TREEMAP 1.0
User's Guide

by

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1. What is TREEMAP?

TREEMAP is designed as a simple tool for visually comparing host and parasite phylogenies: you can view the host and parasite trees, interactively create reconstructions of the history of the host-parasite association, perform randomisation tests of tree similarity, and (if you have branch length information such as might be obtained from DNA sequence data) compare branch lengths in the two trees.

I should emphasise that TREEMAP is an experimental program for comparing host and parasite trees. It started out as a test bed for my research, and is not a finished product. It is offered free and on an "as-is" basis to anyone interested in host-parasite cospeciation. It runs on Apple® Macintosh®'s and under Microsoft® Windows™.

1.1 Copyright notice

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1.3 Acknowledgements

TREEMAP would not have been ported to the Macintosh without Eddie Holmes and Paul Harvey lending me their PowerBooks. Andrew Rambaut offer advice on things Macintosh. Writing the program was made easier by using ideas from the National Center for Biotechnology's VIBRANT library written by Jonathon Kans. TREEMAP is written in C++ and compiled with Microsoft Visual C++ 1.0 (Windows) and Symantec C++ 6.1 (Macintosh).

2. Getting started

2.1 Obtaining TREEMAP

TREEMAP can be obtained by anonymous ftp from the server evolve.zps.ox.ac.uk in the directory /packages/treemap. There are two files present in this directory:

- TreeMap.sea.hqx (Macintosh BinHexed self-extracting archive)
- TREEMAP.ZIP (zip compressed Windows version)

2.2 Requirements

TREEMAP requires either an Apple Macintosh running System 7.0 or later, or a PC running Microsoft Windows 3.1 or later.

2.3 Differences between Macintosh and Windows versions

I've tried to make the two versions as similar as possible; for example the data file formats are identical, as are the menus, and most key commands. However, some compromises have had to be made in order be able to develop the software on both Mac's and PC's at a reasonable speed. Hence some parts of the interface are incomplete and rather clumsy, but I hope to fix this eventually.

In this manual the following symbols indicate comments specific to one or other version of the program:

Apple Macintosh

Microsoft Windows

2.4 Installing TREEMAP

The Macintosh version of TreeMap is stored on the “Harvey group” ftp server as a BinHexed file. Unless your ftp software automatically decodes BinHex files (as does Fetch, for example) you will need to use BinHex 4.0 to obtain the self-extracting archive TreeMap.sea. The latter will automatically extract the TREEMAP application and supporting files.

To install TREEMAP, uncompress the TREEMAP.ZIP file using a program such as XTree for Windows, WinZip, unzip, or PKUnzip, then copy the files into a directory on your hard disk. The file TREEMAP.EXE contains the program, the remaining files are support files and example data files. You can add TREEMAP to the Program manager, or if you prefer, simply launch it from the File Manager or a similar program (see your Windows documentation for details).

2.5 Background Reading

The concept of tree mapping is discussed in Page (1994). The method implemented in TREEMAP is described in detail in Page (1995) — I strongly recommend that you read Page (1995) before using this program.

3. Overview of program

This section provides an overview of the program.

3.1 Starting TreeMap

Macintosh

You can start TreeMap by:

- Double-clicking on the TREEMAP icon.
- Double-clicking on a TREEMAP document.
- Dragging a TREEMAP document onto the TREEMAP application icon.

You can start TREEMAP by:

- Double clicking on the TREEMAP icon if you've add TREEMAP to Program Manager (see your Windows documentation on how to do this).

