

# Package ‘ape’

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## Description

ape provides functions for reading, writing, plotting, and manipulating phylogenetic trees, analyses of comparative data in a phylogenetic framework, ancestral character analyses, analyses of diversification and macroevolution, computing distances from allelic and nucleotide data, reading and writing nucleotide sequences, and several tools such as Mantel's test, generalized skyline plots, graphical exploration of phylogenetic data (alex, trex, kronoviz), estimation of absolute evolutionary rates and clock-like trees using mean path lengths and penalized likelihood. Phylogeny estimation can be done with the NJ, BIONJ, ME, MVR, SDM, and triangle methods, and several methods handling incomplete distance matrices (NJ\*, BIONJ\*, MVR\*, and the corresponding triangle method). Some functions call external applications (PhyML, Clustal, T-Coffee, Muscle) whose results are returned into R.

**License** GPL (>= 2)

**URL** <http://ape-package.ird.fr/>

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ape-package

*Analyses of Phylogenetics and Evolution***Description**

**ape** provides functions for reading and manipulating phylogenetic trees and DNA sequences, computing DNA distances, estimating trees with distance-based methods, and a range of methods for comparative analyses and analysis of diversification. Functionalities are also provided for programming new phylogenetic methods.

The complete list of functions can be displayed with `library(help = ape)`.

More information on **ape** can be found at <http://ape-package.ird.fr/>.

**Author(s)**

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## References

- Paradis, E. (2012) *Analysis of Phylogenetics and Evolution with R (Second Edition)*. New York: Springer.
- Paradis, E., Claude, J. and Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

---

ace

*Ancestral Character Estimation*

---

## Description

This function estimates ancestral character states, and the associated uncertainty, for continuous and discrete characters.

logLik, deviance, and AIC are generic functions used to extract the log-likelihood, the deviance, or the Akaike information criterion of a fitted object. If no such values are available, NULL is returned.

anova is another generic function which is used to compare nested models: the significance of the additional parameter(s) is tested with likelihood ratio tests. You must ensure that the models are effectively nested (if they are not, the results will be meaningless). It is better to list the models from the smallest to the largest.

## Usage

```
ace(x, phy, type = "continuous", method = if (type == "continuous")
  "REML" else "ML", CI = TRUE,
  model = if (type == "continuous") "BM" else "ER",
  scaled = TRUE, kappa = 1, corStruct = NULL, ip = 0.1,
  use.expm = FALSE, use.eigen = TRUE)
## S3 method for class 'ace'
print(x, digits = 4, ...)
## S3 method for class 'ace'
logLik(object, ...)
## S3 method for class 'ace'
deviance(object, ...)
## S3 method for class 'ace'
AIC(object, ..., k = 2)
## S3 method for class 'ace'
anova(object, ...)
```

## Arguments

- x                    a vector or a factor; an object of class "ace" in the case of print.
- phy                  an object of class "phylo".
- type                 the variable type; either "continuous" or "discrete" (or an abbreviation of these).

method	a character specifying the method used for estimation. Four choices are possible: "ML", "REML", "pic", or "GLS".
CI	a logical specifying whether to return the 95% confidence intervals of the ancestral state estimates (for continuous characters) or the likelihood of the different states (for discrete ones).
model	a character specifying the model (ignored if method = "GLS"), or a numeric matrix if type = "discrete" (see details).
scaled	a logical specifying whether to scale the contrast estimate (used only if method = "pic").
kappa	a positive value giving the exponent transformation of the branch lengths (see details).
corStruct	if method = "GLS", specifies the correlation structure to be used (this also gives the assumed model).
ip	the initial value(s) used for the ML estimation procedure when type == "discrete" (possibly recycled).
use.expm	a logical specifying whether to use the package <b>expm</b> to compute the matrix exponential (relevant only if type = "d"). If FALSE, the function <code>matexpo</code> from <b>ape</b> is used (see details). This option is ignored if use.eigen = TRUE (see next).
use.eigen	a logical (relevant if type = "d"); if TRUE then the probability matrix is computed with an eigen decomposition instead of a matrix exponential (see details).
digits	the number of digits to be printed.
object	an object of class "ace".
k	a numeric value giving the penalty per estimated parameter; the default is $k = 2$ which is the classical Akaike information criterion.
...	further arguments passed to or from other methods.

## Details

If type = "continuous", the default model is Brownian motion where characters evolve randomly following a random walk. This model can be fitted by residual maximum likelihood (the default), maximum likelihood (Felsenstein 1973, Schluter et al. 1997), least squares (method = "pic", Felsenstein 1985), or generalized least squares (method = "GLS", Martins and Hansen 1997, Cunningham et al. 1998). In the last case, the specification of `phy` and `model` are actually ignored: it is instead given through a correlation structure with the option `corStruct`.

In the setting `method = "ML"` and `model = "BM"` (this used to be the default until **ape** 3.0-7) the maximum likelihood estimation is done simultaneously on the ancestral values and the variance of the Brownian motion process; these estimates are then used to compute the confidence intervals in the standard way. The REML method first estimates the ancestral value at the root (aka, the phylogenetic mean), then the variance of the Brownian motion process is estimated by optimizing the residual log-likelihood. The ancestral values are finally inferred from the likelihood function giving these two parameters. If `method = "pic"` or "GLS", the confidence intervals are computed using the expected variances under the model, so they depend only on the tree.

It could be shown that, with a continuous character, REML results in unbiased estimates of the variance of the Brownian motion process while ML gives a downward bias. Therefore the former is recommended.

For discrete characters (`type = "discrete"`), only maximum likelihood estimation is available (Pagel 1994) (see [MPR](#) for an alternative method). The model is specified through a numeric matrix with integer values taken as indices of the parameters. The numbers of rows and of columns of this matrix must be equal, and are taken to give the number of states of the character. For instance, `matrix(c(0, 1, 1, 0), 2)` will represent a model with two character states and equal rates of transition, `matrix(c(0, 1, 2, 0), 2)` a model with unequal rates, `matrix(c(0, 1, 1, 1, 0, 1, 1, 1, 0), 3)` a model with three states and equal rates of transition (the diagonal is always ignored). There are short-cuts to specify these models: "ER" is an equal-rates model (e.g., the first and third examples above), "ARD" is an all-rates-different model (the second example), and "SYM" is a symmetrical model (e.g., `matrix(c(0, 1, 2, 1, 0, 3, 2, 3, 0), 3)`). If a short-cut is used, the number of states is determined from the data.

With discrete characters it is necessary to compute the exponential of the rate matrix. The only possibility until **ape** 3.0-7) was the function `matexpo` in **ape**. If `use.expm = TRUE` and `use.eigen = FALSE`, the function `expm`, in the package of the same name, is used. `matexpo` is faster but quite inaccurate for large and/or asymmetric matrices. In case of doubt, use the latter. Since **ape** 3.0-10, it is possible to use an eigen decomposition avoiding the need to compute the matrix exponential; see details in Lebl (2013, sect. 3.8.3). This is much faster and is now the default.

### Value

an object of class "ace" with the following elements:

<code>ace</code>	if <code>type = "continuous"</code> , the estimates of the ancestral character values.
<code>CI95</code>	if <code>type = "continuous"</code> , the estimated 95% confidence intervals.
<code>sigma2</code>	if <code>type = "continuous"</code> , <code>model = "BM"</code> , and <code>method = "ML"</code> , the maximum likelihood estimate of the Brownian parameter.
<code>rates</code>	if <code>type = "discrete"</code> , the maximum likelihood estimates of the transition rates.
<code>se</code>	if <code>type = "discrete"</code> , the standard-errors of estimated rates.
<code>index.matrix</code>	if <code>type = "discrete"</code> , gives the indices of the rates in the rate matrix.
<code>loglik</code>	if <code>method = "ML"</code> , the maximum log-likelihood.
<code>lik.anc</code>	if <code>type = "discrete"</code> , the scaled likelihoods of each ancestral state.
<code>call</code>	the function call.

### Author(s)

Emmanuel Paradis, Ben Bolker

### References

- Cunningham, C. W., Omland, K. E. and Oakley, T. H. (1998) Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology & Evolution*, **13**, 361–366.
- Felsenstein, J. (1973) Maximum likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics*, **25**, 471–492.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.



Lebl, J. (2013) *Notes on Diffy Qs: Differential Equations for Engineers*. <http://www.jirka.org/diffyqs/>.

Martins, E. P. and Hansen, T. F. (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist*, **149**, 646–667.

Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **255**, 37–45.

Schluter, D., Price, T., Mooers, A. O. and Ludwig, D. (1997) Likelihood of ancestor states in adaptive radiation. *Evolution*, **51**, 1699–1711.

### See Also

[MPR](#), [corBrownian](#), [corGrafen](#), [corMartins](#), [compar.ou](#), [anova](#)

### Examples

```
### Just some random data...
data(bird.orders)
x <- rnorm(23)
### Compare the three methods for continuous characters:
ace(x, bird.orders)
ace(x, bird.orders, method = "pic")
ace(x, bird.orders, method = "GLS",
     corStruct = corBrownian(1, bird.orders))
### For discrete characters:
x <- factor(c(rep(0, 5), rep(1, 18)))
ans <- ace(x, bird.orders, type = "d")
#### Showing the likelihoods on each node:
plot(bird.orders, type = "c", FALSE, label.offset = 1)
co <- c("blue", "yellow")
tiplabels(pch = 22, bg = co[as.numeric(x)], cex = 2, adj = 1)
nodelabels(thermo = ans$lik.anc, piecol = co, cex = 0.75)
```

---

add.scale.bar

*Add a Scale Bar to a Phylogeny Plot*

---

### Description

This function adds a horizontal bar giving the scale of the branch lengths to a plot of a phylogenetic tree on the current graphical device.

### Usage

```
add.scale.bar(x, y, length = NULL, ask = FALSE,
             lwd = 1, lcol = "black", ...)
```

**Arguments**

x	x location of the bar (can be left missing).
y	y location of the bar (can be left missing).
length	a numeric value giving the length of the scale bar. If none is supplied, a value is calculated from the data.
ask	a logical; if TRUE the user is asked to click where to draw the bar. The default is FALSE.
lwd	the width of the bar.
lcol	the colour of the bar (use col for the colour of the text).
...	further arguments to be passed to text.

**Details**

By default, the bar is placed in a corner of the graph depending on the direction of the tree. Otherwise both x and y must be specified (if only one is given it is ignored).

The further arguments (...) are used to format the text. They may be font, cex, col, and so on (see examples below, and the help page on [text](#)).

The function [locator](#) may be used to determine the x and y arguments.

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#), [axisPhylo](#), [locator](#)

**Examples**

```
tr <- rtree(10)
layout(matrix(1:2, 2, 1))
plot(tr)
add.scale.bar()
plot(tr)
add.scale.bar(cex = 0.7, font = 2, col = "red")
layout(matrix(1))
```

---

additive

*Incomplete Distance Matrix Filling*

---

**Description**

Fills missing entries from incomplete distance matrix using the additive or the ultrametric procedure (see reference for details).

**Usage**

```
additive(X)
ultrametric(X)
```

**Arguments**

X a distance matrix or an object of class "dist".

**Value**

a distance matrix.

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

**References**

Makarenkov, V. and Lapointe, F.-J. (2004) A weighted least-squares approach for inferring phylogenies from incomplete distance matrices. *Bioinformatics*, **20**, 2113–2121. <http://dx.doi.org/10.1093/bioinformatics/bth211>

---

alex

*Alignment Explorer With Multiple Devices*

---

**Description**

This function helps to explore DNA alignments by zooming in. The user clicks twice defining the opposite corners of the portion which is extracted and drawn on a new window.

**Usage**

```
alex(x, ...)
```

**Arguments**

x an object of class "DNAbin".  
... further arguments to pass to image.DNAbin.

### Details

This function works with a DNA alignment (freshly) plotted on an interactive graphical device (i.e., not a file) with `image`. After calling `alex`, the user clicks twice defining a rectangle in the alignment, then this portion of the alignment is extracted and plotted on a *new* window. The user can click as many times on the alignment. The process is stopped by a right-click. If the user clicks twice outside the alignment, a message “Try again!” is printed.

Each time `alex` is called, the alignment is plotted on a new window without closing or deleting those possibly already plotted.

In all cases, the device where `x` is plotted is the active window after the operation. It should *not* be closed during the whole process.

### Value

NULL

### Author(s)

Emmanuel Paradis

### See Also

[image.DNAbin](#), [trex](#)

### Examples

```
## Not run:
data(woodmouse)
image(woodmouse)
alex(woodmouse)

## End(Not run)
```

---

all.equal.phylo

*Global Comparison of two Phylogenies*

---

### Description

This function makes a global comparison of two phylogenetic trees.

### Usage

```
## S3 method for class 'phylo'
all.equal(target, current, use.edge.length = TRUE,
          use.tip.label = TRUE, index.return = FALSE,
          tolerance = .Machine$double.eps ^ 0.5,
          scale = NULL, ...)
```

**Arguments**

target	an object of class "phylo".
current	an object of class "phylo".
use.edge.length	if FALSE only the topologies are compared; the default is TRUE.
use.tip.label	if FALSE the unlabelled trees are compared; the default is TRUE.
index.return	if TRUE the function returns a two-column matrix giving the correspondence between the nodes of both trees.
tolerance	the numeric tolerance used to compare the branch lengths.
scale	a positive number, comparison of branch lengths is made after scaling (i.e., dividing) them by this number.
...	further arguments passed to or from other methods.

**Details**

This function is meant to be an adaptation of the generic function `all.equal` for the comparison of phylogenetic trees.

A single phylogenetic tree may have several representations in the Newick format and in the "phylo" class of objects used in 'ape'. One aim of the present function is to be able to identify whether two objects of class "phylo" represent the same phylogeny.

**Value**

A logical value, or a two-column matrix.

**Note**

The algorithm used here does not work correctly for the comparison of topologies (i.e., ignoring tip labels) of unrooted trees. This also affects `unique.multiPhylo` which calls the present function. See:

<https://stat.ethz.ch/pipermail/r-sig-phylo/2011-August/001562.html>

**Author(s)**

Benoît Durand <b.durand@alfort.AFSSA.FR>

**See Also**

`all.equal` for the generic R function

**Examples**

```
### maybe the simplest example of two representations
### for the same rooted tree...:
t1 <- read.tree(text = "(a:1,b:1);")
t2 <- read.tree(text = "(b:1,a:1);")
all.equal(t1, t2)
```

```
### ... compare with this:
identical(t1, t2)
### one just slightly more complicated...:
t3 <- read.tree(text = "((a:1,b:1):1,c:2);")
t4 <- read.tree(text = "(c:2,(a:1,b:1):1);")
all.equal(t3, t4) # == all.equal.phylo(t3, t4)
### ... here we force the comparison as lists:
all.equal.list(t3, t4)
```

---

as.alignment

*Conversion Among DNA Sequence Internal Formats*


---

## Description

These functions transform a set of DNA sequences among various internal formats.

## Usage

```
as.alignment(x)
as.DNAbin(x, ...)

## S3 method for class 'character'
as.DNAbin(x, ...)

## S3 method for class 'list'
as.DNAbin(x, ...)

## S3 method for class 'alignment'
as.DNAbin(x, ...)

## S3 method for class 'DNAbin'
as.character(x, ...)
```

## Arguments

`x` a matrix or a list containing the DNA sequences, or an object of class "alignment".  
`...` further arguments to be passed to or from other methods.

## Details

For `as.alignment`, the sequences given as argument should be stored as matrices or lists of single-character strings (the format used in **ape** before version 1.10). The returned object is in the format used in the package **seqinr** to store aligned sequences.

`as.DNAbin` is a generic function with methods so that it works with sequences stored into vectors, matrices, or lists.

`as.character` is a generic function: the present method converts objects of class "DNAbin" into the format used before **ape** 1.10 (matrix of single characters, or list of vectors of single characters). This function must be used first to convert objects of class "DNAbin" into the class "alignment".

**Value**

an object of class "alignment" in the case of "as.alignment"; an object of class "DNAbin" in the case of "as.DNAbin"; a matrix of mode character or a list containing vectors of mode character in the case of "as.character".

**Author(s)**

Emmanuel Paradis

**See Also**

[DNAbin](#), [read.dna](#), [read.GenBank](#), [write.dna](#)

**Examples**

```
data(woodmouse)
x <- as.character(woodmouse)
x[, 1:20]
str(as.alignment(x))
identical(as.DNAbin(x), woodmouse)
```

---

as.bitsplits

*Split Frequencies and Conversion Among Split Classes*

---

**Description**

bitsplits returns the bipartitions (aka splits) for a single tree or a list of trees.

countBipartitions returns the frequencies of the bipartitions from a reference tree (phy) observed in a list of trees (X).

as.bitsplits and as.prop.part are generic functions for converting between the "bitsplits" and "prop.part" classes.

**Usage**

```
bitsplits(x)
countBipartitions(phy, X)
as.bitsplits(x)
## S3 method for class 'prop.part'
as.bitsplits(x)
## S3 method for class 'bitsplits'
print(x, ...)
as.prop.part(x)
## S3 method for class 'bitsplits'
as.prop.part(x)
```

### Arguments

x	an object of the appropriate class.
phy	an object of class "phylo".
X	an object of class "multiPhylo".
...	further arguments passed to or from other methods.

### Details

These functions count bipartitions as defined by internal branches, so they do not work with rooted trees (see examples). The structure of the class "bitsplits" is described in a separate document on ape's web site.

### Value

bitsplits and as.bitsplits return an object of class "bitsplits".

countBipartitions returns a vector of integers.

as.prop.part returns an object of class "prop.part".

### Author(s)

Emmanuel Paradis

### See Also

[prop.part](#)

### Examples

```
tr <- rtree(20)
pp <- prop.part(tr)
as.bitsplits(pp)
## doesn't work for rooted trees...:
countBipartitions(rtree(10), rmtree(100, 10))
## ... but OK with unrooted trees:
countBipartitions(rtree(10, rooted = FALSE), rmtree(100, 10, rooted = FALSE))
```

### Description

These functions convert objects between the classes "phylo" and "matching".



**Usage**

```
as.matching(x, ...)  
## S3 method for class 'phylo'  
as.matching(x, labels = TRUE, ...)  
## S3 method for class 'matching'  
as.phylo(x, ...)
```

**Arguments**

x	an object to convert as an object of class "matching" or of class "phylo".
labels	a logical specifying whether the tip and node labels should be included in the returned matching.
...	further arguments to be passed to or from other methods.

**Details**

A matching is a representation where each tip and each node are given a number, and sibling groups are grouped in a "matching pair" (see Diaconis and Holmes 1998, for details). This coding system can be used only for binary (fully dichotomous) trees.

Diaconis and Holmes (1998) gave some conventions to insure that a given tree has a unique representation as a matching. I have tried to follow them in the present functions.

**Value**

as.matching returns an object of class "matching" with the following component:

matching	a two-column numeric matrix where the columns represent the sibling pairs.
tip.label	(optional) a character vector giving the tip labels where the ith element is the label of the tip numbered i in matching.
node.label	(optional) a character vector giving the node labels in the same order than in matching (i.e. the ith element is the label of the node numbered i + n in matching, with n the number of tips).

as.phylo.matching returns an object of class "phylo".

**Note**

Branch lengths are not supported in the present version.

**Author(s)**

Emmanuel Paradis

**References**

Diaconis, P. W. and Holmes, S. P. (1998) Matchings and phylogenetic trees. *Proceedings of the National Academy of Sciences USA*, **95**, 14600–14602.

**See Also**[as.phylo](#)**Examples**

```

data(bird.orders)
m <- as.matching(bird.orders)
str(m)
m
tr <- as.phylo(m)
all.equal(tr, bird.orders, use.edge.length = FALSE)

```

---

**as.phylo***Conversion Among Tree and Network Objects*

---

**Description**

as.phylo is a generic function which converts an object into a tree of class "phylo". There are currently two methods for objects of class "hclust" and of class "phylog" (implemented in the package ade4).

as.hclust.phylo is a method of the generic [as.hclust](#) which converts an object of class "phylo" into one of class "hclust". This can be used to convert an object of class "phylo" into one of class "dendrogram" (see examples).

as.network and as.igraph convert trees of class "phylo" into these respective classes defined in the packages of the same names (where the generics are defined).

old2new.phylo and new2old.phylo are utility functions for converting between the old and new coding of the class "phylo".

**Usage**

```

as.phylo(x, ...)
## S3 method for class 'hclust'
as.phylo(x, ...)
## S3 method for class 'phylog'
as.phylo(x, ...)
## S3 method for class 'phylo'
as.hclust(x, ...)
old2new.phylo(phy)
new2old.phylo(phy)
## S3 method for class 'phylo'
as.network(x, directed = is.rooted(x), ...)
## S3 method for class 'phylo'
as.igraph(x, directed = is.rooted(x), use.labels = TRUE, ...)

```

**Arguments**

x	an object to be converted into another class.
directed	a logical value: should the network be directed? By default, this depends on whether the tree is rooted or not.
use.labels	a logical specifying whether to use labels to build the network of class "igraph". If TRUE and the tree has no node labels, then some default labels are created first. If FALSE, the network is built with integers.
...	further arguments to be passed to or from other methods.
phy	an object of class "phylo".

**Value**

An object of class "hclust", "phylo", "network", or "igraph".

**Note**

In an object of class "hclust", the height gives the distance between the two sets that are being agglomerated. So these distances are divided by two when setting the branch lengths of a phylogenetic tree.

**Author(s)**

Emmanuel Paradis

**See Also**

[hclust](#), [as.hclust](#), [dendrogram](#), [phylog](#), [as.phylo.formula](#)

**Examples**

```
data(bird.orders)
hc <- as.hclust(bird.orders)
tr <- as.phylo(hc)
all.equal(bird.orders, tr) # FALSE, but...
tr$edge.length <- 2 * tr$edge.length
all.equal(bird.orders, tr) # ... TRUE

### shows the three plots for tree objects:
dend <- as.dendrogram(hc)
layout(matrix(c(1:3, 3), 2, 2))
plot(bird.orders, font = 1)
plot(hc)
par(mar = c(8, 0, 0, 0)) # leave space for the labels
plot(dend)

### how to get (nearly) identical plots with
### plot.phylo and plot.dendrogram:
layout(matrix(1:2, 2, 1))
plot(bird.orders, font = 1, no.margin = TRUE)
```

```

par(mar = c(0, 0, 0, 8))
plot(dend, horiz = TRUE)
layout(matrix(1))

## Not run:
### convert into networks:
if (require(network)) {
  x <- as.network(rtree(10))
  print(x)
  plot(x, vertex.cex = 1:4)
  plot(x, displaylabels = TRUE)
}
tr <- rtree(5)
if (require(igraph)) {
  print((x <- as.igraph(tr)))
  plot(x)
  print(as.igraph(tr, TRUE, FALSE))
  print(as.igraph(tr, FALSE, FALSE))
}

## End(Not run)

```

---

as.phylo.formula

*Conversion from Taxonomy Variables to Phylogenetic Trees*


---

## Description

The function `as.phylo.formula` (short form `as.phylo`) builds a phylogenetic tree (an object of class `phylo`) from a set of nested taxonomic variables.

## Usage

```

## S3 method for class 'formula'
as.phylo(x, data = parent.frame(), ...)

```

## Arguments

<code>x</code>	a right-side formula describing the taxonomic relationship: $\sim C1/C2/\dots/Cn$ .
<code>data</code>	the <code>data.frame</code> where to look for the variables (default to environment).
<code>...</code>	further arguments to be passed from other methods.

## Details

Taxonomic variables must be nested and passed in the correct order: the higher clade must be on the left of the formula, for instance  $\sim Order/Family/Genus/Species$ . In most cases, the resulting tree will be unresolved and contain polytomies.

**Value**

An object of class phylo.

**Author(s)**

Julien Dutheil <Julien.Dutheil@univ-montp2.fr>

**See Also**

[as.phylo](#), [read.tree](#) for a description of phylo objects, [multi2di](#)

**Examples**

```
data(carnivora)
plot(as.phylo(~SuperFamily/Family/Genus/Species, data=carnivora))
```

---

axisPhylo

*Axis on Side of Phylogeny*

---

**Description**

This function adds a scaled axis on the side of a phylogeny plot.

**Usage**

```
axisPhylo(side = 1, ...)
```

**Arguments**

side	a numeric value specifying the side where the axis is plotted: 1: below, 2: left, 3: above, 4: right.
...	further arguments to be passed to axis.

**Details**

The further arguments (...) are used to format the axis. They may be font, cex, col, las, and so on (see the help pages on [axis](#) and [par](#)).

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#), [add.scale.bar](#), [axis](#), [par](#)

### Examples

```
tr <- rtree(30)
ch <- rcoal(30)
plot(ch)
axisPhylo()
plot(tr, "c", FALSE, direction = "u")
axisPhylo(2, las = 1)
```

---

balance

*Balance of a Dichotomous Phylogenetic Tree*

---

### Description

This function computes the balance of a phylogenetic tree, that is for each node of the tree the numbers of descendants (i.e. tips) on each of its daughter-branch. The tree must be fully dichotomous.

### Usage

```
balance(phy)
```

### Arguments

phy            an object of class "phylo".

### Value

a numeric matrix with two columns and one row for each node of the tree. The columns give the numbers of descendants on each daughter-branches (the order of both columns being arbitrary). If the phylogeny phy has an element `node.label`, this is used as rownames for the returned matrix; otherwise the numbers (of mode character) of the matrix edge of phy are used as rownames.

### Author(s)

Emmanuel Paradis

### References

Aldous, D. J. (2001) Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. *Statistical Science*, **16**, 23–34.

---

`base.freq`*Base frequencies from DNA Sequences*

---

**Description**

`base.freq` computes the frequencies (absolute or relative) of the four DNA bases (adenine, cytosine, guanine, and thymidine) from a sample of sequences.

`GC.content` computes the proportion of G+C (using the previous function). All missing or unknown sites are ignored.

`Ftab` computes the contingency table with the absolute frequencies of the DNA bases from a pair of sequences.

**Usage**

```
base.freq(x, freq = FALSE, all = FALSE)
GC.content(x)
Ftab(x, y = NULL)
```

**Arguments**

<code>x</code>	a vector, a matrix, or a list which contains the DNA sequences.
<code>y</code>	a vector with a single DNA sequence.
<code>freq</code>	a logical specifying whether to return the proportions (the default) or the absolute frequencies (counts).
<code>all</code>	a logical; by default only the counts of A, C, G, and T are returned. If <code>all = TRUE</code> , all counts of bases, ambiguous codes, missing data, and alignment gaps are returned.

**Details**

The base frequencies are computed over all sequences in the sample.

For `Ftab`, if the argument `y` is given then both `x` and `y` are coerced as vectors and must be of equal length. If `y` is not given, `x` must be a matrix or a list and only the two first sequences are used.

**Value**

A numeric vector with names `c("a", "c", "g", "t")` (and possibly `"r", "m", ...`, a single numeric value, or a four by four matrix with similar dimnames.

**Author(s)**

Emmanuel Paradis

**See Also**

[seg.sites](#), [nuc.div](#), [DNAbin](#)

**Examples**

```

data(woodmouse)
base.freq(woodmouse)
base.freq(woodmouse, TRUE)
base.freq(woodmouse, TRUE, TRUE)
GC.content(woodmouse)
Ftab(woodmouse)
Ftab(woodmouse[1, ], woodmouse[2, ]) # same than above
Ftab(woodmouse[14:15, ]) # between the last two

```

---

bd.ext

*Extended Version of the Birth-Death Models to Estimate Speciation  
and Extinction Rates*

---

**Description**

This function fits by maximum likelihood a birth-death model to the combined phylogenetic and taxonomic data of a given clade. The phylogenetic data are given by a tree, and the taxonomic data by the number of species for the its tips.

**Usage**

```
bd.ext(phy, S, conditional = TRUE)
```

**Arguments**

phy	an object of class "phylo".
S	a numeric vector giving the number of species for each tip.
conditional	whether probabilities should be conditioned on no extinction (mainly to compare results with previous analyses; see details).

**Details**

A re-parametrization of the birth-death model studied by Kendall (1948) so that the likelihood has to be maximized over  $d/b$  and  $b - d$ , where  $b$  is the birth rate, and  $d$  the death rate.

The standard-errors of the estimated parameters are computed using a normal approximation of the maximum likelihood estimates.

If the argument `S` has names, then they are matched to the tip labels of `phy`. The user must be careful here since the function requires that both series of names perfectly match, so this operation may fail if there is a typing or syntax error. If both series of names do not match, the values `S` are taken to be in the same order than the tip labels of `phy`, and a warning message is issued.

Note that the function does not check that the tree is effectively ultrametric, so if it is not, the returned result may not be meaningful.

If `conditional = TRUE`, the probabilities of the taxonomic data are calculated conditioned on no extinction (Rabosky et al. 2007). In previous versions of the present function (until ape 2.6-1), unconditional probabilities were used resulting in underestimated extinction rate. Though it does



not make much sense to use `conditional = FALSE`, this option is provided to compare results from previous analyses: if the species richnesses are relatively low, both versions will give similar results (see examples).

### Author(s)

Emmanuel Paradis

### References

Paradis, E. (2003) Analysis of diversification: combining phylogenetic and taxonomic data. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **270**, 2499–2505.

Rabosky, D. L., Donnellan, S. C., Talaba, A. L. and Lovette, I. J. (2007) Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **274**, 2915–2923.

### See Also

[birthdeath](#), [branching.times](#), [diversi.gof](#), [diversi.time](#), [ltt.plot](#), [yule](#), [yule.cov](#), [bd.time](#)

### Examples

```
### An example from Paradis (2003) using the avian orders:
data(bird.orders)
### Number of species in each order from Sibley and Monroe (1990):
S <- c(10, 47, 69, 214, 161, 17, 355, 51, 56, 10, 39, 152,
      6, 143, 358, 103, 319, 23, 291, 313, 196, 1027, 5712)
bd.ext(bird.orders, S)
bd.ext(bird.orders, S, FALSE) # same than older versions
```

---

bd.time

*Time-Dependent Birth-Death Models*

---

### Description

This function fits a user-defined time-dependent birth-death model.

### Usage

```
bd.time(phy, birth, death, BIRTH = NULL, DEATH = NULL,
        ip, lower, upper, fast = FALSE, boot = 0, trace = 0)
```

**Arguments**

phy	an object of class "phylo".
birth	either a numeric (if speciation rate is assumed constant), or a (vectorized) function specifying how the birth (speciation) probability changes through time (see details).
death	id. for extinction probability.
BIRTH	(optional) a vectorized function giving the primitive of birth.
DEATH	id. for death.
ip	a numeric vector used as initial values for the estimation procedure. If missing, these values are guessed.
lower, upper	the lower and upper bounds of the parameters. If missing, these values are guessed too.
fast	a logical value specifying whether to use faster integration (see details).
boot	the number of bootstrap replicates to assess the confidence intervals of the parameters. Not run by default.
trace	an integer value. If non-zero, the fitting procedure is printed every trace steps. This can be helpful if convergence is particularly slow.

**Details**

Details on how to specify the birth and death functions and their primitives can be found in the help page of [yule.time](#).

The model is fitted by minimizing the least squares deviation between the observed and the predicted distributions of branching times. These computations rely heavily on numerical integrations. If `fast = FALSE`, integrations are done with R's [integrate](#) function. If `fast = TRUE`, a faster but less accurate function provided in **ape** is used. If fitting a complex model to a large phylogeny, a strategy might be to first use the latter option, and then to use the estimates as starting values with `fast = FALSE`.

**Value**

A list with the following components:

- `para` vector of estimates with names taken from the parameters in the specified functions.
- `SS` the minimized sum of squares.
- `convergenceoutput` convergence criterion from [nlminb](#).
- `messageid`.
- `iterationsid`.
- `evaluationsid`.

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (2011) Time-dependent speciation and extinction from phylogenies: a least squares approach. *Evolution*, **65**, 661–672.

**See Also**

[ltt.plot](#), [birthdeath](#), [yule.time](#), [LTT](#)

**Examples**

```
set.seed(3)
tr <- rbdtree(0.1, 0.02)
bd.time(tr, 0, 0) # fits a simple BD model
bd.time(tr, 0, 0, ip = c(.1, .01)) # 'ip' is useful here
## the classic logistic:
birth.logis <- function(a, b) 1/(1 + exp(-a*t - b))
## Not run:
bd.time(tr, birth.logis, 0, ip = c(0, -2, 0.01))
## slow to get:
## $par
##          a          b          death
## -0.003486961 -1.995983179  0.016496454
##
## $SS
## [1] 20.73023

## End(Not run)
```

---

bind.tree

*Binds Trees*


---

**Description**

This function binds together two phylogenetic trees to give a single object of class "phylo".

**Usage**

```
bind.tree(x, y, where = "root", position = 0, interactive = FALSE)
x + y
```

**Arguments**

x	an object of class "phylo".
y	an object of class "phylo".
where	an integer giving the number of the node or tip of the tree x where the tree y is binded ("root" is a short-cut for the root).
position	a numeric value giving the position from the tip or node given by node where the tree y is binded; negative values are ignored.

interactive      if TRUE the user is asked to choose the tip or node of x by clicking on the tree which must be plotted.

### Details

The argument x can be seen as the receptor tree, whereas y is the donor tree. The root of y is then grafted on a location of x specified by where and, possibly, position. If y has a root edge, this is added as an internal branch in the resulting tree.

x + y is a shortcut for:

```
bind.tree(x, y, position = if (is.null(x$root.edge)) 0 else
x$root.edge)
```

If only one of the trees has no branch length, the branch lengths of the other one are ignored with a warning.

If one (or both) of the trees has no branch length, it is possible to specify a value of 'position' to graft 'y' below the node of 'x' specified by 'where'. In this case, the exact value of 'position' is not important as long as it is greater than zero. The new node will be multichotomous if 'y' has no root edge. This can be solved by giving an arbitrary root edge to 'y' beforehand (e.g., y\$root.edge <- 1); it will be deleted during the binding operation.

### Value

an object of class "phylo".

### Author(s)

Emmanuel Paradis

### See Also

[drop.tip](#), [root](#)

### Examples

```
### binds the two clades of bird orders
cat("((Struthioniformes:21.8,Tinamiformes:21.8):4.1,",
"((Craciformes:21.6,Galliformes:21.6):1.3,Anseriformes:22.9):3.0):2.1;",
file = "ex1.tre", sep = "\n")
cat("((Turniciformes:27.0,(Piciformes:26.3,((Galbuliformes:24.4,",
"((Bucerotiformes:20.8,Upupiformes:20.8):2.6,",
"(Trogoniformes:22.1,Coraciiformes:22.1):1.3):1.0):0.6,",
"(Coliiformes:24.5,(Cuculiformes:23.7,(Psittaciformes:23.1,",
"((Apodiformes:21.3,Trochiliformes:21.3):0.6,",
"(Musophagiformes:20.4,Strigiformes:20.4):1.5):0.6,",
"((Columbiformes:20.8,(Gruiformes:20.1,Ciconiiformes:20.1):0.7):0.8,",
"Passeriformes:21.6):0.9):0.6):0.6):0.8):0.5):1.3):0.7):1.0;",
file = "ex2.tre", sep = "\n")
tree.bird1 <- read.tree("ex1.tre")
```

```

tree.bird2 <- read.tree("ex2.tre")
unlink(c("ex1.tre", "ex2.tre")) # clean-up
(birds <- tree.bird1 + tree.bird2)
layout(matrix(c(1, 2, 3, 3), 2, 2))
plot(tree.bird1)
plot(tree.bird2)
plot(birds)

### examples with random trees
x <- rtree(4, tip.label = LETTERS[1:4])
y <- rtree(4, tip.label = LETTERS[5:8])
x <- makeNodeLabel(x, prefix = "x_")
y <- makeNodeLabel(y, prefix = "y_")
x$root.edge <- y$root.edge <- .2

z <- bind.tree(x, y, po=.2)
plot(y, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("y")
plot(x, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("x")
plot(z, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("z <- bind.tree(x, y, po=.2)")

z <- bind.tree(x, y, 2, .1)
plot(y, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("y")
plot(x, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("x")
plot(z, show.node.label = TRUE, font = 1, root.edge = TRUE)
title("z <- bind.tree(x, y, 2, .1)")

x <- rtree(50)
y <- rtree(50)
x$root.edge <- y$root.edge <- .2
z <- x + y
plot(y, show.tip.label = FALSE, root.edge = TRUE); axisPhylo()
title("y")
plot(x, show.tip.label = FALSE, root.edge = TRUE); axisPhylo()
title("x")
plot(z, show.tip.label = FALSE, root.edge = TRUE); axisPhylo()
title("z <- x + y")
layout(1)

```

**Description**

This function performs the BIONJ algorithm of Gascuel (1997).

**Usage**

```
bionj(X)
```

**Arguments**

X a distance matrix; may be an object of class "dist".

**Value**

an object of class "phylo".

**Author(s)**

original C code by Hoa Sien Cuong and Olivier Gascuel; adapted and ported to R by Vincent Lefort <vincent.lefort@lirmm.fr>

**References**

Gascuel, O. (1997) BIONJ: an improved version of the NJ algorithm based on a simple model of sequence data. *Molecular Biology and Evolution*, **14**:, 685–695.

**See Also**

[nj](#), [fastme](#), [mvr](#), [bionjs](#), [SDM](#), [dist.dna](#)

**Examples**

```
### From Saitou and Nei (1987, Table 1):
x <- c(7, 8, 11, 13, 16, 13, 17, 5, 8, 10, 13,
      10, 14, 5, 7, 10, 7, 11, 8, 11, 8, 12,
      5, 6, 10, 9, 13, 8)
M <- matrix(0, 8, 8)
M[lower.tri(M)] <- x
M <- t(M)
M[lower.tri(M)] <- x
dimnames(M) <- list(1:8, 1:8)
tr <- bionj(M)
plot(tr, "u")
### a less theoretical example
data(woodmouse)
trw <- bionj(dist.dna(woodmouse))
plot(trw)
```

**Description**

This data set describes the phylogenetic relationships of the families of birds as reported by Sibley and Ahlquist (1990). Sibley and Ahlquist inferred this phylogeny from an extensive number of DNA/DNA hybridization experiments. The “tapestry” reported by these two authors (more than 1000 species out of the ca. 9000 extant bird species) generated a lot of debates.

The present tree is based on the relationships among families. A few families were not included in the figures in Sibley and Ahlquist, and thus are not included here as well. The branch lengths were calculated from the values of  $\Delta T_{50}H$  as found in Sibley and Ahlquist (1990, figs. 354, 355, 356, and 369).

**Usage**

```
data(bird.families)
```

**Format**

The data are stored as an object of class “phylo” which structure is described in the help page of the function [read.tree](#).

**Source**

Sibley, C. G. and Ahlquist, J. E. (1990) Phylogeny and classification of birds: a study in molecular evolution. New Haven: Yale University Press.

**See Also**

[read.tree](#), [bird.orders](#)

**Examples**

```
data(bird.families)
op <- par()
par(cex = 0.3)
plot(bird.families)
par(op)
```

---

`bird.orders`*Phylogeny of the Orders of Birds From Sibley and Ahlquist*

---

**Description**

This data set describes the phylogenetic relationships of the orders of birds as reported by Sibley and Ahlquist (1990). Sibley and Ahlquist inferred this phylogeny from an extensive number of DNA/DNA hybridization experiments. The “tapestry” reported by these two authors (more than 1000 species out of the ca. 9000 extant bird species) generated a lot of debates.

The present tree is based on the relationships among orders. The branch lengths were calculated from the values of  $\Delta T_{50}H$  as found in Sibley and Ahlquist (1990, fig. 353).

**Usage**

```
data(bird.orders)
```

**Format**

The data are stored as an object of class “phylo” which structure is described in the help page of the function [read.tree](#).

**Source**

Sibley, C. G. and Ahlquist, J. E. (1990) Phylogeny and classification of birds: a study in molecular evolution. New Haven: Yale University Press.

**See Also**

[read.tree](#), [bird.families](#)

**Examples**

```
data(bird.orders)
plot(bird.orders)
```

---

`birthdeath`*Estimation of Speciation and Extinction Rates With Birth-Death Models*

---

**Description**

This function fits by maximum likelihood a birth-death model to the branching times computed from a phylogenetic tree using the method of Nee et al. (1994).



**Usage**

```
birthdeath(phy)
## S3 method for class 'birthdeath'
print(x, ...)
```

**Arguments**

phy	an object of class "phylo".
x	an object of class "birthdeath".
...	further arguments passed to the print function.

**Details**

Nee et al. (1994) used a re-parametrization of the birth-death model studied by Kendall (1948) so that the likelihood has to be maximized over  $d/b$  and  $b - d$ , where  $b$  is the birth rate, and  $d$  the death rate. This is the approach used by the present function.

This function computes the standard-errors of the estimated parameters using a normal approximations of the maximum likelihood estimates: this is likely to be inaccurate because of asymmetries of the likelihood function (Nee et al. 1995). In addition, 95 intervals of both parameters are computed using profile likelihood: they are particularly useful if the estimate of  $d/b$  is at the boundary of the parameter space (i.e. 0, which is often the case).

Note that the function does not check that the tree is effectively ultrametric, so if it is not, the returned result may not be meaningful.

**Value**

An object of class "birthdeath" which is a list with the following components:

tree	the name of the tree analysed.
N	the number of species.
dev	the deviance (= $-2 \log \text{lik}$ ) at its minimum.
para	the estimated parameters.
se	the corresponding standard-errors.
CI	the 95% profile-likelihood confidence intervals.

**Author(s)**

Emmanuel Paradis

**References**

- Kendall, D. G. (1948) On the generalized "birth-and-death" process. *Annals of Mathematical Statistics*, **19**, 1–15.
- Nee, S., May, R. M. and Harvey, P. H. (1994) The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, **344**, 305–311.

Nee, S., Holmes, E. C., May, R. M. and Harvey, P. H. (1995) Estimating extinctions from molecular phylogenies. in *Extinction Rates*, eds. Lawton, J. H. and May, R. M., pp. 164–182, Oxford University Press.

### See Also

[branching.times](#), [diversi.gof](#), [diversi.time](#), [lft.plot](#), [yule](#), [bd.ext](#), [yule.cov](#), [bd.time](#)

---

boot.phylo

*Tree Bipartition and Bootstrapping Phylogenies*

---

### Description

These functions analyse bipartitions found in a series of trees.

`prop.part` counts the number of bipartitions found in a series of trees given as `...`. If a single tree is passed, the returned object is a list of vectors with the tips descending from each node (i.e., clade compositions indexed by node number).

`prop.clades` counts the number of times the bipartitions present in `phy` are present in a series of trees given as `...` or in the list previously computed and given with `part`.

`boot.phylo` performs a bootstrap analysis.

### Usage

```
boot.phylo(phy, x, FUN, B = 100, block = 1,
           trees = FALSE, quiet = FALSE, rooted = FALSE)
prop.part(..., check.labels = TRUE)
prop.clades(phy, ..., part = NULL, rooted = FALSE)
## S3 method for class 'prop.part'
print(x, ...)
## S3 method for class 'prop.part'
summary(object, ...)
## S3 method for class 'prop.part'
plot(x, barcol = "blue", leftmar = 4, ...)
```

### Arguments

<code>phy</code>	an object of class "phylo".
<code>x</code>	in the case of <code>boot.phylo</code> : a taxa (rows) by characters (columns) matrix; in the case of <code>print</code> and <code>plot</code> : an object of class "prop.part".
<code>FUN</code>	the function used to estimate <code>phy</code> (see details).
<code>B</code>	the number of bootstrap replicates.
<code>block</code>	the number of columns in <code>x</code> that will be resampled together (see details).
<code>trees</code>	a logical specifying whether to return the bootstrapped trees (FALSE by default).
<code>quiet</code>	a logical: a progress bar is displayed by default.

rooted	a logical specifying whether the trees should be treated as rooted or not (the default).
...	either (i) a single object of class "phylo", (ii) a series of such objects separated by commas, or (iii) a list containing such objects. In the case of plot further arguments for the plot (see details).
check.labels	a logical specifying whether to check the labels of each tree. If FALSE, it is assumed that all trees have the same tip labels, and that they are in the same order (see details).
part	a list of partitions as returned by prop.part; if this is used then ... is ignored.
object	an object of class "prop.part".
barcol	the colour used for the bars displaying the number of partitions in the upper panel.
leftmar	the size of the margin on the left to display the tip labels.

