Package 'phytools'

June 1, 2020

Version 0.7-47 **Date** 2020-6-01

Title Phylogenetic Tools for Comparative Biology (and Other Things)

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Depends R (>= 3.5.0), ape (>= 4.0), maps

Imports animation, clusterGeneration, coda, combinat, expm, graphics, grDevices, gtools, MASS, methods, mnormt, nlme, numDeriv, phangorn (>= 2.3.1), plotrix, scatterplot3d, stats, utils

Suggests geiger, RColorBrewer, rgl

ZipData no

Description A wide range of functions for phylogenetic analysis. Functionality is concentrated in phylogenetic comparative biology, but also includes numerous methods for visualizing, manipulating, reading or writing, and even inferring phylogenetic trees and data. Included among the functions in phylogenetic comparative biology are various for ancestral state reconstruction, modelfitting, simulation of phylogenies and data, and multivariate analysis. There are a broad range of plotting methods for phylogenies and comparative data which include, but are not restricted to, methods for mapping trait evolution on trees, for projecting trees into phenotypic space or a geographic map, and for visualizing correlated speciation between trees. Finally, there are a number of functions for reading, writing, analyzing, inferring, simulating, and manipulating phylogenetic trees and comparative data not covered by other packages. For instance, there are functions for randomly or non-randomly attaching species or clades to a phylogeny, for estimating supertrees or consensus phylogenies from a set, for simulating trees and phylogenetic data under a range of models, and for a wide variety of other manipulations and analyses that phylogenetic biologists might find useful in their research.

License GPL (>= 2)

URL http://github.com/liamrevell/phytools

Repository CRAN

Date/Publication 2020-06-01 21:00:02 UTC

NeedsCompilation no

R topics documented:

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Description

phytools provides functions for phylogenetic comparative biology; as well as several other functions for tree inference, manipulation, and analysis that are not implemented in other R packages.

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

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The *phytools* development page is http://github.com/liamrevell/phytools/. More information on *phytools* can also be found at http://blog.phytools.org or http://www.phytools.org.

If you use *phytools* (or other packages that depend on *phytools*) in a publication, please *cite it*. The appropriate citation for *phytools* is listed below or can be obtained using citation("phytools") with the package installed.

Author(s)

Liam J. Revell

Maintainer: Liam J. Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

add.arrow

Add an arrow pointing to a tip or node on the tree

Description

This function adds an arrow or a set of arrows to a plotted tree.

Usage

```
add.arrow(tree=NULL, tip, ...)
```

Arguments

tree	an object of class "phylo", "contMap", or "densityMap". If not supplied, the function will obtain the last plotted phylogeny from the environmental variable last_plot.phylo.
tip	label of tip or tip or node number; or vector of such values. If tree=NULL then the tip label(s) or node number(s) must be supplied.
	optional arguments to control the shape and size of the arrow including: its length (arrl) in the units of the plot; the length of the arrowhead (hedl); the total angle between the wings in the arrowhead (angle); the line width for the plotted lines (lwd); the offset from the tip or end of tip label, in character widths (offset); and the color (col).

Details

This function presently works for radial (type="fan") and right facing square phylograms (type="phylogram"). Trees can be plotted using phytools function plotTree, plotSimmap, contMap, densityMap, and ape S3 method plot.phylo.

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Author(s)

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References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

nodelabels

Examples

```
## show arrows with a black outline
data(anoletree)
plotTree(anoletree,type="fan",fsize=0.7,ftype="i")
add.arrow(anoletree,tip=c("cuvieri","krugi",
    "pulchellus", "poncensis", "stratulus",
    "evermanni", "cooki", "cristatellus",
    "gundlachi","occultus"),lwd=5,arrl=1)
add.arrow(anoletree,tip="cuvieri",col="green",
    lwd=3, arrl=1)
add.arrow(anoletree,tip=c("krugi","pulchellus",
    "poncensis"),col="#E4D96F",lwd=3,arrl=1)
add.arrow(anoletree,tip=c("stratulus","evermanni"),
   col="darkgreen",lwd=3,arrl=1)
add.arrow(anoletree,tip=c("cooki","cristatellus",
    "gundlachi"),col="brown",lwd=3,arrl=1)
add.arrow(anoletree,tip="occultus",col="darkgrey",
   lwd=3,arrl=1)
legend(x="topleft",c("crown-giant","grass-bush","trunk-crown","trunk-ground",
    "twig"),pch=22,pt.bg=c("green","#E4D96F","darkgreen",
    "brown", "darkgrey"), cex=0.9,
   pt.cex=2,title="PR ecomorphs",bty="n")
par(mar=c(5.1,4.1,4.1,2.1)) ## reset margins to default
```

add.color.bar

Add color bar to a plot

Description

This function adds a color bar to a plot created by plotBranchbyTrait. A color bar can be added by clicking on a location within the plot (when prompt=TRUE) or by setting prompt=FALSE and supplying x & y coordinates for the object. This function is also used internally by S3 methods plot.contMap and plot.densityMap, as well as by errorbar.contMap.

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Usage

```
add.color.bar(leg, cols, title=NULL, lims=c(0,1), digits=1, prompt=TRUE,
    lwd=4, outline=TRUE, ...)
```

Arguments

leg	numerical value for the length of the legend.
cols	colors for the legend.
title	text to plot above the bar.
lims	range for the bar.
digits	digits for plotted numbers.
prompt	logical value indicating whether the location of the legend should be obtained interactively.
lwd	width of the plotted bar.
outline	logical value indicated whether or not to outline the plotted color bar with a 1 pt line.
	optional arguments including: x x-coordinate of the legend (if prompt=FALSE); y y-coordinate of the legend; subtitle optional legend subtitle; direction direction of the color bar (i.e., increase from left to right or from right to left); and fsize, font size for the legend text.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2013) Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, **4**, 754-759.

See Also

 $\verb|contMap|, densityMap|, errorbar.contMap|, \verb|plotBranchbyTrait||$

add.everywhere	Add tip to all edges in a tree	

Description

This function adds a tip to all branches of the tree and returns a a list of trees as an object of class "multiPhylo".

Usage

```
add.everywhere(tree, tip.name)
```

add.random 9

Arguments

tree an object of class "phylo".

tip. name a string containing the name of the tip to add.

Value

A list of trees as an object of class "multiPhylo". Since the tip can be added to any branch, the length of the list is equal to the number of edges in tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

allFurcTrees, exhaustiveMP

add.random

Add tips at random to the tree

Description

This function adds new tips at random to a tree with branch lengths. If no edge lengths are provided, and the tree is ultrametric, then edge lengths are assigned to keep the tree ultrametric. The probability that at new tip is added along any branch is directly proportional to the length of the branch.

Usage

```
add.random(tree, n=NULL, tips=NULL, edge.length=NULL, order=c("random","input"))
```

Arguments

tree an object of class "phylo".

n a number of tips to add to the tree. If NULL, will use length(tips). If tips is

specified, then n is also ignored, regardless of its value.

tips a set of tip names for the added tips. If NULL, names will be supplied

edge.length terminal edge length for the added tips. If NULL, and is.ultrametric(tree)

==TRUE, then edge lengths will be assigned to keep the tree ultrametric. Note that if edge lengths are assigned and n>1, then the asssigned terminal edge lengths are not guaranteed as subsequent random tip addition could occur along the new

terminal edge.

order addition order for the new tips.

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Details

Note that sometimes the resultant tree plotted with plot.phylo or plotSimmap may display with branches crossing. If so, the tree can be 'untangled' using untangle.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

allFurcTrees, add.everywhere

add.simmap.legend

Add legend to stochastically mapped tree

Description

This function adds a legend (by default, interactively) to a plotted stochastic character mapped tree.

Usage

```
add.simmap.legend(leg=NULL, colors, prompt=TRUE, vertical=TRUE, ...)
```

Arguments

leg	states for the discrete character in the order of colors.
colors	colors for the legend in the order of leg, or, if leg=NULL, named vector of colors in which names (colors are the states of the mapped discrete character.
prompt	logical value indicating whether the location of the legend should be obtained interactively (i.e., by clicking in the plotting area).
vertical	logical value indiciating whether to plot the legend vertically (if TRUE) or horizontally.
• • •	optional arguments including: x x-coordinate of the legend (if prompt=FALSE); y y-coordinate of the legend; and shape which can be shape="square", the default, or shape="circle".

add.species.to.genus 11

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

plotSimmap

add.species.to.genus Add species to g

Add species to genus on a phylogeny or bind simulated species subtrees to a backbone genus tree

Description

add. species.to.genus adds an additional species to a genus on a phylogeny.

genus.to.species.tree simulates pure-birth subtrees and then binds them at a random height along the terminal edge leading to each corresponding genus on a genus-level backbone tree.

Usage

```
add.species.to.genus(tree, species, genus=NULL, where=c("root","random"))
genus.to.species.tree(tree, species)
```

Arguments

tree	an object of class "phylo". In the case of genus.to.species.tree this should be a genus-level backbone tree.
species	string contain species name in the format "Genus_species" or "Genus species".
genus	for add.species.to.genus, optional argument containing the genus to which species is to be attached. If NULL then genus will be extracted from species.
where	for add.species.to.genus, the location to attach species to the tree. where= "root" will cause the species to be attached to the MRCA of all members of genus. where="random" will cause species to be attached at random to the

subtree descended from the MRCA of all members of genus.