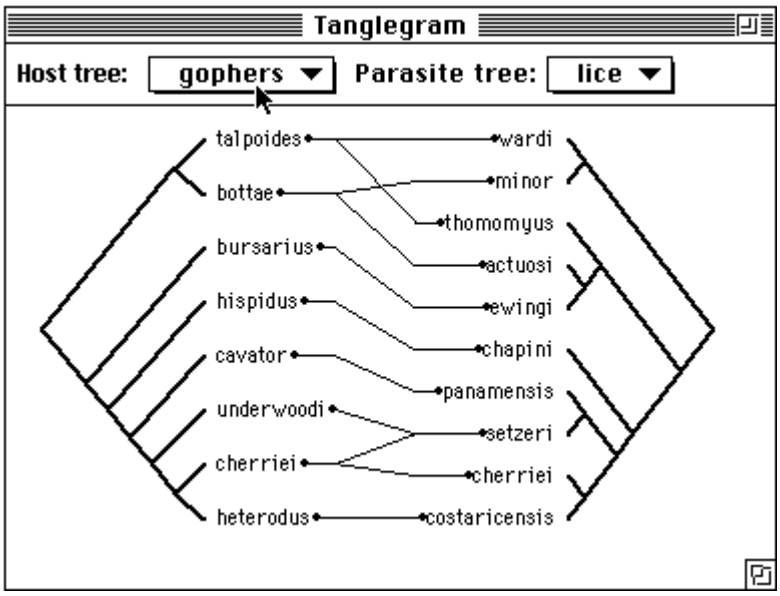
- Dragging a TREEMAP data file onto the TREEMAP.EXE file in File Manager or other file management software (e.g. XTree for Windows).

3.2 Windows

TREEMAP has four main windows which display various views of your data. Windows can be selected by clicking on them, or by using the **Windows** menu. The font used to draw text in each window can be altered using the **Style** menu. The contents of each window can be printed (**File | Print**), copied to the Clipboard (**Edit | Copy**), or saved to disk as a picture (**File | Save Graphics File**) or text (**File | Save Text File**) file. Note that pictures, whether copied to the Clipboard or saved to disk, are formatted to fit on a complete page, they also have the same orientation as the current printer settings. Hence, for some windows you may want to alter the page set-up of your printer (**File | Page setup**) before creating a picture.

3.3 Tanglegram Window

The Tanglegram window displays the current host and parasite trees with parasites connected to hosts by a coloured line:



You can alter the appearance of the trees by changing the font used to draw the labels (using the commands on the **Style** menu), and by rotating descendants about their ancestor, thus "untangling" the trees. To do this, click on the desired branch.

With some practice, you'll quickly be able to obtain a pleasing display. Note that you're not actually altering the phylogenetic relationships specified by the trees, merely how the trees are drawn.

If your trees have branch length information you can display the trees as "phylograms" by choosing the **View | Phylogram** command. To ignore branch lengths choose **View |**

Cladogram. You can also toggle on and off the numbering of the internal nodes of the trees (**View | Internal labels**). These numbers are arbitrary and are used to keep track of the internal nodes. To display branch lengths in host and parasite at the same scale choose **View | Same scale**.

Choosing other trees

If you have more than one host or parasite tree, you can change the tree you're looking at using the popup menus in the Tanglegram window. These list the names of the trees listed in the input file. Because the same trees are being compared in all windows, changing a tree in the Tanglegram window also changes the tree in the Reconstruction window and the Branch lengths window.

3.4 Reconstruction Window

The Reconstruction window displays the parasite tree (in black) overlaid on the host tree (in light grey). This window is the core of TREEMAP, as it is here that you can experiment with different reconstructions, find optimal reconstructions, and perform various randomisation tests.

Creating a reconstruction

By default, TREEMAP reconciles the parasite and hosts trees, however unlike COMPONENT, TREEMAP superimposes the parasite tree on the host tree (cf. Page, 1994: fig. 2c), rather than displaying the reconciled tree itself.

The parasite tree is drawn in black slightly below the host tree (drawn in grey), with each node in the parasite tree draw below the corresponding node in the host tree. You may want to alter the font to improve the display.