### Details

The argument FUN in boot.phylo must be the function used to estimate the tree from the original data matrix. Thus, if the tree was estimated with neighbor-joining (see nj), one maybe wants something like FUN = function(xx) nj(dist.dna(xx)).

block in boot.phylo specifies the number of columns to be resampled altogether. For instance, if one wants to resample at the codon-level, then block = 3 must be used.

Using check.labels = FALSE in prop.part decreases computing times. This requires that (i) all trees have the same tip labels, and (ii) these labels are ordered similarly in all trees (in other words, the element tip.label are identical in all trees).

The plot function represents a contingency table of the different partitions (on the  $x$ -axis) in the lower panel, and their observed numbers in the upper panel. Any further arguments (...) are used to change the aspects of the points in the lower panel: these may be pch, col, bg, cex, etc. This function works only if there is an attribute labels in the object.

The print method displays the partitions and their numbers. The summary method extracts the numbers only.

### Value

prop.part returns an object of class "prop.part" which is a list with an attribute "number". The elements of this list are the observed clades, and the attribute their respective numbers. If the default check.labels = FALSE is used, an attribute "labels" is added, and the vectors of the returned object contains the indices of these labels instead of the labels themselves.

prop.clades and boot.phylo return a numeric vector which  $i$ th element is the number associated to the  $i$ th node of phy. If trees = TRUE, boot.phylo returns a list whose first element (named "BP") is like before, and the second element ("trees") is a list with the bootstrapped trees.

summary returns a numeric vector.

**Note**

prop.clades calls internally prop.part with the option check.labels = TRUE, which may be very slow. If the trees passed as . . . fulfills conditions (i) and (ii) above, then it might be faster to first call, e.g., pp <- prop.part(. . .), then use the option part: prop.clades(phy, part = pp).

You have to be careful that by default prop.clades considers the trees as unrooted and this may result in spurious results if the trees are rooted (see examples).

**Author(s)**

Emmanuel Paradis

**References**

Efron, B., Halloran, E. and Holmes, S. (1996) Bootstrap confidence levels for phylogenetic trees. *Proceedings of the National Academy of Sciences USA*, **93**, 13429–13434.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.

**See Also**

[as.bitsplits](#), [dist.topo](#), [consensus](#), [nodelabels](#)

**Examples**

```
data(woodmouse)
f <- function(x) nj(dist.dna(x))
tr <- f(woodmouse)
### Are bootstrap values stable?
for (i in 1:5)
  print(boot.phylo(tr, woodmouse, f, quiet = TRUE))
### How many partitions in 100 random trees of 10 labels?...
TR <- rmtree(100, 10)
pp10 <- prop.part(TR)
length(pp10)
### ... and in 100 random trees of 20 labels?
TR <- rmtree(100, 20)
pp20 <- prop.part(TR)
length(pp20)
plot(pp10, pch = "x", col = 2)
plot(pp20, pch = "x", col = 2)

set.seed(1)
tr <- rtree(10) # rooted by default
prop.clades(tr, tr) # clearly wrong
prop.clades(tr, tr, rooted = TRUE)
tr <- rtree(10, rooted = FALSE)
prop.clades(tr, tr) # correct
```

---

branching.times	<i>Branching Times of a Phylogenetic Tree</i>
-----------------	---

---

**Description**

This function computes the branching times of a phylogenetic tree, that is the distance from each node to the tips, under the assumption that the tree is ultrametric. Note that the function does not check that the tree is effectively ultrametric, so if it is not, the returned result may not be meaningful.

**Usage**

```
branching.times(phy)
```

**Arguments**

phy            an object of class "phylo".

**Value**

a numeric vector with the branching times. If the phylogeny phy has an element node.label, this is used as names for the returned vector; otherwise the numbers (of mode character) of the matrix edge of phy are used as names.

**Author(s)**

Emmanuel Paradis

**See Also**

[is.ultrametric](#)

---

c.phylo	<i>Building Lists of Trees</i>
---------	--------------------------------

---

**Description**

These functions help to build lists of trees of class "multiPhylo".

**Usage**

```
## S3 method for class 'phylo'  
c(..., recursive = FALSE)  
## S3 method for class 'multiPhylo'  
c(..., recursive = FALSE)  
.compressTipLabel(x)  
.uncompressTipLabel(x)
```

**Arguments**

... one or several objects of class "phylo" or "multiPhylo".  
recursive for compatibility with the generic (do not change).  
x an object of class "phylo" or "multiPhylo".

**Details**

These c methods do not check all the arguments, so it is the user's responsibility to make sure that only objects of the same class (either "phylo" or "multiPhylo") are used.

.compressTipLabel transforms an object of class "multiPhylo" by checking that all trees have the same tip labels and renumbering the tips in the edge matrix so that the tip numbers are also the same taking the first tree as the reference (duplicated labels are not allowed). The returned object has a unique vector of tip labels (attr(x, "TipLabel")).

.uncompressTipLabel does the reverse operation.

**Value**

An object of class "multiPhylo".

**Author(s)**

Emmanuel Paradis

**See Also**

[summary.phylo](#), [multiphylo](#)

**Examples**

```
x <- c(rtree(4), rtree(2))
x
y <- c(rtree(4), rtree(4))
z <- c(x, y)
z
print(z, TRUE)
try(.compressTipLabel(x)) # error
a <- .compressTipLabel(y)
.uncompressTipLabel(a) # back to y
## eventually compare str(a) and str(y)
```

CADM.global

*Congruence among distance matrices***Description**

Function `CADM.global` compute and test the coefficient of concordance among several distance matrices through a permutation test.

Function `CADM.post` carries out a posteriori permutation tests of the contributions of individual distance matrices to the overall concordance of the group.

Use in phylogenetic analysis: to identify congruence among distance matrices (D) representing different genes or different types of data. Congruent D matrices correspond to data tables that can be used together in a combined phylogenetic or other type of multivariate analysis.

**Usage**

```
CADM.global(Dmat, nmat, n, nperm=99, make.sym=TRUE, weights=NULL,
            silent=FALSE)
CADM.post (Dmat, nmat, n, nperm=99, make.sym=TRUE, weights=NULL,
          mult="holm", mantel=FALSE, silent=FALSE)
```

**Arguments**

<code>Dmat</code>	A text file listing the distance matrices one after the other, with or without blank lines in-between. Each matrix is in the form of a square distance matrix with 0's on the diagonal.
<code>nmat</code>	Number of distance matrices in file <code>Dmat</code> .
<code>n</code>	Number of objects in each distance matrix. All matrices must have the same number of objects.
<code>nperm</code>	Number of permutations for the tests of significance.
<code>make.sym</code>	TRUE: turn asymmetric matrices into symmetric matrices by averaging the two triangular portions. FALSE: analyse asymmetric matrices as they are.
<code>weights</code>	A vector of positive weights for the distance matrices. Example: <code>weights = c(1,2,3)</code> . NULL (default): all matrices have same weight in the calculation of W.
<code>mult</code>	Method for correcting P-values in multiple testing. The methods are "holm" (default), "sidak", and "bonferroni". The Bonferroni correction is overly conservative; it is not recommended. It is included to allow comparisons with the other methods.
<code>mantel</code>	TRUE: Mantel statistics will be computed from ranked distances, as well as permutational P-values. FALSE (default): Mantel statistics and tests will not be computed.
<code>silent</code>	TRUE: informative messages will not be printed, but stopping messages will. Option useful for simulation work. FALSE: informative messages will be printed.

## Details

Dmat must contain two or more distance matrices, listed one after the other, all of the same size, and corresponding to the same objects in the same order. Raw data tables can be transformed into distance matrices before comparison with other such distance matrices, or with data that have been obtained as distance matrices, e.g. serological or DNA hybridization data. The distances will be transformed to ranks before computation of the coefficient of concordance and other statistics.

CADM.global tests the global null hypothesis that all matrices are incongruent. If the global null is rejected, function CADM.post can be used to identify the concordant (H0 rejected) and discordant matrices (H0 not rejected) in the group. If a distance matrix has a negative value for the Mantel.mean statistic, that matrix clearly does not belong to the group. Remove that matrix (if there are more than one, remove first the matrix that has the most strongly negative value for Mantel.mean) and run the analysis again.

The corrections used for multiple testing are applied to the list of P-values (P) produced in the a posteriori tests; they take into account the number of tests (k) carried out simulatenously (number of matrices, parameter nmat).

The Holm correction is computed after ordering the P-values in a list with the smallest value to the left. Compute adjusted P-values as:

$$P_{corr} = (k - i + 1) * P$$

where i is the position in the ordered list. Final step: from left to right, if an adjusted  $P_{corr}$  in the ordered list is smaller than the one occurring at its left, make the smallest one equal to the largest one.

The Sidak correction is:

$$P_{corr} = 1 - (1 - P)^k$$

The Bonferonni correction is:

$$P_{corr} = k * P$$

## Value

CADM.global produces a small table containing the W, Chi2, and Prob.perm statistics described in the following list. CADM.post produces a table stored in element A\_posteriori\_tests, containing Mantel.mean, Prob, and Corrected.prob statistics in rows; the columns correspond to the k distance matrices under study, labeled Dmat.1 to Dmat.k. If parameter mantel is TRUE, tables of Mantel statistics and P-values are computed among the matrices.

W	Kendall's coefficient of concordance, W (Kendall and Babington Smith 1939; see also Legendre 2010).
Chi2	Friedman's chi-square statistic (Friedman 1937) used in the permutation test of W.
Prob.perm	Permutational probability.
Mantel.mean	Mean of the Mantel correlations, computed on rank-transformed distances, between the distance matrix under test and all the other matrices in the study.



Prob	Permutational probabilities, uncorrected.
Corrected prob	Permutational probabilities corrected using the method selected in parameter mult.
Mantel.cor	Matrix of Mantel correlations, computed on rank-transformed distances, among the distance matrices.
Mantel.prob	One-tailed P-values associated with the Mantel correlations of the previous table. The probabilities are computed in the right-hand tail. H <sub>0</sub> is tested against the alternative one-tailed hypothesis that the Mantel correlation under test is positive. No correction is made for multiple testing.

### Author(s)

Pierre Legendre, Universite de Montreal

### References

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- Campbell, V., Legendre, P. and Lapointe, F.-J. (2011) The performance of the Congruence Among Distance Matrices (CADM) test in phylogenetic analysis. *BMC Evolutionary Biology*, **11**, 64. <http://www.biomedcentral.com/1471-2148/11/64>.
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- Kendall, M. G. and Babington Smith, B. (1939) The problem of m rankings. *Annals of Mathematical Statistics*, **10**, 275–287.
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- Legendre, P. and Lapointe, F.-J. (2004) Assessing congruence among distance matrices: single malt Scotch whiskies revisited. *Australian and New Zealand Journal of Statistics*, **46**, 615–629.
- Legendre, P. and Lapointe, F.-J. (2005) Congruence entre matrices de distance. P. 178-181 in: Makarenkov, V., G. Cucumel et F.-J. Lapointe [eds] Comptes rendus des 12emes Rencontres de la Societe Francophone de Classification, Montreal, 30 mai - 1er juin 2005.
- Siegel, S. and Castellan, N. J., Jr. (1988) *Nonparametric statistics for the behavioral sciences*. 2nd edition. New York: McGraw-Hill.

### Examples

```
# Examples 1 and 2: 5 genetic distance matrices computed from simulated DNA
# sequences representing 50 taxa having evolved along additive trees with
# identical evolutionary parameters (GTR+ Gamma + I). Distance matrices were
# computed from the DNA sequence matrices using a p distance corrected with the
# same parameters as those used to simulate the DNA sequences. See Campbell et
# al. (2009) for details.
```

```

# Example 1: five independent additive trees. Data provided by V. Campbell.

data(mat5Mrand)
res.global <- CADM.global(mat5Mrand, 5, 50)

# Example 2: three partly similar trees, two independent trees.
# Data provided by V. Campbell.

data(mat5M3ID)
res.global <- CADM.global(mat5M3ID, 5, 50)
res.post <- CADM.post(mat5M3ID, 5, 50, mantel=TRUE)

# Example 3: three matrices respectively representing Serological
# (asymmetric), DNA hybridization (asymmetric) and Anatomical (symmetric)
# distances among 9 families. Data from Lapointe et al. (1999).

data(mat3)
res.global <- CADM.global(mat3, 3, 9, nperm=999)
res.post <- CADM.post(mat3, 3, 9, nperm=999, mantel=TRUE)

# Example 4, showing how to bind two D matrices (cophenetic matrices
# in this example) into a file using rbind(), then run the global test.

a <- rtree(5)
b <- rtree(5)
A <- cophenetic(a)
B <- cophenetic(b)
x <- rownames(A)
B <- B[x, x]
M <- rbind(A, B)
CADM.global(M, 2, 5)

```

---

carnivora

*Carnivora body sizes and life history traits*


---

### Description

Dataset adapted from Gittleman (1986), including 2 morphological variables (body and brain sizes), 8 life history traits variables and 4 taxonomic variables.

### Usage

```
data(carnivora)
```

### Format

A data frame with 112 observations on 17 variables.

```
[,1] Order          factor    Carnivora order
```

[,2]	SuperFamily	factor	Super family (Caniformia or Feliformia)
[,3]	Family	factor	Carnivora family
[,4]	Genus	factor	Carnivora genus
[,5]	Species	factor	Carnivora species
[,6]	FW	numeric	Female body weight (kg)
[,7]	SW	numeric	Average body weight of adult male and adult female (kg)
[,8]	FB	numeric	Female brain weight (g)
[,9]	SB	numeric	Average brain weight of adult male and adult female (g)
[,10]	LS	numeric	Litter size
[,11]	GL	numeric	Gestation length (days)
[,12]	BW	numeric	Birth weight (g)
[,13]	WA	numeric	Weaning age (days)
[,14]	AI	numeric	Age of independence (days)
[,15]	LY	numeric	Longevity (months)
[,16]	AM	numeric	Age of sexual maturity (days)
[,17]	IB	numeric	Inter-birth interval (months)

### Source

Gittleman, J. L. (1986) Carnivore life history patterns: allometric, phylogenetic and ecological associations. *American Naturalist*, **127**: 744–771.

### Examples

```
data(carnivora);
# This is figure 1 of Gittleman 1986:
library(lattice)
trellis.device(color=FALSE)
xyplot(BW ~ FW, groups=Family, data=carnivora, auto.key=TRUE, xlog=TRUE,
       scale=list(log=TRUE), ylim=c(1, 2000))
trellis.device(color=FALSE)
xyplot(BW ~ FB, groups=Family, data=carnivora, auto.key=TRUE, xlog=TRUE,
       scale=list(log=TRUE), ylim=c(1, 2000))
```

---

cherry

*Number of Cherries and Null Models of Trees*

---

### Description

This function calculates the number of cherries (see definition below) on a phylogenetic tree, and tests the null hypotheses whether this number agrees with those predicted from two null models of trees (the Yule model, and the uniform model).

### Usage

cherry(phy)

**Arguments**

phy                    an object of class "phylo".

**Details**

A cherry is a pair of adjacent tips on a tree. The tree can be either rooted or unrooted, but the present function considers only rooted trees. The probability distribution function of the number of cherries on a tree depends on the speciation/extinction model that generated the tree.

McKenzie and Steel (2000) derived the probability distribution function of the number of cherries for two models: the Yule model and the uniform model. Broadly, in the Yule model, each extant species is equally likely to split into two daughter-species; in the uniform model, a branch is added to tree on any of the already existing branches with a uniform probability.

The probabilities are computed using recursive formulae; however, for both models, the probability density function converges to a normal law with increasing number of tips in the tree. The function uses these normal approximations for a number of tips greater than or equal to 20.

**Value**

A NULL value is returned, the results are simply printed.

**Author(s)**

Emmanuel Paradis

**References**

McKenzie, A. and Steel, M. (2000) Distributions of cherries for two models of trees. *Mathematical Biosciences*, **164**, 81–92.

**See Also**

[gammaStat](#)

---

chiroptera

*Bat Phylogeny*

---

**Description**

This phylogeny of bats (Mammalia: Chiroptera) is a supertree (i.e. a composite phylogeny constructed from several sources; see source for details).

**Usage**

data(chiroptera)

**Format**

The data are stored in RData (binary) format.

**Source**

Jones, K. E., Purvis, A., MacLarnon, A., Bininda-Emonds, O. R. P. and Simmons, N. B. (2002) A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews of the Cambridge Philosophical Society*, **77**, 223–259.

**See Also**

[read.nexus](#), [zoom](#)

**Examples**

```
data(chiroptera)
str(chiroptera)
op <- par()
par(cex = 0.3)
plot(chiroptera, type = "c")
par(op)
```

---

chronomPL

*Molecular Dating With Mean Path Lengths*

---

**Description**

This function estimates the node ages of a tree using the mean path lengths method of Britton et al. (2002). The branch lengths of the input tree are interpreted as (mean) numbers of substitutions.

**Usage**

```
chronomPL(phy, se = TRUE, test = TRUE)
```

**Arguments**

phy	an object of class "phylo".
se	a logical specifying whether to compute the standard-errors of the node ages (TRUE by default).
test	a logical specifying whether to test the molecular clock at each node (TRUE by default).

## Details

The mean path lengths (MPL) method estimates the age of a node with the mean of the distances from this node to all tips descending from it. Under the assumption of a molecular clock, standard-errors of the estimates node ages can be computed (Britton et al. 2002).

The tests performed if `test = TRUE` is a comparison of the MPL of the two subtrees originating from a node; the null hypothesis is that the rate of substitution was the same in both subtrees (Britton et al. 2002). The test statistic follows, under the null hypothesis, a standard normal distribution. The returned *P*-value is the probability of observing a greater absolute value (i.e., a two-sided test). No correction for multiple testing is applied: this is left to the user.

Absolute dating can be done by multiplying the edge lengths found by calibrating one node age.

## Value

an object of class "phylo" with branch lengths as estimated by the function. There are, by default, two attributes:

<code>stderr</code>	the standard-errors of the node ages.
<code>Pval</code>	the <i>P</i> -value of the test of the molecular clock for each node.

## Note

The present version requires a dichotomous tree.

## Author(s)

Emmanuel Paradis

## References

Britton, T., Oxelman, B., Vinnersten, A. and Bremer, K. (2002) Phylogenetic dating with confidence intervals using mean path lengths. *Molecular Phylogenetics and Evolution*, **24**, 58–65.

## See Also

[chronopl](#)

## Examples

```
tr <- rtree(10)
tr$edge.length <- 5*tr$edge.length
chr <- chronomPL(tr)
layout(matrix(1:4, 2, 2, byrow = TRUE))
plot(tr)
title("The original tree")
plot(chr)
axisPhylo()
title("The dated MPL tree")
plot(chr)
nodeLabels(round(attr(chr, "stderr"), 3))
```

```

title("The standard-errors")
plot(tr)
nodelabels(round(attr(chr, "Pval"), 3))
title("The tests")

```

---

chronopl

*Molecular Dating With Penalized Likelihood*


---

### Description

This function estimates the node ages of a tree using a semi-parametric method based on penalized likelihood (Sanderson 2002). The branch lengths of the input tree are interpreted as mean numbers of substitutions (i.e., per site).

### Usage

```

chronopl(phy, lambda, age.min = 1, age.max = NULL,
         node = "root", S = 1, tol = 1e-8,
         CV = FALSE, eval.max = 500, iter.max = 500, ...)

```

### Arguments

phy	an object of class "phylo".
lambda	value of the smoothing parameter.
age.min	numeric values specifying the fixed node ages (if age.max = NULL) or the youngest bound of the nodes known to be within an interval.
age.max	numeric values specifying the oldest bound of the nodes known to be within an interval.
node	the numbers of the nodes whose ages are given by age.min; "root" is a short-cut for the root.
S	the number of sites in the sequences; leave the default if branch lengths are in mean number of substitutions.
tol	the value below which branch lengths are considered effectively zero.
CV	whether to perform cross-validation.
eval.max	the maximal number of evaluations of the penalized likelihood function.
iter.max	the maximal number of iterations of the optimization algorithm.
...	further arguments passed to control nlmnb.

## Details

The idea of this method is to use a trade-off between a parametric formulation where each branch has its own rate, and a nonparametric term where changes in rates are minimized between contiguous branches. A smoothing parameter ( $\lambda$ ) controls this trade-off. If  $\lambda = 0$ , then the parametric component dominates and rates vary as much as possible among branches, whereas for increasing values of  $\lambda$ , the variation are smoother to tend to a clock-like model (same rate for all branches).

$\lambda$  must be given. The known ages are given in `age.min`, and the corresponding node numbers in `node`. These two arguments must obviously be of the same length. By default, an age of 1 is assumed for the root, and the ages of the other nodes are estimated.

If `age.max = NULL` (the default), it is assumed that `age.min` gives exactly known ages. Otherwise, `age.max` and `age.min` must be of the same length and give the intervals for each node. Some node may be known exactly while the others are known within some bounds: the values will be identical in both arguments for the former (e.g., `age.min = c(10, 5)`, `age.max = c(10, 6)`, `node = c(15, 18)` means that the age of node 15 is 10 units of time, and the age of node 18 is between 5 and 6).

If two nodes are linked (i.e., one is the ancestor of the other) and have the same values of `age.min` and `age.max` (say, 10 and 15) this will result in an error because the medians of these values are used as initial times (here 12.5) giving initial branch length(s) equal to zero. The easiest way to solve this is to change slightly the given values, for instance use `age.max = 14.9` for the youngest node, or `age.max = 15.1` for the oldest one (or similarly for `age.min`).

The input tree may have multichotomies. If some internal branches are of zero-length, they are collapsed (with a warning), and the returned tree will have less nodes than the input one. The presence of zero-lengthed terminal branches of results in an error since it makes little sense to have zero-rate branches.

The cross-validation used here is different from the one proposed by Sanderson (2002). Here, each tip is dropped successively and the analysis is repeated with the reduced tree: the estimated dates for the remaining nodes are compared with the estimates from the full data. For the  $i$ th tip the following is calculated:

$$\sum_{j=1}^{n-2} \frac{(t_j - t_j^{-i})^2}{t_j}$$

,

where  $t_j$  is the estimated date for the  $j$ th node with the full phylogeny,  $t_j^{-i}$  is the estimated date for the  $j$ th node after removing tip  $i$  from the tree, and  $n$  is the number of tips.

The present version uses the `nlm` to optimise the penalized likelihood function: see its help page for details on parameters controlling the optimisation procedure.

## Value

an object of class "phylo" with branch lengths as estimated by the function. There are three or four further attributes:

<code>ploglik</code>	the maximum penalized log-likelihood.
<code>rates</code>	the estimated rates for each branch.





**Arguments**

<code>phy</code>	an object of class "phylo".
<code>lambda</code>	value of the smoothing parameter.
<code>model</code>	a character string specifying the model of substitution rate variation among branches. The possible choices are: "correlated", "relaxed", "discrete", or an unambiguous abbreviation of these.
<code>quiet</code>	a logical value; by default the calculation progress are displayed.
<code>calibration</code>	a data frame (see details).
<code>control</code>	a list of parameters controlling the optimisation procedure (see details).
<code>x</code>	an object of class <code>c("chronos", "phylo")</code> .
<code>node</code>	a vector of integers giving the node numbers for which a calibration point is given. The default is a short-cut for the root.
<code>age.min, age.max</code>	vectors of numerical values giving the minimum and maximum ages of the nodes specified in <code>node</code> .
<code>interactive</code>	a logical value. If TRUE, then <code>phy</code> is plotted and the user is asked to click close to a node and enter the ages on the keyboard.
<code>soft.bounds</code>	(currently unused)
<code>...</code>	in the case of <code>chronos.control</code> : one of the five parameters controlling optimisation (unused in the case of <code>print.chronos</code> ).

**Details**

`chronos` replaces `chronopl` but with a different interface and some extensions (see References).

The known dates (argument `calibration`) must be given in a data frame with the following column names: `node`, `age.min`, `age.max`, and `soft.bounds` (the last one is yet unused). For each row, these are, respectively: the number of the node in the "phylo" coding standard, the minimum age for this node, the maximum age, and a logical value specifying whether the bounds are soft. If `age.min = age.max`, this means that the age is exactly known. This data frame can be built with `makeChronosCalib` which returns by default a data frame with a single row giving `age = 1` for the root. The data frame can be built interactively by clicking on the plotted tree.

The argument `control` allows one to change some parameters of the optimisation procedure. This must be a list with names. The available options with their default values are:

- `tol = 1e-8`: tolerance for the estimation of the substitution rates.
- `iter.max = 1e4`: the maximum number of iterations at each optimization step.
- `eval.max = 1e4`: the maximum number of function evaluations at each optimization step.
- `nb.rate.cat = 10`: the number of rate categories if `model = "discrete"` (set this parameter to 1 to fit a strict clock model).
- `dual.iter.max = 20`: the maximum number of alternative iterations between rates and dates.

The command `chronos.control()` returns a list with the default values of these parameters. They may be modified by passing them to this function, or directly in the list.

**Value**

chronos returns an object of class `c("chronos", "phylo")`. There is a print method for it. There are additional attributes which can be visualised with `str` or extracted with `attr`.

`makeChronosCalib` returns a data frame.

`chronos.control` returns a list.

**Author(s)**

Emmanuel Paradis

**References**

Kim, J. and Sanderson, M. J. (2008) Penalized likelihood phylogenetic inference: bridging the parsimony-likelihood gap. *Systematic Biology*, **57**, 665–674.

Paradis, E. (2013) Molecular dating of phylogenies by likelihood methods: a comparison of models and a new information criterion. *Molecular Phylogenetics and Evolution*, **67**, 436–444.

Sanderson, M. J. (2002) Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution*, **19**, 101–109.

**See Also**

[chronomPL](#)

**Examples**

```
tr <- rtree(10)
### the default is the correlated rate model:
chr <- chronos(tr)
### strict clock model:
ctrl <- chronos.control(nb.rate.cat = 1)
chr.clock <- chronos(tr, model = "discrete", control = ctrl)
### How different are the rates?
attr(chr, "rates")
attr(chr.clock, "rates")
## Not run:
cal <- makeChronosCalib(tr, interactive = TRUE)
cal
### if you made mistakes, you can edit the data frame with:
### fix(cal)
chr <- chronos(tr, calibration = cal)

## End(Not run)
```

**Description**

These functions call their respective program from R to align a set of nucleotide sequences of class "DNABin".

**Usage**

```
clustal(x, pw.gapopen = 10, pw.gapext = 0.1,
        gapopen = 10, gapext = 0.2, exec = NULL,
        MoreArgs = "", quiet = TRUE, original.ordering = TRUE)
muscle(x, exec = "muscle", MoreArgs = "", quiet = TRUE,
        original.ordering = TRUE)
tcoffee(x, exec = "t_coffee", MoreArgs = "", quiet = TRUE,
         original.ordering = TRUE)
```

**Arguments**

x	an object of class "DNABin".
pw.gapopen, pw.gapext	gap opening and gap extension penalties used by Clustal during pairwise alignments.
gapopen, gapext	idem for global alignment.
exec	a character string giving the name of the program, with its path if necessary. clustal tries to guess it depending on the operating system (see details).
MoreArgs	a character string giving additional options.
quiet	a logical: the default is to not print on R's console the messages from the external program.
original.ordering	a logical specifying whether to return the aligned sequences in the same order than in x.

**Details**

clustal tries to guess the name of the executable program depending on the operating system. Specifically, the followings are used: "clustalw" under Linux, "clustalw2" under MacOS, or "C:/Program Files/ClustalW2/clustalw2" under Windows.

The calculations are done in a temporary directory which is deleted when R is quit. So it is possible to find the files created by the last call in the directory printed by tempdir().

When called without arguments (i.e., clustal(), ...), the function prints the options of the program which may be passed to MoreArgs.

**Value**

an object of class "DNABin" with the aligned sequences.

**Author(s)**

Emmanuel Paradis

**References**

Chenna, R., Sugawara, H., Koike, T., Lopez, R., Gibson, T. J., Higgins, D. G. and Thompson, J. D. (2003) Multiple sequence alignment with the Clustal series of programs. *Nucleic Acids Research* **31**, 3497–3500. <http://www.clustal.org/>

Edgar, R. C. (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797. [http://www.drive5.com/muscle/muscle\\_userguide3.8.html](http://www.drive5.com/muscle/muscle_userguide3.8.html)

Notredame, C., Higgins, D. and Heringa, J. (2000) T-Coffee: A novel method for multiple sequence alignments. *Journal of Molecular Biology*, **302**, 205–217. [http://www.tcoffee.org/Documentation/t\\_coffee/t\\_coffee\\_technical.htm](http://www.tcoffee.org/Documentation/t_coffee/t_coffee_technical.htm)

**See Also**

[image.DNABin](#), [del.gaps](#), [alex](#)

The package **phyloch** which has similar functions for the MAFFT and Prank.

**Examples**

```
## Not run:
### display the options:
clustal()
muscle()
tcoffee()

data(woodmouse)
### open gaps more easily:
clustal(woodmouse, pw.gapopen = 1, pw.gapext = 1)
### T-Coffee requires negative values (quite slow; muscle is much faster):
tcoffee(woodmouse, MoreArgs = "-gapopen=-10 -gapext=-2")

## End(Not run)
```

---

coalescent.intervals *Coalescent Intervals*

---

**Description**

This function extracts or generates information about coalescent intervals (number of lineages, interval lengths, interval count, total depth) from a phylogenetic tree or a list of internode distances. The input tree needs to be ultra-metric (i.e. clock-like).

**Usage**

```
coalescent.intervals(x)
```

**Arguments**

x either an ultra-metric phylogenetic tree (i.e. an object of class "phylo") or, alternatively, a vector of interval lengths.

**Value**

An object of class "coalescentIntervals" with the following entries:

lineages A vector with the number of lineages at the start of each coalescent interval.  
interval.length A vector with the length of each coalescent interval.  
interval.count The total number of coalescent intervals.  
total.depth The sum of the lengths of all coalescent intervals.

**Author(s)**

Korbinian Strimmer (<http://www.stat.uni-muenchen.de/~strimmer/>)

**See Also**

[branching.times](#), [collapsed.intervals](#), [read.tree](#).

**Examples**

```
data("hivtree.newick") # example tree in NH format
tree.hiv <- read.tree(text = hivtree.newick) # load tree

ci <- coalescent.intervals(tree.hiv) # from tree
ci

data("hivtree.table") # same tree, but in table format
ci <- coalescent.intervals(hivtree.table$size) # from vector of interval lengths
ci
```

---

collapse.singles      *Collapse Single Nodes*

---

**Description**

This function deletes the single nodes (i.e., with a single descendant) in a tree.

**Usage**

```
collapse.singles(tree)
```

**Arguments**

tree            an object of class "phylo".

**Value**

an object of class "phylo".

**Author(s)**

Ben Bolker

**See Also**

[plot.phylo](#), [read.tree](#)

---

collapsed.intervals    *Collapsed Coalescent Intervals*

---

**Description**

This function takes a "coalescentIntervals" objects and collapses neighbouring coalescent intervals into a single combined interval so that every collapsed interval is larger than epsilon. Collapsed coalescent intervals are used, e.g., to obtain the generalized skyline plot ([skyline](#)). For  $\text{epsilon} = 0$  no interval is collapsed.

**Usage**

```
collapsed.intervals(ci, epsilon=0)
```

**Arguments**

ci            coalescent intervals (i.e. an object of class "coalescentIntervals").

epsilon       collapsing parameter that controls the amount of smoothing (allowed range: from 0 to ci\$total.depth)

**Details**

Proceeding from the tips to the root of the tree each small interval is pooled with the neighboring interval closer to the root. If the neighboring interval is also small, then pooling continues until the composite interval is larger than epsilon. Note that this approach prevents the occurrence of zero-length intervals at the present. For more details see Strimmer and Pybus (2001).

**Value**

An object of class "collapsedIntervals" with the following entries:

lineages	A vector with the number of lineages at the start of each coalescent interval.
interval.length	A vector with the length of each coalescent interval.
collapsed.interval	A vector indicating for each coalescent interval to which collapsed interval it belongs.
interval.count	The total number of coalescent intervals.
collapsed.interval.count	The number of collapsed intervals.
total.depth	The sum of the lengths of all coalescent intervals.
epsilon	The value of the underlying smoothing parameter.

**Author(s)**

Korbinian Strimmer (<http://www.stat.uni-muenchen.de/~strimmer/>)

**References**

Strimmer, K. and Pybus, O. G. (2001) Exploring the demographic history of DNA sequences using the generalized skyline plot. *Molecular Biology and Evolution*, **18**, 2298–2305.

**See Also**

[coalescent.intervals,skyline.](#)

**Examples**

```
data("hivtree.table") # example tree

# colescent intervals from vector of interval lengths
ci <- coalescent.intervals(hivtree.table$size)
ci

# collapsed intervals
c11 <- collapsed.intervals(ci,0)
c12 <- collapsed.intervals(ci,0.0119)

c11
c12
```



---

compar.cheverud      *Cheverud's Comparative Method*

---

## Description

This function computes the phylogenetic variance component and the residual deviation for continuous characters, taking into account the phylogenetic relationships among species, following the comparative method described in Cheverud et al. (1985). The correction proposed by Rohlf (2001) is used.

## Usage

```
compar.cheverud(y, W, tolerance = 1e-06, gold.tol = 1e-04)
```

## Arguments

y	A vector containing the data to analyse.
W	The phylogenetic connectivity matrix. All diagonal elements will be ignored.
tolerance	Minimum difference allowed to consider eigenvalues as distinct.
gold.tol	Precision to use in golden section search algorithm.

## Details

Model:

$$y = \rho W y + e$$

where  $e$  is the error term, assumed to be normally distributed.  $\rho$  is estimated by the maximum likelihood procedure given in Rohlf (2001), using a golden section search algorithm. The code of this function is indeed adapted from a MatLab code given in appendix in Rohlf's article, to correct a mistake in Cheverud's original paper.

## Value

A list with the following components:

rho	The maximum likelihood estimate of $\rho$
Wnorm	The normalized version of W
residuals	Error terms ( $e$ )

## Author(s)

Julien Dutheil <julien.dutheil@univ-montp2.fr>

## References

- Cheverud, J. M., Dow, M. M. and Leutenegger, W. (1985) The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution*, **39**, 1335–1351.
- Rohlf, F. J. (2001) Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution*, **55**, 2143–2160.
- Harvey, P. H. and Pagel, M. D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press.

## See Also

[compar.lynch](#)

## Examples

```
### Example from Harvey and Pagel's book:
y<-c(10,8,3,4)
W <- matrix(c(1,1/6,1/6,1/6,1/6,1,1/2,1/2,1/6,1/2,1,1,1/6,1/2,1,1), 4)
compar.cheverud(y,W)
### Example from Rohlf's 2001 article:
W<- matrix(c(
  0,1,1,2,0,0,0,0,
  1,0,1,2,0,0,0,0,
  1,1,0,2,0,0,0,0,
  2,2,2,0,0,0,0,0,
  0,0,0,0,0,1,1,2,
  0,0,0,0,1,0,1,2,
  0,0,0,0,1,1,0,2,
  0,0,0,0,2,2,2,0
),8)
W <- 1/W
W[W == Inf] <- 0
y<-c(-0.12,0.36,-0.1,0.04,-0.15,0.29,-0.11,-0.06)
compar.cheverud(y,W)
```

---

compar.gee

*Comparative Analysis with GEEs*

---

## Description

compar.gee performs the comparative analysis using generalized estimating equations as described by Paradis and Claude (2002).

drop1 tests single effects of a fitted model output from compar.gee.

predict returns the predicted (fitted) values of the model.

**Usage**

```

compar.gee(formula, data = NULL, family = "gaussian", phy, corStruct,
            scale.fix = FALSE, scale.value = 1)
## S3 method for class 'compar.gee'
drop1(object, scope, quiet = FALSE, ...)
## S3 method for class 'compar.gee'
predict(object, newdata = NULL, type = c("link", "response"), ...)

```

**Arguments**

formula	a formula giving the model to be fitted.
data	the name of the data frame where the variables in formula are to be found; by default, the variables are looked for in the global environment.
family	a function specifying the distribution assumed for the response; by default a Gaussian distribution (with link identity) is assumed (see ?family for details on specifying the distribution, and on changing the link function).
phy	an object of class "phylo" (ignored if corStruct is used).
corStruct	a (phylogenetic) correlation structure.
scale.fix	logical, indicates whether the scale parameter should be fixed (TRUE) or estimated (FALSE, the default).
scale.value	if scale.fix = TRUE, gives the value for the scale (default: scale.value = 1).
object	an object of class "compar.gee" resulting from fitting compar.gee.
scope	<unused>.
quiet	a logical specifying whether to display a warning message about eventual "marginality principle violation".
newdata	a data frame with column names matching the variables in the formula of the fitted object (see <a href="#">predict</a> for details).
type	a character string specifying the type of predicted values. By default, the linear (link) prediction is returned.
...	further arguments to be passed to drop1.

**Details**

If a data frame is specified for the argument data, then its rownames are matched to the tip labels of phy. The user must be careful here since the function requires that both series of names perfectly match, so this operation may fail if there is a typing or syntax error. If both series of names do not match, the values in the data frame are taken to be in the same order than the tip labels of phy, and a warning message is issued.

If data = NULL, then it is assumed that the variables are in the same order than the tip labels of phy.

**Value**

compar.gee returns an object of class "compar.gee" with the following components:

call	the function call, including the formula.
effect.assign	a vector of integers assigning the coefficients to the effects (used by drop1).
nobs	the number of observations.
QIC	the quasiliikelihood information criterion as defined by Pan (2001).
coefficients	the estimated coefficients (or regression parameters).
residuals	the regression residuals.
family	a character string, the distribution assumed for the response.
link	a character string, the link function used for the mean function.
scale	the scale (or dispersion parameter).
W	the variance-covariance matrix of the estimated coefficients.
dfP	the phylogenetic degrees of freedom (see Paradis and Claude for details on this).

drop1 returns an object of class "anova".

predict returns a vector or a data frame if newdata is used.

**Note**

The calculation of the phylogenetic degrees of freedom is likely to be approximative for non-Brownian correlation structures (this will be refined soon).

The calculation of the quasiliikelihood information criterion (QIC) needs to be tested.

**Author(s)**

Emmanuel Paradis

**References**

Pan, W. (2001) Akaike's information criterion in generalized estimating equations. *Biometrics*, **57**, 120–125.

Paradis, E. and Claude J. (2002) Analysis of comparative data using generalized estimating equations. *Journal of theoretical Biology*, **218**, 175–185.

**See Also**

[read.tree](#), [pic](#), [compar.lynch](#), [drop1](#)

**Examples**

```
### The example in Phylip 3.5c (originally from Lynch 1991)
### (the same analysis than in help(pic)... )
tr <- "(((Homo:0.21,Pongo:0.21):0.28,Macaca:0.49):0.13,Ateles:0.62):0.38,Galago:1.00);"
tree.primates <- read.tree(text = tr)
X <- c(4.09434, 3.61092, 2.37024, 2.02815, -1.46968)
Y <- c(4.74493, 3.33220, 3.36730, 2.89037, 2.30259)
### Both regressions... the results are quite close to those obtained
### with pic().
compar.gee(X ~ Y, phy = tree.primates)
compar.gee(Y ~ X, phy = tree.primates)
### Now do the GEE regressions through the origin: the results are quite
### different!
compar.gee(X ~ Y - 1, phy = tree.primates)
compar.gee(Y ~ X - 1, phy = tree.primates)
```

---

compar.lynch

*Lynch's Comparative Method*


---

**Description**

This function computes the heritable additive value and the residual deviation for continuous characters, taking into account the phylogenetic relationships among species, following the comparative method described in Lynch (1991).

**Usage**

```
compar.lynch(x, G, eps = 1e-4)
```

**Arguments**

x	either a matrix, a vector, or a data.frame containing the data with species as rows and variables as columns.
G	a matrix that can be interpreted as an among-species correlation matrix.
eps	a numeric value to detect convergence of the EM algorithm.

**Details**

The parameter estimates are computed following the EM (expectation-maximization) algorithm. This algorithm usually leads to convergence but may lead to local optima of the likelihood function. It is recommended to run several times the function in order to detect these potential local optima. The 'optimal' value for eps depends actually on the range of the data and may be changed by the user in order to check the stability of the parameter estimates. Convergence occurs when the differences between two successive iterations of the EM algorithm leads to differences between both residual and additive values less than or equal to eps.

**Value**

A list with the following components:

vare	estimated residual variance-covariance matrix.
vara	estimated additive effect variance covariance matrix.
u	estimates of the phylogeny-wide means.
A	additive value estimates.
E	residual values estimates.
lik	logarithm of the likelihood for the entire set of observed taxon-specific mean.

**Note**

The present function does not perform the estimation of ancestral phenotypes as proposed by Lynch (1991). This will be implemented in a future version.

**Author(s)**

Julien Claude <claude@isem.univ-montp2.fr>

**References**

Lynch, M. (1991) Methods for the analysis of comparative data in evolutionary biology. *Evolution*, **45**, 1065–1080.

**See Also**

[pic](#), [compar.gee](#)

**Examples**

```
### The example in Lynch (1991)
cat("(((Homo:0.21,Pongo:0.21):0.28,",
    "Macaca:0.49):0.13,Ateles:0.62):0.38,Galago:1.00);",
    file = "ex.tre", sep = "\n")
tree.primates <- read.tree("ex.tre")
unlink("ex.tre")
X <- c(4.09434, 3.61092, 2.37024, 2.02815, -1.46968)
Y <- c(4.74493, 3.33220, 3.36730, 2.89037, 2.30259)
compar.lynch(cbind(X, Y),
             G = vcv.phylo(tree.primates, cor = TRUE))
```

compar.ou

*Ornstein–Uhlenbeck Model for Continuous Characters***Description**

This function fits an Ornstein–Uhlenbeck model giving a phylogenetic tree, and a continuous character. The user specifies the node(s) where the optimum changes. The parameters are estimated by maximum likelihood; their standard-errors are computed assuming normality of these estimates.

**Usage**

```
compar.ou(x, phy, node = NULL, alpha = NULL)
```

**Arguments**

x	a numeric vector giving the values of a continuous character.
phy	an object of class "phylo".
node	a vector giving the number(s) of the node(s) where the parameter 'theta' (the trait optimum) is assumed to change. The node(s) can be specified with their labels if phy has node labels. By default there is no change (same optimum throughout lineages).
alpha	the value of $\alpha$ to be used when fitting the model. By default, this parameter is estimated (see details).

**Details**

The Ornstein–Uhlenbeck (OU) process can be seen as a generalization of the Brownian motion process. In the latter, characters are assumed to evolve randomly under a random walk, that is change is equally likely in any direction. In the OU model, change is more likely towards the direction of an optimum (denoted  $\theta$ ) with a strength controlled by a parameter denoted  $\alpha$ .

The present function fits a model where the optimum parameter  $\theta$ , is allowed to vary throughout the tree. This is specified with the argument node:  $\theta$  changes after each node whose number is given there. Note that the optimum changes *only* for the lineages which are descendants of this node.

Hansen (1997) recommends to not estimate  $\alpha$  together with the other parameters. The present function allows this by giving a numeric value to the argument alpha. By default, this parameter is estimated, but this seems to yield very large standard-errors, thus validating Hansen's recommendation. In practice, a "poor man estimation" of  $\alpha$  can be done by repeating the function call with different values of alpha, and selecting the one that minimizes the deviance (see Hansen 1997 for an example).