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Details

For add.species.to.genus, if genus contains only one species and where="root", then species will be attached midway along the branch leading to the one species. If where="random" then species will be added at a random position along the edge. If genus cannot be found in the tree, then the original tree is returned and a warning printed. If the tree is not ultrametric, then the resultant tree may not contain branch lengths and a warning will be printed. Note that for some cases in which a tree is read in from file, R may initially think it is ultrametric, but then later (as tips are added) decide that it is not due to rounding of the edge lengths when it was written to file. This can most likely be resolved by using force.ultrametric to coerce the tree to be exactly ultrametric (to the maximum numerical precision permitted by R) before adding tips to the tree. If genus is non-monophyletic then species will be attached to the most inclusive group containing members of genus and a warning will be printed.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
add.random, bind.tip
```

aic.w

Computes AIC weights

Description

This function computes AIC weights for a set of fitted models. It returns an object of class "aic.w" which is just a vector which allows it to be automatically printed with a numerical precision of 8 significant digits.

Usage

aic.w(aic)

Arguments

aic

vector of AIC values for different fitted models. If the vector has names, these names will be inherited by the vector returned by the function.

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Value

A vector of AIC weights.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

allFurcTrees

Generate all bi- and multifurcating unrooted trees

Description

This function creates all possible unrooted bi- and multifurcating trees and returns a list of trees as an object of class "multiPhylo".

Usage

```
allFurcTrees(n, tip.label=NULL, to.plot=TRUE)
```

Arguments

n an integer giving the desired number of species.

tip.label an optional vector of length n containing the tip names.

to.plot an optional logical value indicating whether or not to plot the trees.

Details

This function should be used with caution for n greater than about 8, as in this case the number of possible trees is extremely large.

Value

A list of trees as an object of class "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. 2004. Inferring Phylogenies. Sinauer.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

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See Also

```
add.everywhere, exhaustiveMP
```

Examples

anc.Bayes

Bayesian ancestral character estimation

Description

This function uses Bayesian MCMC to sample from the posterior distribution for the states at internal nodes in the tree.

Usage

```
anc.Bayes(tree, x, ngen=10000, control=list(), ...)
## S3 method for class 'anc.Bayes'
plot(x, ...)
## S3 method for class 'anc.Bayes'
density(x, ...)
```

Arguments

tree an object of class "phylo".

x a vector of tip values for species; names (x) should be the species names. In the

case of the plot and density methods, an object of class "anc.Bayes".

ngen a integer indicating the number of generations for the MCMC.

control a list of control parameters containing the following elements: sig2: starting

value for σ^2 (BM rate); a: starting for the state at the root node; y: starting values for the states at all internal nodes excluding the root (should be labeled with node numbers); pr.mean: means for the prior distributions in the following order - sig2, a, y, note that the prior probability distribution is exponential for sig2 and normal for a and y; pr.var: variances on the prior distributions, same order as pr.mean (but the variance is not used for sig2); prop: variances on the normal proposal distributions in the same order as pr.mean; sample: sample

frequency from the MCMC.

... optional arguments, including to be passed to plot and density methods.

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Details

plot.anc.Bayes generates a likelihood profile plot of the MCMC by default, but can also create a profile plot for any of the sampled variables by using the optional argument what. For instance, what=40 (or, equivalently, what="40") will create a profile plot of the MCMC for node 40. Additional arguments are passed to plot.

density.anc.Bayes computes a posterior density from the MCMC sample. Like plot.anc.Bayes takes the optional argument what, but unlike plot.anc.Bayes computes the posterior density for the root node by default. The object computed by this function is of class "density" and can be visualized using plot.density. Burn-in (in generations) can be set using the optional argument burnin, otherwise it will be assumed to be 20

The print and summary methods for this object class also return (invisibly) a vector of estimated ancestral states based on a user-supplied burn-in (or 20% of the number of generations of MCMC, if no burn-in is provided). Burn-in can be specified with the optional argument burnin.

Value

anc.Bayes returns an object of class "anc.Bayes" including at least two components:

mcmc a data frame with rows ngen/sample+1 containing the posterior sample and

likelihoods. Matrix columns are labeled either sig2 or by the node number of

the internal node.

tree our input phylogeny.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, anc.ML, anc.trend, evol.rate.mcmc, fastAnc
```

Examples

```
## set seed
set.seed(77)
## load data from Garland et al. (1992)
data(mammal.tree)
data(mammal.data)
## extract character of interest
ln.bodyMass<-log(setNames(mammal.data$bodyMass,
    rownames(mammal.data)))
## run MCMC (should be run at least 1e6 generations)
mcmc<-anc.Bayes(mammal.tree,ln.bodyMass,
    ngen=50000)</pre>
```

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anc.ML

Ancestral character estimation using likelihood

Description

This function estimates the evolutionary parameters and ancestral states for Brownian evolution using likelihood. It is also possible (for model="BM") to allow for missing data for some tip taxa.

Usage

```
anc.ML(tree, x, maxit=2000, model=c("BM","OU","EB"), ...)
```

Arguments

tree	an object of class "phylo".
X	a vector of tip values for species; names(x) should be the species names.
maxit	an optional integer value indicating the maximum number of iterations for optimization.
model	model of continuous character evolution ont he tree. It's possible that only model="BM" & model="EB" work in the present version as model="OU" has not be thoroughly tested & some bugs were reported for an earlier version.
	other arguments.

Details

Because this function relies on a high dimensional numerical optimization of the likelihood function, fastAnc should probably be preferred for most purposes. If using anc.ML, users should be cautious to ensure convergence. This has been ameliorated in *phytools* >= 0.2-48 by seeding the ML optimization with the result from fastAnc. For model="EB" this should also not be a problem as the numerical optimization is performed for only sig2 and r, while the ML values of the ancestral states are obtained during every iteration of the optimization algorithmically using the re-rooting method.

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Value

An object of class "anc.ML" with at least the following four elements (if not more, depending on model):

sig2 the variance of the BM process.
ace a vector with the ancestral states.

logLik the log-likelihood.

convergence the value of convergence returned by optim (0 is good).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

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

See Also

```
ace, anc. Bayes, fastAnc, optim
```

Examples

anc.trend

Ancestral character estimation with a trend

Description

This function estimates the evolutionary parameters and ancestral states for Brownian evolution with directional trend.

Usage

```
anc.trend(tree, x, maxit=2000)
```

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Arguments

tree an object of class "phylo".

x a vector of tip values for species; names(x) should be the species names.

maxit an optional integer value indicating the maximum number of iterations for opti-

mization.

Details

Note that this will generally only work and produce sensible results for a phylogeny with some non-contemporary tips (i.e., a tree with some fossil species). The function uses optim with method="L-BFGS-B"; however optimization is only constrained for the sig2 which must be >0.

Value

An object of class "anc. trend" with the following components:

ace a vector with the ancestral states. mu a trend parameter per unit time. sig2 the variance of the BM process, σ^2 .

logL the log-likelihood.

convergence the value of \$convergence returned by optim() (0 is good).

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, anc.Bayes, anc.ML, optim
```

Examples

```
## simulate tree & data using fastBM with a trend (m!=0)
tree<-rtree(n=26,tip.label=LETTERS)
x<-fastBM(tree,mu=4,internal=TRUE)
a<-x[as.character(1:tree$Nnode+Ntip(tree))]
x<-x[tree$tip.label]
## fit no trend model
fit.bm<-anc.ML(tree,x,model="BM")
print(fit.bm)
## fit trend model
fit.trend<-anc.trend(tree,x)
print(fit.trend)
## compare trend vs. no-trend models & estimates</pre>
```

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```
AIC(fit.bm, fit.trend)
layout(matrix(c(3,4,1,2,5,6),3,2,byrow=TRUE),
   heights=c(1.5,3,1.5), widths=c(3,3))
xlim<-ylim<-range(c(a,fit.bm$ace,</pre>
   fit.trend$ace))
plot(a,fit.bm$ace,pch=19,
   col=make.transparent("blue",0.5),
   xlab="true ancestral states",
   ylab="ML estimates",
   main=paste("Comparison of true and estimated",
    "\nstates under a no-trend model"),font.main=3,
   cex.main=1.2,bty="1",cex=1.5,
    xlim=xlim,ylim=ylim)
lines(xlim,ylim,lty="dotted")
plot(a,fit.trend$ace,pch=19,
    col=make.transparent("blue",0.5),
   xlab="true ancestral states",
   ylab="ML estimates",
   main=paste("Comparison of true and estimated",
    "\nstates under a trend model"), font.main=3,
   cex.main=1.2,bty="1",cex=1.5,
   xlim=xlim,ylim=ylim)
lines(xlim,ylim,lty="dotted")
par(mfrow=c(1,1))
```

ancThresh

Ancestral character estimation under the threshold model using Bayesian MCMC

Description

This function uses Bayesian MCMC to estimate ancestral states and thresholds for a discrete character under the threshold model from quantitative genetics (Felsenstein 2012).

Usage

```
ancThresh(tree, x, ngen=100000, sequence=NULL, method="mcmc",
    model=c("BM","OU","lambda"), control=list(), ...)
```

Arguments

tree	phylogenetic tree.
X	a named vector containing discrete character states; or a matrix containing the tip species, in rows, and probabilities of being in each state, in columns.
ngen	number of generations to run the MCMC.
sequence	assumed ordering of the discrete character state. If not supplied and x is a vector then numerical/alphabetical order is assumed; if not supplied and x is a matrix, then the column order of x is used.