Interpreting the reconstruction

Reconstructions can be best explained using an example. The file SIMPLE.NEX contains two small trees:

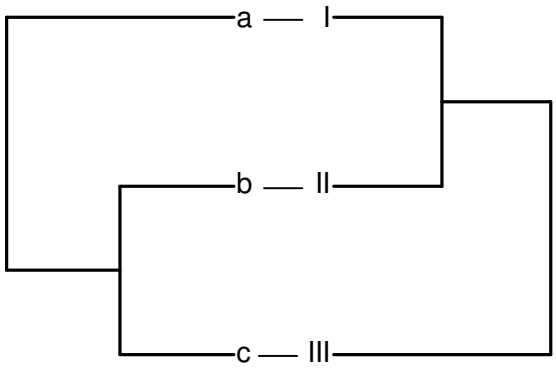


Fig. 1 Host and parasite trees from the file SIMPLE.NEX.

As you can see they are incongruent. Go to the Reconstruction window to see the reconciled tree:

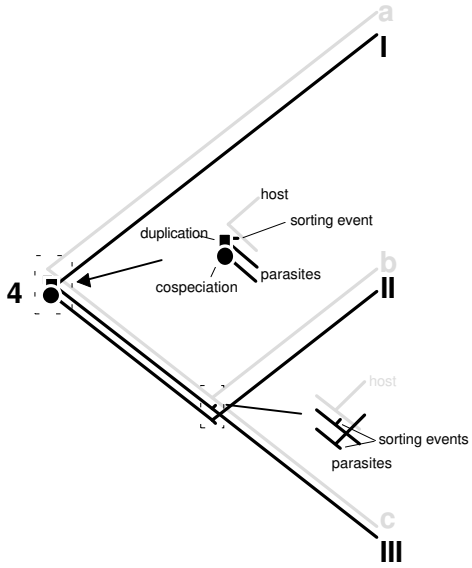


Fig. 2 Reconciled tree for the host and parasite trees in Fig. 1. This tree has one cospeciation event, one duplication event, and three sorting events

Reconciled trees are discussed in detail in Page (1994). In the figure above, the two internal nodes on the parasite tree comprise a *cospeciation* event (●) and a *duplication* (■). Along the bottom of the Reconstruction window the status line appears showing the statistics for this reconstruction.

Sorting events occur when parasites go extinct, or are differentially sorted amongst hosts. For example, two sorting events occurred when host 4 speciated into b and c. Given that host 4 harbours two parasites, we might have expected each to speciate, so that hosts b and c each had two parasites. Either this did not happen (hence parasite II was passed on to host b, and parasite III was passed onto host c) or there was speciation, but only one descendant of each event survived. The other sorting event is associated with the duplication event at the base of the parasite tree.

Host switching

The reconciled tree prohibits association by colonisation, that is, it prohibits host switching. Let's suppose that parasite "I" is associated with its host "a" by colonisation, not by descent. To see what that reconstruction looks like simply click on the parasite's name ("I"). You should now see a new reconstruction:

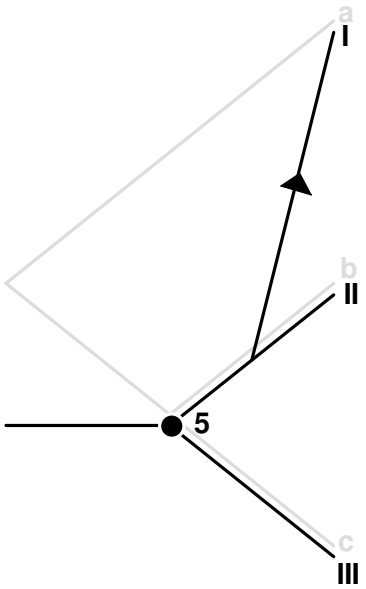


Fig. 3 A reconstruction with one instance of host switching (the line marked with the arrow ➤)

This reconstruction also has one instance of cospeciation, but no duplications or sorting events. By clicking on "I" again you revert to the reconciled tree. Now try clicking on "II":

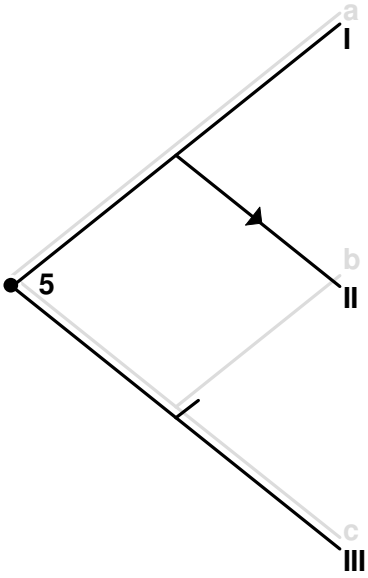


Fig. 4 An alternative reconstruction

This reconstruction also has one cospeciation and one host-switch, but in addition it has a single sorting event (on parasite lineage III where host 4 speciates into b and c).