If x has names, its values are matched to the tip labels of phy, otherwise its values are taken to be in the same order than the tip labels of phy.

The user must be careful here since the function requires that both series of names perfectly match, so this operation may fail if there is a typing or syntax error. If both series of names do not match, the values in the x are taken to be in the same order than the tip labels of phy, and a warning message is issued.

**Value**

an object of class "compar.ou" which is list with the following components:

deviance	the deviance (= -2 * loglik).
para	a data frame with the maximum likelihood estimates and their standard-errors.
call	the function call.

**Note**

The inversion of the variance-covariance matrix in the likelihood function appeared as somehow problematic. The present implementation uses a Cholevski decomposition with the function [chol2inv](#) instead of the usual function [solve](#).

**Author(s)**

Emmanuel Paradis

**References**

Hansen, T. F. (1997) Stabilizing selection and the comparative analysis of adaptation. *Evolution*, **51**, 1341–1351.

**See Also**

[ace](#), [compar.lynch](#), [corBrownian](#), [corMartins](#), [pic](#)

**Examples**

```
data(bird.orders)
### This is likely to give you estimates close to 0, 1, and 0
### for alpha, sigma^2, and theta, respectively:
compar.ou(x <- rnorm(23), bird.orders)
### Much better with a fixed alpha:
compar.ou(x, bird.orders, alpha = 0.1)
### Let us 'mimick' the effect of different optima
### for the two clades of birds...
x <- c(rnorm(5, 0), rnorm(18, 5))
### ... the model with two optima:
compar.ou(x, bird.orders, node = 25, alpha = .1)
### ... and the model with a single optimum:
compar.ou(x, bird.orders, node = NULL, alpha = .1)
### => Compare both models with the difference in deviances
##      which follows a chi^2 with df = 1.
```



---

compute.brLen	<i>Branch Lengths Computation</i>
---------------	-----------------------------------

---

### Description

This function computes branch lengths of a tree using different methods.

### Usage

```
compute.brLen(phy, method = "Grafen", power = 1, ...)
```

### Arguments

phy	an object of class phylo representing the tree.
method	the method to be used to compute the branch lengths; this must be one of the followings: (i) "Grafen" (the default), (ii) a numeric vector, or (iii) a function.
power	The power at which heights must be raised (see below).
...	further argument(s) to be passed to method if it is a function.

### Details

Grafen's (1989) computation of branch lengths: each node is given a 'height', namely the number of leaves of the subtree minus one, 0 for leaves. Each height is scaled so that root height is 1, and then raised at power 'rho' (> 0). Branch lengths are then computed as the difference between height of lower node and height of upper node.

If one or several numeric values are provided as method, they are recycled if necessary. If a function is given instead, further arguments are given in place of ... (they must be named, see examples).

Zero-length branches are not treated as multichotomies, and thus may need to be collapsed (see [di2multi](#)).

### Value

An object of class phylo with branch lengths.

### Author(s)

Julien Dutheil <julien.dutheil@univ-montp2.fr> and Emmanuel Paradis

### References

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal society of London. Series B. Biological Sciences*, **326**, 119–157.

### See Also

[read.tree](#) for a description of phylo objects, [di2multi](#), [multi2di](#)

## Examples

```
data(bird.orders)
plot(compute.brtime(bird.orders, 1))
plot(compute.brtime(bird.orders, runif, min = 0, max = 5))
layout(matrix(1:4, 2, 2))
plot(compute.brtime(bird.orders, power=1), main=expression(rho==1))
plot(compute.brtime(bird.orders, power=3), main=expression(rho==3))
plot(compute.brtime(bird.orders, power=0.5), main=expression(rho==0.5))
plot(compute.brtime(bird.orders, power=0.1), main=expression(rho==0.1))
layout(1)
```

---

compute.brtime

*Compute and Set Branching Times*

---

## Description

This function computes the branch lengths of a tree giving its branching times (aka node ages or heights).

## Usage

```
compute.brtime(phy, method = "coalescent", force.positive = NULL)
```

## Arguments

`phy` an object of class "phylo".

`method` either "coalescent" (the default), or a numeric vector giving the branching times.

`force.positive` a logical value (see details).

## Details

By default, a set of random branching times is generated from a simple coalescent, and the option `force.positive` is set to TRUE so that no branch length is negative.

If a numeric vector is passed to `method`, it is taken as the branching times of the nodes with respect to their numbers (i.e., the first element of `method` is the branching time of the node numbered  $n + 1$  [= the root], the second element of the node numbered  $n + 2$ , and so on), so `force.positive` is set to FALSE. This may result in negative branch lengths. To avoid this, one should use `force.positive = TRUE` in which case the branching times are eventually reordered.

## Value

An object of class "phylo" with branch lengths and ultrametric.

## Author(s)

Emmanuel Paradis

**See Also**

[compute.brLen](#), [branching.times](#)

**Examples**

```
tr <- rtree(10)
layout(matrix(1:4, 2))
plot(compute.brtime(tr)); axisPhylo()
plot(compute.brtime(tr, force.positive = FALSE)); axisPhylo()
plot(compute.brtime(tr, 1:9)); axisPhylo() # a bit nonsense
plot(compute.brtime(tr, 1:9, TRUE)); axisPhylo()
layout(1)
```

---

 consensus

*Concensus Trees*


---

**Description**

Given a series of trees, this function returns the consensus tree. By default, the strict-consensus tree is computed. To get the majority-rule consensus tree, use  $p = 0.5$ . Any value between 0.5 and 1 can be used.

**Usage**

```
consensus(..., p = 1, check.labels = TRUE)
```

**Arguments**

...	either (i) a single object of class "phylo", (ii) a series of such objects separated by commas, or (iii) a list containing such objects.
p	a numeric value between 0.5 and 1 giving the proportion for a clade to be represented in the consensus tree.
check.labels	a logical specifying whether to check the labels of each tree. If FALSE (the default), it is assumed that all trees have the same tip labels, and that they are in the same order (see details).

**Details**

Using `check.labels = FALSE` results in considerable decrease in computing times. This requires that all trees have the same tip labels, *and* these labels are ordered similarly in all trees (in other words, the element `tip.label` are identical in all trees).

**Value**

an object of class "phylo".

**Author(s)**

Emmanuel Paradis

**References**

Felsenstein, J. (2004) *Inferring Phylogenies*. Sunderland: Sinauer Associates.

**See Also**

[prop.part](#), [dist.topo](#)

---

cophenetic.phylo

*Pairwise Distances from a Phylogenetic Tree*

---

**Description**

cophenetic.phylo computes the pairwise distances between the pairs of tips from a phylogenetic tree using its branch lengths.

dist.nodes does the same but between all nodes, internal and terminal, of the tree.

**Usage**

```
## S3 method for class 'phylo'  
cophenetic(x)  
dist.nodes(x)
```

**Arguments**

x                    an object of class "phylo".

**Value**

a numeric matrix with colnames and rownames set to the names of the tips (as given by the element tip.label of the argument phy), or, in the case of dist.nodes, the numbers of the tips and the nodes (as given by the element edge).

**Author(s)**

Emmanuel Paradis

**See Also**

[read.tree](#) to read tree files in Newick format, [cophenetic](#) for the generic function

---

cophyloplot

*Plots two phylogenetic trees face to face with links between the tips.*


---

### Description

This function plots two trees face to face with the links if specified. It is possible to rotate the branches of each tree around the nodes by clicking.

### Usage

```
cophyloplot(x, y, assoc = NULL, use.edge.length = FALSE, space = 0,
            length.line = 1, gap = 2, type = "phylogram", rotate = FALSE,
            col = par("fg"), lwd = par("lwd"), lty = par("lty"),
            show.tip.label = TRUE, font = 3, ...)
```

### Arguments

<code>x, y</code>	two objects of class "phylo".
<code>assoc</code>	a matrix with 2 columns specifying the associations between the tips. If <code>NULL</code> , no links will be drawn.
<code>use.edge.length</code>	a logical indicating whether the branch lengths should be used to plot the trees; default is <code>FALSE</code> .
<code>space</code>	a positive value that specifies the distance between the two trees.
<code>length.line</code>	a positive value that specifies the length of the horizontal line associated to each taxa. Default is 1.
<code>gap</code>	a value specifying the distance between the tips of the phylogeny and the lines.
<code>type</code>	a character string specifying the type of phylogeny to be drawn; it must be one of "phylogram" (the default) or "cladogram".
<code>rotate</code>	a logical indicating whether the nodes of the phylogeny can be rotated by clicking. Default is <code>FALSE</code> .
<code>col</code>	a character vector indicating the color to be used for the links; recycled as necessary.
<code>lwd</code>	id. for the width.
<code>lty</code>	id. for the line type.
<code>show.tip.label</code>	a logical indicating whether to show the tip labels on the phylogeny (defaults to 'TRUE', i.e. the labels are shown).
<code>font</code>	an integer specifying the type of font for the labels: 1 (plain text), 2 (bold), 3 (italic, the default), or 4 (bold italic).
<code>...</code>	(unused)

## Details

The aim of this function is to plot simultaneously two phylogenetic trees with associated taxa. The two trees do not necessarily have the same number of tips and more than one tip in one phylogeny can be associated with a tip in the other.

The association matrix used to draw the links has to be a matrix with two columns containing the names of the tips. One line in the matrix represents one link on the plot. The first column of the matrix has to contain tip labels of the first tree (phy1) and the second column of the matrix, tip labels of the second tree (phy2). There is no limit (low or high) for the number of lines in the matrix. A matrix with two columns and one line will give a plot with one link.

Arguments `gap`, `length.line` and `space` have to be changed to get a nice plot of the two phylogenies. Note that the function takes into account the length of the character strings corresponding to the names at the tips, so that the lines do not overwrite those names.

The `rotate` argument can be used to transform both phylogenies in order to get the more readable plot (typically by decreasing the number of crossing lines). This can be done by clicking on the nodes. The escape button or right click take back to the console.

## Author(s)

Damien de Vienne <damien.de-vienne@u-psud.fr>

## See Also

[plot.phylo](#), [rotate](#), [rotateConstr](#)

## Examples

```
#two random trees
tree1 <- rtree(40)
tree2 <- rtree(20)

#creation of the association matrix:
association <- cbind(tree1$tip.label, tree2$tip.label)

cophyloplot(tree1, tree2, assoc = association,
            length.line = 4, space = 28, gap = 3)

#plot with rotations
## Not run:
cophyloplot(tree1, tree2, assoc=association, length.line=4, space=28, gap=3, rotate=TRUE)

## End(Not run)
```

corBlomberg

*Blomberg et al.'s Correlation Structure***Description**

The “ACDC” (accelerated/decelerated) model assumes that continuous traits evolve under a Brownian motion model which rates accelerates (if  $g < 1$ ) or decelerates (if  $g > 1$ ) through time. If  $g = 1$ , then the model reduces to a Brownian motion model.

**Usage**

```
corBlomberg(value, phy, form = ~1, fixed = FALSE)
## S3 method for class 'corBlomberg'
corMatrix(object, covariate = getCovariate(object),
          corr = TRUE, ...)
## S3 method for class 'corBlomberg'
coef(object, unconstrained = TRUE, ...)
```

**Arguments**

value	the (initial) value of the parameter $g$ .
phy	an object of class "phylo".
form	(ignored).
fixed	a logical specifying whether gls should estimate $\gamma$ (the default) or keep it fixed.
object	an (initialized) object of class "corBlomberg".
covariate	(ignored).
corr	a logical value specifying whether to return the correlation matrix (the default) or the variance-covariance matrix.
unconstrained	a logical value. If TRUE (the default), the coefficients are returned in unconstrained form (the same used in the optimization algorithm). If FALSE the coefficients are returned in “natural”, possibly constrained, form.
...	further arguments passed to or from other methods.

**Value**

an object of class "corBlomberg", the coefficients from an object of this class, or the correlation matrix of an initialized object of this class. In most situations, only corBlomberg will be called by the user.

**Author(s)**

Emmanuel Paradis

**References**

Blomberg, S. P., Garland, Jr, T., and Ives, A. R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

---

 corBrownian

*Brownian Correlation Structure*


---

### Description

Expected covariance under a Brownian model (Felsenstein 1985, Martins and Hansen 1997)

$$V_{ij} = \gamma \times t_a$$

where  $t_a$  is the distance on the phylogeny between the root and the most recent common ancestor of taxa  $i$  and  $j$  and  $\gamma$  is a constant.

### Usage

```
corBrownian(value=1, phy, form=~1)
## S3 method for class 'corBrownian'
coef(object, unconstrained = TRUE, ...)
## S3 method for class 'corBrownian'
corMatrix(object, covariate = getCovariate(object), corr = TRUE, ...)
```

### Arguments

value	The $\gamma$ parameter (default to 1)
phy	An object of class phylo representing the phylogeny (with branch lengths) to consider
object	An (initialized) object of class corBrownian
corr	a logical value. If 'TRUE' the function returns the correlation matrix, otherwise it returns the variance/covariance matrix.
form	ignored for now.
covariate	ignored for now.
unconstrained	a logical value. If 'TRUE' the coefficients are returned in unconstrained form (the same used in the optimization algorithm). If 'FALSE' the coefficients are returned in "natural", possibly constrained, form. Defaults to 'TRUE'
...	some methods for these generics require additional arguments. None are used in these methods.

### Value

An object of class corBrownian, or the coefficient from an object of this class (actually sends `numeric(0)`), or the correlation matrix of an initialized object of this class.

### Author(s)

Julien Dutheil <julien.dutheil@univ-montp2.fr>



## References

- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- Martins, E. P. and Hansen, T. F. (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist*, **149**, 646–667.

## See Also

[corClasses](#)

---

corClasses	<i>Phylogenetic Correlation Structures</i>
------------	--

---

## Description

Classes of phylogenetic correlation structures ("corPhyl") available in **ape**.

- corBrownianBrownian motion model (Felsenstein 1985)
- corMartinsThe covariance matrix defined in Martins and Hansen (1997)
- corGrafenThe covariance matrix defined in Grafen (1989)
- corPagelThe covariance matrix defined in Freckelton et al. (2002)
- corBlombergThe covariance matrix defined in Blomberg et al. (2003)

See the help page of each class for references and detailed description.

## Author(s)

Julien Dutheil <julien.dutheil@univ-montp2.fr>, Emmanuel Paradis

## See Also

[corClasses](#) and [gls](#) in the **nlme** librarie, [corBrownian](#), [corMartins](#), [corGrafen](#), [corPagel](#), [corBlomberg](#)

## Examples

```
library(nlme)
cat("(((Homo:0.21,Pongo:0.21):0.28,",
"Macaca:0.49):0.13,Ateles:0.62):0.38,Galago:1.00);",
file = "ex.tre", sep = "\n")
tree.primates <- read.tree("ex.tre")
X <- c(4.09434, 3.61092, 2.37024, 2.02815, -1.46968)
Y <- c(4.74493, 3.33220, 3.36730, 2.89037, 2.30259)
unlink("ex.tre") # delete the file "ex.tre"
m1 <- gls(Y ~ X, correlation=corBrownian(1, tree.primates))
summary(m1)
m2 <- gls(Y ~ X, correlation=corMartins(1, tree.primates))
```

```
summary(m2)
corMatrix(m2$modelStruct$corStruct)
m3 <- gls(Y ~ X, correlation=corGrafen(1, tree.primates))
summary(m3)
corMatrix(m3$modelStruct$corStruct)
```

---

corGrafen

*Grafen's (1989) Correlation Structure*


---

### Description

Grafen's (1989) covariance structure. Branch lengths are computed using Grafen's method (see [compute.br1en](#)). The covariance matrix is then the traditional variance-covariance matrix for a phylogeny.

### Usage

```
corGrafen(value, phy, form=~1, fixed = FALSE)
## S3 method for class 'corGrafen'
coef(object, unconstrained = TRUE, ...)
## S3 method for class 'corGrafen'
corMatrix(object,
           covariate = getCovariate(object), corr = TRUE, ...)
```

### Arguments

value	The $\rho$ parameter
phy	An object of class phylo representing the phylogeny (branch lengths are ignored) to consider
object	An (initialized) object of class corGrafen
corr	a logical value. If 'TRUE' the function returns the correlation matrix, otherwise it returns the variance/covariance matrix.
fixed	an optional logical value indicating whether the coefficients should be allowed to vary in the optimization, or kept fixed at their initial value. Defaults to 'FALSE', in which case the coefficients are allowed to vary.
form	ignored for now.
covariate	ignored for now.
unconstrained	a logical value. If 'TRUE' the coefficients are returned in unconstrained form (the same used in the optimization algorithm). If 'FALSE' the coefficients are returned in "natural", possibly constrained, form. Defaults to 'TRUE'
...	some methods for these generics require additional arguments. None are used in these methods.

**Value**

An object of class corGrafen or the rho coefficient from an object of this class or the correlation matrix of an initialized object of this class.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr>

**References**

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal society of London. Series B. Biological Sciences*, **326**, 119–157.

**See Also**

[corClasses](#), [compute.brLen](#), [vcv.phylo](#).

---

corMartins

*Martins's (1997) Correlation Structure*

---

**Description**

Martins and Hansen's (1997) covariance structure:

$$V_{ij} = \gamma \times e^{-\alpha t_{ij}}$$

where  $t_{ij}$  is the phylogenetic distance between taxa  $i$  and  $j$  and  $\gamma$  is a constant.

**Usage**

```
corMartins(value, phy, form = ~1, fixed = FALSE)
## S3 method for class 'corMartins'
coef(object, unconstrained = TRUE, ...)
## S3 method for class 'corMartins'
corMatrix(object,
covariate = getCovariate(object), corr = TRUE, ...)
```

**Arguments**

value	The $\alpha$ parameter
phy	An object of class phylo representing the phylogeny (with branch lengths) to consider
object	An (initialized) object of class corMartins
corr	a logical value. If 'TRUE' the function returns the correlation matrix, otherwise it returns the variance/covariance matrix.

fixed	an optional logical value indicating whether the coefficients should be allowed to vary in the optimization, or kept fixed at their initial value. Defaults to 'FALSE', in which case the coefficients are allowed to vary.
form	ignored for now.
covariate	ignored for now.
unconstrained	a logical value. If 'TRUE' the coefficients are returned in unconstrained form (the same used in the optimization algorithm). If 'FALSE' the coefficients are returned in "natural", possibly constrained, form. Defaults to 'TRUE'
...	some methods for these generics require additional arguments. None are used in these methods.

**Value**

An object of class `corMartins` or the alpha coefficient from an object of this class or the correlation matrix of an initialized object of this class.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr>

**References**

Martins, E. P. and Hansen, T. F. (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist*, **149**, 646–667.

**See Also**

[corClasses](#).

---

corPagel

*Pagel's "lambda" Correlation Structure*

---

**Description**

The correlation structure from the present model is derived from the Brownian motion model by multiplying the off-diagonal elements (i.e., the covariances) by  $\lambda$ . The variances are thus the same than for a Brownian motion model.

**Usage**

```
corPagel(value, phy, form = ~1, fixed = FALSE)
## S3 method for class 'corPagel'
corMatrix(object, covariate = getCovariate(object),
          corr = TRUE, ...)
## S3 method for class 'corPagel'
coef(object, unconstrained = TRUE, ...)
```

**Arguments**

value	the (initial) value of the parameter $\lambda$ .
phy	an object of class "phylo".
form	(ignored).
fixed	a logical specifying whether gls should estimate $\lambda$ (the default) or keep it fixed.
object	an (initialized) object of class "corPagel".
covariate	(ignored).
corr	a logical value specifying whether to return the correlation matrix (the default) or the variance-covariance matrix.
unconstrained	a logical value. If TRUE (the default), the coefficients are returned in unconstrained form (the same used in the optimization algorithm). If FALSE the coefficients are returned in "natural", possibly constrained, form.
...	further arguments passed to or from other methods.

**Value**

an object of class "corPagel", the coefficients from an object of this class, or the correlation matrix of an initialized object of this class. In most situations, only corPagel will be called by the user.

**Author(s)**

Emmanuel Paradis

**References**

- Freckleton, R. P., Harvey, P. H. and M. Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist*, **160**, 712–726.
- Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

---

correlogram.formula    *Phylogenetic Correlogram*

---

**Description**

This function computes a correlogram from taxonomic levels.

**Usage**

```
correlogram.formula(formula, data = NULL, use = "all.obs")
```

**Arguments**

formula	a formula of the type $y_1 + \dots + y_n \sim g_1 / \dots / g_n$ , where the $y$ 's are the data to analyse and the $g$ 's are the taxonomic levels.
data	a data frame containing the variables specified in the formula. If NULL, the variables are sought in the user's workspace.
use	a character string specifying how to handle missing values (i.e., NA). This must be one of "all.obs", "complete.obs", or "pairwise.complete.obs", or any unambiguous abbreviation of these. In the first case, the presence of missing values produces an error. In the second case, all rows with missing values will be removed before computation. In the last case, missing values are removed on a case-by-case basis.

**Details**

See the vignette in R: `vignette("MoranI")`.

**Value**

An object of class `correlogram` which is a data frame with three columns:

obs	the computed Moran's I
p.values	the corresponding P-values
labels	the names of each level

or an object of class `correlogramList` containing a list of objects of class `correlogram` if several variables are given as response in formula.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr> and Emmanuel Paradis

**See Also**

[plot.correlogram](#), [Moran.I](#)

**Examples**

```
data(carnivora)
### Using the formula interface:
co <- correlogram.formula(SW ~ Order/SuperFamily/Family/Genus,
  data=carnivora)
co
plot(co)
### Several correlograms on the same plot:
cos <- correlogram.formula(SW + FW ~ Order/SuperFamily/Family/Genus,
  data=carnivora)
cos
plot(cos)
```

---

`data.nex`*NEXUS Data Example*

---

**Description**

Example of Protein data in NEXUS format (Maddison et al., 1997). Data is written in interleaved format using a single DATA block. Original data from Rokas et al (2002).

**Usage**`data(cynipids)`**Format**

ASCII text in NEXUS format

**References**

Maddison, D. R., Swofford, D. L. and Maddison, W. P. (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology*, **46**, 590–621.

Rokas, A., Nylander, J. A. A., Ronquist, F. and Stone, G. N. (2002) A maximum likelihood analysis of eight phylogenetic markers in Gallwasps (Hymenoptera: Cynipidae): implications for insect phylogenetic studies. *Molecular Phylogenetics and Evolution*, **22**, 206–219.

---

`dbd`*Probability Density Under Birth–Death Models*

---

**Description**

These functions compute the probability density under some birth–death models, that is the probability of obtaining  $x$  species after a time  $t$  giving how speciation and extinction probabilities vary through time (these may be constant, or even equal to zero for extinction).

**Usage**

```
dyule(x, lambda = 0.1, t = 1, log = FALSE)
dbd(x, lambda, mu, t, conditional = FALSE, log = FALSE)
dbdTime(x, birth, death, t, conditional = FALSE,
        BIRTH = NULL, DEATH = NULL, fast = FALSE)
```

**Arguments**

<code>x</code>	a numeric vector of species numbers (see <a href="#">Details</a> ).
<code>lambda</code>	a numerical value giving the probability of speciation; can be a vector with several values for <code>dyule</code> .
<code>mu</code>	id. for extinction.
<code>t</code>	id. for the time(s).
<code>log</code>	a logical value specifying whether the probabilities should be returned log-transformed; the default is <code>FALSE</code> .
<code>conditional</code>	a logical specifying whether the probabilities should be computed conditional under the assumption of no extinction after time <code>t</code> .
<code>birth, death</code>	a (vectorized) function specifying how the speciation or extinction probability changes through time (see <a href="#">yule.time</a> and below).
<code>BIRTH, DEATH</code>	a (vectorized) function giving the primitive of birth or death.
<code>fast</code>	a logical value specifying whether to use faster integration (see <a href="#">bd.time</a> ).

**Details**

These three functions compute the probabilities to observe `x` species starting from a single one after time `t` (assumed to be continuous). The first function is a short-cut for the second one with `mu = 0` and with default values for the two other arguments. `dbdTime` is for time-varying `lambda` and `mu` specified as `R` functions.

`dyule` is vectorized simultaneously on its three arguments `x`, `lambda`, and `t`, according to `R`'s rules of recycling arguments. `dbd` is vectorized simultaneously `x` and `t` (to make likelihood calculations easy), and `dbdTime` is vectorized only on `x`; the other arguments are eventually shortened with a warning if necessary.

The returned value is, logically, zero for values of `x` out of range, i.e., negative or zero for `dyule` or if `conditional = TRUE`. However, it is not checked if the values of `x` are positive non-integers and the probabilities are computed and returned.

The details on the form of the arguments `birth`, `death`, `BIRTH`, `DEATH`, and `fast` can be found in the links below.

**Value**

a numeric vector.

**Note**

If you use these functions to calculate a likelihood function, it is strongly recommended to compute the log-likelihood with, for instance in the case of a Yule process, `sum(dyule( , log = TRUE))` (see examples).

**Author(s)**

Emmanuel Paradis



**References**

Kendall, D. G. (1948) On the generalized “birth-and-death” process. *Annals of Mathematical Statistics*, **19**, 1–15.

**See Also**

[bd.time](#), [yule.time](#)

**Examples**

```
x <- 0:10
plot(x, dyule(x), type = "h", main = "Density of the Yule process")
text(7, 0.85, expression(list(lambda == 0.1, t == 1)))

y <- dbd(x, 0.1, 0.05, 10)
z <- dbd(x, 0.1, 0.05, 10, conditional = TRUE)
d <- rbind(y, z)
colnames(d) <- x
barplot(d, beside = TRUE, ylab = "Density", xlab = "Number of species",
        legend = c("unconditional", "conditional on\nno extinction"),
        args.legend = list(bty = "n"))
title("Density of the birth-death process")
text(17, 0.4, expression(list(lambda == 0.1, mu == 0.05, t == 10)))

## Not run:
### generate 1000 values from a Yule process with lambda = 0.05
x <- replicate(1e3, Ntip(rlineage(0.05, 0)))

### the correct way to calculate the log-likelihood...:
sum(dyule(x, 0.05, 50, log = TRUE))

### ... and the wrong way:
log(prod(dyule(x, 0.05, 50)))

### a third, less preferred, way:
sum(log(dyule(x, 0.05, 50)))

## End(Not run)
```

---

del.gaps

*Delete Alignment Gaps in DNA Sequences*


---

**Description**

This function removes the insertion gaps (“-”) in a sample of DNA sequences.

**Usage**

```
del.gaps(x)
```

**Arguments**

`x` a matrix, a list, or a vector containing the DNA sequences.

**Details**

The sequences can be either in "DNABin" or in character format, but the returned object is always of class "DNABin". If `x` is a vector, then a vector is returned; if it is a list or a matrix, then a list is returned.

**Value**

A vector (if there is only one input sequence) or a list of class "DNABin".

**Author(s)**

Emmanuel Paradis

**See Also**

[base.freq](#), [GC.content](#), [seg.sites](#), [image.DNABin](#)

---

delta.plot

*Delta Plots*

---

**Description**

This function makes a  $\delta$  plot following Holland et al. (2002).

**Usage**

```
delta.plot(X, k = 20, plot = TRUE, which = 1:2)
```

**Arguments**

`X` a distance matrix, may be an object of class "dist".

`k` an integer giving the number of intervals in the plot.

`plot` a logical specifying whether to draw the  $\delta$  plot (the default).

`which` a numeric vector indicating which plots are done; 1: the histogram of the  $\delta_q$  values, 2: the plot of the individual  $\bar{\delta}$  values. By default, both plots are done.

**Details**

See Holland et al. (2002) for details and interpretation.

The computing time of this function is proportional to the fourth power of the number of observations ( $O(n^4)$ ), so calculations may be very long with only a slight increase in sample size.

**Value**

This function returns invisibly a named list with two components:

- countsthe counts for the histogram of  $\delta_q$  values
- delta.barthe mean  $\delta$  value for each observation

**Author(s)**

Emmanuel Paradis

**References**

Holland, B. R., Huber, K. T., Dress, A. and Moulton, V. (2002) Delta plots: a tool for analyzing phylogenetic distance data. *Molecular Biology and Evolution*, **12**, 2051–2059.

**See Also**

[dist.dna](#)

**Examples**

```
data(woodmouse)
d <- dist.dna(woodmouse)
delta.plot(d)
layout(1)
delta.plot(d, 40, which = 1)
```

---

dist.dna

*Pairwise Distances from DNA Sequences*

---

**Description**

This function computes a matrix of pairwise distances from DNA sequences using a model of DNA evolution. Eleven substitution models (and the raw distance) are currently available.

**Usage**

```
dist.dna(x, model = "K80", variance = FALSE,
         gamma = FALSE, pairwise.deletion = FALSE,
         base.freq = NULL, as.matrix = FALSE)
```

## Arguments

<code>x</code>	a matrix or a list containing the DNA sequences; this must be of class "DNABin" (use <code>as.DNABin</code> if they are stored as character).
<code>model</code>	a character string specifying the evolutionary model to be used; must be one of "raw", "N", "TS", "TV", "JC69", "K80" (the default), "F81", "K81", "F84", "BH87", "T92", "TN93", "GG95", "logdet", "paralin", "indel", or "indelblock".
<code>variance</code>	a logical indicating whether to compute the variances of the distances; defaults to FALSE so the variances are not computed.
<code>gamma</code>	a value for the gamma parameter possibly used to apply a correction to the distances (by default no correction is applied).
<code>pairwise.deletion</code>	a logical indicating whether to delete the sites with missing data in a pairwise way. The default is to delete the sites with at least one missing data for all sequences (ignored if <code>model = "indel" or "indelblock"</code> ).
<code>base.freq</code>	the base frequencies to be used in the computations (if applicable). By default, the base frequencies are computed from the whole set of sequences.
<code>as.matrix</code>	a logical indicating whether to return the results as a matrix. The default is to return an object of class <code>dist</code> .

## Details

The molecular evolutionary models available through the option `model` have been extensively described in the literature. A brief description is given below; more details can be found in the References.

- `raw, N`: This is simply the proportion or the number of sites that differ between each pair of sequences. This may be useful to draw "saturation plots". The options `variance` and `gamma` have no effect, but `pairwise.deletion` can.
- `TS, TV`: These are the numbers of transitions and transversions, respectively.
- `JC69`: This model was developed by Jukes and Cantor (1969). It assumes that all substitutions (i.e. a change of a base by another one) have the same probability. This probability is the same for all sites along the DNA sequence. This last assumption can be relaxed by assuming that the substitution rate varies among site following a gamma distribution which parameter must be given by the user. By default, no gamma correction is applied. Another assumption is that the base frequencies are balanced and thus equal to 0.25.
- `K80`: The distance derived by Kimura (1980), sometimes referred to as "Kimura's 2-parameters distance", has the same underlying assumptions than the Jukes–Cantor distance except that two kinds of substitutions are considered: transitions ( $A \leftrightarrow G, C \leftrightarrow T$ ), and transversions ( $A \leftrightarrow C, A \leftrightarrow T, C \leftrightarrow G, G \leftrightarrow T$ ). They are assumed to have different probabilities. A transition is the substitution of a purine (C, T) by another one, or the substitution of a pyrimidine (A, G) by another one. A transversion is the substitution of a purine by a pyrimidine, or vice-versa. Both transition and transversion rates are the same for all sites along the DNA sequence. Jin and Nei (1990) modified the Kimura model to allow for variation among sites following a gamma distribution. Like for the Jukes–Cantor model, the gamma parameter must be given by the user. By default, no gamma correction is applied.

- F81: Felsenstein (1981) generalized the Jukes–Cantor model by relaxing the assumption of equal base frequencies. The formulae used in this function were taken from McGuire et al. (1999).
- K81: Kimura (1981) generalized his model (Kimura 1980) by assuming different rates for two kinds of transversions: A <-> C and G <-> T on one side, and A <-> T and C <-> G on the other. This is what Kimura called his “three substitution types model” (3ST), and is sometimes referred to as “Kimura’s 3-parameters distance”.
- F84: This model generalizes K80 by relaxing the assumption of equal base frequencies. It was first introduced by Felsenstein in 1984 in Phylip, and is fully described by Felsenstein and Churchill (1996). The formulae used in this function were taken from McGuire et al. (1999).
- BH87: Barry and Hartigan (1987) developed a distance based on the observed proportions of changes among the four bases. This distance is not symmetric.
- T92: Tamura (1992) generalized the Kimura model by relaxing the assumption of equal base frequencies. This is done by taking into account the bias in G+C content in the sequences. The substitution rates are assumed to be the same for all sites along the DNA sequence.
- TN93: Tamura and Nei (1993) developed a model which assumes distinct rates for both kinds of transition (A <-> G versus C <-> T), and transversions. The base frequencies are not assumed to be equal and are estimated from the data. A gamma correction of the inter-site variation in substitution rates is possible.
- GG95: Galtier and Gouy (1995) introduced a model where the G+C content may change through time. Different rates are assumed for transitsons and transversions.
- logdet: The Log-Det distance, developed by Lockhart et al. (1994), is related to BH87. However, this distance is symmetric. Formulae from Gu and Li (1996) are used. `dist.logdet` in **phangorn** uses a different implementation that gives substantially different distances for low-diverging sequences.
- paralin: Lake (1994) developed the parilinear distance which can be viewed as another variant of the Barry–Hartigan distance.
- indel: this counts the number of sites where there is an insertion/deletion gap in one sequence and not in the other.
- indelblock: same than before but contiguous gaps are counted as a single unit. Note that the distance between -A- and A-- is 3 because there are three different blocks of gaps, whereas the “indel” distance will be 2.

### Value

an object of class `dist` (by default), or a numeric matrix if `as.matrix = TRUE`. If `model = "BH87"`, a numeric matrix is returned because the Barry–Hartigan distance is not symmetric.

If `variance = TRUE` an attribute called "variance" is given to the returned object.

### Author(s)

Emmanuel Paradis

## References

- Barry, D. and Hartigan, J. A. (1987) Asynchronous distance between homologous DNA sequences. *Biometrics*, **43**, 261–276.
- Felsenstein, J. (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, **17**, 368–376.
- Felsenstein, J. and Churchill, G. A. (1996) A Hidden Markov model approach to variation among sites in rate of evolution. *Molecular Biology and Evolution*, **13**, 93–104.
- Galtier, N. and Gouy, M. (1995) Inferring phylogenies from DNA sequences of unequal base compositions. *Proceedings of the National Academy of Sciences USA*, **92**, 11317–11321.
- Gu, X. and Li, W.-H. (1996) Bias-corrected paralinear and LogDet distances and tests of molecular clocks and phylogenies under nonstationary nucleotide frequencies. *Molecular Biology and Evolution*, **13**, 1375–1383.
- Jukes, T. H. and Cantor, C. R. (1969) Evolution of protein molecules. in *Mammalian Protein Metabolism*, ed. Munro, H. N., pp. 21–132, New York: Academic Press.
- Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.
- Kimura, M. (1981) Estimation of evolutionary distances between homologous nucleotide sequences. *Proceedings of the National Academy of Sciences USA*, **78**, 454–458.
- Jin, L. and Nei, M. (1990) Limitations of the evolutionary parsimony method of phylogenetic analysis. *Molecular Biology and Evolution*, **7**, 82–102.
- Lake, J. A. (1994) Reconstructing evolutionary trees from DNA and protein sequences: paralinear distances. *Proceedings of the National Academy of Sciences USA*, **91**, 1455–1459.
- Lockhart, P. J., Steel, M. A., Hendy, M. D. and Penny, D. (1994) Recovering evolutionary trees under a more realistic model of sequence evolution. *Molecular Biology and Evolution*, **11**, 605–602.
- McGuire, G., Prentice, M. J. and Wright, F. (1999). Improved error bounds for genetic distances from DNA sequences. *Biometrics*, **55**, 1064–1070.
- Tamura, K. (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G + C-content biases. *Molecular Biology and Evolution*, **9**, 678–687.
- Tamura, K. and Nei, M. (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, **10**, 512–526.

## See Also

[read.GenBank](#), [read.dna](#), [write.dna](#), [DNAbin](#), [dist.gene](#), [cophenetic.phylo](#), [dist](#)

---

dist.gene	<i>Pairwise Distances from Genetic Data</i>
-----------	---

---

### Description

This function computes a matrix of distances between pairs of individuals from a matrix or a data frame of genetic data.

### Usage

```
dist.gene(x, method = "pairwise", pairwise.deletion = FALSE,  
          variance = FALSE)
```

### Arguments

x	a matrix or a data frame (will be coerced as a matrix).
method	a character string specifying the method used to compute the distances; two choices are available: "pairwise" and "percentage", or any unambiguous abbreviation of these.
pairwise.deletion	a logical indicating whether to delete the columns with missing data on a pairwise basis. The default is to delete the columns with at least one missing observation.
variance	a logical, indicates whether the variance of the distances should be returned (default to FALSE).

### Details

This function is meant to be very general and accepts different kinds of data (alleles, haplotypes, SNP, DNA sequences, ...). The rows of the data matrix represent the individuals, and the columns the loci.

In the case of the pairwise method, the distance  $d$  between two individuals is the number of loci for which they differ, and the associated variance is  $d(L - d)/L$ , where  $L$  is the number of loci.

In the case of the percentage method, this distance is divided by  $L$ , and the associated variance is  $d(1 - d)/L$ .

For more elaborate distances with DNA sequences, see the function `dist.dna`.

### Value

an object of class `dist`. If `variance = TRUE` an attribute called "variance" is given to the returned object.

### Note

Missing data (NA) are coded and treated in R's usual way.

**Author(s)**

Emmanuel Paradis

**See Also**

[dist.dna](#), [cophenetic.phylo](#), [dist](#)

---

dist.topo

*Topological Distances Between Two Trees*

---

**Description**

This function computes the topological distance between two phylogenetic trees using different methods.

**Usage**

```
dist.topo(x, y, method = "PH85")
```

**Arguments**

x	an object of class "phylo".
y	an object of class "phylo".
method	a character string giving the method to be used: either "PH85", or "score".

**Details**

Two methods are available: the one by Penny and Hendy (1985), and the branch length score by Kuhner and Felsenstein (1994). The trees are always considered as unrooted.

The topological distance is defined as twice the number of internal branches defining different bipartitions of the tips (Penny and Hendy 1985). Rzhetsky and Nei (1992) proposed a modification of the original formula to take multifurcations into account.

The branch length score may be seen as similar to the previous distance but taking branch lengths into account. Kuhner and Felsenstein (1994) proposed to calculate the square root of the sum of the squared differences of the (internal) branch lengths defining similar bipartitions (or splits) in both trees.

**Value**

a single numeric value.

**Note**

The geodesic distance of Billera et al. (2001) has been disabled: see the package **distory** on CRAN.



**Author(s)**

Emmanuel Paradis

**References**

Billera, L. J., Holmes, S. P. and Vogtmann, K. (2001) Geometry of the space of phylogenetic trees. *Advances in Applied Mathematics*, **27**, 733–767.

Kuhner, M. K. and Felsenstein, J. (1994) Simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Molecular Biology and Evolution*, **11**, 459–468.

Nei, M. and Kumar, S. (2000) *Molecular Evolution and Phylogenetics*. Oxford: Oxford University Press.

Penny, D. and Hendy, M. D. (1985) The use of tree comparison metrics. *Systematic Zoology*, **34**, 75–82.

Rzhetsky, A. and Nei, M. (1992) A simple method for estimating and testing minimum-evolution trees. *Molecular Biology and Evolution*, **9**, 945–967.

**See Also**

[read.tree](#) to read tree files in Newick format, [cophenetic.phylo](#), [prop.part](#)

**Examples**

```
ta <- rtree(30)
tb <- rtree(30)
dist.topo(ta, ta) # = 0
dist.topo(ta, tb) # This is unlikely to be 0 !
```

---

diversi.gof

*Tests of Constant Diversification Rates*

---

**Description**

This function computes two tests of the distribution of branching times using the Cramér–von Mises and Anderson–Darling goodness-of-fit tests. By default, it is assumed that the diversification rate is constant, and an exponential distribution is assumed for the branching times. In this case, the expected distribution under this model is computed with a rate estimated from the data. Alternatively, the user may specify an expected cumulative density function (z): in this case, x and z must be of the same length. See the examples for how to compute the latter from a sample of expected branching times.

**Usage**

```
diversi.gof(x, null = "exponential", z = NULL)
```

**Arguments**

x	a numeric vector with the branching times.
null	a character string specifying the null distribution for the branching times. Only two choices are possible: either "exponential", or "user".
z	used if null = "user"; gives the expected distribution under the model.

**Details**

The Cramér–von Mises and Anderson–Darling tests compare the empirical density function (EDF) of the observations to an expected cumulative density function. By contrast to the Kolmogorov–Smirnov test where the greatest difference between these two functions is used, in both tests all differences are taken into account.

The distributions of both test statistics depend on the null hypothesis, and on whether or not some parameters were estimated from the data. However, these distributions are not known precisely and critical values were determined by Stephens (1974) using simulations. These critical values were used for the present function.

**Value**

A NULL value is returned, the results are simply printed.

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (1998) Testing for constant diversification rates using molecular phylogenies: a general approach based on statistical tests for goodness of fit. *Molecular Biology and Evolution*, **15**, 476–479.

Stephens, M. A. (1974) EDF statistics for goodness of fit and some comparisons. *Journal of the American Statistical Association*, **69**, 730–737.

**See Also**

[branching.times](#), [diversi.time](#) [lft.plot](#), [birthdeath](#), [yule](#), [yule.cov](#)

**Examples**

```
data(bird.families)
x <- branching.times(bird.families)
### suppose we have a sample of expected branching times `y`;
### for simplicity, take them from a uniform distribution:
y <- runif(500, 0, max(x) + 1) # + 1 to avoid A2 = Inf
### now compute the expected cumulative distribution:
x <- sort(x)
N <- length(x)
ecdf <- numeric(N)
for (i in 1:N) ecdf[i] <- sum(y <= x[i])/500
```

```
### finally do the test:  
diversi.gof(x, "user", z = ecdf)
```

---

`diversi.time`*Analysis of Diversification with Survival Models*

---

## Description

This functions fits survival models to a set of branching times, some of them may be known approximately (censored). Three models are fitted, Model A assuming constant diversification, Model B assuming that diversification follows a Weibull law, and Model C assuming that diversification changes with a breakpoint at time 'Tc'. The models are fitted by maximum likelihood.

## Usage

```
diversi.time(x, census = NULL, censoring.codes = c(1, 0), Tc = NULL)
```

## Arguments

x	a numeric vector with the branching times.
census	a vector of the same length than 'x' used as an indicator variable; thus, it must have only two values, one coding for accurately known branching times, and the other for censored branching times. This argument can be of any mode (numeric, character, logical), or can even be a factor.
censoring.codes	a vector of length two giving the codes used for census: by default 1 (accurately known times) and 0 (censored times). The mode must be the same than the one of census.
Tc	a single numeric value specifying the break-point time to fit Model C. If none is provided, then it is set arbitrarily to the mean of the analysed branching times.

## Details

The principle of the method is to consider each branching time as an event: if the branching time is accurately known, then it is a failure event; if it is approximately known then it is a censoring event. An analogy is thus made between the failure (or hazard) rate estimated by the survival models and the diversification rate of the lineage. Time is here considered from present to past.

Model B assumes a monotonically changing diversification rate. The parameter that controls the change of this rate is called beta. If beta is greater than one, then the diversification rate decreases through time; if it is lesser than one, the the rate increases through time. If beta is equal to one, then Model B reduces to Model A.

## Value

A NULL value is returned, the results are simply printed.

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (1997) Assessing temporal variations in diversification rates from phylogenies: estimation and hypothesis testing. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **264**, 1141–1147.