20 ancThresh

method only method currently available is "mcmc".

model model for the evolution of the liability. Options are "BM" (Brownian motion, the

default), "OU" (Ornstein-Uhlenbeck), or "lambda" (the λ model).

control list containing the following elements: sample, the sampling interval; propliab

variance of the proposal distribution for liabilities; propthresh variance on the proposal distribution for the thresholds; propalpha variance on the proposal distribution for alpha (for model="OU"); pr.anc prior probability distribution on the ancestral states for each node, in a matrix - not all nodes need to be supplied; pr.th prior density on the thresholds; burnin number of generations to exclude for burn-in when plotting posterior probabilities on the tree; plot logical value indicating whether or not to plot the posterior probabilities; print logical value indicating whether or not to print the state of the MCMC; piecol colors for the posterior probabilities plotted as pie charts at internal nodes; and tipcol which indicates whether the tip colors should be based on the input data ("input") or sampled tip liabilities ("estimated"). These will only differ if there is uncertainty in the tip states.

... additional arguments to be passed to plotThresh (called internally).

Details

print and plot S3 methods are now available for the object class "ancThresh".

Value

This function returns an object of class "ancThresh" containing the posterior sample from our analysis, although with other components.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Felsenstein, J. (2012) A comparative method for both discrete and continuous characters using the threshold model. *American Naturalist*, **179**, 145-156.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, **68**, 743-759.

See Also

```
anc.Bayes, threshBayes
```

Examples

```
## Not run:
## load data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## extract character of interest
```

anoletree 21

anoletree

Phylogenetic datasets

Description

anoletree is a phylogeny of Greater Antillean anole species with a mapped discrete character - *ecomorph class*. anole.data is a data frame of morphological characters. Data and tree are from Mahler et al. (2010).

mammal.tree and mammal.data are the phylogeny and dataset for mammal body size and home range size from Garland et al. (1992).

salamanders is a phylogeny of *Plethodon* salamanders from Highton and Larson (1979). According to Wikipedia, the genus *Plethodon* contains 55 species in total.

sunfish.tree and sunfish.data are the phylogeny and dataset for Centrarchidae and buccal morphology (respectively) from Revell and Collar (2009).

wasp. trees and wasp. data are the phylogeny and host-parasite associations from Lopez-Vaamonde et al. (2001).

Usage

```
data(anole.data)
data(anoletree)
data(mammal.data)
data(mammal.tree)
data(salamanders)
data(sunfish.data)
data(sunfish.tree)
data(wasp.data)
data(wasp.trees)
```

Format

```
anoletree is an object of class "simmap". anole.data is a data frame. mammal.tree is an object of class "phylo". mammal.data is a data frame. salamanders is an object of class "phylo". sunfish.tree is an object of class "simmap". sunfish.data is a data frame. wasp.trees is an object of class "multiPhylo". wasp.data is a data frame.
```

22 applyBranchLengths

Source

Garland, T., Jr., P. H. Harvey, and A. R. Ives. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41**, 18-32.

Highton, R., and A. Larson. (1979) The genetic relationships of the salamanders of the genus *Plethodon. Systematic Zoology*, **28**, 579-599.

Lopez-Vaamonde, C., J. Y. Rasplus, G. D. Weiblen, and J. M. Cook. (2001) Molecular phylogenies of fig wasps: Partial cocladogenesis of pollinators and parasites. *Molecular Phylogenetics and Evolution*, **21**, 55-71.

Mahler, D. L, L. J. Revell, R. E. Glor, and J. B. Losos. (2010) Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution*, **64**, 2731-2745.

Revell, L. J., and D. C. Collar. (2009) Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution*, **63**, 1090-1100.

applyBranchLengths

Applies the branch lengths of a reference tree to a target

Description

This function applies the set of branch lengths from a reference tree to a target tree while reconciling any mappings (as in read.simmap) with the new branch lengths.

Usage

```
applyBranchLengths(tree, edge.length)
```

Arguments

tree target tree.

edge.length number of digits for rounding. Passed to round.

Value

An object of class "phylo" or "simmap".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

as.multiPhylo 23

as.multiPhylo	Conversion to object of class "multiPhylo"
---------------	--

Description

This function converts between object classes.

Usage

```
as.multiPhylo(x, ...)
## S3 method for class 'multiSimmap'
as.multiPhylo(x, ...)
## S3 method for class 'phylo'
as.multiPhylo(x, ...)
```

Arguments

x object to be converted to "multiPhylo". Presently an object of class "multiSimmap", or an object of class "phylo". In the latter case an object of class "multiPhylo" with length 1 is generated.

... optional arguments.

Value

An object of class "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

as.Qmatrix Convert a fitted Mk model to a Q-matrix

Description

This function extracts a Q-matrix (in the form of an object of class "Qmatrix" from a fitted Mk model.

24 ave.rates

Usage

```
as.Qmatrix(x, ...)
## S3 method for class 'fitMk'
as.Qmatrix(x, ...)
## S3 method for class 'Qmatrix'
plot(x, ...)
## S3 method for class 'Qmatrix'
print(x, ...)
```

Arguments

x fitted Mk model. (For instance, an object of class "fitMk".) In the case of print.Qmatrix, an object of class "Qmatrix".

... optional arguments.

Value

An object of class "Qmatrix".

Author(s)

Liam Revell liam.revell@umb.edu>, Joan Maspons

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

fitMk

ave.rates

Average the posterior rates

Description

Primarily used internally by posterior.evolrate.

Usage

```
ave.rates(tree, shift, tips, sig1, sig2, ave.shift, showTree=TRUE)
```

averageTree 25

Arguments

```
tree a tree.  
shift the shift point for this sample.  
tips tip names tipward of shift.  
sig1 \sigma_1^2.  
sig2 \sigma_2^2.  
ave.shift average shift from all samples.  
showTree logical value indicating whether to plot the rate-stretched tree.
```

Value

A list of the rates.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
evol.rate.mcmc, minSplit, posterior.evolrate
```

averageTree

Compute an average tree from a set of trees and related operations

Description

These functions compute average trees or consensus trees by various criteria.

Usage

```
averageTree(trees, start=NULL, method="quadratic.path.difference",
    tol=1e-12, quiet=FALSE, ...)
ls.consensus(trees, start=NULL, tol=1e-12, quiet=FALSE, ...)
minTreeDist(tree, trees, method="quadratic.path.difference", ...)
```

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Arguments

trees object of class "multiPhylo".

tree object of class "phylo". For minTreeDist the tree on which to find the edge

lengths that minimize the distance to the phylogenies in trees.

start starting tree for optimization.

method distance criterion for minimization. Options are "symmetric.difference",

"branch.score.difference", "path.difference", and "quadratic.path.difference".

tol tolerance value for optimization.

quiet logical value indicating whether to run "quietly" or not.

... other arguments to be passed internally.

Value

An object of class "phylo" with edge lengths.

Author(s)

Liam Revell liam.revell@umb.edu>

bd Convert object of class "birthdeath" to raw birth & death rates

Description

This function converts an object of class "birthdeath" to a vector with the ML birth & death rates.

Note that this is somewhat unnecessary as *phytools* now contains functions to fit birth-death and pure-birth diversification models from trees (fit.bd and fit.yule) that also take into account incomplete sampling fraction.

Usage

bd(x)

Arguments

x object of class "birthdeath".

Value

A vector.

Author(s)

Liam Revell liam.revell@umb.edu>

bind.tip 27

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
birthdeath, fit.bd, fit.yule
```

bind.tip

Attaches a new tip to a tree

Description

Functions adds a new tip to the tree. If the tree is ultrametric and no branch length is specified, then edge. length is scaled so that the tree remains ultrametric after the new tip is added.

Usage

```
bind.tip(tree, tip.label, edge.length=NULL, where=NULL, position=0,
  interactive=FALSE, ...)
```

Arguments

tree receptor tree. tip.label a string containing the species name for the new tip. edge.length edge length for the new tip (a scalar). where node number to attach new tip. If position>0 then then tip will be attached rootward of the specified node. Node numbers can also be tips, in which case the new tip will be added along the terminal edge. To find out the tip number for given species with name "species" type: which(tree\$tip.label=="species"). position distance rootward of the node to add the new tip. interactive logical value indicating whether or not the species should be added interactively. (Defaults to FALSE.) arguments to be passed to plotTree (for interactive=TRUE.)

Details

Wrapper function for 'ape' bind.tree. Note that interactive=TRUE works only for right-facing phylograms.

Value

An object of class "phylo".

28 bind.tree.simmap

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
set.seed(123)
## generate tree
tree<-pbtree(b=0.1, n=10)
## plot original tree
plot(tree)
axisPhylo()
## add an extant tip ("t_extant") sister to taxon 't5'
## with divergence time of 4.5 Ma
node <- which(tree$tip.label=="t5")</pre>
tree <- bind.tip(tree, tip.label="t_extant",</pre>
    where=node, position=4.5)
# plot to see the result
plot(tree)
axisPhylo()
## add an extinct tip ("t_extinct") sister to 't2' with
## divergence time of 7.8 Ma and duration (edge length) of
## 3.3 Ma
node <- which(tree$tip.label=="t2")</pre>
tree <- bind.tip(tree, tip.label="t_extinct", where=node,</pre>
    position=7.8, edge.length=3.3)
## plot to see the result
plot(tree)
axisPhylo()
```

bind.tree.simmap

Attaches a new tip to a tree

Description

This function grafts tree y onto tree x at node where.

Usage