Prohibited host switches

Note that TREEMAP will not allow some host-switches. Specifically it requires that:

- the ancestral host for all parasites be defined, and
- all host switches are between contemporaneous hosts.

The first requirement means that the root of the parasite tree and its two immediate descendants cannot disperse. The second requirement prohibits spurious dispersals such as from a host onto an ancestor of that host, which by definition no longer exists. These requirements are discussed in Page (in press).

Host-switches need not be restricted to terminal taxa. In larger phylogenies you can click on the internal nodes to create ancestral host-switching events.

3.5 Histogram Window

The Histogram window displays histograms obtained when you perform randomisation tests (see below). You have the option of viewing the histogram as a graphic or as a text summary, by choosing the **View | Graphic as text** command.

Output

The histogram TREEMAP draws is rather unattractive. If you copy it to the Clipboard you can paste it into a graphics program for editing.

You can use the **File | Save as text file** to create a text file containing a text summary of the histogram.

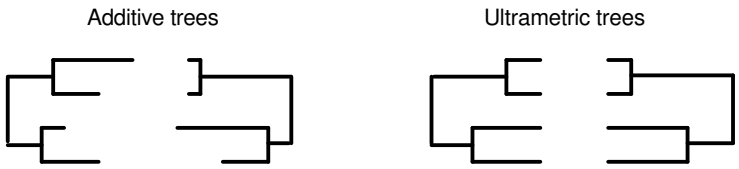
3.6 Branch Lengths Window

If your host and parasite trees have branch lengths, TREEMAP displays a Branch Lengths Window containing a bivariate plot of the lengths of the corresponding branch lengths. It computes and displays the correlation coefficient between the branch lengths in the two trees. Again, this plot will not win any prizes for graphic design. The **File | Save text file...** command allows you to create a text file listing each data point which can be imported into a spreadsheet or charting program to produce nicer graphics.

Types of plot

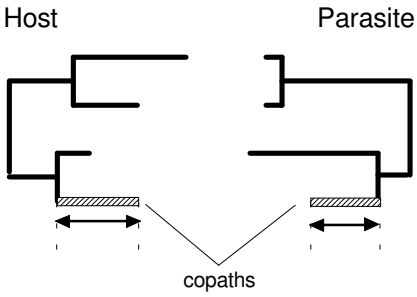
The types of branch length plot available depend on the types of tree you have. If the tips of the trees all line up then the trees are ultrametric (see below). *Ultrametric trees*

are produced by phylogeny programs that assume a molecular clock, such as KITSCH and DNAMLK in PHYLIP. *Additive trees* need not have all tips line up, and hence do not assume a molecular clock.



If the current host and parasite trees are not ultrametric trees then TREEMAP plots the lengths of the copaths (see below) in the two trees. However, if you have ultrametric trees then you have two options, plotting branch lengths (copaths) or plotting coalescences times.

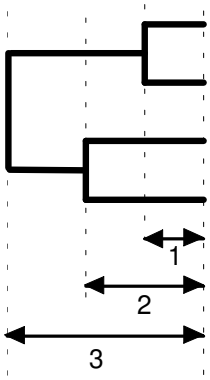
Copaths



A *copath* is a path between successive cospeciation events, or between a terminal taxon and its most recent ancestor that is also a cospeciation event; hence a copath traces out equivalent paths in the host and parasite tree. In the Branch Lengths window the data points are labelled with the number of the host and parasite nodes that are most distant from the root. If either of these nodes is a terminal taxon, the data point is labelled with the name of that taxon.