**See Also**

[branching.times](#), [diversi.gof](#) [ltt.plot](#), [birthdeath](#), [bd.ext](#), [yule](#), [yule.cov](#)

---

diversity.contrast.test

*Diversity Contrast Test*

---

**Description**

This function performs the diversity contrast test comparing pairs of sister-clades.

**Usage**

```
diversity.contrast.test(x, method = "ratiolog",  
                       alternative = "two.sided", nrep = 0, ...)
```

**Arguments**

x	a matrix or a data frame with at least two columns: the first one gives the number of species in clades with a trait supposed to increase or decrease diversification rate, and the second one the number of species in the sister-clades without the trait. Each row represents a pair of sister-clades.
method	a character string specifying the kind of test: "ratiolog" (default), "proportion", "difference", "logratio", or any unambiguous abbreviation of these.
alternative	a character string defining the alternative hypothesis: "two.sided" (default), "less", "greater", or any unambiguous abbreviation of these.
nrep	the number of replications of the randomization test; by default, a Wilcoxon test is done.
...	arguments passed to the function <a href="#">wilcox.test</a> .

### Details

If `method = "ratiolog"`, the test described in Barraclough et al. (1996) is performed. If `method = "proportion"`, the version in Barraclough et al. (1995) is used. If `method = "difference"`, the signed difference is used (Sargent 2004). If `method = "logratio"`, then this is Wiegmann et al.'s (1993) version. These four tests are essentially different versions of the same test (Vamosi and Vamosi 2005, Vamosi 2007). See Paradis (2012) for a comparison of their statistical performance with other tests.

If `nrep = 0`, a Wilcoxon test is done on the species diversity contrasts with the null hypothesis is that they are distributed around zero. If `nrep > 0`, a randomization procedure is done where the signs of the diversity contrasts are randomly chosen. This is used to create a distribution of the test statistic which is compared with the observed value (the sum of the diversity contrasts).

### Value

a single numeric value with the *P*-value.

### Author(s)

Emmanuel Paradis

### References

- Barraclough, T. G., Harvey, P. H. and Nee, S. (1995) Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **259**, 211–215.
- Barraclough, T. G., Harvey, P. H., and Nee, S. (1996) Rate of *rbcL* gene sequence evolution and species diversification in flowering plants (angiosperms). *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **263**, 589–591.
- Paradis, E. (2012) Shift in diversification in sister-clade comparisons: a more powerful test. *Evolution*, **66**, 288–295.
- Sargent, R. D. (2004) Floral symmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **271**, 603–608.
- Vamosi, S. M. (2007) Endless tests: guidelines for analysing non-nested sister-group comparisons. An addendum. *Evolutionary Ecology Research*, **9**, 717.
- Vamosi, S. M. and Vamosi, J. C. (2005) Endless tests: guidelines for analysing non-nested sister-group comparisons. *Evolutionary Ecology Research*, **7**, 567–579.
- Wiegmann, B., Mitter, C. and Farrell, B. 1993. Diversification of carnivorous parasitic insects: extraordinary radiation or specialized dead end? *American Naturalist*, **142**, 737–754.

### See Also

[slowskiguyer.test](#), [mconwaysims.test](#) [richness.yule.test](#)

## Examples

```
### data from Vamosi & Vamosi (2005):
fleshy <- c(1, 1, 1, 1, 1, 3, 3, 5, 9, 16, 33, 40, 50, 100, 216, 393, 850, 947,1700)
dry <- c(2, 64, 300, 89, 67, 4, 34, 10, 150, 35, 2, 60, 81, 1, 3, 1, 11, 1, 18)
x <- cbind(fleshy, dry)
diversity.contrast.test(x)
diversity.contrast.test(x, alt = "g")
diversity.contrast.test(x, alt = "g", nrep = 1e4)
slowinskiguyer.test(x)
mcconwaysims.test(x)
```

---

 DNAbin

---

*Manipulate DNA Sequences in Bit-Level Format*


---

## Description

These functions help to manipulate DNA sequences coded in the bit-level coding scheme.

## Usage

```
## S3 method for class 'DNAbin'
print(x, printlen = 6, digits = 3, ...)
## S3 method for class 'DNAbin'
rbind(...)
## S3 method for class 'DNAbin'
cbind(..., check.names = TRUE, fill.with.gaps = FALSE,
       quiet = FALSE)
## S3 method for class 'DNAbin'
x[i, j, drop = FALSE]
## S3 method for class 'DNAbin'
as.matrix(x, ...)
## S3 method for class 'DNAbin'
c(..., recursive = FALSE)
## S3 method for class 'DNAbin'
as.list(x, ...)
## S3 method for class 'DNAbin'
labels(object, ...)
```

## Arguments

<code>x</code> , <code>object</code>	an object of class "DNAbin".
<code>...</code>	either further arguments to be passed to or from other methods in the case of <code>print</code> , <code>as.matrix</code> , and <code>labels</code> , or a series of objects of class "DNAbin" in the case of <code>rbind</code> , <code>cbind</code> , and <code>c</code> .
<code>printlen</code>	the number of labels to print (6 by default).
<code>digits</code>	the number of digits to print (3 by default).

<code>check.names</code>	a logical specifying whether to check the rownames before binding the columns (see details).
<code>fill.with.gaps</code>	a logical indicating whether to keep all possible individuals as indicated by the rownames, and eventually filling the missing data with insertion gaps (ignored if <code>check.names = FALSE</code> ).
<code>quiet</code>	a logical to switch off warning messages when some rows are dropped.
<code>i, j</code>	indices of the rows and/or columns to select or to drop. They may be numeric, logical, or character (in the same way than for standard R objects).
<code>drop</code>	logical; if TRUE, the returned object is of the lowest possible dimension.
<code>recursive</code>	for compatibility with the generic (unused).

### Details

These are all ‘methods’ of generic functions which are here applied to DNA sequences stored as objects of class "DNAbin". They are used in the same way than the standard R functions to manipulate vectors, matrices, and lists. Additionally, the operators `[]` and `$` may be used to extract a vector from a list. Note that the default of `drop` is not the same than the generic operator: this is to avoid dropping rownames when selecting a single sequence.

These functions are provided to manipulate easily DNA sequences coded with the bit-level coding scheme. The latter allows much faster comparisons of sequences, as well as storing them in less memory compared to the format used before **ape** 1.10.

For `cbind`, the default behaviour is to keep only individuals (as indicated by the rownames) for which there are no missing data. If `fill.with.gaps = TRUE`, a ‘complete’ matrix is returned, eventually with insertion gaps as missing data. If `check.names = TRUE` (the default), the rownames of each matrix are checked, and the rows are reordered if necessary. If `check.names = FALSE`, the matrices must all have the same number of rows, and are simply binded; the rownames of the first matrix are used. See the examples.

`as.matrix` may be used to convert DNA sequences (of the same length) stored in a list into a matrix while keeping the names and the class. `as.list` does the reverse operation.

### Value

an object of class "DNAbin" in the case of `rbind`, `cbind`, and `[]`.

### Author(s)

Emmanuel Paradis

### References

- Paradis, E. (2007) A Bit-Level Coding Scheme for Nucleotides. [http://ape.mpl.ird.fr/misc/BitLevelCodingScheme\\_20April2007.pdf](http://ape.mpl.ird.fr/misc/BitLevelCodingScheme_20April2007.pdf)
- Paradis, E. (2012) *Analysis of Phylogenetics and Evolution with R (Second Edition)*. New York: Springer.

**See Also**

[as.DNABin](#), [read.dna](#), [read.GenBank](#), [write.dna](#), [image.DNABin](#)

The corresponding generic functions are documented in the package **base**.

**Examples**

```
data(woodmouse)
woodmouse
print(woodmouse, 15, 6)
print(woodmouse[1:5, 1:300], 15, 6)
### Just to show how distances could be influenced by sampling:
dist.dna(woodmouse[1:2, ])
dist.dna(woodmouse[1:3, ])
### cbind and its options:
x <- woodmouse[1:2, 1:5]
y <- woodmouse[2:4, 6:10]
as.character(cbind(x, y)) # gives warning
as.character(cbind(x, y, fill.with.gaps = TRUE))
## Not run:
as.character(cbind(x, y, check.names = FALSE)) # gives an error

## End(Not run)
```

---

drop.tip

*Remove Tips in a Phylogenetic Tree*

---

**Description**

`drop.tip` removes the terminal branches of a phylogenetic tree, possibly removing the corresponding internal branches.

`extract.clade` does the inverse operation: it keeps all the tips from a given node, and deletes all the other tips.

**Usage**

```
drop.tip(phy, tip, trim.internal = TRUE, subtree = FALSE,
         root.edge = 0, rooted = is.rooted(phy), interactive = FALSE)
extract.clade(phy, node, root.edge = 0, interactive = FALSE)
```

**Arguments**

<code>phy</code>	an object of class "phylo".
<code>tip</code>	a vector of mode numeric or character specifying the tips to delete.
<code>trim.internal</code>	a logical specifying whether to delete the corresponding internal branches.
<code>subtree</code>	a logical specifying whether to output in the tree how many tips have been deleted and where.



root.edge	an integer giving the number of internal branches to be used to build the new root edge. This has no effect if trim.internal = FALSE.
rooted	a logical indicating whether the tree must be treated as rooted or not. This allows to force the tree to be considered as unrooted (see examples).
node	a node number or label.
interactive	if TRUE the user is asked to select the tips or the node by clicking on the tree which must be plotted.

### Details

The argument `tip` can be either character or numeric. In the first case, it gives the labels of the tips to be deleted; in the second case the numbers of these labels in the vector `phy$tip.label` are given.

This also applies to `node`, but if this argument is character and the tree has no node label, this results in an error. If more than one value is given with `node` (i.e., a vector of length two or more), only the first one is used with a warning.

If `trim.internal = FALSE`, the new tips are given "NA" as labels, unless there are node labels in the tree in which case they are used.

If `subtree = TRUE`, the returned tree has one or several terminal branches indicating how many tips have been removed (with a label "[x\_tips]"). This is done for as many monophyletic groups that have been deleted.

Note that `subtree = TRUE` implies `trim.internal = TRUE`.

To understand how the option `root.edge` works, see the examples below.

### Value

an object of class "phylo".

### Author(s)

Emmanuel Paradis

### See Also

[bind.tree](#), [root](#)

### Examples

```
data(bird.families)
tip <- c(
  "Eopsaltriidae", "Acanthisittidae", "Pittidae", "Eurylaimidae",
  "Philepittidae", "Tyrannidae", "Thamnophilidae", "Furnariidae",
  "Formicariidae", "Conopophagidae", "Rhinocryptidae", "Climacteridae",
  "Menuridae", "Ptilonorhynchidae", "Maluridae", "Meliphagidae",
  "Pardalotidae", "Petroicidae", "Irenidae", "Orthonychidae",
  "Pomatostomidae", "Laniidae", "Vireonidae", "Corvidae",
  "Callaeatidae", "Picathartidae", "Bombycillidae", "Cinclidae",
  "Muscicapidae", "Sturnidae", "Sittidae", "Certhiidae",
```

```

"Paridae", "Aegithalidae", "Hirundinidae", "Regulidae",
"Pycnonotidae", "Hypocoliidae", "Cisticolidae", "Zosteropidae",
"Sylviidae", "Alaudidae", "Nectariniidae", "Melanocharitidae",
"Paramythiidae", "Passeridae", "Fringillidae")
plot(drop.tip(bird.families, tip))
plot(drop.tip(bird.families, tip, trim.internal = FALSE))
data(bird.orders)
plot(drop.tip(bird.orders, 6:23, subtree = TRUE))
plot(drop.tip(bird.orders, c(1:5, 20:23), subtree = TRUE))
plot(drop.tip(bird.orders, c(1:20, 23), subtree = TRUE))
plot(drop.tip(bird.orders, c(1:20, 23), subtree = TRUE, rooted = FALSE))
### Examples of the use of `root.edge`
tr <- read.tree(text = "(A:1,(B:1,(C:1,(D:1,E:1):1):1):1):1;")
drop.tip(tr, c("A", "B"), root.edge = 0) # = (C:1,(D:1,E:1):1);
drop.tip(tr, c("A", "B"), root.edge = 1) # = (C:1,(D:1,E:1):1):1;
drop.tip(tr, c("A", "B"), root.edge = 2) # = (C:1,(D:1,E:1):1):2;
drop.tip(tr, c("A", "B"), root.edge = 3) # = (C:1,(D:1,E:1):1):3;

```

---

edges

*Draw Additional Edges on a Plotted Tree*


---

## Description

edges draws edges on a plotted tree. fancyarrows enhances [arrows](#) with triangle and harpoon heads; it can be called from edges.

## Usage

```

edges(nodes0, nodes1, arrows = 0, type = "classical", ...)
fancyarrows(x0, y0, x1, y1, length = 0.25, angle = 30, code = 2,
            col = par("fg"), lty = par("lty"), lwd = par("lwd"),
            type = "triangle", ...)

```

## Arguments

nodes0, nodes1	vectors of integers giving the tip and/or node numbers where to start and to end the edges (eventually recycled).
arrows	an integer between 0 and 3; 0: lines (the default); 1: an arrow head is drawn at nodes0; 2: at nodes1; 3: both.
type	if the previous argument is not 0, the type of arrow head: "classical" (just lines, the default), "triangle", "harpoon", or any unambiguous abbreviations of these. For fancyarrows only the last two are available.
x0, y0, x1, y1	the coordinates of the start and end points for fancyarrows (these are not recycled and so should be vectors of the same length).
length, angle, code, col, lty, lwd	default options similar to those of <a href="#">arrows</a> .
...	further arguments passed to <a href="#">segments</a> .

## Details

The first function is helpful when drawing reticulations on a phylogeny, especially if computed from the edge matrix.

## Author(s)

Emmanuel Paradis

## See Also

[plot.phylo](#), [nodelabels](#)

## Examples

```
set.seed(2)
tr <- rcoal(6)
plot(tr, "c")
edges(10, 9, col = "red", lty = 2)
edges(10:11, 8, col = c("blue", "green")) # recycling of 'nodes1'
edges(1, 2, lwd = 2, type = "h", arrows = 3, col = "green")
nodelabels()
```

---

evonet

*Evolutionary Networks*

---

## Description

evonet builds a network from a tree of class "phylo". There are print and plot methods as well as a few conversion functions.

## Usage

```
evonet(phy, from, to = NULL)
## S3 method for class 'evonet'
print(x, ...)
## S3 method for class 'evonet'
plot(x, col = "blue", lty = 1, lwd = 1, alpha = 0.5,
      arrows = 0, arrow.type = "classical", ...)
## S3 method for class 'evonet'
as.phylo(x, ...)
## S3 method for class 'evonet'
as.networx(x, weight = NA, ...)
## S3 method for class 'evonet'
as.network(x, directed = TRUE, ...)
## S3 method for class 'evonet'
as.igraph(x, directed = TRUE, use.labels = TRUE, ...)
```

**Arguments**

phy, x	an object of class "phylo" or "evonet".
from	a vector (or a matrix if to = NULL) giving the node or tip numbers involved in the reticulations.
to	a vector of the same length than from.
col, lty, lwd	colors, line type and width of the reticulations (recycled if necessary).
alpha	a value between 0 and 1 specifying the transparency of the reticulations.
arrows	see <a href="#">fancyarrows</a> .
arrow.type	idem.
weight	a numeric vector giving the weights for the reticulations when converting to the class "networx" (recycled or shortened if needed).
directed	a logical: should the network be considered as directed? TRUE by default.
use.labels	a logical specifying whether to use the tip and node labels when building the network of class "igraph".
...	arguments passed to other methods.

**Details**

evonet is a constructor function that checks the arguments.

The classes "networx", "network", and "igraph" are defined in the packages **phangorn**, **network**, and **igraph**, respectively.

**Value**

an object of class c("evonet", "phylo") which is made of an object of class "phylo" plus an element reticulation coding additional edges among nodes and uses the same coding rules than the edge matrix.

The conversion functions return an object of the appropriate class.

**Author(s)**

Emmanuel Paradis

**See Also**

[as.networx](#) in package **phangorn**

**Examples**

```
tr <- rcoal(5)
(x <- evonet(tr, 6:7, 8:9))
plot(x)
```

**Description**

This function implements a method for checking whether an incomplete set of distances satisfy certain conditions that might make it uniquely determine the edge weights of a given topology,  $T$ . It prints information about whether the graph with vertex set the set of leaves, denoted by  $X$ , and edge set the set of non-missing distance pairs, denoted by  $L$ , is connected or strongly non-bipartite. It then also checks whether  $L$  is a triplet cover for  $T$ .

**Usage**

```
ewLasso(X, phy)
```

**Arguments**

$X$	a distance matrix.
phy	an unrooted tree of class "phylo".

**Details**

Missing values must be represented by either NA or a negative value.

This implements a method for checking whether an incomplete set of distances satisfies certain conditions that might make it uniquely determine the edge weights of a given topology,  $T$ . It prints information about whether the graph,  $G$ , with vertex set the set of leaves, denoted by  $X$ , and edge set the set of non-missing distance pairs, denoted by  $L$ , is connected or strongly non-bipartite. It also checks whether  $L$  is a triplet cover for  $T$ . If  $G$  is not connected, then  $T$  does not need to be the only topology satisfying the input incomplete distances. If  $G$  is not strongly non-bipartite then the edge-weights of the edges of  $T$  are not the unique ones for which the input distance is satisfied. If  $L$  is a triplet cover, then the input distance matrix uniquely determines the edge weights of  $T$ . See Dress et al. (2012) for details.

**Value**

NULL, the results are printed in the console.

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

**References**

Dress, A. W. M., Huber, K. T., and Steel, M. (2012) ‘Lassoing’ a phylogentic tree I: basic properties, shellings and covers. *Journal of Mathematical Biology*, **65**(1), 77–105.

---

FastME

*Tree Estimation Based on the Minimum Evolution Algorithm*

---

### Description

The two FastME functions (balanced and OLS) perform the minimum evolution algorithm of Desper and Gascuel (2002).

### Usage

```
fastme.bal(X, nni = TRUE, spr = TRUE, tbr = TRUE)
fastme.ols(X, nni = TRUE)
```

### Arguments

X	a distance matrix; may be an object of class "dist".
nni	a boolean value; TRUE to do NNIs (default).
spr	ditto for SPRs.
tbr	ditto for TBRs.

### Value

an object of class "phylo".

### Author(s)

original C code by Richard Desper; adapted and ported to R by Vincent Lefort <vincent.lefort@lirmm.fr>

### References

Desper, R. and Gascuel, O. (2002) Fast and accurate phylogeny reconstruction algorithms based on the minimum-evolution principle. *Journal of Computational Biology*, **9(5)**, 687–705.

### See Also

[nj](#), [bionj](#), [write.tree](#), [read.tree](#), [dist.dna](#)

### Examples

```
### From Saitou and Nei (1987, Table 1):
x <- c(7, 8, 11, 13, 16, 13, 17, 5, 8, 10, 13,
      10, 14, 5, 7, 10, 7, 11, 8, 11, 8, 12,
      5, 6, 10, 9, 13, 8)
M <- matrix(0, 8, 8)
M[lower.tri(M)] <- x
M <- t(M)
M[lower.tri(M)] <- x
dimnames(M) <- list(1:8, 1:8)
```

```
tr <- fastme.bal(M)
plot(tr, "u")
### a less theoretical example
data(woodmouse)
trw <- fastme.bal(dist.dna(woodmouse))
plot(trw)
```

---

gammaStat

*Gamma-Statistic of Pybus and Harvey*

---

### Description

This function computes the gamma-statistic which summarizes the information contained in the inter-node intervals of a phylogeny. It is assumed that the tree is ultrametric. Note that the function does not check that the tree is effectively ultrametric, so if it is not, the returned result may not be meaningful.

### Usage

```
gammaStat(phy)
```

### Arguments

phy                    an object of class "phylo".

### Details

The gamma-statistic is a summary of the information contained in the inter-node intervals of a phylogeny; it follows, under the assumption that the clade diversified with constant rates, a normal distribution with mean zero and standard-deviation unity (Pybus and Harvey 2000). Thus, the null hypothesis that the clade diversified with constant rates may be tested with  $2 \times (1 - \text{pnorm}(\text{abs}(\text{gammaStat}(\text{phy}))))$  for a two-tailed test, or  $1 - \text{pnorm}(\text{abs}(\text{gammaStat}(\text{phy})))$  for a one-tailed test, both returning the corresponding P-value.

### Value

a numeric vector of length one.

### Author(s)

Emmanuel Paradis

### References

Pybus, O. G. and Harvey, P. H. (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **267**, 2267–2272.

**See Also**

[branching.times](#), [ltt.plot](#), [skyline](#)

---

hivtree

*Phylogenetic Tree of 193 HIV-1 Sequences*

---

**Description**

This data set describes an estimated clock-like phylogeny of 193 HIV-1 group M sequences sampled in the Democratic Republic of Congo.

**Usage**

```
data(hivtree.newick)
data(hivtree.table)
```

**Format**

`hivtree.newick` is a string with the tree in Newick format. The data frame `hivtree.table` contains the corresponding internode distances.

**Source**

This is a data example from Strimmer and Pybus (2001).

**References**

Strimmer, K. and Pybus, O. G. (2001) Exploring the demographic history of DNA sequences using the generalized skyline plot. *Molecular Biology and Evolution*, **18**, 2298–2305.

**Examples**

```
# example tree in NH format (a string)
data("hivtree.newick")
hivtree.newick

# generate file "hivtree.phy" in working directory
cat(hivtree.newick, file = "hivtree.phy", sep = "\n")
tree.hiv <- read.tree("hivtree.phy") # load tree
unlink("hivtree.phy") # delete the file "hivtree.phy"

plot(tree.hiv)

# table with list of internode distances
data("hivtree.table")
hivtree.table

# construct coalescence intervals
```



```
ci <- coalescent.intervals(tree.hiv) # from tree
ci <- coalescent.intervals(hivtree.table$size) #from intervals
ci
```

---

 howmanytrees

*Calculate Numbers of Phylogenetic Trees*


---

## Description

This function calculates the number of possible phylogenetic trees for a given number of tips.

## Usage

```
howmanytrees(n, rooted = TRUE, binary = TRUE,
             labeled = TRUE, detail = FALSE)
```

## Arguments

n	a positive numeric integer giving the number of tips.
rooted	a logical indicating whether the trees are rooted (default is TRUE).
binary	a logical indicating whether the trees are bifurcating (default is TRUE).
labeled	a logical indicating whether the trees have tips labeled (default is TRUE).
detail	a logical indicating whether the eventual intermediate calculations should be returned (default is FALSE). This applies only for the multifurcating trees, and the bifurcating, rooted, unlabeled trees (aka tree shapes).

## Details

In the cases of labeled binary trees, the calculation is done directly and a single numeric value is returned.

For multifurcating trees, and bifurcating, rooted, unlabeled trees, the calculation is done iteratively for 1 to n tips. Thus the user can print all the intermediate values if `detail = TRUE`, or only a single value if `detail = FALSE` (the default).

For multifurcating trees, if `detail = TRUE`, a matrix is returned with the number of tips as rows (named from 1 to n), and the number of nodes as columns (named from 1 to n - 1). For bifurcating, rooted, unlabeled trees, a vector is returned with names equal to the number of tips (from 1 to n).

The number of unlabeled trees (aka tree shapes) can be computed only for the rooted binary cases.

Note that if an infinite value (Inf) is returned this does not mean that there is an infinite number of trees (this cannot be if the number of tips is finite), but that the calculation is beyond the limits of the computer.

## Value

a single numeric value, or in the case where `detail = TRUE` is used, a named vector or matrix.

**Author(s)**

Emmanuel Paradis

**References**Felsenstein, J. (2004) *Inferring Phylogenies*. Sunderland: Sinauer Associates.**Examples**

```
### Table 3.1 in Felsenstein 2004:
for (i in c(1:20, 30, 40, 50))
  cat(paste(i, howmanytrees(i), sep = "\t"), sep = "\n")
### Table 3.6:
howmanytrees(8, binary = FALSE, detail = TRUE)
```

---

 identify.phylo

*Graphical Identification of Nodes and Tips*


---

**Description**

This function allows to identify a clade on a plotted tree by clicking on the plot with the mouse. The tree, specified in the argument `x`, must be plotted beforehand.

**Usage**

```
## S3 method for class 'phylo'
identify(x, nodes = TRUE, tips = FALSE,
         labels = FALSE, quiet = FALSE, ...)
```

**Arguments**

<code>x</code>	an object of class "phylo".
<code>nodes</code>	a logical specifying whether to identify the node.
<code>tips</code>	a logical specifying whether to return the tip information.
<code>labels</code>	a logical specifying whether to return the labels; by default only the numbers are returned.
<code>quiet</code>	a logical controlling whether to print a message inviting the user to click on the tree.
<code>...</code>	further arguments to be passed to or from other methods.

**Details**

By default, the clade is identified by its number as found in the 'edge' matrix of the tree. If `tips = TRUE`, the tips descending from the identified node are returned, possibly together with the node. If `labels = TRUE`, the labels are returned (if the tree has no node labels, then the node numbered is returned).

The node is identified by the shortest distance where the click occurs. If the click occurs close to a tip, the function returns its information.

**Value**

A list with one or two vectors named "tips" and/or "nodes" with the identification of the tips and/or of the nodes.

**Note**

This function does not add anything on the plot, but it can be wrapped with, e.g., [nodelabels](#) (see example), or its results can be sent to, e.g., [drop.tip](#).

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#), [nodelabels](#), [identify](#) for the generic function

**Examples**

```
## Not run:
tr <- rtree(20)
f <- function(col) {
  o <- identify(tr)
  nodelabels(node=o$nodes, pch = 19, col = col)
}
plot(tr)
f("red") # click close to a node
f("green")

## End(Not run)
```

---

image.DNAbin

*Plot of DNA Sequence Alignment*

---

**Description**

This function plots an image of an alignment of nucleotide sequences.

**Usage**

```
## S3 method for class 'DNAbin'
image(x, what, col, bg = "white", xlab = "", ylab = "",
      show.labels = TRUE, cex.lab = 1, legend = TRUE, ...)
```

**Arguments**

x	a matrix of DNA sequences (class "DNAbin").
what	a vector of characters specifying the bases to visualize. If missing, this is set to "a", "g", "c", "t", "n", and "-" (in this order).
col	a vector of colours. If missing, this is set to "red", "yellow", "green", "blue", "grey", and "black". If it is shorter (or longer) than what, it is recycled (or shortened).
bg	the colour used for nucleotides whose base is not among what.
xlab	the label for the <i>x</i> -axis; none by default.
ylab	Idem for the <i>y</i> -axis. Note that by default, the labels of the sequences are printed on the <i>y</i> -axis (see next option).
show.labels	a logical controlling whether the sequence labels are printed (TRUE by default).
cex.lab	a single numeric controlling the size of the sequence labels. Use <code>cex.axis</code> to control the size of the annotations on the <i>x</i> -axis.
legend	a logical controlling whether the legend is plotted (TRUE by default).
...	further arguments passed to <code>image.default</code> (e.g., <code>cex.axis</code> ).

**Details**

The idea of this function is to allow flexible plotting and colouring of a nucleotide alignment. By default, the most common bases (a, g, c, t, and n) and alignment gap are plotted using a standard colour scheme.

It is possible to plot only one base specified as `what` with a chosen colour: this might be useful to check, for instance, the distribution of alignment gaps (`image(x, "-")`) or missing data (see examples).

**Author(s)**

Emmanuel Paradis

**See Also**

[DNAbin](#), [del.gaps](#), [alex](#), [clustal](#), [grid](#)

**Examples**

```
data(woodmouse)
image(woodmouse)
image(woodmouse, "n", "blue") # show missing data
image(woodmouse, c("g", "c"), "green") # G+C
par(mfcol = c(2, 2))
### barcoding style:
for (x in c("a", "g", "c", "t"))
  image(woodmouse, x, "black", cex.lab = 0.5, cex.axis = 0.7)
par(mfcol = c(1, 1))
### zoom on a portion of the data:
image(woodmouse[11:15, 1:50], c("a", "n"), c("blue", "grey"))
```

```
grid(50, 5, col = "black")
### see the guanines on a black background:
image(woodmouse, "g", "yellow", "black")
```

---

Initialize.corPhyl      *Initialize a 'corPhyl' Structure Object*

---

### Description

Initialize a corPhyl correlation structure object. Does the same as Initialize.corStruct, but also checks the row names of data and builds an index.

### Usage

```
## S3 method for class 'corPhyl'
Initialize(object, data, ...)
```

### Arguments

object	An object inheriting from class corPhyl.
data	The data to use. If it contains rownames, they are matched with the tree tip labels, otherwise data are supposed to be in the same order than tip labels and a warning is sent.
...	some methods for this generic require additional arguments. None are used in this method.

### Value

An initialized object of same class as object.

### Author(s)

Julien Dutheil <julien.dutheil@univ-montp2.fr>

### See Also

[corClasses](#), [Initialize.corStruct](#).

---

`is.binary.tree`*Test for Binary Tree*

---

**Description**

This function tests whether a phylogenetic tree is binary.

**Usage**

```
is.binary.tree(phy)
```

**Arguments**

`phy` an object of class "phylo".

**Details**

The test differs slightly whether the tree is rooted or not. An unrooted tree is considered binary if all its nodes are of degree three (i.e., three edges connect to each node). A rooted tree is considered binary if all nodes (including the root node) have exactly two descendant nodes, so that they are of degree three except the root which is of degree 2.

**Value**

`is.binary.tree` returns TRUE if tree is a fully binary phylogenetic tree, otherwise it returns FALSE.

**Author(s)**

Korbinian Strimmer (<http://www.stat.uni-muenchen.de/~strimmer/>)

**See Also**

[is.rooted](#), [is.ultrametric](#), [multi2di](#)

**Examples**

```
data("hivtree.newick") # example tree in NH format
tree.hiv <- read.tree(text = hivtree.newick)
is.binary.tree(tree.hiv)
plot(tree.hiv)
```

---

is.compatible	<i>Check Compatibility of Splits</i>
---------------	--------------------------------------

---

**Description**

is.compatible is a generic function with a method for the class "bitsplits". It checks whether a set of splits is compatible using the arecompatible function.

**Usage**

```
is.compatible(obj)
## S3 method for class 'bitsplits'
is.compatible(obj)
arecompatible(x, y, n)
```

**Arguments**

obj	an object of class "bitsplits".
x, y	a vector of mode raw.
n	the number of taxa in the splits.

**Value**

TRUE if the splits are compatible, FALSE otherwise.

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

---

is.monophyletic	<i>Is Group Monophyletic</i>
-----------------	------------------------------

---

**Description**

This function tests whether a list of tip labels is monophyletic on a given tree.

**Usage**

```
is.monophyletic(phy, tips, reroot = !is.rooted(phy), plot = FALSE, ...)
```

**Arguments**

phy	a phylogenetic tree description of class "phylo".
tips	a vector of mode numeric or character specifying the tips to be tested.
reroot	a logical. If FALSE, then the input tree is not unrooted before the test.
plot	a logical. If TRUE, then the tree is plotted with the specified group tips highlighted.
...	further arguments passed to plot.

**Details**

If phy is rooted, the test is done on the rooted tree, otherwise the tree is first unrooted, then arbitrarily rerooted, in order to be independent on the current position of the root. That is, the test asks if tips could be monophyletic given any favourably rooting of phy.

If phy is unrooted the test is done on an unrooted tree, unless reroot = FALSE is specified.

If tip labels in the list tips are given as characters, they need to be spelled as in the object phy.

**Value**

TRUE or FALSE.

**Author(s)**

Johan Nylander <jnylander@users.sourceforge.net>

**See Also**

[which.edge](#), [drop.tip](#), [mrca](#).

**Examples**

```
## Test one monophyletic and one paraphyletic group on the bird.orders tree
## Not run: data("bird.orders")
## Not run: is.monophyletic(phy = bird.orders, tips = c("Ciconiiformes", "Gruiformes"))
## Not run: is.monophyletic(bird.orders, c("Passeriformes", "Ciconiiformes", "Gruiformes"))
```

---

is.ultrametric

*Test if a Tree is Ultrametric*

---

**Description**

This function computes the distances from each tip to the root: if the variance of these distances is null, the tree is considered as ultrametric.

**Usage**

```
is.ultrametric(phy, tol = .Machine$double.eps^0.5)
```



**Arguments**

phy	an object of class "phylo".
tol	a numeric $\geq 0$ , variation below this value are considered non-significant (see details).

**Details**

The default value for `tol` is based on the numerical characteristics of the machine `R` is running on.

**Value**

a logical: TRUE if the tree is ultrametric, FALSE otherwise.

**Author(s)**

Emmanuel Paradis

**See Also**

[is.binary.tree](#), [.Machine](#)

---

kronoviz

*Plot Multiple Chronograms on the Same Scale*

---

**Description**

The main argument is a list of (rooted) trees which are plotted on the same scale.

**Usage**

```
kronoviz(x, layout = length(x), horiz = TRUE, ...)
```

**Arguments**

x	a list of (rooted) trees of class "phylo".
layout	an integer giving the number of trees plotted simultaneously; by default all.
horiz	a logical specifying whether the trees should be plotted rightwards (the default) or upwards.
...	further arguments passed to <code>plot.phylo</code> .

**Details**

The size of the individual plots is proportional to the size of the trees.

**Value**

NULL

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#)

**Examples**

```
TR <- replicate(10, rcoal(sample(11:20, size = 1)), simplify = FALSE)
kronoviz(TR)
kronoviz(TR, horiz = FALSE, type = "c", show.tip.label = FALSE)
```

---

ladderize

*Ladderize a Tree*

---

**Description**

This function reorganizes the internal structure of the tree to get the ladderized effect when plotted.

**Usage**

```
ladderize(phy, right = TRUE)
```

**Arguments**

phy	an object of class "phylo".
right	a logical specifying whether the smallest clade is on the right-hand side (when the tree is plotted upwards), or the opposite (if FALSE).

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#), [reorder.phylo](#)

**Examples**

```
tr <- rcoal(50)
layout(matrix(1:4, 2, 2))
plot(tr, main = "normal")
plot(ladderize(tr), main = "right-ladderized")
plot(ladderize(tr, FALSE), main = "left-ladderized")
layout(matrix(1, 1))
```

---

`landplants`*Gene Tree of 36 Landplant rbcL Sequences*

---

**Description**

This data set describes a gene tree estimated from 36 landplant *rbcL* sequences.

**Usage**

```
data(landplants.newick)
```

**Format**

`landplants.newick` is a string with the tree in Newick format.

**Source**

This tree is described in Sanderson (1997) and is also a data example in the software package `r8s` (<http://ginger.ucdavis.edu/r8s/>).

**References**

Sanderson, M. J. (1997) A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution*, **14**, 1218–1231.

**Examples**

```
# example tree in NH format (a string)
data("landplants.newick")
landplants.newick

# get corresponding phylo object
tree.landplants <- read.tree(text = landplants.newick)

# plot tree
plot(tree.landplants, label.offset = 0.001)
```

---

`lmorigin`*Multiple regression through the origin*

---

**Description**

Function `lmorigin` computes a multiple linear regression and performs tests of significance of the equation parameters (F-test of R-square and t-tests of regression coefficients) using permutations.

The regression line can be forced through the origin. Testing the significance in that case requires a special permutation procedure. This option was developed for the analysis of independent contrasts, which requires regression through the origin. A permutation test, described by Legendre & Desdevises (2009), is needed to analyze contrasts that are not normally distributed.

**Usage**

```
lmorigin(formula, data, origin=TRUE, nperm=999, method=NULL, silent=FALSE)
```

**Arguments**

formula	A formula specifying the bivariate model, as in <code>lm</code> and <code>aov</code> .
data	A data frame containing the two variables specified in the formula.
origin	<code>origin = TRUE</code> (default) to compute regression through the origin; <code>origin = FALSE</code> to compute multiple regression with estimation of the intercept.
nperm	Number of permutations for the tests. If <code>nperm = 0</code> , permutation tests will not be computed. The default value is <code>nperm = 999</code> . For large data files, the permutation test is rather slow since the permutation procedure is not compiled.
method	<code>method = "raw"</code> computes t-tests of the regression coefficients by permutation of the raw data. <code>method = "residuals"</code> computes t-tests of the regression coefficients by permutation of the residuals of the full model. If <code>method = NULL</code> , permutation of the raw data is used to test the regression coefficients in regression through the origin; permutation of the residuals of the full model is used to test the regression coefficients in ordinary multiple regression.
silent	Informative messages and the time to compute the tests will not be written to the R console if <code>silent=TRUE</code> . Useful when the function is called by a numerical simulation function.

**Details**

The permutation F-test of R-square is always done by permutation of the raw data. When there is a single explanatory variable, permutation of the raw data is used for the t-test of the single regression coefficient, whatever the method chosen by the user. The rationale is found in Anderson & Legendre (1999).

The `print.lmorigin` function prints out the results of the parametric tests (in all cases) and the results of the permutational tests (when `nperm > 0`).

**Value**

reg	The regression output object produced by function <code>lm</code> .
p.param.t.2tail	Parametric probabilities for 2-tailed tests of the regression coefficients.
p.param.t.1tail	Parametric probabilities for 1-tailed tests of the regression coefficients. Each test is carried out in the direction of the sign of the coefficient.
p.perm.t.2tail	Permutational probabilities for 2-tailed tests of the regression coefficients.
p.perm.t.1tail	Permutational probabilities for 1-tailed tests of the regression coefficients. Each test is carried out in the direction of the sign of the coefficient.
p.perm.F	Permutational probability for the F-test of R-square.

origin	TRUE is regression through the origin has been computed, FALSE if multiple regression with estimation of the intercept has been used.
nperm	Number of permutations used in the permutation tests.
method	Permutation method for the t-tests of the regression coefficients: method = "raw" or method = "residuals".
var.names	Vector containing the names of the variables used in the regression.
call	The function call.

**Author(s)**

Pierre Legendre, Universite de Montreal

**References**

Anderson, M. J. and Legendre, P. (1999) An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation*, **62**, 271–303.

Legendre, P. and Desdevises, Y. (2009) Independent contrasts and regression through the origin. *Journal of Theoretical Biology*, **259**, 727–743.

Sokal, R. R. and Rohlf, F. J. (1995) *Biometry - The principles and practice of statistics in biological research. Third edition*. New York: W. H. Freeman.

**Examples**

```
## Example 1 from Sokal & Rohlf (1995) Table 16.1
## SO2 air pollution in 41 cities of the USA
data(lmorigin.ex1)
out <- lmorigin(SO2 ~ ., data=lmorigin.ex1, origin=FALSE, nperm=99)
out

## Example 2: Contrasts computed on the phylogenetic tree of Lamellogadus
## parasites. Response variable: non-specificity index (NSI); explanatory
## variable: maximum host size. Data from Table 1 of Legendre & Desdevises
## (2009).
data(lmorigin.ex2)
out <- lmorigin(NSI ~ MaxHostSize, data=lmorigin.ex2, origin=TRUE, nperm=99)
out

## Example 3: random numbers
y <- rnorm(50)
X <- as.data.frame(matrix(rnorm(250),50,5))
out <- lmorigin(y ~ ., data=X, origin=FALSE, nperm=99)
out
```

**Description**

This function draws the lineage-through time (LTT) plots predicted under a speciation-extinction model (aka birth-death model) with specified values of speciation and extinction rates (which may vary with time).

A prediction interval is plotted by default which requires to define a sample size (100 by default), and different curves can be combined.

**Usage**

```
LTT(birth = 0.1, death = 0, N = 100, Tmax = 50, PI = 95,
    scaled = TRUE, eps = 0.1, add = FALSE, backward = TRUE,
    ltt.style = list("black", 1, 1), pi.style = list("blue", 1, 2))
```

**Arguments**

birth	the speciation rate, this may be either a numeric value or a function of time (named <code>t</code> in the code of the function).
death	id. for the extinction rate.
N	the size of the tree.
Tmax	the age of the root of the tree.
PI	the percentage value of the prediction interval; set this value to 0 to not draw this interval.
scaled	a logical values specifying whether to scale the <i>y</i> -axis between 0 and 1.
eps	a numerical value giving the resolution of the time axis.
add	a logical values specifying whether to make a new plot (the default).
backward	a logical value: should the time axis be traced from the present (the default), or from the root of the tree?
ltt.style	a list with three elements giving the style of the LTT curve with, respectively, the colour (" <code>col</code> "), the line thickness (" <code>lwd</code> "), and the line type (" <code>lty</code> ").
pi.style	id. for the prediction interval.

**Details**

For the moment, this works well when birth and death are constant. Some improvements are under progress for time-dependent rates (but see below for an example).

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (2011) Time-dependent speciation and extinction from phylogenies: a least squares approach. *Evolution*, **65**, 661–672.

**See Also**

[ltt.plot](#)

**Examples**

```
### predicted LTT plot under a Yule model with lambda = 0.1
### and 50 species after 50 units of time...
LTT(N = 50)
### ... and with a birth-death model with the same rate of
### diversification (try with N = 500):
LTT(0.2, 0.1, N = 50, PI = 0, add = TRUE, ltt.style = list("red", 2, 1))
### predictions under different tree sizes:
layout(matrix(1:4, 2, 2, byrow = TRUE))
for (N in c(50, 100, 500, 1000)) {
  LTT(0.2, 0.1, N = N)
  title(paste("N =", N))
}
layout(1)
## Not run:
### speciation rate decreasing with time
birth.logis <- function(t) 1/(1 + exp(0.02 * t + 4))
LTT(birth.logis)
LTT(birth.logis, 0.05)
LTT(birth.logis, 0.1)

## End(Not run)
```

---

ltt.plot

---

*Lineages Through Time Plot*


---

**Description**

These functions provide tools for plotting the numbers of lineages through time from phylogenetic trees.

**Usage**

```
ltt.plot(phy, xlab = "Time", ylab = "N",
         backward = TRUE, tol = 1e-6, ...)
ltt.lines(phy, backward = TRUE, tol = 1e-6, ...)
mltt.plot(phy, ..., dcol = TRUE, dlty = FALSE, legend = TRUE,
          xlab = "Time", ylab = "N", log = "", backward = TRUE,
          tol = 1e-6)
ltt.coplot(phy, backward = TRUE, ...)
ltt.plot.coords(phy, backward = TRUE, tol = 1e-6)
```

**Arguments**

phy	an object of class "phylo"; this could be an object of class "multiPhylo" in the case of <code>mltt.plot</code> .
xlab	a character string (or a variable of mode character) giving the label for the $x$ -axis (default is "Time").
ylab	idem for the $y$ -axis (default is "N").
backward	a logical value: should the time axis be traced from the present (the default), or from the root of the tree?
tol	a numeric value (see details).
...	in the cases of <code>ltt.plot()</code> , <code>ltt.lines()</code> , or <code>ltt.coplot()</code> these are further (graphical) arguments to be passed to <code>plot()</code> , <code>lines()</code> , or <code>plot.phylo()</code> , respectively (see details on how to transform the axes); in the case of <code>mltt.plot()</code> these are additional trees to be plotted (see details).
dcol	a logical specifying whether the different curves should be differentiated with colors (default is TRUE).
dltty	a logical specifying whether the different curves should be differentiated with patterns of dots and dashes (default is FALSE).
legend	a logical specifying whether a legend should be plotted.
log	a character string specifying which axis(es) to be log-transformed; must be one of the followings: "", "x", "y", or "xy".

**Details**

`ltt.plot` does a simple lineages through time (LTT) plot. Additional arguments (...) may be used to change, for instance, the limits on the axes (with `xlim` and/or `ylim`) or other graphical settings (`col` for the color, `lwd` for the line thickness, `lty` for the line type may be useful; see [par](#) for an exhaustive listing of graphical parameters). The  $y$ -axis can be log-transformed by adding the following option: `log = "y"`.

The option `tol` is used as follows: first the most distant tip from the root is found, then all tips whose distance to the root is not different from the previous one more than `tol` are considered to be contemporaneous with it.

