

Additional file 3 — Estimation accuracy measures

We adopted two different measures of estimation accuracy, one for branch lengths and the other for gene rates.

- The fraction of variance unexplained is a classical measure in regression analysis which can be seen as a normalised form of the sum of squared errors of prediction of an estimation model. Here, we adapt it to measure the discrepancy between a vector of branch lengths (b_e) and their estimates (\hat{b}_e). We define the *fraction of variance unexplained* of (b_e) relative to (\hat{b}_e) as:

$$\frac{\sum_e (b_e - \hat{b}_e)^2}{\sum_e (b_e - \bar{b})^2}$$

where sums are over all branches in a tree and \bar{b} is the arithmetic mean of the branch lengths in (b_e).

- In order to measure the discrepancy between a collection of m gene rates (r_k) and their estimates (\hat{r}_k), we take the *mean absolute log-ratio* between r_k and \hat{r}_k , that is:

$$\frac{1}{m} \sum_{k=1}^m \left| \log \frac{\hat{r}_k}{r_k} \right|.$$