Coalescence times

The coalescence time is the time two lineages last had a common ancestor. On an ultrametric tree this corresponds to the distance between the ancestral node and any one of its descendants:



In the tree above there are three coalescence events, hence three coalescence times (1-3). Given ultrametric host and parasite trees, we can plot the coalescence time of each pair of cospeciation nodes (Hafner and Page, in press). For example, given these two ultrametric trees,

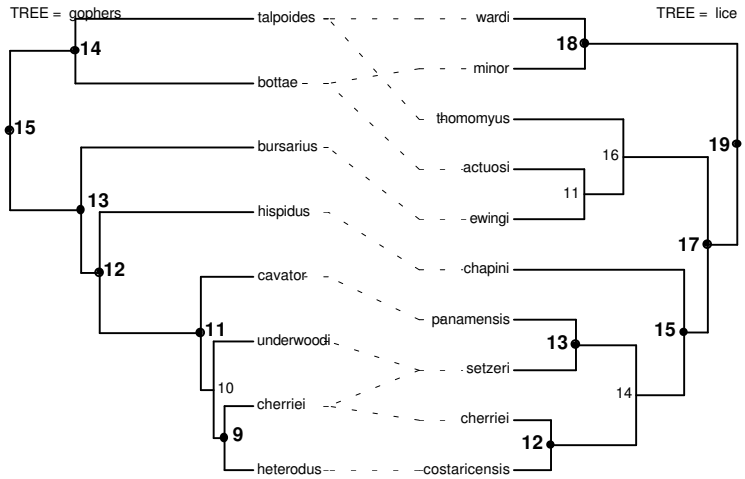


Figure 5. Ultrametric trees for pocket gophers and their lice. Cospeciation nodes are numbered in **bold**

the coalescence plot looks like this:

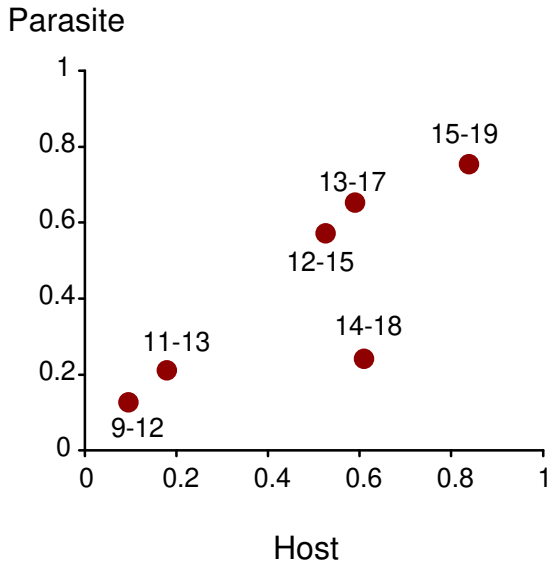


Figure 6. Plot of coalescence times (in units of genetic distance) for the cospeciation events in Fig. 5. Each point is labelled with the numbers of the corresponding nodes in the host and parasite trees, respectively. For example, the point 9-12 plots the coalescence time (measured in units of genetic distance) for the parasite node 12 and its corresponding host node 9.

Because ultrametric trees are constrained to have all pairs of terminal taxa equidistant from their most recent common ancestor these pairs are not independent; hence if you have two ultrametric trees and request **Plot branch lengths** TREEMAP only plots the lengths of the internal copaths.

4 Managing Reconstructions

Having created one reconstruction you may want create others, but in doing so you'll destroy the reconstruction you've just created. TREEMAP lets you save the current reconstruction so you can recall it later. You can also start from scratch by clearing the current reconstruction. The commands that manage the reconstructions are on the **Reconstruction** menu.

4.1 Storing reconstructions

To save the current reconstruction choose the **Store** command from the **Reconstruction** menu. A dialog box will appear: type in the name you want to give your reconstruction (the name can have up to 31 characters) and click on **OK**. TREEMAP will store the current reconstruction in memory.