If the tree is not ultrametric, the plot is done assuming the tips, except the most distant from the root, represent extinction events. If a root edge is present, it is taken into account.

`ltt.lines` adds a LTT curve to an existing plot. Additional arguments (...) may be used to change the settings of the added line.

`mltt.plot` does a multiple LTT plot taking as arguments one or several trees. These trees may be given as objects of class "phylo" (single trees) and/or "multiPhylo" (multiple trees). Any number of objects may be given. This function is mainly for exploratory analyses with the advantages that the axes are set properly to view all lines, and the legend is plotted by default. The plot will certainly make sense if all trees have their most-distant-from-the-root tips contemporaneous (i.e., trees with only extinct lineages will not be represented properly). For more flexible settings of line drawings, it may be better to combine `ltt.plot()` with successive calls of `ltt.lines()` (see examples).

`ltt.coplot` is meant to show how to set a tree and a LTT plots on the same scales. All extra arguments modify only the appearance of the tree. The code can be easily edited and tailored.



**Value**

ltt.plot.coords returns a two-column matrix with the time points and the number of lineages, respectively. The  $i$ th value of the second column is the number of lineages for the interval defined by the  $(i - 1)$ th and the  $i$ th values of the first column. These are then plotted with the option `type = "S"` by the other functions.

**Author(s)**

Emmanuel Paradis

**References**

Harvey, P. H., May, R. M. and Nee, S. (1994) Phylogenies without fossils. *Evolution*, **48**, 523–529.  
 Nee, S., Holmes, E. C., Rambaut, A. and Harvey, P. H. (1995) Inferring population history from molecular phylogenies. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, **349**, 25–31.

**See Also**

[kronoviz](#), [skyline](#), [LTT](#), [branching.times](#), [birthdeath](#), [bd.ext](#), [yule.cov](#), [bd.time](#); [plot](#) for the basic plotting function in R

**Examples**

```
data(bird.families)
opar <- par(mfrow = c(2, 1))
ltt.plot(bird.families)
title("Lineages Through Time Plot of the Bird Families")
ltt.plot(bird.families, log = "y")
title(main = "Lineages Through Time Plot of the Bird Families",
      sub = "(with logarithmic transformation of the y-axis)")
par(opar)

### to plot the tree and the LTT plot together
data(bird.orders)
layout(matrix(1:4, 2, 2))
plot(bird.families, show.tip.label = FALSE)
ltt.plot(bird.families, main = "Bird families")
plot(bird.orders, show.tip.label = FALSE)
ltt.plot(bird.orders, main = "Bird orders")
layout(1)

### better with ltt.coplot():
ltt.coplot(bird.families, show.tip.label = FALSE, x.lim = 27.5)
data(chiroptera)
chiroptera <- compute.brlen(chiroptera)
ltt.coplot(chiroptera, show.tip.label = FALSE, type = "c")

### with extinct lineages and a root edge:
omar <- par("mar")
set.seed(31)
```

```

tr <- rlineage(0.2, 0.15)
tr$root.edge <- 5
ltt.coplot(tr, show.tip.label = FALSE, x.lim = 55)
## compare with:
## ltt.coplot(drop.fossil(tr), show.tip.label = FALSE)
layout(1)
par(mar = omar)

mltt.plot(bird.families, bird.orders)
### Generates 10 random trees with 23 tips:
TR <- replicate(10, rcoal(23), FALSE)
### Give names to each tree:
names(TR) <- paste("random tree", 1:10)
### And specify the class of the list so that mltt.plot()
### does not trash it!
class(TR) <- "multiPhylo"
mltt.plot(TR, bird.orders)
### And now for something (not so) completely different:
ltt.plot(bird.orders, lwd = 2)
for (i in 1:10) ltt.lines(TR[[i]], lty = 2)
legend(-20, 10, lwd = c(2, 1), lty = c(1, 2), bty = "n",
       legend = c("Bird orders", "Random (coalescent) trees"))

```

---

makeLabel

*Label Management*


---

## Description

This is a generic function with methods for character vectors, trees of class "phylo", lists of trees of class "multiPhylo", and DNA sequences of class "DNAbin". All options for the class character may be used in the other methods.

## Usage

```

makeLabel(x, ...)
## S3 method for class 'character'
makeLabel(x, len = 99, space = "_", make.unique = TRUE,
          illegal = "()::,[]", quote = FALSE, ...)
## S3 method for class 'phylo'
makeLabel(x, tips = TRUE, nodes = TRUE, ...)
## S3 method for class 'multiPhylo'
makeLabel(x, tips = TRUE, nodes = TRUE, ...)
## S3 method for class 'DNAbin'
makeLabel(x, ...)

```

## Arguments

**x** a vector of mode character or an object for which labels are to be changed.

**len** the maximum length of the labels: those longer than 'len' will be truncated.

space	the character to replace spaces, tabulations, and linebreaks.
make.unique	a logical specifying whether duplicate labels should be made unique by appending numerals; TRUE by default.
illegal	a string specifying the characters to be deleted.
quote	a logical specifying whether to quote the labels; FALSE by default.
tips	a logical specifying whether tip labels are to be modified; TRUE by default.
nodes	a logical specifying whether node labels are to be modified; TRUE by default.
...	further arguments to be passed to or from other methods.

### Details

The option `make.unique` does not work exactly in the same way then the function of the same name: numbers are suffixed to all labels that are identical (without separator). See the examples.

If there are 10–99 identical labels, the labels returned are "xxx01", "xxx02", etc, or "xxx001", "xxx002", etc, if they are 100–999, and so on. The number of digits added preserves the option 'len'.

The default for 'len' makes labels short enough to be read by PhyML. Clustal accepts labels up to 30 character long.

### Value

An object of the appropriate class.

### Note

The current version does not perform well when trying to make very short unique labels (e.g., less than 5 character long).

### Author(s)

Emmanuel Paradis

### See Also

[makeNodeLabel](#), [make.unique](#), [make.names](#), [abbreviate](#), [mixedFontLabel](#)

### Examples

```
x <- rep("a", 3)
makeLabel(x)
make.unique(x) # <- from R's base
x <- rep("aaaa", 2)
makeLabel(x, len = 3) # made unique and of length 3
makeLabel(x, len = 3, make.unique = FALSE)
```

---

makeNodeLabel	<i>Makes Node Labels</i>
---------------	--------------------------

---

### Description

This function makes node labels in a tree in a flexible way.

### Usage

```
makeNodeLabel(phy, method = "number", prefix = "Node", nodeList = list(), ...)
```

### Arguments

phy	an object of class "phylo".
method	a character string giving the method used to create the labels. Three choices are possible: "number" (the default), "md5sum", and "user", or any unambiguous abbreviation of these.
prefix	the prefix used if method = "number".
nodeList	a named list specifying how nodes are names if method = "user" (see details and examples).
...	further arguments passed to <code>grep</code> .

### Details

The three methods are described below:

- "number" The labels are created with 1, 2, ... prefixed with the argument `prefix`; thus the default is to have Node1, Node2, ... Set `prefix = ""` to have only numbers.
- "md5sum" For each node, the labels of the tips descendant from this node are extracted, sorted alphabetically, and written into a temporary file, then the md5sum of this file is extracted and used as label. This results in a 32-character string which is unique (even accross trees) for a given set of tip labels.
- "user" the argument `nodeList` must be a list with names, the latter will be used as node labels. For each element of `nodeList`, the tip labels of the tree are searched for patterns present in this element: this is done using `grep`. Then the most recent common ancestor of the matching tips is given the corresponding names as labels. This is repeated for each element of `nodeList`.

The method "user" can be used in combination with either of the two others (see examples). Note that this method only modifies the specified node labels (so that if the other nodes have already labels they are not modified) while the two others change all labels.

### Value

an object of class "phylo".

**Author(s)**

Emmanuel Paradis <Emmanuel.Paradis@mpl.ird.fr>

**See Also**

[makeLabel](#), [grep](#), [mixedFontLabel](#)

**Examples**

```
tr <-
"((Pan_paniscus,Pan_troglodytes),((Homo_sapiens,Homo_erectus),Homo_abilis));"
tr <- read.tree(text = tr)
tr <- makeNodeLabel(tr, "u", nodeList = list(Pan = "Pan", Homo = "Homo"))
plot(tr, show.node.label = TRUE)
### does not erase the previous node labels:
tr <- makeNodeLabel(tr, "u", nodeList = list(Hominid = c("Pan","Homo")))
plot(tr, show.node.label = TRUE)
### the two previous commands could be combined:
L <- list(Pan = "Pan", Homo = "Homo", Hominid = c("Pan","Homo"))
tr <- makeNodeLabel(tr, "u", nodeList = L)
### combining different methods:
tr <- makeNodeLabel(tr, c("n", "u"), prefix = "#", nodeList = list(Hominid = c("Pan","Homo")))
plot(tr, show.node.label = TRUE)
```

---

`mantel.test`

*Mantel Test for Similarity of Two Matrices*

---

**Description**

This function computes Mantel's permutation test for similarity of two matrices. It permutes the rows and columns of the two matrices randomly and calculates a  $Z$ -statistic.

**Usage**

```
mantel.test(m1, m2, nperm = 999, graph = FALSE,
            alternative = "two.sided", ...)
```

**Arguments**

<code>m1</code>	a numeric matrix giving a measure of pairwise distances, correlations, or similarities among observations.
<code>m2</code>	a second numeric matrix giving another measure of pairwise distances, correlations, or similarities among observations.
<code>nperm</code>	the number of times to permute the data.
<code>graph</code>	a logical indicating whether to produce a summary graph (by default the graph is not plotted).

`alternative` a character string defining the alternative hypothesis: "two.sided" (default), "less", "greater", or any unambiguous abbreviation of these.

`...` further arguments to be passed to `plot()` (to add a title, change the axis labels, and so on).

### Details

The function calculates a  $Z$ -statistic for the Mantel test, equal to the sum of the pairwise product of the lower triangles of the permuted matrices, for each permutation of rows and columns. It compares the permuted distribution with the  $Z$ -statistic observed for the actual data.

If `graph = TRUE`, the functions plots the density estimate of the permutation distribution along with the observed  $Z$ -statistic as a vertical line.

The `...` argument allows the user to give further options to the `plot` function: the title main be changed with `main=`, the axis labels with `xlab =`, and `ylab =`, and so on.

### Value

`z.stat` the  $Z$ -statistic (sum of rows\*columns of lower triangle) of the data matrices.

`p`  $P$ -value (quantile of the observed  $Z$ -statistic in the permutation distribution).

`alternative` the alternative hypothesis.

### Author(s)

Original code in S by Ben Bolker, ported to R by Julien Claude

### References

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.

Manly, B. F. J. (1986) *Multivariate statistical methods: a primer*. London: Chapman & Hall.

### Examples

```
q1 <- matrix(runif(36), nrow = 6)
q2 <- matrix(runif(36), nrow = 6)
mantel.test(q1, q2, graph = TRUE,
            main = "Mantel test: a random example with 6 X 6 matrices",
            xlab = "z-statistic", ylab = "Density",
            sub = "The vertical line shows the observed z-statistic")
```

---

mat3	<i>Three Matrices</i>
------	-----------------------

---

**Description**

Three matrices respectively representing Serological (asymmetric), DNA hybridization (asymmetric) and Anatomical (symmetric) distances among 9 families.

**Usage**

```
data(mat3)
```

**Format**

A data frame with 27 observations and 9 variables.

**Source**

Lapointe, F.-J., J. A. W. Kirsch and J. M. Hutcheon. 1999. Total evidence, consensus, and bat phylogeny: a distance-based approach. *Molecular Phylogenetics and Evolution* 11: 55-66.

**See Also**

[mat5Mrand](#), [mat5M3ID](#)

---

mat5M3ID	<i>Five Trees</i>
----------	-------------------

---

**Description**

Three partly similar trees, two independent trees.

**Usage**

```
data(mat5M3ID)
```

**Format**

A data frame with 250 observations and 50 variables.

**Source**

Data provided by V. Campbell.

**See Also**

[mat5Mrand](#), [mat3](#)

mat5Mrand

*Five Independent Trees*

---

**Description**

Five independent additive trees.

**Usage**

```
data(mat5Mrand)
```

**Format**

A data frame with 250 observations and 50 variables.

**Source**

Data provided by V. Campbell.

**See Also**

[mat5M3ID](#), [mat3](#)

---

matexpo

*Matrix Exponential*

---

**Description**

This function computes the exponential of a square matrix using a spectral decomposition.

**Usage**

```
matexpo(x)
```

**Arguments**

x                    a square matrix of mode numeric.

**Value**

a numeric matrix of the same dimensions than 'x'.

**Author(s)**

Emmanuel Paradis



## Examples

```
### a simple rate matrix:
m <- matrix(0.1, 4, 4)
diag(m) <- -0.3
### towards equilibrium:
for (t in c(1, 5, 10, 50)) print(matexpo(m*t))
```

---

mcconwaysims.test      *McConway-Sims Test of Homogeneous Diversification*

---

## Description

This function performs the McConway–Sims test that a trait or variable does not affect diversification rate.

## Usage

```
mcconwaysims.test(x)
```

## Arguments

**x**                      a matrix or a data frame with at least two columns: the first one gives the number of species in clades with a trait supposed to increase or decrease diversification rate, and the second one the number of species in the sister-clades without the trait. Each row represents a pair of sister-clades.

## Details

The McConway–Sims test compares a series of sister-clades where one of the two is characterized by a trait supposed to affect diversification rate. The null hypothesis is that the trait does not affect diversification. The alternative hypothesis is that diversification rate is increased or decreased by the trait (by contrast to the Slowinski–Guyer test). The test is a likelihood-ratio of a null Yule model and an alternative model with two parameters.

## Value

a data frame with the  $\chi^2$ , the number of degrees of freedom, and the *P*-value.

## Author(s)

Emmanuel Paradis

## References

McConway, K. J. and Sims, H. J. (2004) A likelihood-based method for testing for nonstochastic variation of diversification rates in phylogenies. *Evolution*, **58**, 12–23.

Paradis, E. (2012) Shift in diversification in sister-clade comparisons: a more powerful test. *Evolution*, **66**, 288–295.

**See Also**

[balance](#), [slowinskiguyer.test](#), [rc](#) in [geiger](#), [shift.test](#) in [apTreeshape](#)

**Examples**

```
### simulate 10 clades with lambda = 0.1 and mu = 0.09:
n0 <- replicate(10, balance(rbdtree(.1, .09, Tmax = 35))[1])
### simulate 10 clades with lambda = 0.15 and mu = 0.1:
n1 <- replicate(10, balance(rbdtree(.15, .1, Tmax = 35))[1])
x <- cbind(n1, n0)
mconwaysims.test(x)
slowinskiguyer.test(x)
richness.yule.test(x, 35)
```

---

mcmc.popsiz
*Reversible Jump MCMC to Infer Demographic History*


---

**Description**

These functions implement a reversible jump MCMC framework to infer the demographic history, as well as corresponding confidence bands, from a genealogical tree. The computed demographic history is a continuous and smooth function in time. `mcmc.popsiz` runs the actual MCMC chain and outputs information about the sampling steps, `extract.popsiz` generates from this MCMC output a table of population size in time, and `plot.popsiz` and `lines.popsiz` provide utility functions to plot the corresponding demographic functions.

**Usage**

```
mcmc.popsiz(tree, nstep, thinning=1, burn.in=0, progress.bar=TRUE,
  method.prior.changepts=c("hierarchical", "fixed.lambda"), max.nodes=30,
  lambda=0.5, gamma.shape=0.5, gamma.scale=2,
  method.prior.heights=c("skyline", "constant", "custom"),
  prior.height.mean,
  prior.height.var)
extract.popsiz(mcmc.out, credible.interval=0.95, time.points=200, thinning=1, burn.in=0)
## S3 method for class 'popsiz'
plot(x, show.median=TRUE, show.years=FALSE, subst.rate, present.year, ...)
## S3 method for class 'popsiz'
lines(x, show.median=TRUE, show.years=FALSE, subst.rate, present.year, ...)
```

**Arguments**

`tree` Either an ultrametric tree (i.e. an object of class "phylo"), or coalescent intervals (i.e. an object of class "coalescentIntervals").

`nstep` Number of MCMC steps, i.e. length of the Markov chain (suggested value: 10,000-50,000).

thinning	Thinning factor (suggest value: 10-100).
burn.in	Number of steps dropped from the chain to allow for a burn-in phase (suggest value: 1000).
progress.bar	Show progress bar during the MCMC run.
method.prior.changepoints	If hierarchical is chosen (the default) then the smoothing parameter lambda is drawn from a gamma distribution with some specified shape and scale parameters. Alternatively, for fixed.lambda the value of lambda is a given constant.
max.nodes	Upper limit for the number of internal nodes of the approximating spline (default: 30).
lambda	Smoothing parameter. For method="fixed.lambda" the specified value of lambda determines the mean of the prior distribution for the number of internal nodes of the approximating spline for the demographic function (suggested value: 0.1-1.0).
gamma.shape	Shape parameter of the gamma function from which lambda is drawn for method="hierarchical".
gamma.scale	Scale parameter of the gamma function from which lambda is drawn for method="hierarchical".
method.prior.heights	Determines the prior for the heights of the change points. If custom is chosen then two functions describing the mean and variance of the heights in dependence of time have to be specified (via prior.height.mean and prior.height.var options). Alternatively, two built-in priors are available: constant assumes constant population size and variance determined by Felsenstein (1992), and skyline assumes a skyline plot (see Opgen-Rhein et al. 2004 for more details).
prior.height.mean	Function describing the mean of the prior distribution for the heights (only used if method.prior.heights = custom).
prior.height.var	Function describing the variance of the prior distribution for the heights (only used if method.prior.heights = custom).
mcmc.out	Output from mcmc.popsiz - this is needed as input for extract.popsiz.
credible.interval	Probability mass of the confidence band (default: 0.95).
time.points	Number of discrete time points in the table output by extract.popsiz.
x	Table with population size versus time, as computed by extract.popsiz.
show.median	Plot median rather than mean as point estimate for demographic function (default: TRUE).
show.years	Option that determines whether the time is plotted in units of substitutions (default) or in years (requires specification of substitution rate and year of present).
subst.rate	Substitution rate (see option show.years).
present.year	Present year (see option show.years).
...	Further arguments to be passed on to plot.

**Details**

Please refer to Opgen-Rhein et al. (2005) for methodological details, and the help page of [skyline](#) for information on a related approach.

**Author(s)**

Rainer Opgen-Rhein and Korbinian Strimmer (<http://strimmerlab.org>). Parts of the rjMCMC sampling procedure are adapted from R code by Karl Brodman (<http://www.biostat.wisc.edu/~kbroman/>)

**References**

Opgen-Rhein, R., Fahrmeir, L. and Strimmer, K. 2005. Inference of demographic history from genealogical trees using reversible jump Markov chain Monte Carlo. *BMC Evolutionary Biology*, 5, 6.

**See Also**

[skyline](#) and [skylineplot](#).

**Examples**

```
# get tree
data("hivtree.newick") # example tree in NH format
tree.hiv <- read.tree(text = hivtree.newick) # load tree

# run mcmc chain
mcmc.out <- mcmc.popsizetree(tree.hiv, nstep=100, thinning=1, burn.in=0, progress.bar=FALSE) # toy run
#mcmc.out <- mcmc.popsizetree(tree.hiv, nstep=10000, thinning=5, burn.in=500) # remove comments!!

# make list of population size versus time
popsizetree <- extract.popsizetree(mcmc.out)

# plot and compare with skyline plot
sk <- skyline(tree.hiv)
plot(sk, lwd=1, lty=3, show.years=TRUE, subst.rate=0.0023, present.year = 1997)
lines(popsizetree, show.years=TRUE, subst.rate=0.0023, present.year = 1997)
```

---

mixedFontLabel

*Mixed Font Labels for Plotting*


---

**Description**

This function helps to format labels with bits of text in different font shapes (italics, bold, or bolditalics) and different separators. The output is intended to be used for plotting.

**Usage**

```
mixedFontLabel(..., sep = " ", italic = NULL, bold = NULL,
               parenthesis = NULL,
               always.uptight = c("sp.", "spp.", "ssp."))
```

**Arguments**

`...` vectors of mode character to be formatted. They may be of different lengths in which case the shortest ones are recycled.

`sep` a vector of mode character giving the separators to be printed between the elements in `...`

`italic` a vector of integers specifying the elements in `...` to be printed in italics.

`bold` id. in boldface.

`parenthesis` id. within parentheses.

`always.uptight` of vector of mode character giving the strings to not print in italics. Use `always.uptight = ""` to cancel this option.

**Details**

The idea is to have different bits of text in different vectors that are put together to make a vector of R expressions. This vector is interpreted by graphical functions to format the text. A simple use may be `mixedFontLabel(genus, species)`, `italic = 1:2`, but it is more interesting when mixing fonts (see examples).

To have an element in bolditalics, its number must given in both `italic` and `bold`.

The vector returned by this function may be assigned as the `tip.label` element of a tree of class "phylo", or even as its `node.label` element.

**Value**

A vector of mode expression.

**Author(s)**

Emmanuel Paradis

**See Also**

[makeLabel](#), [makeNodeLabel](#), `taxo.fonts` in package **phyloch** for fancy alignments

**Examples**

```
tr <- read.tree(text = "((a,(b,c)),d);")
genus <- c("Gorilla", "Pan", "Homo", "Pongo")
species <- c("gorilla", "spp.", "sapiens", "pygmaeus")
geo <- c("Africa", "Africa", "World", "Asia")
tr$tip.label <- mixedFontLabel(genus, species, geo, italic = 1:2,
                             parenthesis = 3)
layout(matrix(c(1, 2), 2))
```

```

plot(tr)
tr$tip.label <- mixedFontLabel(genus, species, geo, sep = c(" ", " | "),
  italic = 1:2, bold = 3)
plot(tr)
layout(1)

```

---

Moran.I

*Moran's I Autocorrelation Index*


---

### Description

This function computes Moran's I autocorrelation coefficient of  $x$  giving a matrix of weights using the method described by Gittleman and Kot (1990).

### Usage

```

Moran.I(x, weight, scaled = FALSE, na.rm = FALSE,
  alternative = "two.sided")

```

### Arguments

<code>x</code>	a numeric vector.
<code>weight</code>	a matrix of weights.
<code>scaled</code>	a logical indicating whether the coefficient should be scaled so that it varies between -1 and +1 (default to FALSE).
<code>na.rm</code>	a logical indicating whether missing values should be removed.
<code>alternative</code>	a character string specifying the alternative hypothesis that is tested against the null hypothesis of no phylogenetic correlation; must be of one "two.sided", "less", or "greater", or any unambiguous abbreviation of these.

### Details

The matrix weight is used as "neighbourhood" weights, and Moran's I coefficient is computed using the formula:

$$I = \frac{n}{S_0} \frac{\sum_{i=1}^n \sum_{j=1}^n w_{i,j} (y_i - \bar{y})(y_j - \bar{y})}{\sum_{i=1}^n (y_i - \bar{y})^2}$$

with

- $y_i$  = observations
- $w_{i,j}$  = distance weight
- $n$  = number of observations
- $S_0 = \sum_{i=1}^n \sum_{j=1}^n w_{i,j}$

The null hypothesis of no phylogenetic correlation is tested assuming normality of  $I$  under this null hypothesis. If the observed value of  $I$  is significantly greater than the expected value, then the values of  $x$  are positively autocorrelated, whereas if  $I_{\text{observed}} < I_{\text{expected}}$ , this will indicate negative autocorrelation.

**Value**

A list containing the elements:

observed	the computed Moran's I.
expected	the expected value of I under the null hypothesis.
sd	the standard deviation of I under the null hypothesis.
p.value	the P-value of the test of the null hypothesis against the alternative hypothesis specified in alternative.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr> and Emmanuel Paradis

**References**

Gittleman, J. L. and Kot, M. (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology*, **39**, 227–241.

**See Also**

[weight.taxo](#)

**Examples**

```
tr <- rtree(30)
x <- rnorm(30)
## weights w[i,j] = 1/d[i,j]:
w <- 1/cophenetic(tr)
## set the diagonal w[i,i] = 0 (instead of Inf...):
diag(w) <- 0
Moran.I(x, w)
Moran.I(x, w, alt = "l")
Moran.I(x, w, alt = "g")
Moran.I(x, w, scaled = TRUE) # usually the same
```

**Description**

This function does ancestral character reconstruction by parsimony as described in Hanazawa et al. (1995) and modified by Narushima and Hanazawa (1997).

**Usage**

```
MPR(x, phy, outgroup)
```

**Arguments**

x	a vector of integers.
phy	an object of class "phylo"; the tree must be unrooted and fully dichotomous.
outgroup	an integer or a character string giving the tip of phy used as outgroup.

**Details**

Hanazawa et al. (1995) and Narushima and Hanazawa (1997) used Farris's (1970) and Swofford and Maddison's (1987) framework to reconstruct ancestral states using parsimony. The character is assumed to take integer values. The algorithm finds the sets of values for each node as intervals with lower and upper values.

It is recommended to root the tree with the outgroup before the analysis, so plotting the values with [nodeLabels](#) is simple.

**Value**

a matrix of integers with two columns named "lower" and "upper" giving the lower and upper values of the reconstructed sets for each node.

**Author(s)**

Emmanuel Paradis

**References**

- Farris, J. M. (1970) Methods for computing Wagner trees. *Systematic Zoology*, **19**, 83–92.
- Hanazawa, M., Narushima, H. and Minaka, N. (1995) Generating most parsimonious reconstructions on a tree: a generalization of the Farris–Swofford–Maddison method. *Discrete Applied Mathematics*, **56**, 245–265.
- Narushima, H. and Hanazawa, M. (1997) A more efficient algorithm for MPR problems in phylogeny. *Discrete Applied Mathematics*, **80**, 231–238.
- Swofford, D. L. and Maddison, W. P. (1987) Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences*, **87**, 199–229.

**See Also**

[ace](#), [root](#), [nodeLabels](#)

**Examples**

```
## the example in Narushima and Hanazawa (1997):
tr <- read.tree(text = "(((i,j)c,(k,l)b)a,(h,g)e,f)d;")
x <- c(1, 3, 0, 6, 5, 2, 4)
names(x) <- letters[6:12]
(o <- MPR(x, tr, "f"))
plot(tr)
nodeLabels(paste("[", o[, 1], ",", o[, 2], "]", sep = ""))
tiplabels(x[tr$tip.label], adj = -2)
```



```
## some random data:  
x <- rpois(30, 1)  
tr <- rtree(30, rooted = FALSE)  
MPR(x, tr, "t1")
```

---

mrca

*Find Most Recent Common Ancestors Between Pairs*

---

### Description

mrca returns for each pair of tips (and nodes) its most recent common ancestor (MRCA).

getMRCA returns the MRCA of two or more tips.

### Usage

```
mrca(phy, full = FALSE)  
getMRCA(phy, tip)
```

### Arguments

phy	an object of class "phylo".
full	a logical indicating whether to return the MRCAs among all tips and nodes (if TRUE); the default is to return only the MRCAs among tips.
tip	a vector of mode numeric or character specifying the tips.

### Details

For mrca, the diagonal is set to the number of the tips (and nodes if full = TRUE). If full = FALSE, the colnames and rownames are set with the tip labels of the tree; otherwise the numbers are given as names.

For getMRCA, if tip is of length one or zero then NULL is returned.

### Value

a matrix of mode numeric (mrca) or a single numeric value (getMRCA).

### Author(s)

Emmanuel Paradis

---

**mst***Minimum Spanning Tree*

---

**Description**

The function `mst` finds the minimum spanning tree between a set of observations using a matrix of pairwise distances.

The plot method plots the minimum spanning tree showing the links where the observations are identified by their numbers.

**Usage**

```
mst(X)
## S3 method for class 'mst'
plot(x, graph = "circle", x1 = NULL, x2 = NULL, ...)
```

**Arguments**

<code>X</code>	either a matrix that can be interpreted as a distance matrix, or an object of class "dist".
<code>x</code>	an object of class "mst" (e.g. returned by <code>mst()</code> ).
<code>graph</code>	a character string indicating the type of graph to plot the minimum spanning tree; two choices are possible: "circle" where the observations are plotted regularly spaced on a circle, and "nsca" where the two first axes of a non-symmetric correspondence analysis are used to plot the observations (see Details below). If both arguments <code>x1</code> and <code>x2</code> are given, the argument <code>graph</code> is ignored.
<code>x1</code>	a numeric vector giving the coordinates of the observations on the <i>x</i> -axis. Both <code>x1</code> and <code>x2</code> must be specified to be used.
<code>x2</code>	a numeric vector giving the coordinates of the observations on the <i>y</i> -axis. Both <code>x1</code> and <code>x2</code> must be specified to be used.
<code>...</code>	further arguments to be passed to <code>plot()</code> .

**Details**

These functions provide two ways to plot the minimum spanning tree which try to space as much as possible the observations in order to show as clearly as possible the links. The option `graph = "circle"` simply plots regularly the observations on a circle, whereas `graph = "nsca"` uses a non-symmetric correspondence analysis where each observation is represented at the centroid of its neighbours.

Alternatively, the user may use any system of coordinates for the observations, for instance a principal components analysis (PCA) if the distances were computed from an original matrix of continuous variables.

**Value**

an object of class "mst" which is a square numeric matrix of size equal to the number of observations with either 1 if a link between the corresponding observations was found, or 0 otherwise. The names of the rows and columns of the distance matrix, if available, are given as rownames and colnames to the returned object.

**Author(s)**

Yvonnick Noel <noel@univ-lille3.fr>, Julien Claude <claud@isem.univ-montp2.fr> and Emmanuel Paradis

**See Also**

[dist.dna](#), [dist.gene](#), [dist](#), [plot](#)

**Examples**

```
require(stats)
X <- matrix(runif(200), 20, 10)
d <- dist(X)
PC <- prcomp(X)
M <- mst(d)
opar <- par()
par(mfcol = c(2, 2))
plot(M)
plot(M, graph = "nsca")
plot(M, x1 = PC$x[, 1], x2 = PC$x[, 2])
par(opar)
```

---

multi2di

*Collapse and Resolve Multichotomies*

---

**Description**

These two functions collapse or resolve multichotomies in phylogenetic trees.

**Usage**

```
multi2di(phy, random = TRUE)
di2multi(phy, tol = 1e-08)
```

**Arguments**

phy	an object of class "phylo".
random	a logical value specifying whether to resolve the multichotomies randomly (the default) or in the order they appear in the tree (if random = FALSE).
tol	a numeric value giving the tolerance to consider a branch length significantly greater than zero.

**Details**

`multi2di` transforms all multichotomies into a series of dichotomies with one (or several) branch(es) of length zero.

`di2multi` deletes all branches smaller than `tol` and collapses the corresponding dichotomies into a multichotomy.

**Value**

Both functions return an object of class "phylo".

**Author(s)**

Emmanuel Paradis

**See Also**

[is.binary.tree](#)

**Examples**

```
data(bird.families)
is.binary.tree(bird.families)
is.binary.tree(multi2di(bird.families))
all.equal(di2multi(multi2di(bird.families)), bird.families)
### To see the results of randomly resolving a trichotomy:
tr <- read.tree(text = "(a:1,b:1,c:1);")
layout(matrix(1:4, 2, 2))
for (i in 1:4)
  plot(multi2di(tr), use.edge.length = FALSE, cex = 1.5)
layout(matrix(1))
```

---

multiphylo

---

*Manipulating Lists of Trees*


---

**Description**

These are extraction and replacement operators for lists of trees stored in the class "multiPhylo".

**Usage**

```
## S3 method for class 'multiPhylo'
x[i]
## S3 method for class 'multiPhylo'
x[[i]]
## S3 method for class 'multiPhylo'
x$name
## S3 replacement method for class 'multiPhylo'
x[...] <- value
```

```
## S3 replacement method for class 'multiPhylo'
x[[...]] <- value
## S3 replacement method for class 'multiPhylo'
x$... <- value
```

### Arguments

x, value	an object of class "phylo" or "multiPhylo".
i	index(ices) of the tree(s) to select from a list; this may be a vector of integers, logicals, or names.
name	a character string specifying the tree to be extracted.
...	index(ices) of the tree(s) to replace; this may be a vector of integers, logicals, or names.

### Details

The subsetting operator [ keeps the class correctly ("multiPhylo").

The replacement operators check the labels of value if x has a single vector of tip labels for all trees (see examples).

### Value

An object of class "phylo" ([[, \$) or of class "multiPhylo" ([ and the replacement operators).

### Author(s)

Emmanuel Paradis

### See Also

[summary.phylo](#), [c.phylo](#)

### Examples

```
x <- rmtree(10, 20)
names(x) <- paste("tree", 1:10, sep = "")
x[1:5]
x[1] # subsetting
x[[1]] # extraction
x$tree1 # same than above
x[[1]] <- rtree(20)

y <- .compressTipLabel(x)
## up to here 'x' and 'y' have exactly the same information
## but 'y' has a unique vector of tip labels for all the trees
x[[1]] <- rtree(10) # no error
try(y[[1]] <- rtree(10)) # error

try(x[1] <- rtree(20)) # error
## use instead one of the two:
```

```
x[1] <- list(rtree(20))
x[1] <- c(rtree(20))

x[1:5] <- rmtree(5, 20) # replacement
x[11:20] <- rmtree(10, 20) # elongation
x # 20 trees
```

---

mvr

*Minimum Variance Reduction*

---

### Description

Phylogenetic tree construction based on the minimum variance reduction.

### Usage

```
mvr(X, V)
mvr(X, V, fs = 15)
```

### Arguments

X	a distance matrix.
V	a variance matrix.
fs	agglomeration criterion parameter: it is coerced as an integer and must at least equal to one.

### Details

The MVR method can be seen as a version of BIONJ which is not restricted to the Poisson model of variance (Gascuel 2000).

### Value

an object of class "phylo".

### Author(s)

Andrei Popescu <niteloerpopescu@gmail.com>

### References

Criscuolo, A. and Gascuel, O. (2008). Fast NJ-like algorithms to deal with incomplete distance matrices. *BMC Bioinformatics*, 9.

Gascuel, O. (2000). Data model and classification by trees: the minimum variance reduction (MVR) method. *Journal of Classification*, 17, 67–99.

**See Also**

[bionj](#), [fastme](#), [njs](#), [SDM](#)

**Examples**

```
data(woodmouse)
rt <- dist.dna(woodmouse, variance = TRUE)
v <- attr(rt, "variance")
tr <- mvr(rt, v)
plot(tr, "u")
```

---

nj

*Neighbor-Joining Tree Estimation*

---

**Description**

This function performs the neighbor-joining tree estimation of Saitou and Nei (1987).

**Usage**

```
nj(X)
```

**Arguments**

X                    a distance matrix; may be an object of class "dist".

**Value**

an object of class "phylo".

**Author(s)**

Emmanuel Paradis

**References**

Saitou, N. and Nei, M. (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, **4**, 406–425.

Studier, J. A. and Keppler, K. J. (1988) A note on the neighbor-joining algorithm of Saitou and Nei. *Molecular Biology and Evolution*, **5**, 729–731.

**See Also**

[write.tree](#), [read.tree](#), [dist.dna](#), [bionj](#), [fastme](#), [njs](#)

**Examples**

```

### From Saitou and Nei (1987, Table 1):
x <- c(7, 8, 11, 13, 16, 13, 17, 5, 8, 10, 13,
      10, 14, 5, 7, 10, 7, 11, 8, 11, 8, 12,
      5, 6, 10, 9, 13, 8)
M <- matrix(0, 8, 8)
M[lower.tri(M)] <- x
M <- t(M)
M[lower.tri(M)] <- x
dimnames(M) <- list(1:8, 1:8)
tr <- nj(M)
plot(tr, "u")
### a less theoretical example
data(woodmouse)
trw <- nj(dist.dna(woodmouse))
plot(trw)

```

---

njs

*Tree Reconstruction from Incomplete Distances With NJ\* or bio-NJ\**


---

**Description**

Reconstructs a phylogenetic tree from a distance matrix with possibly missing values.

**Usage**

```

njs(X, fs = 15)
bionjs(X, fs = 15)

```

**Arguments**

X	a distance matrix.
fs	argument <i>s</i> of the agglomerative criterion: it is coerced as an integer and must at least equal to one.

**Details**

Missing values represented by either NA or any negative number.

Basically, the  $Q^*$  criterion is applied to all the pairs of leaves, and the *s* highest scoring ones are chosen for further analysis by the agglomeration criteria that better handle missing distances (see references for details).

**Value**

an object of class "phylo".



**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

**References**

<http://www.biomedcentral.com/1471-2105/9/166>

**See Also**

[nj](#), [bionj](#), [triangMtds](#)

**Examples**

```
data(woodmouse)
d <- dist.dna(woodmouse)
dm <- d
dm[sample(length(dm), size = 3)] <- NA
dist.topo(njs(dm), nj(d)) # often 0
dm[sample(length(dm), size = 10)] <- NA
dist.topo(njs(dm), nj(d)) # sometimes 0
```

---

node.depth

*Depth and Heights of Nodes and Tips*

---

**Description**

These functions return the depths or heights of nodes and tips.

**Usage**

```
node.depth(phy, method = 1)
node.depth.edgelen(phy)
node.height(phy, clado.style = FALSE)
node.height.clado(phy)
```

**Arguments**

**phy** an object of class "phylo".

**method** an integer value (1 or 2); 1: the node depths are proportional to the number of tips descending from each node, 2: they are evenly spaced.

**clado.style** a logical value; if TRUE, the node heights are calculated for a cladogram.

**Details**

`node.depth` computes the depth of a node depending on the value of `method` (see the option `node.depth` in [plot.phylo](#)). The value of 1 is given to the tips.

`node.depth.edglength` does the same but using branch lengths.

`node.height` computes the heights of nodes and tips as plotted by a phylogram or a cladogram.

`node.height.clado` does the same but for a cladogram (this function will be removed soon as `node.height(phy, clado.style = TRUE)` does the same thing).

**Value**

A numeric vector indexed with the node numbers of the matrix ‘edge’ of `phy`.

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#)

---

nodelabels

*Labelling the Nodes, Tips, and Edges of a Tree*

---

**Description**

These functions add labels to or near the nodes, the tips, or the edges of a tree using text or plotting symbols. The text can be framed.

**Usage**

```
nodelabels(text, node, adj = c(0.5, 0.5), frame = "rect",
           pch = NULL, thermo = NULL, pie = NULL, piecol = NULL,
           col = "black", bg = "lightblue", horiz = FALSE,
           width = NULL, height = NULL, ...)
tiplabels(text, tip, adj = c(0.5, 0.5), frame = "rect",
          pch = NULL, thermo = NULL, pie = NULL, piecol = NULL,
          col = "black", bg = "yellow", horiz = FALSE,
          width = NULL, height = NULL, ...)
edgelabels(text, edge, adj = c(0.5, 0.5), frame = "rect",
           pch = NULL, thermo = NULL, pie = NULL, piecol = NULL,
           col = "black", bg = "lightgreen", horiz = FALSE,
           width = NULL, height = NULL, date = NULL, ...)
```

**Arguments**

text	a vector of mode character giving the text to be printed. Can be left empty.
node	a vector of mode numeric giving the numbers of the nodes where the text or the symbols are to be printed. Can be left empty.
tip	a vector of mode numeric giving the numbers of the tips where the text or the symbols are to be printed. Can be left empty.
edge	a vector of mode numeric giving the numbers of the edges where the text or the symbols are to be printed. Can be left empty.
adj	one or two numeric values specifying the horizontal and vertical, respectively, justification of the text or symbols. By default, the text is centered horizontally and vertically. If a single value is given, this alters only the horizontal position of the text.
frame	a character string specifying the kind of frame to be printed around the text. This must be one of "rect" (the default), "circle", "none", or any unambiguous abbreviation of these.
pch	a numeric giving the type of plotting symbol to be used; this is eventually recycled. See <a href="#">par</a> for R's plotting symbols. If pch is used, then text is ignored.
thermo	a numeric vector giving some proportions (values between 0 and 1) for each node, or a numeric matrix giving some proportions (the rows must sum to one).
pie	same than thermo.
piecol	a list of colours (given as a character vector) to be used by thermo or pie; if left NULL, a series of colours given by the function rainbow is used.
col	a character string giving the color to be used for the text or the plotting symbols; this is eventually recycled.
bg	a character string giving the color to be used for the background of the text frames or of the plotting symbols if it applies; this is eventually recycled.
...	further arguments passed to the text or points functions (e.g. cex to alter the size of the text or the symbols, or font for the text; see the examples below).
horiz, width, height	parameters controlling the aspect of thermometers; by default, their width and height are determined automatically.
date	specifies the positions of labels on edges of chronograms with respect to the time scale.

**Details**

These three functions have the same optional arguments and the same functioning.

If the arguments text is missing and pch and thermo are left as NULL, then the numbers of the nodes (or of the tips) are printed.

If node, tip, or edge is missing, then the text or the symbols are printed on all nodes, tips, or edges.

The option cex can be used to change the size of all types of labels.

A simple call of these functions with no arguments (e.g., nodelabels()) prints the numbers of all nodes (or tips).

In the case of `tiplabels`, it would be useful to play with the options `x.lim` and `label.offset` (and possibly `show.tip.label`) of `plot.phylo` in most cases (see the examples).

### Author(s)

Emmanuel Paradis, Ben Bolker, and Jim Lemon

### See Also

[plot.phylo](#), [edges](#), [mixedFontLabel](#)

### Examples

```
tr <- read.tree(text = "((Homo,Pan),Gorilla);")
plot(tr)
nodelabels("7.3 Ma", 4, frame = "r", bg = "yellow", adj = 0)
nodelabels("5.4 Ma", 5, frame = "c", bg = "tomato", font = 3)

data(bird.orders)
plot(bird.orders, use.edge.length = FALSE, font = 1)
bs <- round(runif(22, 90, 100), 0) # some imaginary bootstrap values
bs2 <- round(runif(22, 90, 100), 0)
bs3 <- round(runif(22, 90, 100), 0)
nodelabels(bs, adj = 1.2)
nodelabels(bs2, adj = -0.2, bg = "yellow")

### something more classical
plot(bird.orders, use.edge.length = FALSE, font = 1)
nodelabels(bs, adj = -0.2, frame = "n", cex = 0.8)
nodelabels(bs2, adj = c(1.2, 1), frame = "n", cex = 0.8)
nodelabels(bs3, adj = c(1.2, -0.2), frame = "n", cex = 0.8)

### the same but we play with the font
plot(bird.orders, use.edge.length = FALSE, font = 1)
nodelabels(bs, adj = -0.2, frame = "n", cex = 0.8, font = 2)
nodelabels(bs2, adj = c(1.2, 1), frame = "n", cex = 0.8, font = 3)
nodelabels(bs3, adj = c(1.2, -0.2), frame = "n", cex = 0.8)

plot(bird.orders, "c", use.edge.length = FALSE, font = 1)
nodelabels(thermo = runif(22), cex = .8)

plot(bird.orders, "u", FALSE, font = 1, lab4ut = "a")
nodelabels(cex = .75, bg = "yellow")

### representing two characters at the tips (you could have as many
### as you want)
plot(bird.orders, "c", FALSE, font = 1, label.offset = 3,
      x.lim = 31, no.margin = TRUE)
tiplabels(pch = 21, bg = gray(1:23/23), cex = 2, adj = 1.4)
tiplabels(pch = 19, col = c("yellow", "red", "blue"), adj = 2.5, cex = 2)
### This can be used to highlight tip labels:
plot(bird.orders, font = 1)
```

```

i <- c(1, 7, 18)
tiplabels(bird.orders$tip.label[i], i, adj = 0)
### Some random data to compare piecharts and thermometres:
tr <- rtree(15)
x <- runif(14, 0, 0.33)
y <- runif(14, 0, 0.33)
z <- runif(14, 0, 0.33)
x <- cbind(x, y, z, 1 - x - y - z)
layout(matrix(1:2, 1, 2))
plot(tr, "c", FALSE, no.margin = TRUE)
nodelabels(pie = x, cex = 1.3)
text(4.5, 15, "Are you \"pie\"...", font = 4, cex = 1.5)
plot(tr, "c", FALSE, no.margin = TRUE)
nodelabels(thermo = x, col = rainbow(4), cex = 1.3)
text(4.5, 15, "... or \"thermo\"?", font = 4, cex = 1.5)
plot(tr, "c", FALSE, no.margin = TRUE)
nodelabels(thermo = x, col = rainbow(4), cex = 1.3)
plot(tr, "c", FALSE, no.margin = TRUE)
nodelabels(thermo = x, col = rainbow(4), width = 3, horiz = TRUE)
layout(matrix(1))
plot(tr, main = "Showing Edge Lengths")
edgelabels(round(tr$edge.length, 3), srt = 90)
plot(tr, "p", FALSE)
edgelabels("above", adj = c(0.5, -0.25), bg = "yellow")
edgelabels("below", adj = c(0.5, 1.25), bg = "lightblue")

```

opsin

*Gene Tree of 32 opsin Sequences***Description**

This data set describes a gene tree estimated from 32 opsin sequences.

