

Interactive web-based visualization of phylogenetic trees using Phylogeny.IO

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Traditional static publication formats make visualization, exploration and sharing of massive phylogenetic trees difficult. Web-based technologies, such as the Data Driven Document (D3) JavaScript library, exist to overcome such challenges by allowing interactive display of complex data sets. We here we an open-source web-based application that applies the power of D3 to the visualization of phylogenetic trees. Phylogeny.IO (<http://phyloeny.io>) displays trees together with a range of static (e.g., such as shapes and colors) and dynamic (e.g., pop-up text and images) annotations. Annotated trees can be shared as IFrame HTML objects easily embeddable in any web page.

Traditional static publishing formats struggle with the display of 'big data', including large phylogenetic trees. Typically such trees become split across multiple figures, sometime spanning pages, which makes them difficult to navigate, or are shrunk down, which makes them difficult to read. Even more problematically, there are often multiple layers of information available for each phylogeny, including error bars for node date estimates, taxon images, and various other types of annotations that cannot be displayed simultaneously without crowding the figure. Consequently, the same tree may appear in multiple figures, each one highlighting different aspects of the data. Spreading the layers of information across multiple figures makes it more challenging to see how they interrelate, and can increase publication costs, which are often calculated by figure.

In response to this limitation, a wide range electronic solutions have exist to help visualize trees, particularly for the web, including EvolView, iTol, and PhyloWidget, as well as many others (Letunic & Bork, 2007, 2011; Jordan & Piel, 2008; Smits & Ouverney, 2010; Zhang et al., 2012). These applications have rich feature sets, and produce beautifully rendered trees, but tend to focus on visualization of the tree within the application itself. This makes it difficult to share the tree without exporting them into a graphics format, or installing the application locally, which is not always possible either. Furthermore, some also require locally installed software or third-party packages such as Java or Adobe Flash, which limit compatibility and could pose security concerns. The jsPhyloSVG library (Smits & Ouverney, 2010) takes advantage of JavaScript for phylogenetic tree display, making rich interactive figures for local display. However, it has a relatively difficult syntax and no graphical user interface, which require a steep learning curve.

Our goal was to develop an open-source application using general purpose JavaScript libraries, specifically D3.js, for phylogenetic tree display. As a result, the application works with modern browsers, including mobile devices, and allows interactive phylogenetic trees to be easily

embedded into static web pages for sharing. The use of JavaScript for phylogenetic tree visualization has several advantages. First, the visualization is performed client-side by the web browser, decreasing computational load on the server hosting the trees. This enhances deployment scalability, allowing the server to handle many requests. Second, all of the data used to render and annotate the tree are therefore accessible to the user, making the process reproducible and transparent.

For phylogeny manipulation and annotation, we borrowed heavily from the user interface of FigTree, a popular tree viewer associated with the BEAST software package (Rambaut; Drummond & Rambaut, 2007). Trees can be uploaded and annotated using the interface hosted at <http://phylogeny.io>. It currently supports Newick and some Nexus file formats (namely those produced by BEAST) (Maddison, Swofford & Maddison, 1997), and a custom JSON format that is also used for exporting annotated trees. Once a tree has been annotated, it can be shared as a HTML iframe document and embedded into any static web page.

One disadvantage of JavaScript for visualizing large data sets is that images have to be rendered in web browsers locally. This limits the size of the tree that can be visualized without slowing down the browser. As a result, the visualization is currently limited to 4000 leaf nodes total, though only 1000 leafs can be displayed simultaneously. Consequently, when larger trees are loaded, some branches are automatically collapsed to speed up rendering.

We illustrate the advantages of this approach using a large tree from a large study of ant phylogenetics by Moreau and Bell (2013), which produced a fossil-calibrated phylogeny of 311 taxa. In paper, the phylogeny occupies nearly three manuscript pages, together with a separate figure depicting a dated chronogram with leaf labels in 1.5 point font. The annotated phylogram, combining elements of of Figures 1 and 2 in the original data set can be seen as an example on phylogeny.IO website. In addition, named species have images hyperlinked from AntWeb.

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