4.2 Choosing reconstructions

To recall a reconstruction chose the desired reconstruction from the popup menu at the top of the Reconstruction window. Choosing the reconstruction “none” clears the current reconstruction.

4.3 Clearing the reconstruction

At any time you can clear the current reconstruction (that is, revert to the reconciled tree) by choosing **Clear** from the **Reconstruction** menu. If the current reconstruction has not been stored the program will ask you if you want to store it.

5 Finding the best reconstruction(s)

In this context the “best” reconstruction is defined as that with the greatest number of cospeciation events (see Page, in press). TREEMAP offers two ways of finding the best, a simple heuristic search and an exhaustive search.

5.1 Heuristic search

The heuristic search uses a simple algorithm that attempts to find a single optimal reconstruction introducing successive host-switches until the number of cospeciations no longer increases. It is quick but is not guaranteed to find the best reconstruction (although in practise it does rather well). Note that it finds only **one** reconstruction — there may be others that are equally good, or better.

The heuristic algorithm is a useful way of quickly estimating the maximum number of cospeciation events. It is also used by the randomisation tests described below.

The reconstruction found by the program is not automatically stored, so if you want to keep it you will have to store it using the **Store** command (see above).

5.2 Exact search

TREEMAP also features an exact algorithm that will find all the optimal reconstructions. This algorithm is (a lot) slower than the heuristic method.

Be warned that if you use the exact search all currently stored reconstructions will be lost as TREEMAP uses that storage space for the optimal reconstructions. Also, the exact search can take a long time. However, the program can sit in the background allowing you to get on with other tasks (Windows version only).

Choose the **Exact** command from the **Reconstruction** menu. TREEMAP will display a dialog box showing its progress. You can abandon the search by clicking on the **Cancel** or **Stop** button.

Once the search is completed the optimal reconstructions are stored in memory and can be accessed using the popup menu in the Reconstruction window (see above).

6. Randomisation tests

TREEMAP offers a range of randomisation tests (some more experimental than others) designed to help evaluate the relationship between host and parasite phylogenies.

6.1 Is there evidence for cospeciation?

Given that the "best" reconstruction requires *n* cospeciation events, how do we know if this is meaningful or not? One approach is to ask what are the chances of getting *n* cospeciations by chance alone. TREEMAP allows you to randomise either the host or the parasite tree, or both simultaneously. For each randomised tree (or pair of trees), TREEMAP uses its heuristic algorithm to compute the maximum number of cospeciation events between the two trees.

6.2 Generating random trees

You can choose to randomise either the host tree, the parasite tree, or both simultaneously. Once you have chosen which option you desire, TREEMAP then displays a dialog box asking you how many random trees you want to generate, under which model they are generated, and how to seed the random number generator.

If you choose **User value** then TREEMAP uses the value you supply, otherwise TREEMAP takes a seed from your computer's system clock. If you supply a seed it

must be in the range 1 to 2,147,483,646. If you use the same seed each time then the same set of random trees will be generated.

The result of the randomisation test is a histogram of the frequency of the maximum number of cospeciation events between the pairs of trees generated. This is displayed in the Histogram window.

6.3 Comparing branch lengths

If your trees have branch lengths (e.g., amounts of sequence divergence) then you can do one or more simple randomisation tests to assess the significance of the correlation between branch lengths in the host and parasite trees.

Choose the **Randomise | Branch lengths** command. TREEMAP displays a dialog box similar to the one for random trees:

Additive trees

If you have additive trees, TREEMAP will randomly reassign the observed branch lengths in the parasite tree, then compute the correlation coefficient between the randomised branch lengths and the observed host branch lengths.

Ultrametric trees (molecular clock)

If you have ultrametric host and parasite trees, you can either use a simple Yule model to generate random coalescent times for the parasites, or randomise the intervals between the observed coalescence times to generate new coalescence times (this will be described in more detail elsewhere).

Results

As with the random trees, the Histogram Window displays the results of the randomisation test.

7. Managing TREEMAP files

This section describes the file formats used by TREEMAP, and how you can create your own data files.