```
bind.tree.simmap(x, y, where="root")
```

bmPlot 29

Arguments

X	an object of class "simmap". (The receptor tree.)
у	an object of class "simmap". (The tree being grafted.)
where	node number to attach new tip, or the root node if where="root".

Details

This function wraps around bind.tree for objects of class "simmap"; however it presently only allows y to be grafted at a node of x and it does not allow y to possess a root edge.

Value

An object of class "simmap".

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

bmPlot	Simulates and visualizes discrete-time Brownian evolution on a phylogeny

Description

This function conducts discrete-time Brownian motion simulation on an input tree, plots the outcome, and returns the tip and internal node states to the user as a named vector.

The function will first rescale and round the branch lengths to integer length, if they are not already in integer values. If integer branch lengths are provided, the user should also set ngen to be equal to the total height of the tree in generations (and thus avoid rescaling).

For type="threshold" the visualization is of the threshold model (Felsenstein 2012), in which the evolving character is liability and the segments of evolution are colored by their value for the threshold trait. If type="threshold" is used, the function requires at least one addition input: thresholds, a vector containing the ordered thresholds between states. The user can also provide the colors for plotting in colors. Note that one more color than threshold should be provided as one threshold implies two states; two thresholds, three states; etc. If no value for colors is provided, the function will recycle a set of four colors up to the number of times required by thresholds. Finally, the optional argument return.tree=TRUE will tell the function to return a list with the tip and note states and an object of class "phylo" with (for type="threshold"), the state for the threshold model through time mapped on the branches of the tree in discrete time.

30 bmPlot

Usage

```
bmPlot(tree, type="BM", anc=0, sig2=1/1000, ngen=1000, ...)
```

Arguments

tree	a phylogenetic tree in "phylo" format.
type	the type of plot to create. See Description.
anc	the ancestral value for the root node.
sig2	the BM rate (variance of the Brownian evolution process), σ^2 .
ngen	number of generations for the simulation: will rescale the tree to this total length.
	arguments to be passed to different methods.

Value

This function conducts and plots discrete time Brownian simulation and returns a vector containing the simulated states at internal nodes and tips of the tree.

It also returns, by default (although this can be turned off) a tree with the branch lengths in discrete time and with a mapped discrete character (for type="threshold").

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. 2012. A comparative method for both discrete and continuous characters using the threshold model. *American Naturalist*, **179**, 145-156.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, bold68, 743-759.

See Also

fastBM, pbtree, phenogram, threshBayes

Examples

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```
par(mfrow=c(1,2),mar=c(5.1,4.1,4.1,0.1))
tt<-bmPlot(tree,type="threshold",thresholds=c(0,1,2),
    bty="1")
plot(tt$tree,direction="upwards",
    mar=c(5.1,0.1,4.1,1.1),ftype="off",
    colors=setNames(c("black","red","blue"),
    letters[1:3]),lwd=3)
## reset par to default values
par(mfrow=c(1,1),mar=c(5.1,4.1,4.1,2.1))</pre>
```

branching.diffusion

Animation of branching random diffusion

Description

This function creates an animation of branching random diffusion (i.e., BM with speciation).

Usage

```
branching.diffusion(sig2=1, b=0.0023, time.stop=1000, ylim=NULL,
    smooth=TRUE, pause=0.02, record=NULL, path=NULL, ...)
```

Arguments

sig2	variance of BM process, σ^2 .
b	birthrate for branching process.
time.stop	number of generations to run.
ylim	y limits (for plotting).
smooth	no longer used.
pause	pause (in s) between generations.
record	filename for video file output (no video if NULL).
path	full path to file for video rendering. (By default branching.diffusion will look for the executable ffmpeg.exe in the directory C:/Program Files/ffmpeg/bin, even though this will not make sense on non-Windows machines.)
	optional arguments.

Value

An animated plot and (optionally) a recorded video file. For animation to be recorded to file, the function requires the package *animation* as well as a video renderer.

Author(s)

Liam Revell liam.revell@umb.edu>

32 brownie.lite

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

bmPlot, fastBM

brownie.lite

Likelihood test for rate variation in a continuous trait

Description

This function takes an object of class "phylo" or class "simmap" with a mapped binary or multistate trait (see read.simmap) and data for a single continuously valued character. It then fits the Brownian rate variation ("noncensored") model of O'Meara et al. (2006; *Evolution*). This is also the basic model implemented in Brian O'Meara's *Brownie* software.

Usage

```
brownie.lite(tree, x, maxit=2000, test="chisq", nsim=100, se=NULL, ...)
```

Arguments

t	tree	a phylogenetic tree either as an object of class "phylo" or "simmap". (See read.simmap, make.simmap, or paintSubTree for more details about the latter object class.)
>	(a vector of tip values for species. names(x) should be the species names.
n	naxit	an optional integer value indicating the maximum number of iterations for optimization - may need to be increased for large trees.
t	test	an optional string indicating the method for hypothesis testing - options are "chisq" or "simulation".
r	nsim	number of simulations (only used if test="simulation").
5	se	a vector containing the standard errors for each estimated mean in x.
		optional arguments.

Details

Sampling error in the estimation of species means can also be accounted for by assigning the vector se with the species specific sampling errors for x.

brownie.lite 33

Value

An object of class "brownie.lite" containing the following components:

sig2. single is the rate, σ^2 , for a single-rate model. This is usually the "null" model.

a.single is the estimated state at the root node for the single rate model.

var.single variance on the single rate estimator - obtained from the Hessian.

logL1 log-likelihood of the single-rate model.

k1 number of parameters in the single rate model (always 2).

sig2.multiple is a length p (for p rates) vector of BM rates (σ_1^2 , σ_2^2 , and so on) from the multi-

rate model.

a.multiple is the estimated state at the root node for the multi-rate model.

var.multiple p x p variance-covariance matrix for the p rates - the square-roots of the diago-

nals should give the standard error for each rate.

logL.multiple log-likelihood of the multi-rate model.

k2 number of parameters in the multi-rate model (p+1).

P.chisq P-value for a likelihood ratio test against the χ^2 distribution; or P.sim P-value for a likelihood ratio test agains a simulated null distribution.

convergence logical value indicating if the likelihood optimization converged.

Author(s)

Liam Revell liam.revell@umb.edu>

References

O'Meara, B. C., C. Ane, M. J. Sanderson, and P. C. Wainwright. (2006) Testing for different rates of continuous trait evolution using likelihood. *Evolution*, **60**, 922-933.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

brownieREML, evol.vcv, ratebytree

Examples

```
## load data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## extract character of interest
buccal.length<-setNames(sunfish.data$buccal.length,
    rownames(sunfish.data))
## fit model
multiBM.fit<-brownie.lite(sunfish.tree,
    buccal.length)
print(multiBM.fit)</pre>
```

34 brownieREML

brownieREML

REML version of brownie.lite

Description

This function takes an object of class "phylo" or an object of class "simmap" with a mapped binary or multistate trait (see read.simmap) and data for a single continuously valued character. It then uses restricted maximum likelihood (REML) to fit the Brownian rate variation ("noncensored") model of O'Meara et al. (2006; *Evolution*). This function is similar to brownie.lite but uses REML (which is faster and unbiased) instead of ML. REML optimization takes advantage of Felsenstein's (1985) contrasts algorithm.

Usage

```
brownieREML(tree, x, maxit=2000, ...)
```

Arguments

tree	an object of class "phylo" or "simmap". (See read.simmap and make.simmap for more information about the latter object class.)
X	a vector of tip values for species. names(x) should be the species names.
maxit	an optional integer value indicating the maximum number of iterations for optimization - may need to be increased for large trees.
	optional arguments.

Value

An object of class "brownieREML" containing the following components:

sig2.single is the rate, σ^2 , for a single rate model - this is usually the "null" model.

logL1 log-likelihood of the single-rate model.

sig2.multiple is a length p (for p rates) vector of BM rates (σ_1^2 , σ_2^2 , and so on) from the multi-

rate model.

logL2 log-likelihood of the multi-rate model.

convergence numerical value from optim.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, **125**, 1-15.

O'Meara, B. C., C. Ane, M. J. Sanderson, and P. C. Wainwright. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution*, **60**, 922-933.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

cladelabels 35

See Also

brownie.lite, evol.vcv, evol.rate.mcmc, ratebytree

cla	delabels	Add labels to subtrees of a plotted phylogeny

Description

This function adds clade labels to a plotted tree.

Usage

```
cladelabels(tree=NULL, text, node, offset=NULL, wing.length=NULL, cex=1,
    orientation="vertical")
arc.cladelabels(tree=NULL, text, node=NULL, ln.offset=1.02,
    lab.offset=1.06, cex=1, orientation="curved",...)
```

Arguments

tree	an object of class "phylo". If not supplied, the function will obtain the last plotted phylogeny from the environmental variable last_plot.phylo.
text	desired clade label text.
node	node number for the most recent common ancestor of members of the clade. For arc.cladelabels this defaults to NULL which means that the node of the clade to be labeled should be specified interactively (that is, by clicking on the graphical device).
offset	offset (as a multiplier of character width) for the label. Defaults to offset=1 if tree is supplied or offset=8 otherwise.
wing.length	length of the wings to add to the top & bottom of the label bar (in character widths).
cex	character expansion factor.
orientation	orientation of the text. Can be orientation = "vertical" (the default) or "horizontal".
ln.offset	line offset (as a function of total tree height) for arc.cladelabels.
lab.offset	label offset for arc.cladelabels.
	optional arguments for arc.cladelabels.

Details

cladelabels presently works only for rightward facing plotted phylogenies - but no warning will be returned if your tree does not conform to this requirement!

arc.cladelabels is designed to do a similar thing to cladelabels, but for plotted fan trees. This function checks to ensure that the most recently plotted tree was plotted with type="fan" style.

36 collapse.to.star

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

nodelabels

collapse.to.star

Collapse a subtree to a star phylogeny

Description

This function collapses a subtree to a star. If the tree has edge lengths, the function will keep the tips at the same height above the root as in the original tree.