**Usage**

```
data(opsin.newick)
```

**Format**

opsin.newick is a string with the tree in Newick format.

**Source**

This tree is described in Misawa and Tajima (2000) as an example for application of the Klastorin (1982) classification method.

**References**

Misawa, K. (2000) A simple method for classifying genes and a bootstrap test for classifications. *Molecular Biology and Evolution*, **17**, 1879–1884.

**Examples**

```
# example tree in NH format (a string)
data("opsin.newick")
opsin.newick

# get corresponding phylo object
tree.opsin <- read.tree(text = opsin.newick)

# plot tree
plot(tree.opsin, label.offset = 0.01)
```

---

parafit

*Test of host-parasite coevolution*


---

**Description**

Function `parafit` tests the hypothesis of coevolution between a clade of hosts and a clade of parasites. The null hypothesis (H0) of the global test is that the evolution of the two groups, as revealed by the two phylogenetic trees and the set of host-parasite association links, has been independent. Tests of individual host-parasite links are also available as an option.

The method, which is described in detail in Legendre et al. (2002), requires some estimates of the phylogenetic trees or phylogenetic distances, and also a description of the host-parasite associations (H-P links) observed in nature.

**Usage**

```
parafit(host.D, para.D, HP, nperm = 999, test.links = FALSE,
        seed = NULL, correction = "none", silent = FALSE)
```

**Arguments**

<code>host.D</code>	A matrix of phylogenetic or patristic distances among the hosts (object class: <code>matrix</code> , <code>data.frame</code> or <code>dist</code> ). A matrix of patristic distances exactly represents the information in a phylogenetic tree.
<code>para.D</code>	A matrix of phylogenetic or patristic distances among the parasites (object class: <code>matrix</code> , <code>data.frame</code> or <code>dist</code> ). A matrix of patristic distances exactly represents the information in a phylogenetic tree.
<code>HP</code>	A rectangular matrix with hosts as rows and parasites as columns. The matrix contains 1's when a host-parasite link has been observed in nature between the host in the row and the parasite in the column, and 0's otherwise.
<code>nperm</code>	Number of permutations for the tests. If <code>nperm = 0</code> , permutation tests will not be computed. The default value is <code>nperm = 999</code> . For large data files, the permutation test is rather slow since the permutation procedure is not compiled.
<code>test.links</code>	<code>test.links = TRUE</code> will test the significance of individual host-parasite links. Default: <code>test.links = FALSE</code> .

seed	seed = NULL (default): a seed is chosen at random by the function. That seed is used as the starting point for all tests of significance, i.e. the global H-P test and the tests of individual H-P links if they are requested. Users can select a seed of their choice by giving any integer value to seed, for example seed = -123456. Running the function again with the same seed value will produce the exact same test results.
correction	Correction methods for negative eigenvalues (details below): correction="lingoes" and correction="cailliez". Default value: "none".
silent	Informative messages and the time to compute the tests will not be written to the R console if silent=TRUE. Useful when the function is called by a numerical simulation function.

## Details

Two types of test are produced by the program: a global test of coevolution and, optionally, a test on the individual host-parasite (H-P) link.

The function computes principal coordinates for the host and the parasite distance matrices. The principal coordinates (all of them) act as a complete representation of either the phylogenetic distance matrix or the phylogenetic tree.

Phylogenetic distance matrices are normally Euclidean. Patristic distance matrices are additive, thus they are metric and Euclidean. Euclidean matrices are fully represented by real-valued principal coordinate axes. For non-Euclidean matrices, negative eigenvalues are produced; complex principal coordinate axes are associated with the negative eigenvalues. So, the program rejects matrices that are not Euclidean and stops.

Negative eigenvalues can be corrected for by one of two methods: the Lingoes or the Caillez correction. It is up to the user to decide which correction method should be applied. This is done by selecting the option correction="lingoes" or correction="cailliez". Details on these correction methods are given in the help file of the pcoa function.

The principle of the global test is the following (H0: independent evolution of the hosts and parasites): (1) Compute matrix  $D = C t(A) B$ . Note: D is a fourth-corner matrix (sensu Legendre et al. 1997), where A is the H-P link matrix, B is the matrix of principal coordinates computed from the host.D matrix, and C is the matrix of principal coordinates computed from the para.D matrix. (2) Compute the statistic ParaFitGlobal, the sum of squares of all values in matrix D. (3) Permute at random, separately, each row of matrix A, obtaining matrix A.perm. Compute  $D.perm = C$

The test of each individual H-P link is carried out as follows (H0: this particular link is random): (1) Remove one link (k) from matrix A. (2) Compute matrix  $D = C t(A) B$ . (3a) Compute trace(k), the sum of squares of all values in matrix D. (3b) Compute the statistic ParaFitLink1 = (trace - trace(k)) where trace is the ParaFitGlobal statistic. (3c) Compute the statistic ParaFitLink2 = (trace - trace(k)) / (tracemax - trace) where tracemax is the maximum value that can be taken by trace. (4) Permute at random, separately, each row of matrix A, obtaining A.perm. Use the same sequences of permutations as were used in the test of ParaFitGlobal. Using the values of trace and trace.perm saved during the global test, compute the permuted values of the two statistics, ParaFit1.perm and ParaFit2.perm. (5) Repeat step 4 a large number of times. (6) Add the reference value of ParaFit1 to the distribution of ParaFit1.perm values; add the reference value of ParaFit2 to the distribution of ParaFit2.perm values. Calculate the permutational probabilities associated to ParaFit1 and ParaFit2.

The print.parafit function prints out the results of the global test and, optionally, the results of the tests of the individual host-parasite links.

**Value**

ParaFitGlobal	The statistic of the global H-P test.
p.global	The permutational p-value associated with the ParaFitGlobal statistic.
link.table	The results of the tests of individual H-P links, including the ParaFitLink1 and ParaFitLink2 statistics and the p-values obtained from their respective permutational tests.
para.per.host	Number of parasites per host.
host.per.para	Number of hosts per parasite.
nperm	Number of permutations for the tests.

**Author(s)**

Pierre Legendre, Universite de Montreal

**References**

- Hafner, M. S, P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes and S. A. Nadler. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science*, **265**, 1087–1090.
- Legendre, P., Y. Desdevises and E. Bazin. 2002. A statistical test for host-parasite coevolution. *Systematic Biology*, **51(2)**, 217–234.

**See Also**

[pcoa](#)

**Examples**

```
## Gopher and lice data from Hafner et al. (1994)

data(gopher.D)
data(lice.D)
data(HP.links)

res <- parafit(gopher.D, lice.D, HP.links, nperm=99, test.links=TRUE)
# res      # or else: print(res)
```

---

pcoa

*Principal Coordinate Analysis*

---

**Description**

Function [pcoa](#) computes principal coordinate decomposition (also called classical scaling) of a distance matrix D (Gower 1966). It implements two correction methods for negative eigenvalues.



**Usage**

```
pcoa(D, correction="none", rn=NULL)

## S3 method for class 'pcoa'
biplot(x, Y=NULL, plot.axes = c(1,2), dir.axis1=1, dir.axis2=1, rn=NULL, ...)
```

**Arguments**

D	A distance matrix of class <code>dist</code> or <code>matrix</code> .
correction	Correction methods for negative eigenvalues (details below): "lingoes" and "cailliez". Default value: "none".
rn	An optional vector of row names, of length n, for the n objects.
x	Output object from <code>pcoa</code> .
Y	Any rectangular data table containing explanatory variables to be projected onto the ordination plot. That table may contain, for example, the community composition data used to compute D, or any transformation of these data; see examples.
plot.axes	The two PCoA axes to plot.
dir.axis1	= -1 to revert axis 1 for the projection of points and variables. Default value: +1.
dir.axis2	= -1 to revert axis 2 for the projection of points and variables. Default value: +1.
...	Other graphical arguments passed to function.

**Details**

This function implements two methods for correcting for negative values in principal coordinate analysis (PCoA). Negative eigenvalues can be produced in PCoA when decomposing distance matrices produced by coefficients that are not Euclidean (Gower and Legendre 1986, Legendre and Legendre 1998).

In `pcoa`, when negative eigenvalues are present in the decomposition results, the distance matrix D can be modified using either the Lingoes or the Cailliez procedure to produce results without negative eigenvalues.

In the Lingoes (1971) procedure, a constant  $c_1$ , equal to twice absolute value of the largest negative value of the original principal coordinate analysis, is added to each original squared distance in the distance matrix, except the diagonal values. A new principal coordinate analysis, performed on the modified distances, has at most  $(n-2)$  positive eigenvalues, at least 2 null eigenvalues, and no negative eigenvalue.

In the Cailliez (1983) procedure, a constant  $c_2$  is added to the original distances in the distance matrix, except the diagonal values. The calculation of  $c_2$  is described in Legendre and Legendre (1998). A new principal coordinate analysis, performed on the modified distances, has at most  $(n-2)$  positive eigenvalues, at least 2 null eigenvalues, and no negative eigenvalue.

In all cases, only the eigenvectors corresponding to positive eigenvalues are shown in the output list. The eigenvectors are scaled to the square root of the corresponding eigenvalues. Gower (1966) has shown that eigenvectors scaled in that way preserve the original distance (in the D matrix) among the objects. These eigenvectors can be used to plot ordination graphs of the objects.

We recommend not to use PCoA to produce ordinations from the chord, chi-square, abundance profile, or Hellinger distances. It is easier to first transform the community composition data using

the following transformations, available in the `decostand` function of the `vegan` package, and then carry out a principal component analysis (PCA) on the transformed data:

Chord transformation: `decostand(spiders,"normalize")`

Transformation to relative abundance profiles: `decostand(spiders,"total")`

Hellinger transformation: `decostand(spiders,"hellinger")`

Chi-square transformation: `decostand(spiders,"chi.square")`

The ordination results will be identical and the calculations shorter. This two-step ordination method, called transformation-based PCA (tb-PCA), was described by Legendre and Gallagher (2001).

The `biplot.pcoa` function produces plots for any pair of principal coordinates. The original variables can be projected onto the ordination plot.

### Value

<code>correction</code>	The values of parameter <code>correction</code> and variable <code>'correct'</code> in the function.
<code>note</code>	A note describing the type of correction done, if any.
<code>values</code>	The eigenvalues and related information:
<code>Eigenvalues</code>	All eigenvalues (positive, null, negative).
<code>Relative_eig</code>	Relative eigenvalues.
<code>Corr_eig</code>	Corrected eigenvalues (Lingoes correction); Legendre and Legendre (1998, p. 438, eq. 9.27).
<code>Rel_corr_eig</code>	Relative eigenvalues after Lingoes or Cailliez correction.
<code>Broken_stick</code>	Expected fractions of variance under the broken stick model.
<code>Cumul_eig</code>	Cumulative relative eigenvalues.
<code>Cum_corr_eig</code>	Cumulative corrected relative eigenvalues.
<code>Cumul_br_stick</code>	Cumulative broken stick fractions.
<code>vectors</code>	The principal coordinates with positive eigenvalues.
<code>trace</code>	The trace of the distance matrix. This is also the sum of all eigenvalues, positive and negative.
<code>vectors.cor</code>	The principal coordinates with positive eigenvalues from the distance matrix corrected using the method specified by parameter <code>correction</code> .
<code>trace.cor</code>	The trace of the corrected distance matrix. This is also the sum of its eigenvalues.

### Author(s)

Pierre Legendre, Universite de Montreal

## References

- Cailliez, F. (1983) The analytical solution of the additive constant problem. *Psychometrika*, **48**, 305–308.
- Gower, J. C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53**, 325–338.
- Gower, J. C. and Legendre, P. (1986) Metric and Euclidean properties of dissimilarity coefficients. *Journal of Classification*, **3**, 5–48.
- Legendre, P. and Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.
- Legendre, P. and Legendre, L. (1998) *Numerical Ecology, 2nd English edition*. Amsterdam: Elsevier Science BV.
- Lingoes, J. C. (1971) Some boundary conditions for a monotone analysis of symmetric matrices. *Psychometrika*, **36**, 195–203.

## Examples

```
# Oribatid mite data from Borcard and Legendre (1994)

## Not run:
if (require(vegan)) {
data(mite) # Community composition data, 70 peat cores, 35 species

# Select rows 1:30. Species 35 is absent from these rows. Transform to log
mite.log <- log(mite[1:30,-35]+1) # Equivalent: log1p(mite[1:30,-35])

# Principal coordinate analysis and simple ordination plot
mite.D <- vegdist(mite.log, "bray")
res <- pcoa(mite.D)
res$values
biplot(res)

# Project unstandardized and standardized species on the PCoA ordination plot
mite.log.st = apply(mite.log, 2, scale, center=TRUE, scale=TRUE)

par(mfrow=c(1,2))
biplot(res, mite.log)
biplot(res, mite.log.st)

# Reverse the ordination axes in the plot
par(mfrow=c(1,2))
biplot(res, mite.log, dir.axis1=-1, dir.axis2=-1)
biplot(res, mite.log.st, dir.axis1=-1, dir.axis2=-1)
}

## End(Not run)
```

---

phydataplot

*Tree Annotation*

---

### Description

phydataplot plots data on a tree in a way that adapts to the type of tree. ring does the same for circular trees.

Both functions match the data with the labels of the tree.

### Usage

```
phydataplot(x, phy, style = "bars", offset = 1, ...)  
ring(x, phy, style = "ring", offset = 1, ...)
```

### Arguments

x	a vector, a factor, a matrix, or a data frame.
phy	the tree (which must be already plotted).
style	a character string specifying the type of graphics; can be abbreviated (see details).
offset	the space between the tips of the tree and the plot.
...	further arguments passed to the graphical functions.

### Details

The possible values for style are “bars”, “segments”, “image”, or “arrows” for phydataplot, and “ring”, “segments”, or “arrows” for ring.

### Note

For the moment, only rightwards trees are supported (does not apply to circular trees).

### Author(s)

Emmanuel Paradis

### See Also

[plot.phylo](#), [nodelabels](#), [fancyarrows](#)

**Examples**

```

## demonstrates matching with names:
tr <- rcoal(n <- 10)
x <- 1:n
names(x) <- tr$tip.label
plot(tr, x.lim = 11)
phydataplot(x, tr)
## shuffle x but matching names with tip labels reorders them:
phydataplot(sample(x), tr, "s", lwd = 3, lty = 3)

## adapts to the tree:
plot(tr, "f", x.l = c(-11, 11), y.l = c(-11, 11))
phydataplot(x, tr, "s")

## leave more space with x.lim to show 2 barplots:
plot(tr, x.lim = 22)
phydataplot(x, tr, "b")
phydataplot(x, tr, "b", offset = 12, col = "yellow")

ts <- rcoal(N <- 100)
X <- rTraitCont(ts) # names are set
dd <- dist(X)
op <- par(mar = rep(0, 4))
plot(ts, x.lim = 10, cex = 0.4, font = 1)
phydataplot(as.matrix(dd), ts, "i", offset = 0.2)

par(xpd = TRUE, mar = op$mar)
co <- c("blue", "red"); l <- c(-2, 2)
X <- X + abs(min(X)) # move scale so X >= 0
plot(ts, "f", show.tip.label = FALSE, x.lim = 1, y.lim = 1, open.angle = 30)
phydataplot(X, ts, "s", col = co, offset = 0.05)
ring(X, ts, "ring", col = co, offset = max(X) + 0.1) # the same info as a ring

## as many rings as you want...
co <- c("blue", "yellow")
plot(ts, "r", show.tip.label = FALSE, x.l = c(-1, 1), y.l = c(-1, 1))
for (o in seq(0, 0.4, 0.2)) {
  co <- rev(co)
  ring(0.2, ts, "r", col = rep(co, each = 5), offset = o)
}

lim <- c(-5, 5)
co <- rgb(0, 0.4, 1, alpha = 0.1)
y <- seq(0.01, 1, 0.01)
plot(ts, "f", x.lim = lim, y.lim = lim, show.tip.label = FALSE)
ring(y, ts, offset = 0, col = co, lwd = 0.1)
for (i in 1:3) {
  y <- y + 1
  ring(y, ts, offset = 0, col = co, lwd = 0.1)
}

## rings can be in the background

```

```

plot(ts, "r", plot = FALSE)
ring(1, ts, "r", col = rainbow(100), offset = -1)
par(new = TRUE)
plot(ts, "r", font = 1, edge.color = "white")

## might be more useful:
co <- c("lightblue", "yellow")
plot(ts, "r", plot = FALSE)
ring(0.1, ts, "r", col = sample(co, size = N, rep = TRUE), offset = -.1)
par(new = TRUE)
plot(ts, "r", font = 1)

## if x is matrix:
tx <- rcoal(m <- 20)
X <- runif(m, 0, 0.5); Y <- runif(m, 0, 0.5)
X <- cbind(X, Y, 1 - X - Y)
rownames(X) <- tx$tip.label
plot(tx, x.lim = 6)
co <- rgb(diag(3))
phydataplot(X, tx, col = co)
## a variation:
plot(tx, show.tip.label = FALSE, x.lim = 5)
phydataplot(X, tx, col = co, offset = 0.05, border = NA)

plot(tx, "f", show.tip.label = FALSE, open.angle = 180)
ring(X, tx, col = co, offset = 0.05)

```

---

phymltest

*Fits a Bunch of Models with PhyML*


---

## Description

This function calls PhyML and fits successively 28 models of DNA evolution. The results are saved on disk, as PhyML usually does, and returned in **R** as a vector with the log-likelihood value of each model.

## Usage

```

phymltest(seqfile, format = "interleaved", itree = NULL,
          exclude = NULL, execname = NULL, append = TRUE)
## S3 method for class 'phymltest'
print(x, ...)
## S3 method for class 'phymltest'
summary(object, ...)
## S3 method for class 'phymltest'
plot(x, main = NULL, col = "blue", ...)

```

**Arguments**

seqfile	a character string giving the name of the file that contains the DNA sequences to be analysed by PhyML.
format	a character string specifying the format of the DNA sequences: either "interleaved" (the default), or "sequential".
itree	a character string giving the name of a file with a tree in Newick format to be used as an initial tree by PhyML. If NULL (the default), PhyML uses a "BIONJ" tree.
exclude	a vector of mode character giving the models to be excluded from the analysis. These must be among those below, and follow the same syntax.
execname	a character string specifying the name of the PhyML executable. This argument can be left as NULL if PhyML's default names are used: "phym1_3.0_linux32", "phym1_3.0_macintel", or "phym1_3.0_win32.exe", under Linux, MacOS, or Windows respectively.
append	a logical indicating whether to erase previous PhyML output files if present; the default is to not erase.
x	an object of class "phym1test".
object	an object of class "phym1test".
main	a title for the plot; if left NULL, a title is made with the name of the object (use main = "" to have no title).
col	a colour used for the segments showing the AIC values (blue by default).
...	further arguments passed to or from other methods.

**Details**

The present function requires version 3.0.1 of PhyML; it won't work with older versions.

The user must take care to set correctly the three different paths involved here: the path to PhyML's binary, the path to the sequence file, and the path to R's working directory. The function should work if all three paths are different. Obviously, there should be no problem if they are all the same.

The following syntax is used for the models:

```
"X[Y][Z]00[+I][+G]"
```

where "X" is the first letter of the author of the model, "Y" and "Z" are possibly other co-authors of the model, "00" is the year of the publication of the model, and "+I" and "+G" indicates whether the presence of invariant sites and/or a gamma distribution of substitution rates have been specified. Thus, Kimura's model is denoted "K80" and not "K2P". The exception to this rule is the general time-reversible model which is simple denoted "GTR" model.

The seven substitution models used are: "JC69", "K80", "F81", "F84", "HKY85", "TN93", and "GTR". These models are then altered by adding the "+I" and/or "+G", resulting thus in four variants for each of them (e.g., "JC69", "JC69+I", "JC69+G", "JC69+I+G"). Some of these models are described in the help page of [dist.dna](#).

When a gamma distribution of substitution rates is specified, four categories are used (which is PhyML's default behaviour), and the "alpha" parameter is estimated from the data.

For the models with a different substitution rate for transitions and transversions, these rates are left free and estimated from the data (and not constrained with a ratio of 4 as in PhyML's default).

The option `path2exec` has been removed in the present version: the path to PhyML's executable can be specified with the option `execname`.

### Value

`phymltest` returns an object of class "phymltest": a numeric vector with the models as names.

The `print` method prints an object of class "phymltest" as matrix with the name of the models, the number of free parameters, the log-likelihood value, and the value of the Akaike information criterion ( $AIC = -2 * \text{loglik} + 2 * \text{number of free parameters}$ )

The `summary` method prints all the possible likelihood ratio tests for an object of class "phymltest".

The `plot` method plots the values of AIC of an object of class "phymltest" on a vertical scale.

### Note

It is important to note that the models fitted by this function is only a small fraction of the models possible with PhyML. For instance, it is possible to vary the number of categories in the (discretized) gamma distribution of substitution rates, and many parameters can be fixed by the user. The results from the present function should rather be taken as indicative of a best model.

### Author(s)

Emmanuel Paradis

### References

Posada, D. and Crandall, K. A. (2001) Selecting the best-fit model of nucleotide substitution. *Systematic Biology*, **50**, 580–601.

Guindon, S. and Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, **52**, 696–704. <http://www.atgc-montpellier.fr/phyml/>

### See Also

[read.tree](#), [write.tree](#), [dist.dna](#)

### Examples

```
### A 'fake' example with random likelihood values: it does not
### make sense, but does not need PhyML and gives you a flavour
### of what the output looks like:
x <- runif(28, -100, -50)
names(x) <- ape:::phymltest.model
class(x) <- "phymltest"
x
summary(x)
plot(x)
plot(x, main = "", col = "red")
```



```

### This example needs PhyML, copy/paste or type the
### following commands if you want to try them, eventually
### changing setwd() and the options of phym1test()
## Not run:
setwd("D:/phym1_v2.4/exe") # under Windows
data(woodmouse)
write.dna(woodmouse, "woodmouse.txt")
X <- phym1test("woodmouse.txt")
X
summary(X)
plot(X)

## End(Not run)

```

---

pic

*Phylogenetically Independent Contrasts*


---

### Description

Compute the phylogenetically independent contrasts using the method described by Felsenstein (1985).

### Usage

```
pic(x, phy, scaled = TRUE, var.contrasts = FALSE,
    rescaled.tree = FALSE)
```

### Arguments

x	a numeric vector.
phy	an object of class "phylo".
scaled	logical, indicates whether the contrasts should be scaled with their expected variances (default to TRUE).
var.contrasts	logical, indicates whether the expected variances of the contrasts should be returned (default to FALSE).
rescaled.tree	logical, if TRUE the rescaled tree is returned together with the main results.

### Details

If x has names, its values are matched to the tip labels of phy, otherwise its values are taken to be in the same order than the tip labels of phy.

The user must be careful here since the function requires that both series of names perfectly match. If both series of names do not match, the values in the x are taken to be in the same order than the tip labels of phy, and a warning message is issued.

**Value**

either a vector of phylogenetically independent contrasts (if `var.contrasts = FALSE`), or a two-column matrix with the phylogenetically independent contrasts in the first column and their expected variance in the second column (if `var.contrasts = TRUE`). If the tree has node labels, these are used as labels of the returned object.

If `rescaled.tree = TRUE`, a list is returned with two elements named “`contr`” with the above results and “`rescaled.tree`” with the tree and its rescaled branch lengths (see Felsenstein 1985).

**Author(s)**

Emmanuel Paradis

**References**

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.

**See Also**

[read.tree](#), [compar.gee](#), [compar.lynch](#), [pic.ortho](#), [varCompPhylip](#)

**Examples**

```
### The example in Phylip 3.5c (originally from Lynch 1991)
cat("(((Homo:0.21,Pongo:0.21):0.28,",
    "Macaca:0.49):0.13,Ateles:0.62):0.38,Galago:1.00);",
    file = "ex.tre", sep = "\n")
tree.primates <- read.tree("ex.tre")
X <- c(4.09434, 3.61092, 2.37024, 2.02815, -1.46968)
Y <- c(4.74493, 3.33220, 3.36730, 2.89037, 2.30259)
names(X) <- names(Y) <- c("Homo", "Pongo", "Macaca", "Ateles", "Galago")
pic.X <- pic(X, tree.primates)
pic.Y <- pic(Y, tree.primates)
cor.test(pic.X, pic.Y)
lm(pic.Y ~ pic.X - 1) # both regressions
lm(pic.X ~ pic.Y - 1) # through the origin
unlink("ex.tre") # delete the file "ex.tre"
```

---

pic.ortho

*Phylogenetically Independent Orthonormal Contrasts*

---

**Description**

This function computes the orthonormal contrasts using the method described by Felsenstein (2008). Only a single trait can be analyzed; there can be several observations per species.

**Usage**

```
pic.ortho(x, phy, var.contrasts = FALSE, intra = FALSE)
```

**Arguments**

x	a numeric vector or a list of numeric vectors.
phy	an object of class "phylo".
var.contrasts	logical, indicates whether the expected variances of the contrasts should be returned (default to FALSE).
intra	logical, whether to return the intraspecific contrasts.

**Details**

The data `x` can be in two forms: a vector if there is a single observation for each species, or a list whose elements are vectors containing the individual observations for each species. These vectors may be of different lengths.

If `x` has names, its values are matched to the tip labels of `phy`, otherwise its values are taken to be in the same order than the tip labels of `phy`.

**Value**

either a vector of contrasts, or a two-column matrix with the contrasts in the first column and their expected variances in the second column (if `var.contrasts = TRUE`). If the tree has node labels, these are used as labels of the returned object.

If `intra = TRUE`, the attribute "intra", a list of vectors with the intraspecific contrasts or NULL for the species with a one observation, is attached to the returned object.

**Author(s)**

Emmanuel Paradis

**References**

Felsenstein, J. (2008) Comparative methods with sampling error and within-species variation: Contrasts revisited and revised. *American Naturalist*, **171**, 713–725.

**See Also**

[pic](#), [varCompPhylip](#)

**Examples**

```
tr <- rcoal(30)
### a single observation per species:
x <- rTraitCont(tr)
pic.ortho(x, tr)
pic.ortho(x, tr, TRUE)
### different number of observations per species:
x <- lapply(sample(1:5, 30, TRUE), rnorm)
pic.ortho(x, tr, intra = TRUE)
```

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plot.correlogram      *Plot a Correlogram*

---

### Description

These functions plot correlograms previously computed with [correlogram.formula](#).

### Usage

```
## S3 method for class 'correlogram'
plot(x, legend = TRUE, test.level = 0.05,
     col = c("grey", "red"), type = "b", xlab = "",
     ylab = "Moran's I", pch = 21, cex = 2, ...)
## S3 method for class 'correlogramList'
plot(x, lattice = TRUE, legend = TRUE,
     test.level = 0.05, col = c("grey", "red"),
     xlab = "", ylab = "Moran's I",
     type = "b", pch = 21, cex = 2, ...)
```

### Arguments

x	an object of class "correlogram" or of class "correlogramList" (both produced by <a href="#">correlogram.formula</a> ).
legend	should a legend be added on the plot?
test.level	the level used to discriminate the plotting symbols with colours considering the P-values.
col	two colours for the plotting symbols: the first one is used if the P-value is greater than or equal to test.level, the second one otherwise.
type	the type of plot to produce (see <a href="#">plot</a> for possible choices).
xlab	an optional character string for the label on the x-axis (none by default).
ylab	the default label on the y-axis.
pch	the type of plotting symbol.
cex	the default size for the plotting symbols.
lattice	when plotting several correlograms, should they be plotted in trellis-style with lattice (the default), or together on the same plot?
...	other parameters passed to the plot or lines function.

### Details

When plotting several correlograms with lattice, some options have no effect: legend, type, and pch (pch=19 is always used in this situation).

When using pch between 1 and 20 (i.e., non-filled symbols, the colours specified in col are also used for the lines joining the points. To keep black lines, it is better to leave pch between 21 and 25.

**Author(s)**

Emmanuel Paradis

**See Also**[correlogram.formula](#), [Moran.I](#)

plot.phylo

*Plot Phylogenies***Description**

These functions plot phylogenetic trees on the current graphical device.

**Usage**

```
## S3 method for class 'phylo'
plot(x, type = "phylogram", use.edge.length = TRUE,
     node.pos = NULL, show.tip.label = TRUE, show.node.label = FALSE,
     edge.color = "black", edge.width = 1, edge.lty = 1, font = 3,
     cex = par("cex"), adj = NULL, srt = 0, no.margin = FALSE,
     root.edge = FALSE, label.offset = 0, underscore = FALSE,
     x.lim = NULL, y.lim = NULL, direction = "rightwards",
     lab4ut = "horizontal", tip.color = "black", plot = TRUE,
     rotate.tree = 0, open.angle = 0, node.depth = 1, ...)
## S3 method for class 'multiPhylo'
plot(x, layout = 1, ...)
```

**Arguments**

**x** an object of class "phylo" or of class "multiPhylo".

**type** a character string specifying the type of phylogeny to be drawn; it must be one of "phylogram" (the default), "cladogram", "fan", "unrooted", "radial" or any unambiguous abbreviation of these.

**use.edge.length** a logical indicating whether to use the edge lengths of the phylogeny to draw the branches (the default) or not (if FALSE). This option has no effect if the object of class "phylo" has no 'edge.length' element.

**node.pos** a numeric taking the value 1 or 2 which specifies the vertical position of the nodes with respect to their descendants. If NULL (the default), then the value is determined in relation to 'type' and 'use.edge.length' (see details).

**show.tip.label** a logical indicating whether to show the tip labels on the phylogeny (defaults to TRUE, i.e. the labels are shown).

**show.node.label** a logical indicating whether to show the node labels on the phylogeny (defaults to FALSE, i.e. the labels are not shown).

edge.color	a vector of mode character giving the colours used to draw the branches of the plotted phylogeny. These are taken to be in the same order than the component edge of phy. If fewer colours are given than the length of edge, then the colours are recycled.
edge.width	a numeric vector giving the width of the branches of the plotted phylogeny. These are taken to be in the same order than the component edge of phy. If fewer widths are given than the length of edge, then these are recycled.
edge.lty	same than the previous argument but for line types; 1: plain, 2: dashed, 3: dotted, 4: dotdash, 5: longdash, 6: twodash.
font	an integer specifying the type of font for the labels: 1 (plain text), 2 (bold), 3 (italic, the default), or 4 (bold italic).
cex	a numeric value giving the factor scaling of the tip and node labels (Character EXpansion). The default is to take the current value from the graphical parameters.
adj	a numeric specifying the justification of the text strings of the labels: 0 (left-justification), 0.5 (centering), or 1 (right-justification). This option has no effect if type = "unrooted". If NULL (the default) the value is set with respect of direction (see details).
srt	a numeric giving how much the labels are rotated in degrees (negative values are allowed resulting in clock-like rotation); the value has an effect respectively to the value of direction (see Examples). This option has no effect if type = "unrooted".
no.margin	a logical. If TRUE, the margins are set to zero and the plot uses all the space of the device (note that this was the behaviour of plot.phylo up to version 0.2-1 of 'ape' with no way to modify it by the user, at least easily).
root.edge	a logical indicating whether to draw the root edge (defaults to FALSE); this has no effect if 'use.edge.length = FALSE' or if 'type = "unrooted"'.
label.offset	a numeric giving the space between the nodes and the tips of the phylogeny and their corresponding labels. This option has no effect if type = "unrooted".
underscore	a logical specifying whether the underscores in tip labels should be written as spaces (the default) or left as are (if TRUE).
x.lim	a numeric vector of length one or two giving the limit(s) of the x-axis. If NULL, this is computed with respect to various parameters such as the string lengths of the labels and the branch lengths. If a single value is given, this is taken as the upper limit.
y.lim	same than above for the y-axis.
direction	a character string specifying the direction of the tree. Four values are possible: "rightwards" (the default), "leftwards", "upwards", and "downwards".
lab4ut	(= labels for unrooted trees) a character string specifying the display of tip labels for unrooted trees: either "horizontal" where all labels are horizontal (the default), or "axial" where the labels are displayed in the axis of the corresponding terminal branches. This option has an effect only if type = "unrooted".
tip.color	the colours used for the tip labels, eventually recycled (see examples).

plot	a logical controlling whether to draw the tree. If FALSE, the graphical device is set as if the tree was plotted, and the coordinates are saved as well.
rotate.tree	for "fan", "unrooted", or "radial" trees: the rotation of the whole tree in degrees (negative values are accepted).
open.angle	if type = "f", the angle in degrees left blank. Use a non-zero value if you want to call <code>axisPhylo</code> after the tree is plotted.
node.depth	an integer value (1 or 2) used if branch lengths are not used to plot the tree; 1: the node depths are proportional to the number of tips descending from each node (the default and was the only possibility previously), 2: they are evenly spaced.
layout	the number of trees to be plotted simultaneously.
...	further arguments to be passed to plot or to plot.phylo.

### Details

If `x` is a list of trees (i.e., an object of class "multiPhylo"), then any further argument may be passed with `...` and could be any one of those listed above for a single tree.

The font format of the labels of the nodes and the tips is the same.

If `no.margin = TRUE`, the margins are set to zero and are not restored after plotting the tree, so that the user can access the coordinates system of the plot.

The option 'node.pos' allows the user to alter the vertical position (i.e., ordinates) of the nodes. If `node.pos = 1`, then the ordinate of a node is the mean of the ordinates of its direct descendants (nodes and/or tips). If `node.pos = 2`, then the ordinate of a node is the mean of the ordinates of all the tips of which it is the ancestor. If `node.pos = NULL` (the default), then its value is determined with respect to other options: if `type = "phylogram"` then 'node.pos = 1'; if `type = "cladogram"` and `use.edge.length = FALSE` then 'node.pos = 2'; if `type = "cladogram"` and `use.edge.length = TRUE` then 'node.pos = 1'. Remember that in this last situation, the branch lengths make sense when projected on the x-axis.

If `adj` is not specified, then the value is determined with respect to `direction`: if `direction = "leftwards"` then `adj = 1` (0 otherwise).

If the arguments `x.lim` and `y.lim` are not specified by the user, they are determined roughly by the function. This may not always give a nice result: the user may check these values with the (invisibly) returned list (see "Value:").

If you resize manually the graphical device (windows or X11) you may need to replot the tree.

### Value

`plot.phylo` returns invisibly a list with the following components which values are those used for the current plot:

type  
use.edge.length

node.pos  
node.depth

```
show.tip.label
show.node.label
```

```
font
cex
adj
srt
no.margin
label.offset
x.lim
y.lim
direction
tip.color
Ntip
Nnode
```

### Note

The argument `asp` cannot be passed with . . . .

### Author(s)

Emmanuel Paradis

### See Also

[read.tree](#), [trex](#), [kronoviz](#), [add.scale.bar](#), [axisPhylo](#), [nodelabels](#), [edges](#), [plot](#) for the basic plotting function in R

### Examples

```
### An extract from Sibley and Ahlquist (1990)
cat("(((Strix_aluco:4.2,Asio_otus:4.2):3.1,",
    "Athene_noctua:7.3):6.3,Tyto_alba:13.5);",
    file = "ex.tre", sep = "\n")
tree.owls <- read.tree("ex.tre")
plot(tree.owls)
unlink("ex.tre") # delete the file "ex.tre"

### Show the types of trees.
layout(matrix(1:6, 3, 2))
plot(tree.owls, main = "With branch lengths")
plot(tree.owls, type = "c")
plot(tree.owls, type = "u")
plot(tree.owls, use.edge.length = FALSE, main = "Without branch lengths")
plot(tree.owls, type = "c", use.edge.length = FALSE)
plot(tree.owls, type = "u", use.edge.length = FALSE)
```



```

layout(matrix(1))

data(bird.orders)
### using random colours and thickness
plot(bird.orders,
     edge.color = sample(colors(), length(bird.orders$edge)/2),
     edge.width = sample(1:10, length(bird.orders$edge)/2, replace = TRUE))
title("Random colours and branch thickness")
### rainbow colouring...
X <- c("red", "orange", "yellow", "green", "blue", "purple")
plot(bird.orders,
     edge.color = sample(X, length(bird.orders$edge)/2, replace = TRUE),
     edge.width = sample(1:10, length(bird.orders$edge)/2, replace = TRUE))
title("Rainbow colouring")
plot(bird.orders, type = "c", use.edge.length = FALSE,
     edge.color = sample(X, length(bird.orders$edge)/2, replace = TRUE),
     edge.width = rep(5, length(bird.orders$edge)/2))
segments(rep(0, 6), 6.5:1.5, rep(2, 6), 6.5:1.5, lwd = 5, col = X)
text(rep(2.5, 6), 6.5:1.5, paste(X, "..."), adj = 0)
title("Character mapping...")
plot(bird.orders, "u", font = 1, cex = 0.75)
data(bird.families)
plot(bird.families, "u", lab4ut = "axial", font = 1, cex = 0.5)
plot(bird.families, "r", font = 1, cex = 0.5)
### cladogram with oblique tip labels
plot(bird.orders, "c", FALSE, direction = "u", srt = -40, x.lim = 25.5)
### facing trees with different informations...
tr <- bird.orders
tr$tip.label <- rep("", 23)
layout(matrix(1:2, 1, 2), c(5, 4))
plot(bird.orders, "c", FALSE, adj = 0.5, no.margin = TRUE, label.offset = 0.8,
     edge.color = sample(X, length(bird.orders$edge)/2, replace = TRUE),
     edge.width = rep(5, length(bird.orders$edge)/2))
text(7.5, 23, "Facing trees with different informations", font = 2)
plot(tr, "p", direction = "l", no.margin = TRUE,
     edge.width = sample(1:10, length(bird.orders$edge)/2, replace = TRUE))
### Recycling of arguments gives a lot of possibilities
### for tip labels:
plot(bird.orders, tip.col = c(rep("red", 5), rep("blue", 18)),
     font = c(rep(3, 5), rep(2, 17), 1))
plot(bird.orders, tip.col = c("blue", "green"),
     cex = 23:1/23 + .3, font = 1:3)
co <- c(rep("blue", 9), rep("green", 35))
plot(bird.orders, "f", edge.col = co)
plot(bird.orders, edge.col = co)
layout(1)

```

**Description**

Plot previously estimated variance components.

**Usage**

```
## S3 method for class 'varcomp'  
plot(x, xlab = "Levels", ylab = "Variance", type = "b", ...)
```

**Arguments**

x	A <i>varcomp</i> object
xlab	x axis label
ylab	y axis label
type	plot type ("l", "p" or "b", see <a href="#">plot</a> )
...	Further argument sent to the <a href="#">xyplot</a> function.

**Value**

The same as [xyplot](#).

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr>

**See Also**

[varcomp](#)

---

print.phylo

*Compact Display of a Phylogeny*

---

**Description**

These functions prints a compact summary of a phylogeny, or a list of phylogenies, on the console.

**Usage**

```
## S3 method for class 'phylo'  
print(x, printlen = 6 ,...)  
## S3 method for class 'multiPhylo'  
print(x, details = FALSE ,...)  
## S3 method for class 'multiPhylo'  
str(object, ...)
```

**Arguments**

x	an object of class "phylo" or "multiPhylo".
object	an object of class "multiPhylo".
printlen	the number of labels to print (6 by default).
details	a logical indicating whether to print information on all trees.
...	further arguments passed to or from other methods.

**Value**

NULL.

**Author(s)**

Ben Bolker and Emmanuel Paradis

**See Also**

[read.tree](#), [summary.phylo](#), [print](#) for the generic R function

**Examples**

```
x <- rtree(10)
print(x)
print(x, printlen = 10)
x <- rmtree(2, 10)
print(x)
print(x, TRUE)
str(x)
```

---

read.caic

*Read Tree File in CAIC Format*

---

**Description**

This function reads one tree from a CAIC file. A second file containing branch lengths values may also be passed (experimental).

**Usage**

```
read.caic(file, brlen = NULL, skip = 0, comment.char = "#", ...)
```

**Arguments**

file	a file name specified by either a variable of mode character, or a double-quoted string.
brlen	a file name for the branch lengths file.
skip	the number of lines of the input file to skip before beginning to read data (this is passed directly to scan()).
comment.char	a single character, the remaining of the line after this character is ignored (this is passed directly to scan()).
...	Further arguments to be passed to scan().

**Details**

Read a tree from a file in the format used by the CAIC and MacroCAIC program.

**Value**

an object of class "phylo".

**Warning**

The branch length support is still experimental and was not fully tested.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr>

**References**

Purvis, A. and Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *CABIOS*, **11** :241–251.

**See Also**

[read.tree](#), [read.nexus](#)

**Examples**

```
### The same example than in read.tree, without branch lengths.
### An extract from Sibley and Ahlquist (1990)
cat("AAA", "Strix_aluco", "AAB", "Asio_otus",
    "AB", "Athene_noctua", "B", "Tyto_alba",
    file = "ex.tre", sep = "\n")
tree.owls <- read.caic("ex.tre")
plot(tree.owls)
tree.owls
unlink("ex.tre") # delete the file "ex.tre"
```

---

read.dna	<i>Read DNA Sequences in a File</i>
----------	-------------------------------------

---

### Description

These functions read DNA sequences in a file, and returns a matrix or a list of DNA sequences with the names of the taxa read in the file as rownames or names, respectively. By default, the sequences are stored in binary format, otherwise (if `as.character = "TRUE"`) in lower case.

### Usage

```
read.dna(file, format = "interleaved", skip = 0,
         nlines = 0, comment.char = "#",
         as.character = FALSE, as.matrix = NULL)
read.FASTA(file)
```

### Arguments

<code>file</code>	a file name specified by either a variable of mode character, or a double-quoted string.
<code>format</code>	a character string specifying the format of the DNA sequences. Four choices are possible: "interleaved", "sequential", "clustal", or "fasta", or any unambiguous abbreviation of these.
<code>skip</code>	the number of lines of the input file to skip before beginning to read data (ignored for FASTA files; see below).
<code>nlines</code>	the number of lines to be read (by default the file is read until its end; ignored for FASTA files).
<code>comment.char</code>	a single character, the remaining of the line after this character is ignored (ignored for FASTA files).
<code>as.character</code>	a logical controlling whether to return the sequences as an object of class "DNABin" (the default).
<code>as.matrix</code>	(used if <code>format = "fasta"</code> ) one of the three followings: (i) NULL: returns the sequences in a matrix if they are of the same length, otherwise in a list; (ii) TRUE: returns the sequences in a matrix, or stops with an error if they are of different lengths; (iii) FALSE: always returns the sequences in a list.