7.1 Kinds of files

On the Macintosh, TREEMAP creates three kinds of files: TREEMAP data files, PICT files, and text files. These files have the following icons:

PICT files are standard Macintosh picture files, which can be edited by graphics programs, or copied/pasted into a word processor. Text files are used to store text output, and have their creator set to TeachText so you can quickly view their contents using that program.

Under Windows, TREEMAP data files are standard ASCII text files with the default extension *.NEX, and picture files are Windows metafiles (*.WMF). The later can be read by virtually all Windows graphics programs and word processors.

7.2 Opening an existing data file

TREEMAP data files use a variant of the NEXUS format (the details of which are presented later in this manual). To read a TREEMAP file choose the **Open** command from the **File** menu. You will be presented with a standard File Open dialog box that lists the available files. The program comes with several example data files for you to examine.

TREEMAP also supports drag-and-drop opening of files.

Tree information

If your input file contains output comments you can view these using the **Host information** and **Parasite information** commands on the **View** menu.

7..3 Creating a new TREEMAP file

If you have trees for the hosts and parasites (e.g., produced by a phylogenetic tree building program such as PAUP or PHYLIP) then you can create a new TREEMAP file using the **File | New** command. To do this you must have the following two files:

- Fully resolved, rooted trees for the hosts in either NEXUS (e.g. PAUP 3.0 or later, MacClade 3.0) or PHYLIP format.
- Fully resolved, rooted trees for the parasites in either NEXUS or PHYLIP format. Every parasite must have a host.

The **New** command displays the following dialog box.

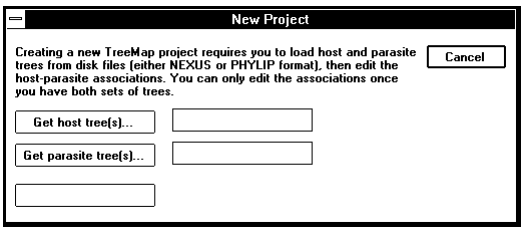


Fig. 7 The New Project dialog box.

To load your tree files click on the **Get host tree(s)...** and **Get parasite tree(s)...** buttons. If the trees are successfully loaded the name of the file will be displayed to the right of the corresponding button. Once you have both sets of trees you can click on the **Edit associations...** button which displays the following dialog:

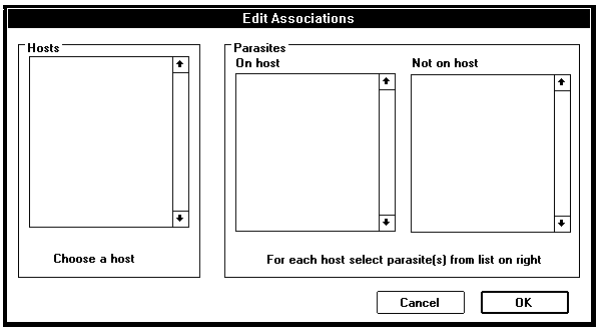


Fig. 8 Edit Associations dialog box.

The dialog displays a list of all host taxa, together with two lists of parasites: those that are on the currently selected host, and those that are not. You can move parasites between the two lists by double clicking on one or more parasite names.

Not every host taxa requires a parasite, but every parasite requires a host. Your changes to the host-parasite associations will not be accepted unless this last requirement is satisfied.

Once you've entered the host-parasite associations, click on **OK** and TREEMAP will display the trees and associations.

7.4 Editing an existing TREEMAP file

You can edit the host-parasite associations using the **Edit | Associations** command. This displays the same dialog box as described in the previous section.

7.5 Importing and exporting COMPONENT 2.0 files

The file formats used by TREEMAP and COMPONENT (Page, 1993) are incompatible. However, TREEMAP can read and write COMPONENT files. To read a COMPONENT file choose **Import** from the **File** menu. A dialog box will appear prompting you for the file name.

Should you wish to export a TREEMAP file for use by COMPONENT (for example, to edit the trees or compute a reconciled tree) choose the **Export** command. Note that any reconstructions you have created cannot be saved to COMPONENT files.