If node is the global root of the tree a star phylogeny will be created.

Usage

```
collapse.to.star(tree, node)
```

Arguments

tree an object of class "phylo".

node node for the clade to be collapsed.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
splitTree, starTree
```

collapseTree 37

collapseTree

Interactive tree visualizer

Description

Function creates an interactive visualization of collapsing & expanding clades on the tree.

Usage

```
collapseTree(tree, ...)
```

Arguments

tree

an object of class "phylo".

. . .

optional arguments. These mostly match the arguments of plotSimmap, but also include the argument drop.extinct=TRUE which will (if the input tree is ultrametric) drop any 'extinct' lineages from the tree that is returned by the

function.

Details

Function first plots a fan style tree, and then the user collapses node on the tree by clicking on them. Collapsed nodes are collapsed to the common ancestor of the clade. Nodes that have been collapsed can also be expanded by clicking. Right-click to end.

Value

Returns the final plotted tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol., 3, 217-223.

See Also

```
plotTree, plotSimmap
```

Examples

```
## Not run:
data(anoletree)
pruned<-collapseTree(anoletree)</pre>
## End(Not run)
```

38 consensus.edges

compare.chronograms	Compares two chronograms with precisely matching nodes in a visual
	manner

Description

This function plots two trees, with semi-transparent colors by default, & uses arrows to highlight differences in depth of corresponding nodes between the trees.

Usage

```
compare.chronograms(t1, t2, ...)
```

Arguments

t1 object of class "phylo".

t2 object of class "phylo" that matches t1 precisely in topology & node rotations,

but differs in edge lengths.

.. optional arguments.

Value

Function creates a plot.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

consensus.edges

Compute consensus edges for a tree under some criterion

Description

This function computes consensus edge lengths by different methods.

Usage

```
consensus.edges(trees, method=c("mean.edge","least.squares"), ...)
```

contMap 39

Arguments

trees object of class "multiPhylo" in which the trees must have edge lengths. This

could be, for instance, a sample from the posterior distribution of trees in a

Bayesian analysis.

method method for computing the edge lengths. Could be the mean of all trees in which

the edge is present, or it could be the least-squares edge lengths computed on the mean patristic distance matrices from the input phylogenies in trees. Note that in the latter case the phangorn function nnls.tree is used and the option

rooted will be set to is.rooted(tree) for the consensus tree.

... optional arguments, the most popular of which is consensus.tree - a user sup-

plied consensus tree. Another optional argument for method="mean.edge" is if.absent which tells the function how to include absent edges in the computation of average edge lengths. Possible values are "zero" (the default) or

"ignore".

Value

An object of class "phylo" with edge lengths.

Author(s)

Liam Revell liam.revell@umb.edu>

contMap

Map continuous trait evolution on the tree

Description

Function plots a tree with a mapped continuous character. The mapping is accomplished by estimating states at internal nodes using ML with fastAnc, and then interpolating the states along each edge using equation [2] of Felsenstein (1985).

errorbar.contMap adds error bars to an existing plot.

Usage

```
contMap(tree, x, res=100, fsize=NULL, ftype=NULL, lwd=4, legend=NULL,
    lims=NULL, outline=TRUE, sig=3, type="phylogram", direction="rightwards",
    plot=TRUE, ...)
## S3 method for class 'contMap'
plot(x, ...)
errorbar.contMap(obj, ...)
```

40 contMap

Arguments

tree object of class "phylo".

x a numerical vector of phenotypic trait values for species. names(x) should con-

tain the species names and match tree\$tip.label. Or, for plot.contMap, an

object of class "contMap".

res resolution for gradient plotting. Larger numbers (to a point) indicate a finer

(smoother) gradient.

fsize relative font size - can be a vector of length 2 in which the first element gives

the font size for the tip labels & the second element giving the font size for the

legend.

ftype font type - see options in plotSimmap. As with fsize, this can be a vector with

the second element giving font type for the legend.

lwd line width for branches. Can be a single integer number or a vector. In the latter

case, the second number will be taken to be the desired legend width.

legend if FALSE no legend is plotted; if a numeric value, it gives the length of the legend

in units of branch length. Default is 0.5 times the total tree length.

lims range for the color map. By default, this will be c(min(x), max(x)), and should

always include this range.

outline logical value indicating whether or not to outline the branches of the tree in

black.

sig the number of decimal places to show on the legend limits.

type type of plot desired. Options are "phylogram" for a rightward square phylo-

gram; and "fan" for a circular phylogram.

direction plotting direction for type="phylogram".

plot logical value indicating whether or not to plot the tree. If plot=FALSE then an

object of class "contMap" will be returned without plotting.

obj object of class "contMap".

... optional arguments for plot. contMap which include all the arguments of contMap

except for tree, x, res, and lims. Also method, "fastAnc", "anc.ML", or "user" (for user-supplied states) specifying which function to use for ancestral state estimation; hold specifies whether or not to hold output to graphical device before plotting (defaults to hold=TRUE); and anc.states a vector containing some or multiple ancestral user-supplied ancestral states at nodes. Some other plotting arguments, such as xlim and ylim, may also work. Optional arguments for errorbar.contMap include x, a vector containing the original trait values mapped onto the tree (otherwise these will be obtained from obj), scale.by.ci, a logical argument (defaulting to TRUE) that determines whether or not the length of the error bars will be scaled by the CI width, and lwd, which

detemines the line width of the plotted error bars.

Value

Plots a tree. An object of class "contMap" is returned invisibly. errorbar.contMap adds colorful error bars to a plotted tree.

cophylo 41

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist, 125, 1-15.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. 2013. Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, **4**, 754-759.

See Also

```
anc.ML, densityMap, fastAnc, plotSimmap
```

Examples

```
## load data from Garland et al. (1992)
data(mammal.tree)
data(mammal.data)
## extract character of interest
ln.bodyMass<-log(setNames(mammal.data$bodyMass,</pre>
    rownames(mammal.data)))
## create "contMap" object
mammal.contMap<-contMap(mammal.tree,</pre>
    ln.bodyMass,plot=FALSE,res=200)
## change color scheme
mammal.contMap<-setMap(mammal.contMap,</pre>
    c("white","#FFFFB2","#FECC5C","#FD8D3C",
    "#E31A1C"))
plot(mammal.contMap,fsize=c(0.7,0.8),
    leg.txt="log(body mass)")
par(mar=c(5.1,4.1,4.1,2.1)) ## reset margins to default
```

cophylo

Creates a co-phylogenetic plot

Description

This function creates an object of class "cophylo" or, in the case of plot.cophylo, plots that object. The function can (optionally) first attempt to rotate the nodes of both trees to optimize vertical matching of tips.

Usage

```
cophylo(tr1, tr2, assoc=NULL, rotate=TRUE, ...) ## S3 method for class 'cophylo' plot(x, ...)
```

42 cophylo

Arguments

tr1 object of class "phylo". tr2 object of class "phylo".

assoc matrix containing the tip labels in tr1 to match to the tip labels in tr2. Note

that not all labels in either tree need to be included; and, furthermore, one label

in tr1 can be matched with more than one label in tr2, or vice versa.

rotate logical argument indicating whether nodes on both trees should be rotated to

attempt to match in vertical position.

in the case of plot.cophylo, an object of class "cophylo" to be plotted. Х

optional arguments to be passed to tipRotate, or, in the case of plot.cophylo, . . .

to the internally used tree plotting function, phylogram. phylogram takes similar arguments to plotSimmap, such as fsize, ftype, lwd, and pts, though not all options from plotSimmap and plotTree are available. If fsize is supplied as a vector, different size fonts for the left & right facing trees may be used. In addition, the optional argument scale.bar, which should be a vector containing the lengths of the scale bars desired for the right & left trees, will add scale bars to the plot when supplied to plot.cophylo. If either tree contains polytomies, the cophylo argument rotate.multi should be set to TRUE. If curved linking lines are desired, the plot.cophylo argument link.type should be set to "curved". Other arguments for the plot method include link.col, link.lty, and link.lwd, which can be supplied as a scalar or a vector in which the order of the elements corresponds to the order of the associations in assoc. Finally, edge.col, a list consisting of two vectors (left and right) can be used to specify the edge colors of the two left & right plotted trees. Note that the edge order is the same as in the *rotated* trees, assuming that a rotation has been performed

on x.

Details

If no matrix of associations, assoc, is provided, then cophylo will look for exact matches of tip labels between trees.

Value

An object of class "cophylo" which includes the following components or a pair of plotted facing phylogenies with links between tips as specified in assoc.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol., 3, 217-223.

cospeciation 43

See Also

```
cophyloplot, plotSimmap
```

Examples

cospeciation

Conducts a statistical test of cospeciation between two trees

Description

This function conducts a test for cospeciation based on tree distance, applying a distance metric selected by the user.

Note that this method should be prone to be quite liberal as the null hypothesis is no similarity between trees!

Usage

```
cospeciation(t1, t2, distance=c("RF","SPR"),
    method=c("simulation","permutation"), assoc=NULL,
    nsim=100, ...)
## S3 method for class 'cospeciation'
plot(x, ...)
## S3 method for class 'cospeciation'
print(x, ...)
```

Arguments

t1	object of class "phylo".
t2	object of class "phylo".

distance method to compare trees.

method method to use (simulation of pure-birth trees, or permutation of tip labels on a

fixed tree) to obtain a null distribution of tree distances via distance.

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assoc	matrix containing the tip labels in t1 to match to the tip labels in t2. Note that
	not all labels in either tree need to be included; however, unlike cophylo, one
	label in t1 cannot be matched with more than one label in t2, nor vice versa. If
	NULL then an exact match of tip labels will be sought.
nsim	number of simulations or permutations.
x	for plot and print methods, an object of class "cospeciation".
	optional arguments.

Value

An object of class "cospeciation", which includes the test-statistic, the null distribution, and a p-value for the test of the null hypothesis of no topological similarity between the two trees.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

cophylo

Examples

countSimmap

Counts the number of character changes on a object of class "simmap" or "multiSimmap"

Description

This function takes a tree or a set of trees with a mapped discrete character (that is, an object of class "simmap" or "multiSimmap"), and computes the total number of character changes as well as the number of character changes between all states.

ctt 45

Usage