### Details

`read.dna` follows the interleaved and sequential formats defined in PHYLIP (Felsenstein, 1993) but with the original feature that there is no restriction on the lengths of the taxa names. For these two formats, the first line of the file must contain the dimensions of the data (the numbers of taxa and the numbers of nucleotides); the sequences are considered as aligned and thus must be of the same lengths for all taxa. For the FASTA format, the conventions defined in the URL below (see References) are followed; the sequences are taken as non-aligned. For all formats, the nucleotides can be arranged in any way with blanks and line-breaks inside (with the restriction that the first ten

nucleotides must be contiguous for the interleaved and sequential formats, see below). The names of the sequences are read in the file. Particularities for each format are detailed below.

- **Interleaved:**the function starts to read the sequences after it finds one or more spaces (or tabulations). All characters before the sequences are taken as the taxa names after removing the leading and trailing spaces (so spaces in taxa names are allowed). It is assumed that the taxa names are not repeated in the subsequent blocks of nucleotides.
- **Sequential:**the same criterion than for the interleaved format is used to start reading the sequences and the taxa names; the sequences are then read until the number of nucleotides specified in the first line of the file is reached. This is repeated for each taxa.
- **Clustal:**this is the format output by the Clustal programs (.aln). It is somehow similar to the interleaved format: the differences being that the dimensions of the data are not indicated in the file, and the names of the sequences are repeated in each block.
- **FASTA:**This looks like the sequential format but the taxa names (or rather a description of the sequence) are on separate lines beginning with a 'greater than' character '>' (there may be leading spaces before this character). These lines are taken as taxa names after removing the '>' and the possible leading and trailing spaces. All the data in the file before the first sequence is ignored.

### Value

a matrix or a list (if `format = "fasta"`) of DNA sequences stored in binary format, or of mode character (if `as.character = TRUE`).

`read.FASTA` always returns a list of class `"DNABin"`.

### Author(s)

Emmanuel Paradis

### References

Anonymous. FASTA format description. <http://www.ncbi.nlm.nih.gov/BLAST/fasta.html>

Anonymous. IUPAC ambiguity codes. <http://www.ncbi.nlm.nih.gov/SNP/iupac.html>

Felsenstein, J. (1993) Phylip (Phylogeny Inference Package) version 3.5c. Department of Genetics, University of Washington. <http://evolution.genetics.washington.edu/phylip/phylip.html>

### See Also

[read.GenBank](#), [write.dna](#), [DNABin](#), [dist.dna](#), [woodmouse](#)

### Examples

```
### a small extract from `data(woodmouse)`
cat("3 40",
    "No305   NTTCGAAAAACACCCCACTACTAAAANTTATCAGTCACT",
    "No304   ATTCGAAAAACACCCCACTACTAAAATTATCAACCACT",
    "No306   ATTCGAAAAACACCCCACTACTAAAATTATCAATCACT",
    file = "exdna.txt", sep = "\n")
```

```

ex.dna <- read.dna("exdna.txt", format = "sequential")
str(ex.dna)
ex.dna
### the same data in interleaved format...
cat("3 40",
    "No305     NTTGAAAAA CACACCCACT",
    "No304     ATTCGAAAAA CACACCCACT",
    "No306     ATTCGAAAAA CACACCCACT",
    "          ACTAAAAANTT ATCAGTCACT",
    "          ACTAAAAATT ATCAACCACT",
    "          ACTAAAAATT ATCAATCACT",
    file = "exdna.txt", sep = "\n")
ex.dna2 <- read.dna("exdna.txt")
### ... in clustal format...
cat("CLUSTAL (ape) multiple sequence alignment", "",
    "No305     NTTGAAAAACACACCCACTACTAAAAANTTATCAGTCACT",
    "No304     ATTCGAAAAACACACCCACTACTAAAAATTATCAACCACT",
    "No306     ATTCGAAAAACACACCCACTACTAAAAATTATCAATCACT",
    "          *****",
    file = "exdna.txt", sep = "\n")
ex.dna3 <- read.dna("exdna.txt", format = "clustal")
### ... and in FASTA format
cat(">No305",
    "NTTCGAAAAACACACCCACTACTAAAAANTTATCAGTCACT",
    ">No304",
    "ATTCGAAAAACACACCCACTACTAAAAATTATCAACCACT",
    ">No306",
    "ATTCGAAAAACACACCCACTACTAAAAATTATCAATCACT",
    file = "exdna.txt", sep = "\n")
ex.dna4 <- read.dna("exdna.txt", format = "fasta")
### The first three are the same!
identical(ex.dna, ex.dna2)
identical(ex.dna, ex.dna3)
identical(ex.dna, ex.dna4)
unlink("exdna.txt") # clean-up

```

---

read.GenBank

*Read DNA Sequences from GenBank via Internet*


---

## Description

This function connects to the GenBank database, and reads nucleotide sequences using accession numbers given as arguments.

## Usage

```

read.GenBank(access.nb, seq.names = access.nb, species.names = TRUE,
             gene.names = FALSE, as.character = FALSE)

```

**Arguments**

access.nb	a vector of mode character giving the accession numbers.
seq.names	the names to give to each sequence; by default the accession numbers are used.
species.names	a logical indicating whether to attribute the species names to the returned object.
gene.names	a logical indicating whether to attribute the gene names to the returned object. It is FALSE by default because this will work correctly only when reading sequences with a single gene.
as.character	a logical controlling whether to return the sequences as an object of class "DNABin" (the default).

**Details**

The function uses the site <http://www.ncbi.nlm.nih.gov/> from where the sequences are downloaded.

If `species.names = TRUE`, the returned list has an attribute "species" containing the names of the species taken from the field "ORGANISM" in GenBank.

If `gene.names = TRUE`, the returned list has an attribute "gene" containing the names of the gene. This will not work correctly if reading a sequence with multiple genes (e.g., a mitochondrial genome).

**Value**

A list of DNA sequences made of vectors of class "DNABin", or of single characters (if `as.character = "TRUE"`).

**Author(s)**

Emmanuel Paradis

**See Also**

[read.dna](#), [write.dna](#), [dist.dna](#), [DNABin](#)

**Examples**

```
### This won't work if your computer is not connected
### to the Internet!!!
###
### Get the 8 sequences of tanagers (Ramphocelus)
### as used in Paradis (1997)
ref <- c("U15717", "U15718", "U15719", "U15720",
        "U15721", "U15722", "U15723", "U15724")
### Copy/paste or type the following commands if you
### want to try them.
## Not run:
Rampho <- read.GenBank(ref)
### get the species names:
attr(Rampho, "species")
### build a matrix with the species names and the accession numbers:
```



```

cbind(attr(Rampho, "species"), names(Rampho))
### print the first sequence
### (can be done with `Rampho$U15717` as well)
Rampho[[1]]
### print the first sequence in a cleaner way
cat(Rampho[[1]], "\n", sep = "")

## End(Not run)

```

---

read.nexus

*Read Tree File in Nexus Format*


---

## Description

This function reads one or several trees in a NEXUS file.

## Usage

```
read.nexus(file, tree.names = NULL)
```

## Arguments

file	a file name specified by either a variable of mode character, or a double-quoted string.
tree.names	if there are several trees to be read, a vector of mode character giving names to the individual trees (by default, this uses the labels in the NEXUS file if these are present).

## Details

The present implementation tries to follow as much as possible the NEXUS standard (but see the restriction below on TRANSLATION tables). Only the block “TREES” is read; the other data can be read with other functions (e.g., [read.dna](#), [read.table](#), ...).

If a TRANSLATION table is present it is assumed that only the tip labels are translated and they are all translated with integers without gap. Consequently, if nodes have labels in the tree(s) they are read as they are and not looked for in the translation table. The logic behind this is that in the vast majority of cases, node labels will be support values rather than proper taxa names. This is consistent with [write.nexus](#) which translates only the tip labels.

‘read.nexus’ tries to represent correctly trees with a badly represented root edge (i.e. with an extra pair of parentheses). For instance, the tree “((A:1,B:1):10);” will be read like “(A:1,B:1):10;” but a warning message will be issued in the former case as this is apparently not a valid Newick format. If there are two root edges (e.g., “(((A:1,B:1):10):10);”), then the tree is not read and an error message is issued.

## Value

an object of class “phylo” or of class “multiPhylo”.

**Author(s)**

Emmanuel Paradis

**References**

Maddison, D. R., Swofford, D. L. and Maddison, W. P. (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology*, **46**, 590–621.

**See Also**

[read.tree](#), [write.nexus](#), [write.tree](#), [read.nexus.data](#), [write.nexus.data](#)

---

 read.nexus.data

*Read Character Data In NEXUS Format*


---

**Description**

This function reads a file with sequences in the NEXUS format.

**Usage**

```
read.nexus.data(file)
```

**Arguments**

`file` a file name specified by either a variable of mode character, or a double-quoted string.

**Details**

This parser tries to read data from a file written in a *restricted* NEXUS format (see examples below).

Please see files 'data.nex' and 'taxacharacters.nex' for examples of formats that will work.

Some noticeable exceptions from the NEXUS standard (non-exhaustive list):

- **I**Comments must be either on separate lines or at the end of lines. Examples:  
 [Comment] — **OK**  
 Taxon ACGTACG [Comment] — **OK**  
 [Comment line 1  
 Comment line 2] — **NOT OK!**  
 Tax[Comment]on ACG[Comment]T — **NOT OK!**
- **I**No spaces (or comments) are allowed in the sequences. Examples:  
 name ACGT — **OK**  
 name AC GT — **NOT OK!**

- **III**No spaces are allowed in taxon names, not even if names are in single quotes. That is, single-quoted names are not treated as such by the parser. Examples:  
 Genus\_species — **OK**  
 'Genus\_species' — **OK**  
 'Genus species' — **NOT OK!**
- **IV**The trailing end that closes the matrix must be on a separate line. Examples:  
 taxon AACCGGT  
 end; — **OK**  
 taxon AACCGGT;  
 end; — **OK**  
 taxon AACCGGT; end; — **NOT OK!**
- **V**Multistate characters are not allowed. That is, NEXUS allows you to specify multiple character states at a character position either as an uncertainty, (XY), or as an actual appearance of multiple states, {XY}. This is information is not handled by the parser. Examples:  
 taxon 0011?110 — **OK**  
 taxon 0011{01}110 — **NOT OK!**  
 taxon 0011(01)110 — **NOT OK!**
- **VI**The number of taxa must be on the same line asntax. The same applies to nchar. Examples:  
 ntax = 12 — **OK**  
 ntax =  
 12 — **NOT OK!**
- **VII**The word “matrix” can not occur anywhere in the file before the actual matrix command, unless it is in a comment. Examples:  
 BEGIN CHARACTERS;  
 TITLE 'Data in file "03a-cytochromeB.nex"';  
 DIMENSIONS NCHAR=382;  
 FORMAT DATATYPE=Protein GAP=- MISSING=?;  
 ["This is The Matrix"] — **OK**  
 MATRIX  
  
 BEGIN CHARACTERS;  
 TITLE 'Matrix in file "03a-cytochromeB.nex"'; — **NOT OK!**  
 DIMENSIONS NCHAR=382;  
 FORMAT DATATYPE=Protein GAP=- MISSING=?;  
 MATRIX

**Value**

A list of sequences each made of a single vector of mode character where each element is a (phylogenetic) character state.

**Author(s)**

Johan Nylander <nylander@scs.fsu.edu>

## References

Maddison, D. R., Swofford, D. L. and Maddison, W. P. (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology*, **46**, 590–621.

## See Also

[read.nexus](#), [write.nexus](#), [write.nexus.data](#)

## Examples

```
## Use read.nexus.data to read a file in NEXUS format into object x
## Not run: x <- read.nexus.data("file.nex")
```

---

read.tree

*Read Tree File in Parenthetic Format*

---

## Description

This function reads a file which contains one or several trees in parenthetic format known as the Newick or New Hampshire format.

## Usage

```
read.tree(file = "", text = NULL, tree.names = NULL, skip = 0,
          comment.char = "#", keep.multi = FALSE, ...)
```

## Arguments

file	a file name specified by either a variable of mode character, or a double-quoted string; if file = "" (the default) then the tree is input on the keyboard, the entry being terminated with a blank line.
text	alternatively, the name of a variable of mode character which contains the tree(s) in parenthetic format. By default, this is ignored (set to NULL, meaning that the tree is read in a file); if text is not NULL, then the argument file is ignored.
tree.names	if there are several trees to be read, a vector of mode character that gives names to the individual trees; if NULL (the default), the trees are named "tree1", "tree2", ...
skip	the number of lines of the input file to skip before beginning to read data (this is passed directly to scan()).
comment.char	a single character, the remaining of the line after this character is ignored (this is passed directly to scan()).
keep.multi	if TRUE and tree.names = NULL then single trees are returned in "multiPhylo" format, with any name that is present (see details). Default is FALSE.
...	further arguments to be passed to scan().

## Details

The default option for `file` allows to type directly the tree on the keyboard (or possibly to copy from an editor and paste in R's console) with, e.g., `mytree <- read.tree()`.

'`read.tree`' tries to represent correctly trees with a badly represented root edge (i.e. with an extra pair of parentheses). For instance, the tree "`((A:1,B:1):10);`" will be read like "`(A:1,B:1):10;`" but a warning message will be issued in the former case as this is apparently not a valid Newick format. If there are two root edges (e.g., "`((A:1,B:1):10):10;`"), then the tree is not read and an error message is issued.

If there are any characters preceding the first "(" in a line then this is assigned to the name. This is returned when a "multiPhylo" object is returned and `tree.names = NULL`.

## Value

an object of class "phylo" with the following components:

<code>edge</code>	a two-column matrix of mode numeric where each row represents an edge of the tree; the nodes and the tips are symbolized with numbers; the tips are numbered 1, 2, ..., and the nodes are numbered after the tips. For each row, the first column gives the ancestor.
<code>edge.length</code>	(optional) a numeric vector giving the lengths of the branches given by edge.
<code>tip.label</code>	a vector of mode character giving the names of the tips; the order of the names in this vector corresponds to the (positive) number in edge.
<code>Nnode</code>	the number of (internal) nodes.
<code>node.label</code>	(optional) a vector of mode character giving the names of the nodes.
<code>root.edge</code>	(optional) a numeric value giving the length of the branch at the root if it exists.

If several trees are read in the file, the returned object is of class "multiPhylo", and is a list of objects of class "phylo". The name of each tree can be specified by `tree.names`, or can be read from the file (see details).

## Author(s)

Emmanuel Paradis and Daniel Lawson <[dan.lawson@bristol.ac.uk](mailto:dan.lawson@bristol.ac.uk)>

## References

- Felsenstein, J. The Newick tree format. <http://evolution.genetics.washington.edu/phylip/newicktree.html>
- Olsen, G. Interpretation of the "Newick's 8:45" tree format standard. [http://evolution.genetics.washington.edu/phylip/newick\\_doc.html](http://evolution.genetics.washington.edu/phylip/newick_doc.html)
- Paradis, E. (2008) Definition of Formats for Coding Phylogenetic Trees in R. [http://ape.mpl.ird.fr/misc/FormatTreeR\\_28July2008.pdf](http://ape.mpl.ird.fr/misc/FormatTreeR_28July2008.pdf)
- Paradis, E. (2012) *Analysis of Phylogenetics and Evolution with R (Second Edition)*. New York: Springer.

**See Also**

[write.tree](#), [read.nexus](#), [write.nexus](#), [scan](#) for the basic R function to read data in a file

**Examples**

```
### An extract from Sibley and Ahlquist (1990)
s <- "owls(((Strix_aluco:4.2,Asio_otus:4.2):3.1,Athene_noctua:7.3):6.3,Tyto_alba:13.5);"
cat(s, file = "ex.tre", sep = "\n")
tree.owls <- read.tree("ex.tre")
str(tree.owls)
tree.owls
tree.owls <- read.tree("ex.tre", keep.multi = TRUE)
tree.owls
names(tree.owls)
unlink("ex.tre") # delete the file "ex.tre"
### Only the first three species using the option `text'
TREE <- "((Strix_aluco:4.2,Asio_otus:4.2):3.1,Athene_noctua:7.3);"
TREE
tree.owls.bis <- read.tree(text = TREE)
str(tree.owls.bis)
tree.owls.bis
```

reorder.phylo

*Internal Reordering of Trees***Description**

This function changes the internal structure of a phylogeny stored as an object of class "phylo". The tree returned is the same than the one input, but the ordering of the edges could be different.

**Usage**

```
## S3 method for class 'phylo'
reorder(x, order = "cladewise", index.only = FALSE, ...)
```

**Arguments**

x	an object of class "phylo".
order	a character string: either "cladewise" (the default), "postorder", "pruningwise", or any unambiguous abbreviation of these.
index.only	should the function return only the ordered indices of the rows of the edge matrix?
...	further arguments passed to or from other methods.

**Details**

Because in a tree coded as an object of class "phylo" each branch is represented by a row in the element 'edge', there is an arbitrary choice for the ordering of these rows. `reorder` allows to reorder these rows according to three rules: in the "cladewise" order each clade is formed by a series of contiguous rows. In the "postorder" order, the rows are arranged so that computations following pruning-like algorithm the tree (or postorder tree traversal) can be done by descending along these rows (conversely, a preorder tree traversal can be performed by moving from the last to the first row). The "pruningwise" order is an alternative "pruning" order which is actually a bottom-up traversal order (Valiente 2002). (This third choice might be removed in the future as it merely duplicates the second one which is more efficient.) The possible multichotomies and branch lengths are preserved.

Note that for a given order, there are several possible orderings of the rows of 'edge'.

**Value**

an object of class "phylo" (with the attribute "order" set accordingly), or a numeric vector if `index.only = TRUE`.

**Author(s)**

Emmanuel Paradis

**References**

Valiente, G. (2002) *Algorithms on Trees and Graphs*. New York: Springer.

**See Also**

[read.tree](#) to read tree files in Newick format, [reorder](#) for the generic function

**Examples**

```
data(bird.families)
tr <- reorder(bird.families, "postorder")
all.equal(bird.families, tr) # uses all.equal.phylo actually
all.equal.list(bird.families, tr) # bypasses the generic
```

---

richness.yule.test      *Test of Diversification-Shift With the Yule Process*

---

**Description**

This function performs a test of shift in diversification rate using probabilities from the Yule process.

**Usage**

```
richness.yule.test(x, t)
```

**Arguments**

- x a matrix or a data frame with at least two columns: the first one gives the number of species in clades with a trait supposed to increase or decrease diversification rate, and the second one the number of species in the sister-clades without the trait. Each row represents a pair of sister-clades.
- t a numeric vector giving the divergence times of each pair of clades in x.

**Value**

a data frame with the  $\chi^2$ , the number of degrees of freedom (= 1), and the *P*-value.

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (2012) Shift in diversification in sister-clade comparisons: a more powerful test. *Evolution*, **66**, 288–295.

**See Also**

[slowinskiguyer.test](#), [mconwaysims.test](#), [diversity.contrast.test](#)

**Examples**

```
### see examples(mconwaysims.test)
```

---

rlineage

*Tree Simulation Under the Time-Dependent Birth–Death Models*


---

**Description**

These two functions simulate phylogenies under any time-dependent birth–death model. `lineage` generates a complete tree including the species that go extinct; `rbdtree` generates a tree with only the species until present; `drop.fossil` is a utility function to remove the extinct species.

**Usage**

```
rlineage(birth, death, Tmax = 50, BIRTH = NULL,
         DEATH = NULL, eps = 1e-6)
rbdtree(birth, death, Tmax = 50, BIRTH = NULL,
        DEATH = NULL, eps = 1e-6)
drop.fossil(phy, tol = 1e-8)
```



**Arguments**

birth, death	a numeric value or a (vectorized) function specifying how speciation and extinction rates vary through time.
Tmax	a numeric value giving the length of the simulation.
BIRTH, DEATH	a (vectorized) function which is the primitive of birth or death. This can be used to speed-up the computation. By default, numerical integration is done.
eps	a numeric value giving the time resolution of the simulation; this may be increased (e.g., 0.001) to shorten computation times.
phy	an object of class "phylo".
tol	a numeric value giving the tolerance to consider a species as extinct.

**Details**

Both functions use continuous-time algorithms described in the references. The models are time-dependent birth–death models as described in Kendall (1948). Speciation (birth) and extinction (death) rates may be constant or vary through time according to an R function specified by the user. In the latter case, BIRTH and/or DEATH may be used if the primitives of birth and death are known. In these functions time is the formal argument and must be named t.

**Value**

An object of class "phylo".

**Author(s)**

Emmanuel Paradis

**References**

- Kendall, D. G. (1948) On the generalized “birth-and-death” process. *Annals of Mathematical Statistics*, **19**, 1–15.
- Paradis, E. (2011) Time-dependent speciation and extinction from phylogenies: a least squares approach. *Evolution*, **65**, 661–672.

**See Also**

[yule](#), [yule.time](#), [birthdeath](#), [rtree](#), [stree](#)

**Examples**

```
plot(rlineage(0.1, 0)) # Yule process with lambda = 0.1
plot(rlineage(0.1, 0.05)) # simple birth-death process
b <- function(t) 1/(1 + exp(0.2*t - 1)) # logistic
layout(matrix(0:3, 2, byrow = TRUE))
curve(b, 0, 50, xlab = "Time", ylab = "")
mu <- 0.07
segments(0, mu, 50, mu, lty = 2)
legend("topright", c(expression(lambda), expression(mu)),
```

```

      lty = 1:2, bty = "n")
plot(rlineage(b, mu), show.tip.label = FALSE)
title("Simulated with 'rlineage'")
plot(rbdtree(b, mu), show.tip.label = FALSE)
title("Simulated with 'rbdtree'")

```

root

*Roots Phylogenetic Trees***Description**

root reroots a phylogenetic tree with respect to the specified outgroup or at the node specified in node.

unroot unroots a phylogenetic tree, or returns it unchanged if it is already unrooted.

is.rooted tests whether a tree is rooted.

**Usage**

```

root(phy, outgroup, node = NULL, resolve.root = FALSE, interactive = FALSE)
unroot(phy)
is.rooted(phy)

```

**Arguments**

phy	an object of class "phylo".
outgroup	a vector of mode numeric or character specifying the new outgroup.
node	alternatively, a node number where to root the tree (this should give the MRCA of the ingroup).
resolve.root	a logical specifying whether to resolve the new root as a bifurcating node.
interactive	if TRUE the user is asked to select the node by clicking on the tree which must be plotted.

**Details**

The argument outgroup can be either character or numeric. In the first case, it gives the labels of the tips of the new outgroup; in the second case the numbers of these labels in the vector phy\$tip.label are given.

If outgroup is of length one (i.e., a single value), then the tree is rerooted using the node below this tip as the new root.

If outgroup is of length two or more, the most recent common ancestor (MRCA) of the ingroup is used as the new root. Note that the tree is unrooted before being rerooted, so that if outgroup is already the outgroup, then the returned tree is not the same than the original one (see examples). If outgroup is not monophyletic, the operation fails and an error message is issued.

If resolve.root = TRUE, root adds a zero-length branch below the MRCA of the ingroup.

A tree is considered rooted if either only two branches connect to the root, or if there is a root.edge element. In all other cases, is.rooted returns FALSE.

**Value**

an object of class "phylo" for root and unroot; a single logical value for `is.rooted`.

**Author(s)**

Emmanuel Paradis

**See Also**

[bind.tree](#), [drop.tip](#), [nodelabels](#), [identify.phylo](#)

**Examples**

```
data(bird.orders)
plot(root(bird.orders, 1))
plot(root(bird.orders, 1:5))

tr <- root(bird.orders, 1)
is.rooted(bird.orders) # yes!
is.rooted(tr)          # no!
### This is because the tree has been unrooted first before rerooting.
### You can delete the outgroup...
is.rooted(drop.tip(tr, "Struthioniformes"))
### ... or resolve the basal trichotomy in two ways:
is.rooted(multi2di(tr))
is.rooted(root(bird.orders, 1, r = TRUE))
### To keep the basal trichotomy but forcing the tree as rooted:
tr$root.edge <- 0
is.rooted(tr)
```

---

rotate

*Swapping Sister Clades*

---

**Description**

For a given node, `rotate` exchanges the position of two clades descending from this node. It can handle dichotomies as well as polytomies. In the latter case, two clades from the polytomy are selected for swapping.

`rotateConstr` rotates internal branches giving a constraint on the order of the tips.

**Usage**

```
rotate(phy, node, polytom = c(1, 2))
rotateConstr(phy, constraint)
```

**Arguments**

phy	an object of class "phylo".
node	a vector of mode numeric or character specifying the number of the node.
polytom	a vector of mode numeric and length two specifying the two clades that should be exchanged in a polytomy.
constraint	a vector of mode character specifying the order of the tips as they should appear when plotting the tree (from bottom to top).

**Details**

phy can be either rooted or unrooted, contain polytomies and lack branch lengths. In the presence of very short branch lengths it is convenient to plot the phylogenetic tree without branch lengths in order to identify the number of the node in question.

node can be any of the interior nodes of a phylogenetic tree including the root node. Number of the nodes can be identified by the `nodelabels` function. Alternatively, you can specify a vector of length two that contains either the number or the names of two tips that coalesce in the node of interest.

If the node subtends a polytomy, any two clades of the the polytomy can be chosen by `polytom`. On a plotted phylogeny, the clades are numbered from bottom to top and `polytom` is used to index the two clades one likes to swop.

**Value**

an object of class "phylo".

**Author(s)**

Christoph Heibl <heibl@lmu.de>, Emmanuel Paradis

**See Also**

[plot.phylo](#), [nodelabels](#), [root](#), [drop.tip](#)

**Examples**

```
# create a random tree:
tre <- rtree(25)

# visualize labels of internal nodes:
plot(tre, use.edge.length=FALSE)
nodelabels()

# rotate clades around node 30:
tre.new <- rotate(tre, 30)

# compare the results:
par(mfrow=c(1,2)) # split graphical device
plot(tre) # plot old tre
plot(tre.new) # plot new tree
```

```

# visualize labels of terminal nodes:
plot(tre)
tiplabels()

# rotate clades containing nodes 12 and 20:
tre.new <- rotate(tre, c(12, 21))

# compare the results:
par(mfrow=c(1,2)) # split graphical device
plot(tre) # plot old tre
plot(tre.new) # plot new tree

# or you might just specify tiplabel names:
tre.new <- rotate(tre, c("t3", "t14"))

# compare the results:
par(mfrow=c(1,2)) # devide graphical device
plot(tre) # plot old tre
plot(tre.new) # plot new tree

# a simple example for rotateConstr:
A <- read.tree(text = "((A,B),(C,D));")
B <- read.tree(text = "((D,C),B),A);")
B <- rotateConstr(B, A$tip.label)
plot(A); plot(B, d = "l")

# something more interesting (from ?cophyloplot):
tr1 <- rtree(40)
## drop 20 randomly chosen tips:
tr2 <- drop.tip(tr1, sample(tr1$tip.label, size = 20))
## rotate the root and reorder the whole:
tr2 <- rotate(tr2, 21)
tr2 <- read.tree(text = write.tree(tr2))
X <- cbind(tr2$tip.label, tr2$tip.label) # association matrix
cophyloplot(tr1, tr2, assoc = X, space = 28)
## before reordering tr2 we have to find the constraint:
co <- tr2$tip.label[order(match(tr2$tip.label, tr1$tip.label))]
newtr2 <- rotateConstr(tr2, co)
cophyloplot(tr1, newtr2, assoc = X, space = 28)

```

## Description

This function simulates the evolution of a continuous character along a phylogeny. The calculation is done recursively from the root. See Paradis (2012, pp. 232 and 324) for an introduction.

**Usage**

```
rTraitCont(phy, model = "BM", sigma = 0.1, alpha = 1, theta = 0,
           ancestor = FALSE, root.value = 0, ...)
```

**Arguments**

phy	an object of class "phylo".
model	a character (either "BM" or "OU") or a function specifying the model (see details).
sigma	a numeric vector giving the standard-deviation of the random component for each branch (can be a single value).
alpha	if model = "OU", a numeric vector giving the strength of the selective constraint for each branch (can be a single value).
theta	if model = "OU", a numeric vector giving the optimum for each branch (can be a single value).
ancestor	a logical value specifying whether to return the values at the nodes as well (by default, only the values at the tips are returned).
root.value	a numeric giving the value at the root.
...	further arguments passed to model if it is a function.

**Details**

There are three possibilities to specify model:

- "BM": a Brownian motion model is used. If the arguments sigma has more than one value, its length must be equal to the the branches of the tree. This allows to specify a model with variable rates of evolution. You must be careful that branch numbering is done with the tree in "pruningwise" order: to see the order of the branches you can use: `tr <- reorder(tr, "p"); plot(tr); edgelabels`. The arguments alpha and theta are ignored.
- "OU": an Ornstein-Uhlenbeck model is used. The above indexing rule is used for the three parameters sigma, alpha, and theta. This may be interesting for the last one to model varying phenotypic optima. The exact updating formula from Gillespie (1996) are used which are reduced to BM formula if alpha = 0.
- A function: it must be of the form `foo(x, l)` where x is the trait of the ancestor and l is the branch length. It must return the value of the descendant. The arguments sigma, alpha, and theta are ignored.

**Value**

A numeric vector with names taken from the tip labels of phy. If ancestor = TRUE, the node labels are used if present, otherwise, "Node1", "Node2", etc.

**Author(s)**

Emmanuel Paradis

## References

- Gillespie, D. T. (1996) Exact numerical simulation of the Ornstein-Uhlenbeck process and its integral. *Physical Review E*, **54**, 2084–2091.
- Paradis, E. (2012) *Analysis of Phylogenetics and Evolution with R (Second Edition)*. New York: Springer.

## See Also

[rTraitDisc](#), [rTraitMult](#), [ace](#)

## Examples

```
data(bird.orders)
rTraitCont(bird.orders) # BM with sigma = 0.1
### OU model with two optima:
tr <- reorder(bird.orders, "postorder")
plot(tr)
edgelabels()
theta <- rep(0, Nedge(tr))
theta[c(1:4, 15:16, 23:24)] <- 2
## sensitive to 'alpha' and 'sigma':
rTraitCont(tr, "OU", theta = theta, alpha=.1, sigma=.01)
### an imaginary model with stasis 0.5 time unit after a node, then
### BM evolution with sigma = 0.1:
foo <- function(x, l) {
  if (l <= 0.5) return(x)
  x + (1 - 0.5)*rnorm(1, 0, 0.1)
}
tr <- rcoal(20, br = runif)
rTraitCont(tr, foo, ancestor = TRUE)
### a cumulative Poisson process:
bar <- function(x, l) x + rpois(1, l)
(x <- rTraitCont(tr, bar, ancestor = TRUE))
plot(tr, show.tip.label = FALSE)
Y <- x[1:20]
A <- x[-(1:20)]
nodelabels(A)
tiplabels(Y)
```

---

rTraitDisc

*Discrete Character Simulation*

---

## Description

This function simulates the evolution of a discrete character along a phylogeny. If `model` is a character or a matrix, evolution is simulated with a Markovian model; the transition probabilities are calculated for each branch with  $P = e^{Qt}$  where  $Q$  is the rate matrix given by `model` and  $t$  is the branch length. The calculation is done recursively from the root. See Paradis (2006, p. 101) for a general introduction applied to evolution.

**Usage**

```
rTraitDisc(phy, model = "ER", k = if (is.matrix(model)) ncol(model) else 2,
           rate = 0.1, states = LETTERS[1:k], freq = rep(1/k, k),
           ancestor = FALSE, root.value = 1, ...)
```

**Arguments**

phy	an object of class "phylo".
model	a character, a square numeric matrix, or a function specifying the model (see details).
k	the number of states of the character.
rate	the rate of change used if model is a character; it is <i>not</i> recycled if model = "ARD" of model = "SYM".
states	the labels used for the states; by default "A", "B", ...
freq	a numeric vector giving the equilibrium relative frequencies of each state; by default the frequencies are equal.
ancestor	a logical value specifying whether to return the values at the nodes as well (by default, only the values at the tips are returned).
root.value	an integer giving the value at the root (by default, it's the first state). To have a random value, use root.value = sample(k).
...	further arguments passed to model if it is a function.

**Details**

There are three possibilities to specify model:

- A matrix: it must be a numeric square matrix; the diagonal is always ignored. The arguments k and rate are ignored.
- A character: these are the same short-cuts than in the function [ace](#): "ER" is an equal-rates model, "ARD" is an all-rates-different model, and "SYM" is a symmetrical model. Note that the argument rate must be of the appropriate length, i.e., 1,  $k(k-1)$ , or  $k(k-1)/2$  for the three models, respectively. The rate matrix  $Q$  is then filled column-wise.
- A function: it must be of the form `foo(x, l)` where x is the trait of the ancestor and l is the branch length. It must return the value of the descendant as an integer.

**Value**

A factor with names taken from the tip labels of phy. If ancestor = TRUE, the node labels are used if present, otherwise, "Node1", "Node2", etc.

**Author(s)**

Emmanuel Paradis

**References**

Paradis, E. (2006) *Analyses of Phylogenetics and Evolution with R*. New York: Springer.



**See Also**

[rTraitCont](#), [rTraitMult](#), [ace](#)

**Examples**

```

data(bird.orders)
### the two followings are the same:
rTraitDisc(bird.orders)
rTraitDisc(bird.orders, model = matrix(c(0, 0.1, 0.1, 0), 2))

### two-state model with irreversibility:
rTraitDisc(bird.orders, model = matrix(c(0, 0, 0.1, 0), 2))

### simple two-state model:
tr <- rcoal(n <- 40, br = runif)
x <- rTraitDisc(tr, ancestor = TRUE)
plot(tr, show.tip.label = FALSE)
nodelabels(pch = 19, col = x[-(1:n)])
tiplabels(pch = 19, col = x[1:n])

### an imaginary model with stasis 0.5 time unit after a node, then
### random evolution:
foo <- function(x, l) {
  if (l < 0.5) return(x)
  sample(2, size = 1)
}
tr <- rcoal(20, br = runif)
x <- rTraitDisc(tr, foo, ancestor = TRUE)
plot(tr, show.tip.label = FALSE)
co <- c("blue", "yellow")
cot <- c("white", "black")
Y <- x[1:20]
A <- x[-(1:20)]
nodelabels(A, bg = co[A], col = cot[A])
tiplabels(Y, bg = co[Y], col = cot[Y])

```

---

rTraitMult

*Multivariate Character Simulation*


---

**Description**

This function simulates the evolution of a multivariate set of traits along a phylogeny. The calculation is done recursively from the root.

**Usage**

```

rTraitMult(phy, model, p = 1, root.value = rep(0, p), ancestor = FALSE,
           asFactor = NULL, trait.labels = paste("x", 1:p, sep = ""), ...)

```

**Arguments**

phy	an object of class "phylo".
model	a function specifying the model (see details).
p	an integer giving the number of traits.
root.value	a numeric vector giving the values at the root.
ancestor	a logical value specifying whether to return the values at the nodes as well (by default, only the values at the tips are returned).
asFactor	the indices of the traits that are returned as factors (discrete traits).
trait.labels	a vector of mode character giving the names of the traits.
...	further arguments passed to model if it is a function.

**Details**

The model is specified with an R function of the form `foo(x, l)` where `x` is a vector of the traits of the ancestor and `l` is the branch length. Other arguments may be added. The function must return a vector of length `p`.

**Value**

A data frame with `p` columns whose names are given by `trait.labels` and row names taken from the labels of the tree.

**Author(s)**

Emmanuel Paradis

**See Also**

[rTraitCont](#), [rTraitDisc](#), [ace](#)

**Examples**

```
## correlated evolution of 2 continuous traits:
mod <- function(x, l) {
  y1 <- rnorm(1, x[1] + 0.5*x[2], 0.1)
  y2 <- rnorm(1, 0.5*x[1] + x[2], 0.1)
  c(y1, y2)
}
set.seed(11)
tr <- makeNodeLabel(rcoal(20))
x <- rTraitMult(tr, mod, 2, ancestor = TRUE)
op <- par(mfcol = c(2, 1))
plot(x, type = "n")
text(x, labels = rownames(x), cex = 0.7)
oq <- par(mar = c(0, 1, 0, 1), xpd = TRUE)
plot(tr, font = 1, cex = 0.7)
odelabels(tr$node.label, cex = 0.7, adj = 1)
par(c(op, oq))
```

---

rtree *Generates Random Trees*

---

### Description

These functions generate trees by splitting randomly the edges (`rtree`) or randomly clustering the tips (`rcoal`). `rtree` generates general trees, and `rcoal` generates coalescent trees. The algorithms are described in Paradis (2012).

### Usage

```
rtree(n, rooted = TRUE, tip.label = NULL, br = runif, ...)
rcoal(n, tip.label = NULL, br = "coalescent", ...)
rmtree(N, n, rooted = TRUE, tip.label = NULL, br = runif, ...)
```

### Arguments

<code>n</code>	an integer giving the number of tips in the tree.
<code>rooted</code>	a logical indicating whether the tree should be rooted (the default).
<code>tip.label</code>	a character vector giving the tip labels; if not specified, the tips "t1", "t2", ..., are given.
<code>br</code>	one of the following: (i) an R function used to generate the branch lengths ( <code>rtree</code> ; use <code>NULL</code> to simulate only a topology), or the coalescence times ( <code>rcoal</code> ); (ii) a character to simulate a genuine coalescent tree for <code>rcoal</code> (the default); or (iii) a numeric vector for the branch lengths or the coalescence times.
<code>...</code>	further argument(s) to be passed to <code>br</code> .
<code>N</code>	an integer giving the number of trees to generate.

### Details

The trees generated are bifurcating. If `rooted = FALSE` in (`rtree`), the tree is trifurcating at its root.

The default function to generate branch lengths in `rtree` is `runif`. If further arguments are passed to `br`, they need to be tagged (e.g., `min = 0`, `max = 10`).

`rmtree` calls successively `rtree` and set the class of the returned object appropriately.

### Value

An object of class "phylo" or of class "multiPhylo" in the case of `rmtree`.

### Author(s)

Emmanuel Paradis

## References

Paradis, E. (2012) *Analysis of Phylogenetics and Evolution with R (Second Edition)*. New York: Springer.

## See Also

[stree](#), [rlineage](#)

## Examples

```
layout(matrix(1:9, 3, 3))
### Nine random trees:
for (i in 1:9) plot(rtree(20))
### Nine random cladograms:
for (i in 1:9) plot(rtree(20, FALSE), type = "c")
### generate 4 random trees of bird orders:
data(bird.orders)
layout(matrix(1:4, 2, 2))
for (i in 1:4)
  plot(rcoal(23, tip.label = bird.orders$tip.label), no.margin = TRUE)
layout(matrix(1))
```

---

SDM

---

*Construction of Consensus Distance Matrix With SDM*


---

## Description

This function implements the SDM method of Criscuolo et al. (2006) for a set of  $n$  distance matrices.

## Usage

```
SDM(...)
```

## Arguments

...                     $2n$  elements (with  $n > 1$ ), the first  $n$  elements are the distance matrices: these can be (symmetric) matrices, objects of class "dist", or a mix of both. The next  $n$  elements are the sequence length from which the matrices have been estimated (can be seen as a degree of confidence in matrices).

## Details

Reconstructs a consensus distance matrix from a set of input distance matrices on overlapping sets of taxa. Potentially missing values in the supermatrix are represented by NA. An error is returned if the input distance matrices can not resolve to a consensus matrix.

**Value**

a 2-element list containing a distance matrix labelled by the union of the set of taxa of the input distance matrices, and a variance matrix associated to the returned distance matrix.

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

**References**

Criscuolo, A., Berry, V., Douzery, E. J. P. , and Gascuel, O. (2006) SDM: A fast distance-based approach for (super)tree building in phylogenomics. *Systematic Biology*, **55**, 740–755.

**See Also**

[bionj](#), [fastme](#), [njs](#), [mvrs](#), [triangMtd](#)

---

seg.sites

*Find Segregating Sites in DNA Sequences*

---

**Description**

This function gives the indices of segregating (polymorphic) sites in a sample of DNA sequences.

**Usage**

```
seg.sites(x)
```

**Arguments**

x                    a matrix or a list which contains the DNA sequences.

**Details**

If the sequences are in a list, all the sequences must be of the same length. Ambiguous nucleotides are ignored.

**Value**

A numeric (integer) vector giving the indices of the segregating sites.

**Note**

The present version looks for the sites which are “variable” in the data in terms of different *letters*. This may give unexpected results if there are ambiguous bases in the data.

**Author(s)**

Emmanuel Paradis

**See Also**

[base.freq](#), [theta.s](#), [nuc.div](#)

**Examples**

```
data(woodmouse)
y <- seg.sites(woodmouse)
y
length(y)
```

---

skyline

*Skyline Plot Estimate of Effective Population Size*


---

**Description**

skyline computes the *generalized skyline plot* estimate of effective population size from an estimated phylogeny. The demographic history is approximated by a step-function. The number of parameters of the skyline plot (i.e. its smoothness) is controlled by a parameter epsilon.

find.skyline.epsilon searches for an optimal value of the epsilon parameter, i.e. the value that maximizes the AICc-corrected log-likelihood (logL.AICc).

**Usage**

```
skyline(x, ...)
## S3 method for class 'phylo'
skyline(x, ...)
## S3 method for class 'coalescentIntervals'
skyline(x, epsilon=0, ...)
## S3 method for class 'collapsedIntervals'
skyline(x, old.style=FALSE, ...)
find.skyline.epsilon(ci, GRID=1000, MINEPS=1e-6, ...)
```

**Arguments**

x	Either an ultrametric tree (i.e. an object of class "phylo"), or coalescent intervals (i.e. an object of class "coalescentIntervals"), or collapsed coalescent intervals (i.e. an object of class "collapsedIntervals").
epsilon	collapsing parameter that controls the amount of smoothing (allowed range: from 0 to ci\$total.depth, default value: 0). This is the same parameter as in <a href="#">collapsed.intervals</a> .
old.style	Parameter to choose between two slightly different variants of the generalized skyline plot (Strimmer and Pybus, pers. comm.). The default value FALSE is recommended.
ci	coalescent intervals (i.e. an object of class "coalescentIntervals")
GRID	Parameter for the grid search for epsilon in find.skyline.epsilon.
MINEPS	Parameter for the grid search for epsilon in find.skyline.epsilon.
...	Any of the above parameters.

**Details**

skyline implements the *generalized skyline plot* introduced in Strimmer and Pybus (2001). For  $\epsilon = 0$  the generalized skyline plot degenerates to the *classic skyline plot* described in Pybus et al. (2000). The latter is in turn directly related to lineage-through-time plots (Nee et al., 1995).

**Value**

skyline returns an object of class "skyline" with the following entries:

time	A vector with the time at the end of each coalescent interval (i.e. the accumulated interval lengths from the beginning of the first interval to the end of an interval)
interval.length	A vector with the length of each interval.
population.size	A vector with the effective population size of each interval.
parameter.count	Number of free parameters in the skyline plot.
epsilon	The value of the underlying smoothing parameter.
logL	Log-likelihood of skyline plot (see Strimmer and Pybus, 2001).
logL.AICc	AICc corrected log-likelihood (see Strimmer and Pybus, 2001).
find.skyline.epsilon	returns the value of the epsilon parameter that maximizes logL.AICc.

**Author(s)**

Korbinian Strimmer (<http://www.stat.uni-muenchen.de/~strimmer/>)

**References**

- Strimmer, K. and Pybus, O. G. (2001) Exploring the demographic history of DNA sequences using the generalized skyline plot. *Molecular Biology and Evolution*, **18**, 2298–2305.
- Pybus, O. G, Rambaut, A. and Harvey, P. H. (2000) An integrated framework for the inference of viral population history from reconstructed genealogies. *Genetics*, **155**, 1429–1437.
- Nee, S., Holmes, E. C., Rambaut, A. and Harvey, P. H. (1995) Inferring population history from molecular phylogenies. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, **349**, 25–31.

**See Also**

[coalescent.intervals](#), [collapsed.intervals](#), [skylineplot](#), [ltt.plot](#).