TREEMAP expects the COMPONENT file to contain a only single DISTRIBUTION block describing the parasite's host distribution and relationships. Multiple DISTRIBUTION blocks are not allowed.

An advantage of using COMPONENT files is that they can be easily created using COMPONENT's text and tree editors. A disadvantage is that COMPONENT is currently only available for Windows PC's.

7.6 Exporting files for Brooks Parsimony Analysis

Brooks parsimony analysis (BPA; Brooks and McLennan, 1991) is another method for exploring the relationship between host and parasite phylogeny. It consists of coding the parasite cladogram as a suite of binary characters which are then analysed using parsimony. You can either use a tree building program to find the most parsimonious host tree based on the parasite phylogeny, or you can optimise the coded parasite phylogeny onto a known host phylogeny (similar to what TREEMAP does). Elsewhere (Page, 1990; 1994) I have been critical of BPA; in particular I have argued that the reconstructions it produces may be spurious. However, I have provided the facility to export files for BPA so that you can explore this issue for yourself.

TREEMAP creates a NEXUS format file that can be read by PAUP 3.1 (Swofford, 1993) and MacClade 3.0 (Maddison and Maddison, 1992). The current parasite tree displayed in the Tanglegram window is additive binary coded using “inclusive ORing” (O'Grady and Deets, 1987), and the host tree (or trees) is written to a TREES block. The binary characters are labelled with either the name of the corresponding terminal parasite taxon or the number displayed when you choose **View | Internal labels** in the Tanglegram window.

On the Macintosh the exported file has its creator set to 'CLAD' so that Finder displays the MacClade icon (shown below). Double clicking on the file will load it into MacClade.

7.7 TREEMAP file format

TREEMAP uses a variant of the NEXUS format to describe the host and parasite trees, the host-parasite associations, and the reconstructions. Extensions to the NEXUS forma are currently being developed (David Maddison, pers. comm.) that will enable me to replace the current format with a more portable format. In the meantime, TREEMAP has its own file format. Here is a simple example:
a simple example:

```
#nexus

begin host;
     tree host=(a,(b,c));
endblock;

begin parasite;
     tree parasite =((I,II),III);
endblock;

begin distribution;
     range
           I     : a;
           II    : b,
           III   : c
           ;
endblock;
```

Each file must contain HOST, PARASITE, and DISTRIBUTION blocks in that order. The HOST and PARASITE blocks describe the host and parasite phylogenies. You can either enter the trees directly (as above) or use the IMPORT command, e.g.

```
begin host;
      import filetype=nexus
             file='\develop\cpwcpp\gophers.tre';
endblock;
```

This example imports a PAUP tree file called GOPHERS.TRE (you can also import PHYLIP files).

The import command will only work if the file being imported is in the same folder as the data file. The **file=** field should contain just the name of the file, without any path information.

The file being imported can reside in any directory, and the **file=** command can contain full path information.

Tree descriptions in the HOST and PARASITE blocks must contain the labels for the host and parasite taxa; e.g., in the example given above, the host tree is described as (a,(b,c)), not (1,(2,3)). If you are importing PAUP or PHYLIP files, TREEMAP automatically obtains the labels from the imported tree file.

TREEMAP requires binary (i.e., fully resolved) rooted trees for both the hosts and parasites. Including non binary trees will cause the program to issue an error message and stop reading your data file.

You can have up to 100 host and parasite trees, each with up to 100 taxa.

If you create one or more reconstructions the file saved by TREEMAP will contain a RECONSTRUCTIONS block describing each reconstruction. Do not attempt to edit this block.

7.8 Creating a data file from scratch

At present TREEMAP has no file editing facilities, so you will need to use a text editor.

Use a text editor such as TeachText or BBEdit.

Use a text editor such as Windows Notepad or the editor provided by COMPONENT.

If you use a word processor be sure to save your file as a text file.

7.9 Saving files

The **Save** command saves any modifications you have made to the original file. The **Save as** command lets you save the trees (and any reconstructions) to a new file.

References

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