```
countSimmap(tree, states=NULL, message=TRUE)
```

Arguments

tree an object of class "simmap" or "multiSimmap".

states optional argument with the states for the mapped character. If not provided,

these will be computed from the tree. This is useful if averaging across many

trees, some of which may lack certain states.

message optional logical argument indicating whether or not to return an informative

message about the function output.

Value

A list with up to three elements: N is an integer value giving the total number of character changes on the tree; Tr gives the number of of transitions between row and column states (or a matrix containing both N and the transitions between states, in rows, for an object of class "multiPhylo"); and (optionally) message contains an explanatory message about the function output.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
## load data from Revell & Collar (2009)
data(anoletree)
anoletree
countSimmap(anoletree)
```

ctt Generates (or simulates) a 'changes through time' plot from a set of stochastic map character histories

Description

This function generates a 'changes through time' plot in the style of a lineage-through-time (LTT) plot. It shows the mean rate or the mean number of changes per unit time from a set of stochastic character map trees.

Usage

```
ctt(trees, segments=20, ...)
sim.ctt(tree, Q, anc=NULL, nmaps=100, ...)
sim.multiCtt(tree, Q, anc=NULL, nmaps=100, nsim=100, ...)
```

Arguments

trees an object of class "multiSimmap".

segments number of segments to break up the history of the tree.

tree for sim.ctt, an object of class "phylo".

Q for sim.ctt, a transition matrix to use for simulation.

anc ancestral state at the root node for simulation.

nmaps number of stochastic maps per simulation.

nsim for sim.multiCtt only, the number of simulations to run.

... optional arguments.

Value

An object of class "ctt" or "multiCtt".

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

ltt

 ${\it density.multiSimmap} \qquad {\it Computes a posterior distribution for the number and types of changes} \\ {\it on the tree}$

Description

This function summarizes the result of one or more stochastic maps.

Usage

```
## S3 method for class 'multiSimmap'
density(x, ...)
## S3 method for class 'changesMap'
plot(x, ...)
```

densityMap 47

Arguments

x object of class "multiSimmap" (see make.simmap), or, in the case plot.changesMap, an object of class "changesMap" produced via a call to density.multiSimmap.

... optional arguments. For density.multiSimmap these consist of bw (bandwidth) & method ("changes", "densityMap", or "timings").

Details

In density.multiSimmap method="changes", the default, results in a posterior distribution of the number & types of changes on the tree. If the package *coda* has been installed, then the function HPD.interval is used to compute a 95-percent high probability density interval for the number of changes of each type on the tree. Otherwise, the central 95-percent of the posterior sample is returned as an estimate of the 95-percent HPD interval for each change type. The method also computes the full posterior density for each change type using a bandwidth specified by the user. method="densityMap" computes a standard "densityMap" object, and thus only permits binary characters. Finally method="changes" has not yet been implemented.

plot.changesMap plots the posterior density returned by density.multiSimmap for method="changes".

Value

For method="changes" density.multiSimmap returns an object of class "changesMap". For method="densityMap" density.multiSimmap returns an object of class "densityMap". plot.changesMap generates a plot.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

densityMap

Plot posterior density of stochastic mapping on a tree

Description

Function plots a tree with the posterior density for a mapped character from stochastic character mapping on the tree. Since the mapped value is the probability of being in state "1", only binary [0,1] characters are allowed.

48 densityMap

Usage

```
densityMap(trees, res=100, fsize=NULL, ftype=NULL, lwd=3, check=FALSE,
    legend=NULL, outline=FALSE, type="phylogram", direction="rightwards",
    plot=TRUE, ...)
## S3 method for class 'densityMap'
plot(x, ...)
```

Arguments

trees	set of phylogenetic trees in a modified "multiPhylo" object. Values for a two-state discrete character are mapped on the tree. See make.simmap and read.simmap for details.
res	resolution for gradient plotting. Larger numbers indicate a finer (smoother) gradient.
fsize	relative font size - can be a vector with the second element giving the font size for the legend.
ftype	font type - see options in plotSimmap. As with fsize, can be a vector with the second element giving font type for the legend.
lwd	line width for branches. If a vector of two elements is supplied, the second element will be taken to be the desired width of the legend bar.
check	check to make sure that the topology and branch lengths of all phylogenies in trees are equal.
legend	if FALSE no legend is plotted; if a numeric value, it gives the length of the legend in units of branch length. Default is 0.5 times the total tree length.
outline	logical value indicating whether or not to outline the branches of the tree in black.
type	type of plot desired. Options are "phylogram" for a rightward square phylogram; and "fan" for a circular phylogram.
plot	logical value indicating whether or not to plot the tree. If plot=FALSE then an object of class "densityMap" will be returned without plotting.
direction	plotting direction for type="phylogram".
x	for plot.densityMap, an object of class "densityMap".
•••	optional arguments for plot.densityMap. These include all the arguments of densityMap except trees and res. Additional optional arguments include mar (margins), offset (tip label offset: in units of the edge length or character widths, as in plotSimmap), and hold (whether or not to use dev.hold to hold output to graphical device before plotting; defaults to hold=TRUE). Also, the argument states can be used to 'order' the states on the probability axis (that is, which state should correspond to a posterior probability of 0 or 1). Some other

plotting arguments, such as xlim and ylim, may also work.

Value

Plots a tree and returns an object of class "densityMap" invisibly.

densityTree 49

Author(s)

Liam Revell liam.revell@umb.edu>

References

Bollback, J. P. 2006. Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Huelsenbeck, J. P., R. Neilsen, and J. P. Bollback. 2003. Stochastic mapping of morphological characters. *Systematic Biology*, **52**, 131-138.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. 2013. Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, **4**, 754-759.

See Also

make.simmap, plotSimmap, read.simmap

Examples

densityTree

Plots a posterior sample of trees

Description

Functions plots a posterior sample of trees, including with mapped discrete characters.

make. transparent is used internally and converts a color to transparent with a certain user-specified alpha level.

50 densityTree

Usage

```
densityTree(trees, colors="blue", alpha=NULL, method="plotTree",
    fix.depth=FALSE, use.edge.length=TRUE, compute.consensus=TRUE,
    use.gradient=FALSE, show.axis=TRUE, ...)
make.transparent(color, alpha)
```

Arguments

trees an object of class "multiPhylo" or "multiSimmap".

colors a color or a named vector of colors in which names correspond to mapped states

in an object of class "multiSimmap".

alpha transparency level for plotted trees which is passed to internally used function,

make.transparent. (0 is fully transparent, which 1 is fully opaque.) By default

will be one divided by the number of trees.

method plotting method to be used internally. Can be "plotTree" or "plotSimmap".

fix.depth logical value indicating whether or not to plot trees with a fixed depth or to

permit plotted trees to have different depths.

use.edge.length

logical value indicating whether to use the edge lengths of the input tree. Defaults to use.edge.length=TRUE unless any input tree edge lengths are NULL.

compute.consensus

logical value indicating whether or not to use the tip order from a consensus tree. (Defaults to compute . consensus=TRUE Defaulted to FALSE in earlier version of

this function.)

use.gradient logical value indicating whether to plot all trees slightly offset using a rainbow

color gradient. (Defaults to use.gradient=FALSE.)

show.axis logical value indicating whether or not to include a horizontal axis in the plot.

... arguments to be passed to plotTree or plotSimmap. Some may be ignored if

they are incompatible with the method.

color in make. transparent, the color (or colors in a vector) to render transparent.

Value

Function creates a plot.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

describe.simmap 51

describe.simmap	Summarizes a stochastic mapped tree or set of trees
-----------------	---

Description

This function summarizes the result of one or more stochastic maps.

Usage

```
describe.simmap(tree, ...)
## S3 method for class 'simmap'
summary(object, ...)
## S3 method for class 'multiSimmap'
summary(object, ...)
## S3 method for class 'describe.simmap'
plot(x, ...)
```

Arguments

tree	a single tree or a set of trees as an object of class "simmap" or "multiSimmap", respectively.
object	object of class "simmap" or "multiSimmap".
x	for S3 plot method, an object of class "describe.simmap".
	optional arguments which include: plot, a logical value indicating whether or not to plot the posterior probabilities at nodes (default is plot=FALSE); check.equal, a logical value indicating whether or not to check if all trees are equal using all.equal.phylo (default is check.equal=FALSE); and message, a logical indicating whether or not to print an informative message to the screen (default is message=TRUE).

Value

An object of class "describe.simmap" with the following elements:

count a matrix containing the number and types of transitions for each tree, if tree is

an object of class "multiSimmap".

times a matrix containg the times spend in each state on each tree.

ace the posterior probabilities of each node being in each state, if tree is an object

of class "multiSimmap".

legend a vector containing the plot legend, if plot=TRUE.

if class(tree)="simmap" then the function simply returns the results of countSimmap combined with the states at each node of the tree and a matrix containing the total and relative times spent in each state on the tree.