**Examples**

```

# get tree
data("hivtree.newick") # example tree in NH format
tree.hiv <- read.tree(text = hivtree.newick) # load tree

# corresponding coalescent intervals
ci <- coalescent.intervals(tree.hiv) # from tree

# collapsed intervals
cl1 <- collapsed.intervals(ci,0)
cl2 <- collapsed.intervals(ci,0.0119)

#### classic skyline plot ####
sk1 <- skyline(cl1)      # from collapsed intervals
sk1 <- skyline(ci)      # from coalescent intervals
sk1 <- skyline(tree.hiv) # from tree
sk1

plot(skyline(tree.hiv))
skylineplot(tree.hiv) # shortcut

plot(sk1, show.years=TRUE, subst.rate=0.0023, present.year = 1997)

#### generalized skyline plot ####

sk2 <- skyline(cl2)      # from collapsed intervals
sk2 <- skyline(ci, 0.0119) # from coalescent intervals
sk2 <- skyline(tree.hiv, 0.0119) # from tree
sk2

plot(sk2)

# classic and generalized skyline plot together in one plot
plot(sk1, show.years=TRUE, subst.rate=0.0023, present.year = 1997, col=c(grey(.8),1))
lines(sk2, show.years=TRUE, subst.rate=0.0023, present.year = 1997)
legend(.15,500, c("classic", "generalized"), col=c(grey(.8),1),lty=1)

# find optimal epsilon parameter using AICc criterion
find.skyline.epsilon(ci)

sk3 <- skyline(ci, -1) # negative epsilon also triggers estimation of epsilon
sk3$epsilon

```



**Description**

These functions provide various ways to draw *skyline plot* graphs on the current graphical device. Note that `skylineplot(z, ...)` is simply a shortcut for `plot(skyline(z, ...))`. The skyline plot itself is an estimate of effective population size through time, and is computed using the function `skyline`.

**Usage**

```
## S3 method for class 'skyline'
plot(x, show.years=FALSE, subst.rate, present.year, ...)
## S3 method for class 'skyline'
lines(x, show.years=FALSE, subst.rate, present.year, ...)
skylineplot(z, ...)
skylineplot.deluxe(tree, ...)
```

**Arguments**

<code>x</code>	skyline plot data (i.e. an object of class "skyline").
<code>z</code>	Either an ultrametric tree (i.e. an object of class "phylo"), or coalescent intervals (i.e. an object of class "coalescentIntervals"), or collapsed coalescent intervals (i.e. an object of class "collapsedIntervals").
<code>tree</code>	ultrametric tree (i.e. an object of class "phylo").
<code>show.years</code>	option that determines whether the time is plotted in units of of substitutions (default) or in years (requires specification of substitution rate and year of present).
<code>subst.rate</code>	substitution rate (see option <code>show.years</code> ).
<code>present.year</code>	present year (see option <code>show.years</code> ).
<code>...</code>	further arguments to be passed on to <code>skyline()</code> and <code>plot()</code> .

**Details**

See `skyline` for more details (incl. references) about the skyline plot method.

**Author(s)**

Korbinian Strimmer (<http://www.stat.uni-muenchen.de/~strimmer/>)

**See Also**

`plot` and `lines` for the basic plotting function in R, `coalescent.intervals`, `skyline`

**Examples**

```
# get tree
data("hivtree.newick") # example tree in NH format
tree.hiv <- read.tree(text = hivtree.newick) # load tree

#### classic skyline plot
```

```

skylineplot(tree.hiv) # shortcut

#### plot classic and generalized skyline plots and estimate epsilon
sk.opt <- skylineplot.deluxe(tree.hiv)
sk.opt$epsilon

#### classic and generalized skyline plot ####
sk1 <- skyline(tree.hiv)
sk2 <- skyline(tree.hiv, 0.0119)

# use years rather than substitutions as unit for the time axis
plot(sk1, show.years=TRUE, subst.rate=0.0023, present.year = 1997, col=c(grey(.8),1))
lines(sk2, show.years=TRUE, subst.rate=0.0023, present.year = 1997)
legend(.15,500, c("classic", "generalized"), col=c(grey(.8),1),lty=1)

#### various skyline plots for different epsilons
layout(mat= matrix(1:6,2,3,byrow=TRUE))
ci <- coalescent.intervals(tree.hiv)
plot(skyline(ci, 0.0));title(main="0.0")
plot(skyline(ci, 0.007));title(main="0.007")
plot(skyline(ci, 0.0119),col=4);title(main="0.0119")
plot(skyline(ci, 0.02));title(main="0.02")
plot(skyline(ci, 0.05));title(main="0.05")
plot(skyline(ci, 0.1));title(main="0.1")
layout(mat= matrix(1:1,1,1,byrow=TRUE))

```

---

slowinskiguyer.test     *Slowinski-Guyer Test of Homogeneous Diversification*

---

## Description

This function performs the Slowinski–Guyer test that a trait or variable does not increase diversification rate.

## Usage

```
slowinskiguyer.test(x, detail = FALSE)
```

## Arguments

x	a matrix or a data frame with at least two columns: the first one gives the number of species in clades with a trait supposed to increase diversification rate, and the second one the number of species in the corresponding sister-clade without the trait. Each row represents a pair of sister-clades.
detail	if TRUE, the individual P-values are appended.

## Details

The Slowinski–Guyer test compares a series of sister-clades where one of the two is characterized by a trait supposed to increase diversification rate. The null hypothesis is that the trait does not affect diversification. If the trait decreased diversification rate, then the null hypothesis cannot be rejected.

The present function has mainly a historical interest. The Slowinski–Guyer test generally performs poorly: see Paradis (2012) alternatives and the functions cited below.

## Value

a data frame with the  $\chi^2$ , the number of degrees of freedom, and the  $P$ -value. If `detail = TRUE`, a list is returned with the data frame and a vector of individual  $P$ -values for each pair of sister-clades.

## Author(s)

Emmanuel Paradis

## References

Paradis, E. (2012) Shift in diversification in sister-clade comparisons: a more powerful test. *Evolution*, **66**, 288–295.

Slowinski, J. B. and Guyer, C. (1993) Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist*, **142**, 1019–1024.

## See Also

[balance](#), [mconwaysims.test](#), [diversity.contrast.test](#), [richness.yule.test](#), [rc](#) in **geiger**, [shift.test](#) in **apTreeshape**

## Examples

```
### from Table 1 in Slowinski and Guyer(1993):
viviparous <- c(98, 8, 193, 36, 7, 128, 2, 3, 23, 70)
oviparous <- c(234, 17, 100, 4, 1, 12, 6, 1, 481, 11)
x <- data.frame(viviparous, oviparous)
slowinskiguyer.test(x, TRUE) # 'P ~ 0.32' in the paper
xalt <- x
xalt[3, 2] <- 1
slowinskiguyer.test(xalt)
```

speciesTree

*Species Tree Estimation***Description**

This function calculates the species tree from a set of gene trees.

**Usage**

```
speciesTree(x, FUN = min)
```

**Arguments**

**x** a list of trees, e.g., an object of class "multiPhylo".  
**FUN** a function used to compute the divergence times of each pair of tips.

**Details**

For all trees in *x*, the divergence time of each pair of tips is calculated: these are then ‘summarized’ with *FUN* to build a new distance matrix used to calculate the species tree with a single-linkage hierarchical clustering. The default for *FUN* computes the maximum tree (maxtree) of Liu et al. (2010). Using *FUN* = mean gives the shallowest divergence tree of Maddison and Knowles (2006).

**Value**

an object of class "phylo".

**Author(s)**

Emmanuel Paradis

**References**

Liu, L., Yu, L. and Pearl, D. K. (2010) Maximum tree: a consistent estimator of the species tree. *Journal of Mathematical Biology*, **60**, 95–106.  
 Maddison, W. P. and Knowles, L. L. (2006) Inferring phylogeny despite incomplete lineage sorting. *Systematic Biology*, **55**, 21–30.

**Examples**

```
### example in Liu et al. (2010):
tr1 <- read.tree(text = "((B:0.05,C:0.05):0.01,D:0.06):0.04,A:0.1);")
tr2 <- read.tree(text = "((A:0.07,C:0.07):0.02,D:0.09):0.03,B:0.12);")
TR <- c(tr1, tr2)
TSmax <- speciesTree(TR) # MAXTREE
TSsha <- speciesTree(TR, mean) # shallowest divergence

layout(matrix(1:4, 1))
```

```
## playing with 'x.lim' is not so complicated
## but this will be improved someday
plot(tr1, "c", d = "u", y.lim = c(-0.07, 0.1), font = 1)
axisPhylo(4); title("Gene tree 1")
plot(tr2, "c", d = "u", y.lim = c(-0.05, 0.12), font = 1)
axisPhylo(4); title("Gene tree 2")
plot(TSmax, "c", d = "u", y.lim = c(-0.1, 0.07), font = 1)
axisPhylo(4); title("Species tree inferred\nby MAXTREE")
plot(TSsha, "c", d = "u", y.lim = c(0, 0.17), font = 1)
axisPhylo(4); title("Species tree inferred\nby Shallowest Divergence")
```

---

stree

*Generates Systematic Regular Trees*


---

## Description

This function generates trees with regular shapes.

## Usage

```
stree(n, type = "star", tip.label = NULL)
```

## Arguments

n	an integer giving the number of tips in the tree.
type	a character string specifying the type of tree to generate; four choices are possible: "star", "balanced", "left", "right", or any unambiguous abbreviation of these.
tip.label	a character vector giving the tip labels; if not specified, the tips "t1", "t2", ..., are given.

## Details

The types of trees generated are:

- "star" a star (or comb) tree with a single internal node.
- "balanced" a fully balanced dichotomous rooted tree; n must be a power of 2 (2, 4, 8, ...).
- "left" a fully unbalanced rooted tree where the largest clade is on the left-hand side when the tree is plotted upwards.
- "right" same than above but in the other direction.

## Value

An object of class "phylo".

## Author(s)

Emmanuel Paradis

**See Also**

[compute.brlen](#), [rtree](#)

**Examples**

```
layout(matrix(1:4, 2, 2))
plot(stree(100))
plot(stree(128, "balanced"))
plot(stree(100, "left"))
plot(stree(100, "right"))
```

---

subtreeplot

*Zoom on a Portion of a Phylogeny by Successive Clicks*

---

**Description**

This function plots simultaneously a whole phylogenetic tree (supposedly large) and a portion of it determined by clicking on the nodes of the phylogeny. On exit, returns the last subtree visualized.

**Usage**

```
subtreeplot(x, wait=FALSE, ...)
```

**Arguments**

<code>x</code>	an object of class "phylo".
<code>wait</code>	a logical indicating whether the node being processed should be printed (useful for big phylogenies).
<code>...</code>	further arguments passed to <code>plot.phylo</code> .

**Details**

This function aims at easily exploring very large trees. The main argument is a phylogenetic tree, and the second one is a logical indicating whether a waiting message should be printed while the calculation is being processed.

The whole tree is plotted on the left-hand side in half of the device. The subtree is plotted on the right-hand side in the other half. The user clicks on the nodes in the complete tree and the subtree corresponding to this node is plotted in the right-hand side. There is no limit for the number of clicks that can be done. On exit, the subtree on the right hand side is returned.

To use a subtree as the new tree in which to zoom, the user has to use the function many times. This can however be done in a single command line (see example 2).

**Author(s)**

Damien de Vienne <damien.de-vienne@u-psud.fr>

**See Also**

[plot.phylo](#), [drop.tip](#), [subtrees](#)

**Examples**

```
## Not run:
#example 1: simple
tree1 <- rtree(50)
tree2 <- subtrees(tree1, wait = TRUE) # on exit, tree2 will be a subtree of tree1

#example 2: more than one zoom
tree1 <- rtree(60)
tree2 <- subtrees(subtrees(subtrees(tree1))) # allow three successive zooms

## End(Not run)
```

---

subtrees

*All subtrees of a Phylogenetic Tree*

---

**Description**

This function returns a list of all the subtrees of a phylogenetic tree.

**Usage**

```
subtrees(tree, wait=FALSE)
```

**Arguments**

tree	an object of class "phylo".
wait	a logical indicating whether the node being processed should be printed (useful for big phylogenies).

**Value**

subtrees returns a list of trees of class "phylo" and returns invisibly for each subtree a list with the following components:

```
tip.label
node.label
Ntip
Nnode
```

**Author(s)**

Damien de Vienne <damien.de-vienne@u-psud.fr>

**See Also**

[zoom](#), [subtreepLOT](#) for functions extracting particular subtrees.

**Examples**

```
### Random tree with 12 leaves
phy<-rtree(12)
par(mfrow=c(4,3))
plot(phy, sub="Complete tree")

### Extract the subtrees
l<-subtrees(phy)

### plot all the subtrees
for (i in 1:11) plot(l[[i]], sub=paste("Node", l[[i]]$node.label[1]))
par(mfrow=c(1,1))
```

---

summary.phylo

---

*Print Summary of a Phylogeny*


---

**Description**

The first function prints a compact summary of a phylogenetic tree (an object of class "phylo"). The three other functions return the number of tips, nodes, or edges, respectively.

**Usage**

```
## S3 method for class 'phylo'
summary(object, ...)
Ntip(phy)
Nnode(phy, internal.only = TRUE)
Nedge(phy)
```

**Arguments**

`object`, `phy` an object of class "phylo".  
`...` further arguments passed to or from other methods.  
`internal.only` a logical indicating whether to return the number of internal nodes only (the default), or of internal and terminal (tips) nodes (if FALSE).

**Details**

The summary includes the numbers of tips and of nodes, summary statistics of the branch lengths (if they are available) with mean, variance, minimum, first quartile, median, third quartile, and maximum, listing of the first ten tip labels, and (if available) of the first ten node labels. It is also printed whether some of these optional elements (branch lengths, node labels, and root edge) are not found in the tree.

summary simply prints its results on the standard output and is not meant for programming.



**Value**

A NULL value in the case of summary, a single numeric value for the three other functions.

**Author(s)**

Emmanuel Paradis

**See Also**

[read.tree](#), [summary](#) for the generic R function, [multiphylo](#), [c.phylo](#)

**Examples**

```
data(bird.families)
summary(bird.families)
Ntip(bird.families)
Nnode(bird.families)
Nedge(bird.families)
```

---

treePop

*Tree Popping*

---

**Description**

Method for reconstructing phylogenetic trees from an object of class splits using tree popping.

**Usage**

```
treePop(obj)
```

**Arguments**

obj            an object of class "bitsplit".

**Value**

an object of class "phylo" which displays all the splits in the input object.

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

---

trex

*Tree Explorer With Multiple Devices*


---

### Description

This function requires a plotted tree: the user is invited to click close to a node and the corresponding subtree (or clade) is plotted on a new window.

### Usage

```
trex(phy, title = TRUE, subbg = "lightyellow3",
     return.tree = FALSE, ...)
```

### Arguments

phy	an object of class "phylo".
title	a logical or a character string (see details).
subbg	a character string giving the background colour for the subtree.
return.tree	a logical: if TRUE, the subtree is returned after being plotted and the operation is stopped.
...	further arguments to pass to plot.phylo.

### Details

This function works with a tree (freshly) plotted on an interactive graphical device (i.e., not a file). After calling `trex`, the user clicks close to a node of the tree, then the clade from this node is plotted on a *new* window. The user can click as many times on the main tree: the clades are plotted successively on the *same* new window. The process is stopped by a right-click. If the user clicks too close to the tips, a message "Try again!" is printed.

Each time `trex` is called, the subtree is plotted on a new window without closing or deleting those possibly already plotted. They may be distinguished with the options `title` and/or `subbg`.

In all cases, the device where `phy` is plotted is the active window after the operation. It should *not* be closed during the whole process.

If `title = TRUE`, a default title is printed on the new window using the node label, or the node number if there are no node labels in the tree. If `title = FALSE`, no title is printed. If `title` is a character string, it is used for the title.

### Value

an object of class "phylo" if `return.tree = TRUE`

### Author(s)

Emmanuel Paradis

**See Also**

[plot.phylo](#), [identify.phylo](#)

**Examples**

```
## Not run:
tr <- rcoal(1000)
plot(tr, show.tip.label = FALSE)
trex(tr) # left-click as many times as you want, then right-click
tr <- makeNodeLabel(tr)
trex(tr, subbg = "lightgreen") # id.

## generate a random colour with control on the darkness:
rRGB <- function(a, b)
  rgb(runif(1, a, b), runif(1, a, b), runif(1, a, b))

### with a random pale background:
trex(tr, subbg = rRGB(0.8, 1))
## the above can be called many times...
graphics.off() # close all graphical devices

## End(Not run)
```

---

triangMtd

*Tree Reconstruction Based on the Triangles Method*

---

**Description**

Fast distance-based construction method. Should only be used when distance measures are fairly reliable.

**Usage**

```
triangMtd(X)
triangMtds(X)
```

**Arguments**

X                    a distance matrix.

**Value**

an object of class "phylo".

**Author(s)**

Andrei Popescu <niteloserpopescu@gmail.com>

**References**

[http://archive.numdam.org/ARCHIVE/RO/RO\\_2001\\_\\_35\\_2/RO\\_2001\\_\\_35\\_2\\_283\\_0/RO\\_2001\\_\\_35\\_2\\_283\\_0.pdf](http://archive.numdam.org/ARCHIVE/RO/RO_2001__35_2/RO_2001__35_2_283_0/RO_2001__35_2_283_0.pdf)

**See Also**

[nj](#), [bionj](#), [fastme](#), [njs](#), [mvrs](#), [SDM](#)

**Examples**

```
data(woodmouse)
tr <- triangMtd(dist.dna(woodmouse))
plot(tr)
```

---

unique.multiPhylo      *Removes Duplicate Trees*

---

**Description**

This function scans a list of trees, and returns a list with the duplicate trees removed. By default the labelled topologies are compared.

**Usage**

```
## S3 method for class 'multiPhylo'
unique(x, incomparables = FALSE,
       use.edge.length = FALSE,
       use.tip.label = TRUE, ...)
```

**Arguments**

`x`                    an object of class "multiPhylo".

`incomparables`       unused (for compatibility with the generic).

`use.edge.length`     a logical specifying whether to consider the edge lengths in the comparisons; the default is FALSE.

`use.tip.label`       a logical specifying whether to consider the tip labels in the comparisons; the default is TRUE.

`...`                further arguments passed to or from other methods.

**Value**

an object of class "multiPhylo" with an attribute "old.index" indicating which trees of the original list are similar (the tree of smaller index is taken as reference).

**Author(s)**

Emmanuel Paradis

**See Also**

`all.equal.phylo`, `unique` for the generic R function, `read.tree`, `read.nexus`

**Examples**

```
TR <- rmtree(50, 4)
length(unique(TR)) # not always 15...
howmanytrees(4)
```

---

varcomp

*Compute Variance Component Estimates*

---

**Description**

Get variance component estimates from a fitted lme object.

**Usage**

```
varcomp(x, scale = FALSE, cum = FALSE)
```

**Arguments**

x	A fitted lme object
scale	Scale all variance so that they sum to 1
cum	Send cumulative variance components.

**Details**

Variance computations is done as in Venables and Ripley (2002).

**Value**

A named vector of class `varcomp` with estimated variance components.

**Author(s)**

Julien Dutheil <julien.dutheil@univ-montp2.fr>

**References**

Venables, W. N. and Ripley, B. D. (2002) *Modern Applied Statistics with S (Fourth Edition)*. New York: Springer-Verlag.

**See Also**[lme](#)**Examples**

```

data(carnivora)
library(nlme)
m <- lme(log10(SW) ~ 1, random = ~ 1|Order/SuperFamily/Family/Genus, data=carnivora)
v <- varcomp(m, TRUE, TRUE)
plot(v)

```

varCompPhylip

*Variance Components with Orthonormal Contrasts***Description**

This function calls Phylip's contrast program and returns the phylogenetic and phenotypic variance-covariance components for one or several traits. There can be several observations per species.

**Usage**

```
varCompPhylip(x, phy, exec = NULL)
```

**Arguments**

x	a numeric vector, a matrix (or data frame), or a list.
phy	an object of class "phylo".
exec	a character string giving the name of the executable contrast program (see details).

**Details**

The data *x* can be in several forms: (i) a numeric vector if there is single trait and one observation per species; (ii) a matrix or data frame if there are several traits (as columns) and a single observation of each trait for each species; (iii) a list of vectors if there is a single trait and several observations per species; (iv) a list of matrices or data frames: same than (ii) but with several traits and the rows are individuals.

If *x* has names, its values are matched to the tip labels of *phy*, otherwise its values are taken to be in the same order than the tip labels of *phy*.

Phylip (version 3.68 or higher) must be accessible on your computer. If you have a Unix-like operating system, the executable name is assumed to be "phylip contrast" (as in Debian); otherwise it is set to "contrast". If this doesn't suit your system, use the option *exec* accordingly. If the executable is not in the path, you may need to specify it, e.g., *exec* = "C:/Program Files/Phylip/contrast".

**Value**

a list with elements `varA` and `varE` with the phylogenetic (additive) and phenotypic (environmental) variance-covariance matrices. If a single trait is analyzed, these contains its variances.

**Author(s)**

Emmanuel Paradis

**References**

Felsenstein, J. (2004) Phylip (Phylogeny Inference Package) version 3.68. Department of Genetics, University of Washington, Seattle, USA. <http://evolution.genetics.washington.edu/phylip/phylip.html>.

Felsenstein, J. (2008) Comparative methods with sampling error and within-species variation: Contrasts revisited and revised. *American Naturalist*, **171**, 713–725.

**See Also**

[pic](#), [pic.ortho](#), [compar.lynch](#)

**Examples**

```
## Not run:
tr <- rcoal(30)
### Five traits, one observation per species:
x <- replicate(5, rTraitCont(tr, sigma = 1))
varCompPhylip(x, tr) # varE is small
x <- replicate(5, rnorm(30))
varCompPhylip(x, tr) # varE is large
### Five traits, ten observations per species:
x <- replicate(30, replicate(5, rnorm(10)), simplify = FALSE)
varCompPhylip(x, tr)

## End(Not run)
```

**Description**

This function computes the expected variances and covariances of a continuous trait assuming it evolves under a given model.

This is a generic function with methods for objects of class "phyl" and "corPhyl".

**Usage**

```
vcv(phy, ...)  
## S3 method for class 'phylo'  
vcv(phy, model = "Brownian", corr = FALSE, ...)  
## S3 method for class 'corPhyl'  
vcv(phy, corr = FALSE, ...)
```

**Arguments**

phy	an object of the correct class (see above).
model	a character giving the model used to compute the variances and covariances; only "Brownian" is available (for other models, a correlation structure may be used).
corr	a logical indicating whether the correlation matrix should be returned (TRUE); by default the variance-covariance matrix is returned (FALSE).
...	further arguments to be passed to or from other methods.

**Value**

a numeric matrix with the names of the tips as colnames and rownames.

**Note**

Do not confuse this function with [vcov](#) which computes the variance-covariance matrix among parameters of a fitted model object.

**Author(s)**

Emmanuel Paradis

**References**

Garland, T. Jr. and Ives, A. R. (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist*, **155**, 346–364.

**See Also**

[corBrownian](#), [corMartins](#), [corGrafen](#), [corPagel](#), [corBlomberg](#)

**Examples**

```
tr <- rtree(5)  
## all are the same:  
vcv(tr)  
vcv(corBrownian(1, tr))  
vcv(corPagel(1, tr))
```



---

weight.taxo	<i>Define Similarity Matrix</i>
-------------	---------------------------------

---

**Description**

weight.taxo computes a matrix whose entries [i, j] are set to 1 if x[i] == x[j], 0 otherwise.

weight.taxo2 computes a matrix whose entries [i, j] are set to 1 if x[i] == x[j] AND y[i] != y[j], 0 otherwise.

The diagonal [i, i] is always set to 0.

The returned matrix can be used as a weight matrix in [Moran.I](#). x and y may be vectors of factors.

See further details in vignette("MoranI").

**Usage**

```
weight.taxo(x)
weight.taxo2(x, y)
```

**Arguments**

x, y            a vector or a factor.

**Value**

a square numeric matrix.

**Author(s)**

Emmanuel Paradis

**See Also**

[Moran.I](#), [correlogram.formula](#)

---

where	<i>Find Patterns in DNA Sequences</i>
-------	---------------------------------------

---

**Description**

This function finds patterns in a single or a set of DNA sequences.

**Usage**

```
where(x, pattern)
```

**Arguments**

x                    an object of class "DNABin".  
pattern            a character string to be searched in x.

**Details**

If x is a vector, the function returns a single vector giving the position(s) where the pattern was found. If x is a matrix or a list, it returns a list with the positions of the pattern for each sequence.

Patterns may be overlapping. For instance, if pattern = "tata" and the sequence starts with 'tatata', then the vector returned will be c(1, 3).

**Value**

a vector of integers or a list of such vectors.

**Author(s)**

Emmanuel Paradis

**See Also**

[DNABin](#), [image.DNABin](#)

**Examples**

```
data(woodmouse)
where(woodmouse, "tata")
```

---

which.edge

*Identifies Edges of a Tree*

---

**Description**

This function identifies the edges that belong to a group (possibly non-monophyletic) specified as a set of tips.

**Usage**

```
which.edge(phy, group)
```

**Arguments**

phy                an object of class "phylo".  
group             a vector of mode numeric or character specifying the tips for which the edges are to be identified.

**Details**

The group of tips specified in 'group' may be non-monophyletic (paraphyletic or polyphyletic), in which case all edges from the tips to their most recent common ancestor are identified.

The identification is made with the indices of the rows of the matrix 'edge' of the "phylo" object.

**Value**

a numeric vector.

**Author(s)**

Emmanuel Paradis

**See Also**

[bind.tree](#), [drop.tip](#), [root](#)

---

woodmouse

*Cytochrome b Gene Sequences of Woodmice*

---

**Description**

This is a set of 15 sequences of the mitochondrial gene cytochrome *b* of the woodmouse (*Apodemus sylvaticus*) which is a subset of the data analysed by Michaux et al. (2003). The full data set is available through GenBank (accession numbers AJ511877 to AJ511987).

**Usage**

```
data(woodmouse)
```

**Format**

The data are stored in an ASCII file using the sequential format for DNA sequences which is read with 'read.dna()'.

**Source**

Michaux, J. R., Magnanou, E., Paradis, E., Nieberding, C. and Libois, R. (2003) Mitochondrial phylogeography of the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Molecular Ecology*, **12**, 685–697.

**See Also**

[read.dna](#), [DNABin](#), [dist.dna](#)

**Examples**

```
data(woodmouse)
str(woodmouse)
```

write.dna

*Write DNA Sequences in a File***Description**

This function writes in a file a list of DNA sequences in sequential, interleaved, or FASTA format.

**Usage**

```
write.dna(x, file, format = "interleaved", append = FALSE,
          nbcpl = 6, colsep = " ", colw = 10, indent = NULL,
          blocksep = 1)
```

**Arguments**

x	a list or a matrix of DNA sequences.
file	a file name specified by either a variable of mode character, or a double-quoted string.
format	a character string specifying the format of the DNA sequences. Three choices are possible: "interleaved", "sequential", or "fasta", or any unambiguous abbreviation of these.
append	a logical, if TRUE the data are appended to the file without erasing the data possibly existing in the file, otherwise the file (if it exists) is overwritten (FALSE the default).
nbcpl	a numeric specifying the number of columns per row (6 by default); may be negative implying that the nucleotides are printed on a single line.
colsep	a character used to separate the columns (a single space by default).
colw	a numeric specifying the number of nucleotides per column (10 by default).
indent	a numeric or a character specifying how the blocks of nucleotides are indented (see details).
blocksep	a numeric specifying the number of lines between the blocks of nucleotides (this has an effect only if 'format = "interleaved"').

**Details**

Three formats are supported in the present function: see the help page of [read.dna](#) and the references below for a description.

If the sequences have no names, then they are given "1", "2", ... as names in the file.

With the interleaved and sequential formats, the sequences must be all of the same length. The names of the sequences are not truncated.

The argument `indent` specifies how the rows of nucleotides are indented. In the interleaved and sequential formats, the rows with the taxon names are never indented; the subsequent rows are indented with 10 spaces by default (i.e., if `indent = NULL`). In the FASTA format, the rows are not indented by default. This default behaviour can be modified by specifying a value to `indent`: the

rows are then indented with “indent” (if it is a character) or ‘indent’ spaces (if it is a numeric). For example, specifying indent = " " or indent = 3 will have the same effect (use indent = "\t" for a tabulation).

The different options are intended to give flexibility in formatting the sequences. For instance, if the sequences are very long it may be judicious to remove all the spaces between columns (colsep = ""), in the margins (indent = 0), and between the blocks (blocksep = 0) to produce a smaller file.

### Value

None (invisible ‘NULL’).

### Note

Specifying a negative value for ‘nbcot’ (meaning that the nucleotides are printed on a single line) gives the same output for the interleaved and sequential formats.

The names of the sequences may be truncated with the function `makeLabel`. In particular, Clustal is limited to 30 characters, and PHYLIP seems limited to 99 characters.

### Author(s)

Emmanuel Paradis

### References

Anonymous. FASTA format description. <http://www.ncbi.nlm.nih.gov/BLAST/fasta.html>

Anonymous. IUPAC ambiguity codes. <http://www.ncbi.nlm.nih.gov/SNP/iupac.html>

Felsenstein, J. (1993) Phylip (Phylogeny Inference Package) version 3.5c. Department of Genetics, University of Washington. <http://evolution.genetics.washington.edu/phylip/phylip.html>

### See Also

`read.dna`, `read.GenBank`, `makeLabel`

---

write.nexus

*Write Tree File in Nexus Format*

---

### Description

This function writes trees in a file with the NEXUS format.

### Usage

```
write.nexus(..., file = "", translate = TRUE)
```

**Arguments**

...	either (i) a single object of class "phylo", (ii) a series of such objects separated by commas, or (iii) a list containing such objects.
file	a file name specified by either a variable of mode character, or a double-quoted string; if file = "" (the default) then the tree is written on the standard output connection.
translate	a logical, if TRUE (the default) a translation of the tip labels is done which are replaced in the parenthetic representation with tokens.

**Details**

If several trees are given, they must all have the same tip labels.

If among the objects given some are not trees of class "phylo", they are simply skipped and not written in the file.

**Value**

None (invisible 'NULL').

**Author(s)**

Emmanuel Paradis

**References**

Maddison, D. R., Swofford, D. L. and Maddison, W. P. (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology*, **46**, 590–621.

**See Also**

[read.nexus](#), [read.tree](#), [write.tree](#), [read.nexus.data](#), [write.nexus.data](#)

---

write.nexus.data

*Write Character Data in NEXUS Format*

---

**Description**

This function writes in a file a list of sequences in the NEXUS format. The names of the vectors of the list are used as taxon names.

**Usage**

```
write.nexus.data(x, file, format = "dna", datablock = TRUE,
                interleaved = TRUE, charsperline = NULL,
                gap = NULL, missing = NULL)
```

**Arguments**

x	a list of sequences each made of a single vector of mode character where each element is a character state (e.g. "A", "C", ...).
file	a file name specified by either a variable of mode character, or a double-quoted string.
format	a character string specifying the format of the sequences. Two choices are possible: dna, or protein, or any unambiguous abbreviation of these. Default is "dna".
datablock	a logical, if TRUE the data are written in a single DATA block. If FALSE data is written in TAXA and CHARACTER blocks. Default is TRUE.
interleaved	a logical, if TRUE the data is written in interleaved format with number of characters per line as specified with <code>charsperline = numerical_value</code> . If FALSE, data is written in sequential format. Default is TRUE.
charsperline	a numeric specifying the number of characters per line when used with <code>interleaved = TRUE</code> . Default is 80.
gap	a character specifying the symbol for gap. Default is "-".
missing	a character specifying the symbol for missing data. Default is "?".

**Details**

If the sequences have no names, then they are given "1", "2", ..., as names in the file.

Sequences must be all of the same length (i.e., aligned).

Default symbols for missing data and gaps can be changed by using the `missing` and `gap` commands.

Please see files 'data.nex' and 'taxacharacters.nex' for examples of output formats.

**Value**

None (invisible 'NULL').

**Note**

...

**Author(s)**

Johan Nylander <nylander@scs.fsu.edu>

**References**

Maddison, D. R., Swofford, D. L. and Maddison, W. P. (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology*, **46**, 590–621.

**See Also**

[read.nexus](#), [write.nexus](#), [read.nexus.data](#)

## Examples

```
## Not run:
## Write interleaved DNA data with 100 characters per line in a DATA block
data("woodmouse")
write.nexus.data(woodmouse, file= "wood.ex.nex", interleaved = TRUE, charsperline = 100)
## Write sequential DNA data in TAXA and CHARACTERS blocks
data("cynipids")
write.nexus.data(cynipids, file = "cyn.ex.nex", format = "protein",
                 datablock = FALSE, interleaved = FALSE)
unlink(c("wood.ex.nex", "cyn.ex.nex"))

## End(Not run)
```

---

write.tree

*Write Tree File in Parenthetic Format*

---

## Description

This function writes in a file a tree in parenthetic format using the Newick (also known as New Hampshire) format.

## Usage

```
write.tree(phy, file = "", append = FALSE,
           digits = 10, tree.names = FALSE)
```

## Arguments

phy	an object of class "phylo" or "multiPhylo".
file	a file name specified by either a variable of mode character, or a double-quoted string; if file = "" (the default) then the tree is written on the standard output connection (i.e. the console).
append	a logical, if TRUE the tree is appended to the file without erasing the data possibly existing in the file, otherwise the file (if it exists) is overwritten (FALSE the default).
digits	a numeric giving the number of digits used for printing branch lengths.
tree.names	either a logical or a vector of mode character. If TRUE then any tree names will be written prior to the tree on each line. If character, specifies the name of "phylo" objects which can be written to the file.

## Details

The node labels and the root edge length, if available, are written in the file.

If tree.names == TRUE then a variant of the Newick format is written for which the name of a tree precedes the Newick format tree (parentheses are eventually deleted beforehand). The tree names are taken from the names attribute if present (they are ignored if tree.names is a character vector).



**Value**

a vector of mode character if `file = ""`, none (invisible NULL) otherwise.

**Author(s)**

Emmanuel Paradis, Daniel Lawson <dan.lawson@bristol.ac.uk>, and Klaus Schliep <kschliep@snv.jussieu.fr>

**References**

Felsenstein, J. The Newick tree format. <http://evolution.genetics.washington.edu/phylip/newicktree.html>

Olsen, G. Interpretation of the "Newick's 8:45" tree format standard. [http://evolution.genetics.washington.edu/phylip/newick\\_doc.html](http://evolution.genetics.washington.edu/phylip/newick_doc.html)

**See Also**

[read.tree](#), [read.nexus](#), [write.nexus](#)

---

yule

*Fits the Yule Model to a Phylogenetic Tree*

---

**Description**

This function fits by maximum likelihood a Yule model, i.e., a birth-only model to the branching times computed from a phylogenetic tree.

**Usage**

```
yule(phy, use.root.edge = FALSE)
```

**Arguments**

`phy` an object of class "phylo".  
`use.root.edge` a logical specifying whether to consider the root edge in the calculations.

**Details**

The tree must be fully dichotomous.

The maximum likelihood estimate of the speciation rate is obtained by the ratio of the number of speciation events on the cumulative number of species through time; these two quantities are obtained with the number of nodes in the tree, and the sum of the branch lengths, respectively.

If there is a 'root.edge' element in the phylogenetic tree, and `use.root.edge = TRUE`, then it is assumed that it has a biological meaning and is counted as a branch length, and the root is counted as a speciation event; otherwise the number of speciation events is the number of nodes - 1.

The standard-error of lambda is computed with the second derivative of the log-likelihood function.

**Value**

An object of class "yule" which is a list with the following components:

lambda	the maximum likelihood estimate of the speciation (birth) rate.
se	the standard-error of lambda.
loglik	the log-likelihood at its maximum.

**Author(s)**

Emmanuel Paradis

**See Also**

[branching.times](#), [diversi.gof](#), [diversi.time](#), [ltt.plot](#), [birthdeath](#), [bd.ext](#), [yule.cov](#)

---

yule.cov

*Fits the Yule Model With Covariates*

---

**Description**

This function fits by maximum likelihood the Yule model with covariates, that is a birth-only model where speciation rate is determined by a generalized linear model.

**Usage**

```
yule.cov(phy, formula, data = NULL)
```

**Arguments**

phy	an object of class "phylo".
formula	a formula specifying the model to be fitted.
data	the name of the data frame where the variables in formula are to be found; by default, the variables are looked for in the global environment.

**Details**

The model fitted is a generalization of the Yule model where the speciation rate is determined by:

$$\ln \frac{\lambda_i}{1 - \lambda_i} = \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \alpha$$

where  $\lambda_i$  is the speciation rate for species  $i$ ,  $x_{i1}, x_{i2}, \dots$  are species-specific variables, and  $\beta_1, \beta_2, \dots, \alpha$  are parameters to be estimated. The term on the left-hand side above is a logit function often used in generalized linear models for binomial data (see [family](#)). The above model can be written in matrix form:

$$\text{logit} \lambda_i = x_i' \beta$$

The standard-errors of the parameters are computed with the second derivatives of the log-likelihood function. (See References for other details on the estimation procedure.)

The function needs three things:

- a phylogenetic tree which may contain multichotomies;
- a formula which specifies the predictors of the model described above: this is given as a standard R formula and has no response (no left-hand side term), for instance:  $\sim x + y$ , it can include interactions ( $\sim x + a * b$ ) (see [formula](#) for details);
- the predictors specified in the formula must be accessible to the function (either in the global space, or through the data option); they can be numeric vectors or factors. The length and the order of these data are important: the number of values (length) must be equal to the number of tips of the tree + the number of nodes. The order is the following: first the values for the tips in the same order than for the labels, then the values for the nodes sequentially from the root to the most terminal nodes (i.e., in the order given by `phy$edge`).

The user must obtain the values for the nodes separately.

Note that the method in its present implementation assumes that the change in a species trait is more or less continuous between two nodes or between a node and a tip. Thus reconstructing the ancestral values with a Brownian motion model may be consistent with the present method. This can be done with the function [ace](#).

### Value

A NULL value is returned, the results are simply printed. The output includes the deviance of the null (intercept-only) model and a likelihood-ratio test of the fitted model against the null model. Note that the deviance of the null model is different from the one returned by [yule](#) because of the different parametrizations.

### Author(s)

Emmanuel Paradis

### References

Paradis, E. (2005) Statistical analysis of diversification with species traits. *Evolution*, **59**, 1–12.

### See Also

[branching.times](#), [diversi.gof](#), [diversi.time](#), [ltt.plot](#), [birthdeath](#), [bd.ext](#), [yule](#)

### Examples

```
### a simple example with some random data
data(bird.orders)
x <- rnorm(45) # the tree has 23 tips and 22 nodes
### the standard-error for x should be as large as
### the estimated parameter
yule.cov(bird.orders, ~ x)
### another example with a tree that has a multichotomy
```

```
data(bird.families)
y <- rnorm(272) # 137 tips + 135 nodes
yule.cov(bird.families, ~ y)
```

---

yule.time	<i>Fits the Time-Dependent Yule Model</i>
-----------	---

---

## Description

This function fits by maximum likelihood the time-dependent Yule model. The time is measured from the past (`root.time`) to the present.

## Usage

```
yule.time(phy, birth, BIRTH = NULL, root.time = 0, opti = "nlm", start = 0.01)
```

## Arguments

phy	an object of class "phylo".
birth	a (vectorized) function specifying how the birth (speciation) probability changes through time (see details).
BIRTH	a (vectorized) function giving the primitive of birth.
root.time	a numeric value giving the time of the root node (time is measured from the past towards the present).
opti	a character string giving the function used for optimisation of the likelihood function. Three choices are possible: "nlm", "nlminb", or "optim", or any unambiguous abbreviation of these.
start	the initial values used in the optimisation.

## Details

The model fitted is a straightforward extension of the Yule model with covariates (see [yule.cov](#)). Rather than having heterogeneity among lineages, the speciation probability is the same for all lineages at a given time, but can change through time.

The function `birth` *must* meet these two requirements: (i) the parameters to be estimated are the formal arguments; (ii) time is named `t` in the body of the function. However, this is the opposite for the primitive `BIRTH`: `t` is the formal argument, and the parameters are used in its body. See the examples.

It is recommended to use `BIRTH` if possible, and required if speciation probability is constant on some time interval. If this primitive cannot be provided, a numerical integration is done with [integrate](#).

The standard-errors of the parameters are computed with the Hessian of the log-likelihood function.

## Value

An object of class "yule" (see [yule](#)).

**Author(s)**

Emmanuel Paradis

**References**

Hubert, N., Paradis, E., Bruggemann, H. and Planes, S. (2011) Community assembly and diversification in Indo-Pacific coral reef fishes. *Ecology and Evolution*, **1**, 229–277.

**See Also**

[branching.times](#), [ltt.plot](#), [birthdeath](#), [yule](#), [yule.cov](#), [bd.time](#)

**Examples**

```
### define two models...
birth.logis <- function(a, b) 1/(1 + exp(-a*t - b)) # logistic
birth.step <- function(l1, l2, Tc1) { # 2 rates with one break-point
  ans <- rep(l1, length(t))
  ans[t > Tc1] <- l2
  ans
}
### ... and their primitives:
BIRTH.logis <- function(t) log(exp(-a*t) + exp(b))/a + t
BIRTH.step <- function(t)
{
  out <- numeric(length(t))
  sel <- t <= Tc1
  if (any(sel)) out[sel] <- t[sel] * l1
  if (any(!sel)) out[!sel] <- Tc1 * l1 + (t[!sel] - Tc1) * l2
  out
}
data(bird.families)
### fit both models:
yule.time(bird.families, birth.logis)
yule.time(bird.families, birth.logis, BIRTH.logis) # same but faster
## Not run: yule.time(bird.families, birth.step) # fails
yule.time(bird.families, birth.step, BIRTH.step,
  opti = "nlminb", start = c(.01, .01, 100))
```

---

 zoom

*Zoom on a Portion of a Phylogeny*


---

**Description**

This function plots simultaneously a whole phylogenetic tree (supposedly large) and a portion of it.

**Usage**

```
zoom(phy, focus, subtree = FALSE, col = rainbow, ...)
```

**Arguments**

phy	an object of class "phylo".
focus	a vector, either numeric or character, or a list of vectors specifying the tips to be focused on.
subtree	a logical indicating whether to show the context of the extracted subtrees.
col	a vector of colours used to show where the subtrees are in the main tree, or a function .
...	further arguments passed to plot.phylo.

**Details**

This function aims at exploring very large trees. The main argument is a phylogenetic tree, and the second one is a vector or a list of vectors specifying the tips to be focused on. The vector(s) can be either numeric and thus taken as the indices of the tip labels, or character in which case it is taken as the corresponding tip labels.

The whole tree is plotted on the left-hand side in a narrower sub-window (about a quarter of the device) without tip labels. The subtrees consisting of the tips in 'focus' are extracted and plotted on the right-hand side starting from the top left corner and successively column-wise.

If the argument 'col' is a vector of colours, as many colours as the number of subtrees must be given. The alternative is to give a function that will create colours or grey levels from the number of subtrees: see [rainbow](#) for some possibilities with colours.

**Author(s)**

Emmanuel Paradis

**See Also**

[plot.phylo](#), [drop.tip](#), [layout](#), [rainbow](#), [grey](#)

**Examples**

```
## Not run:
data(chiroptera)
zoom(chiroptera, 1:20, subtree = TRUE)
zoom(chiroptera, grep("Plecotus", chiroptera$tip.label))
zoom(chiroptera, list(grep("Plecotus", chiroptera$tip.label),
                     grep("Pteropus", chiroptera$tip.label)))

## End(Not run)
```

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