the MP tree and shortest trees not containing the node of interest will always be the same, unless the data matrix as a whole is changed). Partition III, although smaller, contains all the support: \(PBS_{III} = (L(b) + L(c))/2 - L(a) = 1.0\); while partition IV contributes no net support. Again, \(PBS_{III} + PBS_{IV} = BS\).

If multiple equally most-parsimonious trees are discovered in the search of the entire data set, then the length of a partition is calculated on each of these. PBS
is equal to the difference between the average length of the partition among the MP trees and the average length of the partition among the shortest tree(s) not containing the node of interest.

The partition congruence index

One difficulty of BS is that the value is a single number that does not reflect potential underlying disagreement among constituent data partitions. For example, a given branch may be supported by two characters and contradicted by none, or supported by 100 characters and contradicted by 98. Both of these branches will have a BS of two. Goloboff and Farris (2001) developed the idea of the relative fit difference (RFD) to address this ambiguity in terms of homoplasy within an unpartitioned matrix, but (to my knowledge) it has not been addressed in the context of PBS.

The simplest approach to evaluating incongruence among partitions is simply to present the PBS values for
each branch and discuss instances in which there is apparent disagreement among them (e.g., Wahlberg et al., 2005). This is not particularly satisfactory, as it does not provide an objective numerical measure, and results in qualitative value judgments about “well-supported” or “poorly supported” clades. A parameter that took into account both the overall support for a given branch and the disagreement among data partitions underlying that support value could be a useful measure.

The more disagreement there is among partitions, the greater will be the difference between positive PBS values from the partition(s) that provide the BS for a given branch, and the negative PBS values for partition(s) that contradict that branch. John Gatesy (pers. comm.) has suggested the value $BS / \sum|PBS|$ as a measure of this disagreement. This value ranges from 1 when no partition contradicts the branch, to approaching zero, when there are strongly disagreeing partitions (for example, +100 and −99 yield a value of 0.005). This is
Fig. 6. PCI values resulting from a range of conflicting PBS values from an artificial data set with two partitions. PBS2 represents the partition that drives the structure of the data, PBS1 represents the conflicting partition. Conflict in PBS1 ranges from 0 to PBS2-1 for each PBS2 value. The data are presented in Table 1.

Table 1

Artificial data matrix showing the range of PCI values as a function of various PBS values, as graphically depicted in Fig. 6. Top row represents PBS for partition 1, left column represents PBS with increasing degrees of conflict in partition 2.

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a simple measure, but it does not reflect the amount of BS, nor does it increase continuously, like BS values do. A slightly more complex value that incorporates those features is the partition congruence index (PCI), which is defined as follows:

\[
\text{PCI} = \text{BS} - \left( \sum_{i=1}^{n} |\text{PBS}_i| - \text{BS} \right) / \text{BS}
\]

Described in words, the partition congruence index for a given branch equals the BS minus (the difference between the sum of the absolute values of the PBS for each partition and the BS, divided by the BS). The behavior of the PCI relative to various PBS values for a made up data set with two partitions is presented in Fig. 6. The accompanying values are presented in Table 1. As is evident, when there is no conflict among partitions, PCI = BS, but as the conflicting signal between partitions increases, PCI decreases, until it becomes negative. With lower BS values, relatively little conflict results in a negative PCI value, but as BS increases, the degree of conflict must become increasingly severe to produce a negative PCI score.

Figure 7 shows actual BS and PCI scores from two equal-weighted simultaneous analyses of empirical data sets for different groups of nymphalid butterflies (Wahlberg et al., 2005; Brower et al. 2006). As noted
above, the PCI is equal to the BS when there is no conflict among partitions. The impact of conflicting signal in one or more partitions on the PCI is relatively small when BS is large, as indicated by the near linearity of the two graphs when BS is greater than 5. When BS is relatively low, the PCI is much more sensitive to incongruence, and many nodes with positive BS values have negative PCI values. Although the potential exists for very large negative PCI values when there is strong conflict among partitions \((PCI_{min} = -2BS + 2)\), no such values were observed in these data, the lowest PCI value in the Nymphalinae data set was \(-13.2\), and the lowest in the Ithomiini data set was \(-11\).

**Discussion**

The exercise of assessing congruence or incongruence among data partitions is not dependent upon reification of partitions as distinct functional units evolving under homogeneous processes (Bull et al., 1993) or separate parts of organisms (different genes, molecules versus morphology, etc.) (Miyamoto and Fitch, 1995). Instead, partitioning data is a potentially useful way to explore incongruence of signal among characters from different sources. Doing so in the context of the weight of the evidence from the data matrix as a whole using BS and PBS values avoids the problem of implied non-independence of characters within a partition (DeSalle and Brower, 1997). Much of the criticism of support measures (e.g., Kluge and Wolfe, 1993) is focused upon their employment of reanalyses of data subsets or partitions as though they were separate sources of evidence. PBS has the advantage of being based exclusively on parameters of the complete data matrix, and PBS may be calculated for any combination of partitions that the researcher deems useful, or even for individual characters (referred to as “character support”, which is also additive; see Gatesy et al., 1999).

Pablo Goloboff (pers. comm.) has contrived some particular cases in which PBS values behave unpredictably. Multiple, incongruent groups of homoplastic character states in alternate partitions can produce non-intuitive and seemingly inexplicable results due to the differential distribution of homoplasy among partitions in the most parsimonious and subparsimonious trees used to calculate BS and PBS values. PBS also appears to be sensitive to missing data, and can shift dramatically among partitions as missing data are filled into the matrix. Further exploration of the impact of these problems for the interpretation of PBS values will be a valuable contribution to the theoretical investigation of clade quality. However, as Goloboff et al. (2003) have pointed out, no measure of clade quality yet developed is immune from bizarre behavior in certain conceivable instances. Even parsimony analysis itself can be “inconsistent” under the wrong circumstances. A premise of the cladistic approach is that signal from synapomorphies rises above the random noise of homoplasy, even when homoplasy is abundant (Farris, 1983). The detection of strong incongruence among data partitions may imply a violation of this premise, and negative PCI values should be considered as a sign that further inquiry may reveal errors or other interesting phenomena intrinsic to the data.

There are no objective means to set a criterion of rejection of support or stability for a particular branch in a particular cladogram. Given the dependence of the tree on the underlying sample of characters and taxa, support for the current data does not necessarily imply that the support will be robust to the addition of taxa and characters: support today is no guarantee of stability in the future. For this reason, measurements like bootstrap values and Bayesian posterior probabilities that imply a confidence interval are potentially misleading. BS, by contrast, because it has no upper bound, is a more direct and less sophisticated way to document the accumulation of character support for a particular branch in a particular phylogenetic hypothesis. The expectation/hope is that strongly supported branches will remain stable against collapse and perhaps even continue to accumulate further support as additional data are incorporated. The PCI is a simple parametric value that largely mirrors BS, but provides a more refined way of distinguishing between branches that are weakly supported as a result of a small amount of inferred character transformation, and those that are weakly supported as a result of conflict among partitions of the data that imply different topologies.

**Acknowledgments**

Thanks to Niklas Wahlberg and Darlene Judd for support and stability, and for discussions about them. John Gatesy and Pablo Goloboff provided helpful criticisms of an earlier draft of the manuscript. The work was sponsored by US National Science Foundation DEB 0089886 and the Harold and Leona Rice Endowment for Systematic Entomology.

**References**