52 di2multi.simmap

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

di2multi.simmap

Collapse or resolve polytomies in a tree with a character painted on the edges

Description

The method di2multi collapses branches of zero length (or, more specifically, branches with length shorter than tol) to create a polytomy in a tree or set of trees. The method multi2di resolves polytomies by adding branches of zero length (while preserving the mappings) in a tree or set of trees.

Usage

```
## S3 method for class 'simmap'
di2multi(phy, ...)
## S3 method for class 'simmap'
multi2di(phy, ...)
## S3 method for class 'multiSimmap'
di2multi(phy, ...)
## S3 method for class 'multiSimmap'
multi2di(phy, ...)
## S3 method for class 'contMap'
di2multi(phy, ...)
## S3 method for class 'contMap'
multi2di(phy, ...)
## S3 method for class 'densityMap'
di2multi(phy, ...)
## S3 method for class 'densityMap'
multi2di(phy, ...)
```

Arguments

phy object of class "simmap", "multiSimmap", "contMap", or "densityMap" containing a character mapped onto the edges of a tree or set of trees.

optional arguments: tol, length below which edges should be treated as having zero length; and random, specifying whether to resolve polytomies randomly (if TRUE) or in the order in which they are encountered.

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Details

This methods should theoretically behave similarly to di2multi and multi2di from the *ape* package.

Value

An object of class "simmap", "multiSimmap", "contMap", or "densityMap", depending on the class of phy.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
contMap, densityMap, di2multi, make.simmap, multi2di, read.simmap
```

dotTree

Creates a phylogenetic dot plot

Description

Creates a plot in which different sized dots/circles represent different tip values for a quantitative trait.

Usage

Arguments

Х

tree	an object of class	"phylo".

vector of trait values; or a matrix. If x is a vector it must have names that correspond to the tip labels of tree. If x is a matrix (and it probably should be a *matrix*, not a data frame) then the row names of the matrix should correspond to the tip labels of the phylogeny. In the case of dot.legend, the x coordinate

of the legend.

legend logical value indicating whether or not a legend should be plotted.

54 dotTree

method tree plotting method to be used internally. Will switch to method="phylogram"

if the number of traits is greater than one. For dot.legend, it should be the

method that was used for the plot.

standardize a logical value indicating whether or not to standardize x, or each column of x,

to have a mean of zero & variance of one prior to analysis.

y y coordinate of the legend.

min minimum value for dot.legend.
max maximum value for dot.legend.

Ntip number of tips in the plotted tree for dot.legend.

length length of legend.

prompt logical value indicating whether or not to prompt for legend position.

... optional arguments. In the case of dotTree, these will be passed to plotTree

or a different internally used plotting function for method="phylogram". See phylo.heatmap for more detail on these arguments. Other option for dotTree also include data.type ("continuous" or "discrete"), colors, length, for data type "continuous" the length of the legend in terms of plotted circles, x.space, the spacing of the columns in the plotted data matrix, and leg.space, the spacing of the legend dots (again, for data.type="continuous" only).

Value

Function creates a plot.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

drop.clade 55

drop.clade

Drop a clade from a tree

Description

Mostly internal function for posterior.evolrate; function drops the clade containing the species in tip.

Usage

```
drop.clade(tree, tip)
```

Arguments

tree object of class "phylo". tip set of tips in a clade.

Details

Probably should not use unless you know what you're doing.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

drop.leaves

Drop all the leaves (tips) from a tree

Description

Drops all the leaves from a tree, leaving behind only the structure leading to internal nodes.

Usage

```
drop.leaves(tree, ...)
```

56 drop.tip.contMap

Arguments

tree object of class "phylo".

... optional arguments. Presently includes only the logical value keep.tip.labels

which tells the function how to labels the tips on the reduced tree.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

drop.tip.contMap

Drop tip or tips from an object of class "contMap" or "densityMap"

Description

This function drops one or multiple tips from an object of class "contMap" or "densityMap". This function is equivalent to drop. tip but for an object of this class.

Usage

```
drop.tip.contMap(x, tip)
drop.tip.densityMap(x, tip)
```

Arguments

x an object of class "contMap" or "densityMap". tip name or names of species to be dropped.

Details

For more information about objects of class "contMap" or "densityMap", please refer to the documentation pages for contMap or densityMap, respectively.

Value

```
An object of class "contMap" or "densityMap".
```

Author(s)

Liam Revell liam.revell@umb.edu>

drop.tip.simmap 57

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
contMap, densityMap, drop.tip, drop.tip.simmap
```

drop.tip.simmap

Drop tips or extract clade from tree with mapped discrete character

Description

This function drops one or multiple tips from the modified "phylo" object with a mapped binary or multistate trait (see read.simmap) while maintaining the matrix \$mapped.edge and list of mappings by branch maps. This function is equivalent to drop.tip but for a tree with a mapped discrete character.

extract.clade.simmap is functionally equivalent to extract.clade but preserves discrete character mappings on the tree.

Usage

```
drop.tip.simmap(tree, tip)
extract.clade.simmap(tree, node)
```

Arguments

tree a modified object of class "phylo" (see read.simmap).

tip name or names of species to be dropped.

node node number for the root node of the clade to be extracted.

Value

A modified object of class "phylo" containing the elements maps and \$mapped.edge with the time spent in each state along each edge of the tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
brownie.lite, drop.tip, extract.clade, make.simmap, read.simmap, sim.history
```

58 Dtest

Conducts correlational D-test from stochastic mapping

Description

This function conducts the 'D-test' of Huelsenbeck et al. (2003).

Usage

```
Dtest(t1, t2, nsim=100, ...)
```

Arguments

t1	set of stochastic map trees (i.e., object of class "multiSimmap" for character 1. Note that t1 and t2 should be of the same length.
t2	set of stochastic map trees (i.e., object of class "multiSimmap" for character 2. Note that t1 and t2 should be of the same length.
nsim	number of simulations to use in the test.
	arguments to be passed internally to make.simmap. Note that (for now) these must be the same for both t1 and t2 (that is to say, we are not able to assume different trait evolution models for each tree).

Details

Note that this function has been included without much testing, and so the user should be wary.

Value

An object of class "Dtest".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Huelsenbeck, J. P., R. Neilsen, and J. P. Bollback (2003) Stochastic mapping of morphological characters. *Systematic Biology*, **52**, 131-138.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, map.overlap
```

edgeProbs 59

edgeProbs

Compute the relative frequencies of state changes along edges

Description

This function computes the relative frequencies of character state changes along edges from a sample of stochastically mapped character histories. This function assumes that all trees in the sample differ only in their mapped histories & not at all in topology or branch lengths. Note that it only asks whether the starting and ending states of the edge differ in a particular way, and thus ignores multiple-hits along a single edge.

Usage

```
edgeProbs(trees)
```

Arguments

trees

an object of class "multiSimmap" containing a sample of trees that are identical in topology & branch lengths with different stochastically mapped character histories.

Value

The object that is returned is a matrix with the state changes & the relative frequency of each state change. Rows are in the order of the matrix edge for any of the mapped trees.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

plotSimmap

60 estDiversity

estDiversity	Estimate diversity at each node of the tree

Description

This function estimates the lineage density at each node in the tree based on a biogeographic model (based on Mahler et al. 2010).

Usage

```
estDiversity(tree, x, method=c("asr","simulation"), model="ER", ...)
```

Arguments

tree	is a phylogenetic tree in "phylo" format.
x	a vector containing the biogeographic area for each of the tip taxa.
method	method for reconstructing ancestral biogeography.
model	model for ancestral character estimation. In theory, any model from ace; however only symmetric models permitted for method="asr".
	optional arguments. So far, this includes only nsim, the number of stochastic mappings to conduct using make.simmap for method="simulation".

Details

Two different methods are implemented in the current version. For method="asr" the state at the current node, and at each position along each co-extant internal edge, is computed as the marginal (empirical Bayesian) ancestral state reconstruction using the re-rooting method of Yang (2006). The lineage density is then computed as the sum of the marginal reconstructions (posterior probabilities) times the summed marginal ancestral reconstructions across co-extant edges. In method="simulation", stochastic character mapping is used to generate optional argument nsim stochastic maps of ancestral biogeography. Then the lineage density at each node is computed as the number of co-existing lineages with the same biogeography as the focal node, averaged acrossed stochastic maps. The importance of this distinction may depend on the degree to which reconstructions at internal nodes are independent, which relates to the distinction between marginal and joint reconstruction (e.g., see Yang 2006).

Value

A vector containing the estimated lineage density at each node

Author(s)

Liam Revell liam.revell@umb.edu>

evol.rate.mcmc 61

References

Mahler, D. L, L. J. Revell, R. E. Glor, and J. B. Losos. (2010) Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution*, **64**, 2731-2745.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Yang, Z. (2006) Computational Molecular Evolution. Oxford University Press.

See Also

fitDiversityModel

evol.rate.mcmc

Bayesian MCMC method for identifying exceptional phenotypic diversification in a phylogeny

Description

This function takes a phylogenetic tree and data for a single continuously valued character and uses a Bayesian MCMC approach to identify the phylogenetic location of a shift in the evolutionary rate through time.

Usage

```
evol.rate.mcmc(tree, x, ngen=10000, control=list(), ...)
## S3 method for class 'evol.rate.mcmc'
print(x, ...)
## S3 method for class 'evol.rate.mcmc'
summary(object, ...)
## S3 method for class 'summary.evol.rate.mcmc'
print(x, ...)
## S3 method for class 'summary.evol.rate.mcmc'
plot(x, ...)
```

Arguments

tree an object of class "phylo" (a phylogenetic tree).

x a vector of tip values for species in which names(x) contains the species names

of tree, an object of class "evol.rate.mcmc", or (in the case of the S3 summary method) an object of class "summary.evol.rate.mcmc".

ngen an integer value indicating the number of generations for the MCMC.

control a list of control parameters containing the following elements: sig1: starting

value for σ_1^2 ; sig2: starting value for σ_2^2 ; a: starting value for a; sd1: standard deviation for the normal proposal distribution for σ_1^2 ; sd2: standard deviation for the normal proposal distribution for σ_2^2 ; kloc: scaling parameter for tree

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move proposals - $1/\lambda$ for the reflected exponential distribution; sdlnr: standard deviation on the log-normal prior on σ_1^2/σ_2^2 ; rand. shift: probability of proposing a random shift in the tree (improves mixing); print: print frequency for the MCMC correlate exposure to the MCMC correlate exposure to the matter of the proposition of the matter of the matter

for the MCMC; sample: sample frequency.

object for the S3 summary method, an object of class "evol.rate.mcmc".

... other optional arguments.

Details

Default values of control are given in Revell et al. (2012).

Value

An object of class "evol.rate.mcmc" consisting of at least the following elements:

mcmc results from the MCMC run.

tips list of stips in rate σ_1^2 for each sampled generation of MCMC (to polarize the

rate shift).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J., D. L. Mahler, P. Peres-Neto, and B. D. Redelings. (2012) A new method for identifying exceptional phenotypic diversification. *Evolution*, **66**, 135-146.

See Also

anc.Bayes, brownie.lite, evol.vcv, minSplit, posterior.evolrate

evol.vcv	Likelihood test for variation in the evolutionary variance-covariance
	matrix

Description

This function takes an object of class "simmap" with a mapped binary or multistate trait and data for an arbitrary number of continuously valued character. It then fits the multiple evolutionary variance-covariance matrix (rate matrix) model of Revell & Collar (2009; *Evolution*).

Usage

```
evol.vcv(tree, X, maxit=2000, vars=FALSE, ...)
```

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Arguments

tree	an object of class "simmap". If tree is an object of class "phylo" then a simple multivariate Brownian motion model will be fit to the data in X.
X	an n x m matrix of tip values for m continuously valued traits in n species - row names should be species names. If X is supplied as a data frame it will be coerced into a matrix without warning.
maxit	an optional integer value indicating the maximum number of iterations for optimization. This quantity may need to be increased for difficult optimizations.
vars	an optional logical value indicating whether or not to estimate the variances of the parameter estimates from the Hessian matrix.
	optional arguments.

Details

This function performs optimization by maximizing the likelihood with respect to the Cholesky matrices using optim. Optimization is by method="Nelder-Mead". Using box constraints does not make sense here as they would be applied to the Cholesky matrix rather than the target parameters. Users may have to increase maxit for large trees and/or more than two traits.

Value

An object of class "evol.vcv" with the following components:

R.single vcv matrix for the single rate matrix model.

vars.single optionally, a matrix containing the variances of the elements of R. single.

logL1 log-likelihood for single matrix model.

k1 number of parameters in the single marix model.

R.multiple mx mx p array containing the p estimated vcv matrices for the p regimes painted

on the tree.

vars.multiple optionally, an array containing the variances of the parameter estimates in R. multiple.

logL.multiple log-likelihood of the multi-matrix model. k2 number of parameters estimated in this model. P.chisq P-value of the χ^2 test on the likelihood ratio.

convergence logical value indicating whether or not the optimization has converged.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J., and D. C. Collar (2009) Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution*, **63**, 1090-1100.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

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See Also

```
evol.rate.mcmc, brownie.lite
```

Examples

```
## load data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## fit multi-correlation model
sunfish.fit<-evol.vcv(sunfish.tree,sunfish.data[,2:3])
print(sunfish.fit)</pre>
```

evolvcv.lite

Likelihood test for a shift in the evolutionary correlation between traits

Description

This function takes an object of class "simmap" with a mapped binary or multistate trait and data for two and only two continuously valued character. It then fits four different evolutionary models: common rates and correlation; different rates, common correlation; different correlations, common rates; no common structure.

Usage

```
evolvcv.lite(tree, X, maxit=2000, tol=1e-10)
```

Arguments

tree	an object of class "simmap". If tree is an object of class "phylo" then a simple multivariate Brownian motion model will be fit to the data in X.
X	an $n \times m$ matrix of tip values for m continuously valued traits in n species - row names should be species names. If X is supplied as a data frame it will be coerced into a matrix without warning.
maxit	an optional integer value indicating the maximum number of iterations for optimization - may need to be increased for large trees.
tol	tolerance value for "L-BFGS-B" optimization.

Value

A list with the results summarized for each model.

Author(s)

Liam Revell liam.revell@umb.edu>

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References

Revell, L. J., and D. C. Collar (2009) Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution*, **63**, 1090-1100.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
brownie.lite, evol.vcv
```

Examples

```
## load data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## fit heirarchical common-structure models
sunfish.fit<-evolvcv.lite(sunfish.tree,sunfish.data[,2:3])
print(sunfish.fit)</pre>
```

exhaustiveMP

Exhaustive and branch & bound MP optimization

Description

This function does exhaustive and branch & bound MP searches.

Usage

```
exhaustiveMP(data, tree=NULL, method="branch.and.bound")
```

Arguments

data is a phyDat (Schliep 2011) object containing DNA or other data.

tree an optional input tree (used only with method="branch.and.bound").

method an optional string indicating method to use: "branch.and.bound", imple-

menting a branch-and-bound search (obviously), or "exhaustive".

Details

Should probably not be used for more than about 8 species (and definitely not more than 10 species). Performs parsimony calculations using parsimony in the phangorn package (Schliep, 2011).

Value

A "phylo" or "multiPhylo" object that is the MP tree or set of MP trees. It also returns the parsimony scores in attr(trees, "pscore") or attr(trees[[i]], "pscore") for the ith tree.

66 expand.clade

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Felsenstein, J. (2004) Inferring Phylogenies. Sinauer.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Schliep, K. P. (2011) phangorn: phylogenetic analysis in R. Bioinformatics, 27, 592-593.

See Also

```
mrp.supertree, optim.parsimony, pratchet
```

expand.clade

Expands (or contracts) the tip-spacing of a given clade or clades

Description

The purpose of this function is to compute a custom tip-spacing for users who want to expand or contract the tip-spacing of the descendant taxa from a given node or nodes.

Usage

```
expand.clade(tree, node, factor=5)
## S3 method for class 'expand.clade'
plot(x, ...)
```

Arguments

tree an object of class "phylo" or "simmap".

node node index or vector of node indices.

factor expansion factor for the tip-spacing of the taxa descended from node or nodes

in node.

x for plot method, an object of class "expand.clade".

... optional arguments to be passed to plotTree or plotSimmap, depending on the

class of x\$tree.

Value

The function returns an object of class "expand.clade" which consists of the (possibly re-ordered) tree and a numerical vector with the calculated tip spacing based on the expansion factor specified by the user. This object can be plotted using the S3 plot method for the object class; or it can be plotted simplying by calling a standard plotting function on the tree & tip spacings.

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Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

export.as.xml

Export trees & data in XML format

Description

This function exports trees & character data in XML format.

Usage

```
export.as.xml(file, trees, X)
```

Arguments

file filename for export.

trees a phylogenetic tree or trees in "phylo" or "multiPhylo" format.

X a matrix of class "DNAbin" or a matrix with discretely valued non-DNA charac-

ter data.

Details

Can be used to create input file for the program SIMMAP v1.5 (Bollback 2006).

Value

A file.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Bollback, J. P. (2006) Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.nexus, read.simmap, write.simmap
```

fancyTree

Plots special types of phylogenetic trees

Description

This function plots different types of phylogenetic trees.

If type="extinction" (or any unambiguous abbreviation) the function will plot a tree in which branches preceding the MRCA of all extant taxa and branches leading only to extnct lineages are plotted with dashed red lines.

If type="traitgram3d" the function will plot a three dimensional traitgram (that is, a projection of the tree into three dimensional morphospace where two dimensions are the phenotypic trait and the third axis is time since the root). In this case, the additional argument X, a matrix containing the tip values of all species (with species IDs as row names) should be supplied. Optionally, the user can also supply the matrix A, which contains the ancestral states in the tree with rows labeled by node number.

If type="droptip" the function will create a two panel figure in which the first panel is the tree with lineages to be pruned highlighted; and the second panel is the pruned tree. In this case, the additional argument tip, the tip name or vector of tip names to be dropped, must be supplied.

If type="densitymap", a posterior probability density "heat-map" is created based on a set of trees in a "multiPhylo" object containing a binary [0,1] mapped character. (See densityMap for additional optional arguments if type="densitymap".) This option just calls the function densityMap internally.

If type="contmap", reconstructed continuous trait evolution is mapped on the tree. Again, see contMap for additional arguments if type="contmap". Much like type="densitymap", this option just calls the function contMap internally.

If type="phenogram95" a 95-percent phenogram is plotted using transparency to visualize uncertainty at ancestral nodes and along branches. Most of the options of phenogram are available.

Finally, if type="scattergram" a phylogenetic scatter plot matrix containing contMap style trees on the diagonal and phylomorphospace plots in non-diagonal panels is produced. For this type a trait matrix X must also be supplied. The only additional arguments available for this type are ftype, fsize, colors, and label. (See phylomorphospace for details on how these arguments should be used.) This function calls phyloScattergram (which is also now exported to the name space) internally. In addition to creating a plot, phyloScattergram also returns an object of class "phyloScattergram" which can be replotted using different options if desired.

Presently only type="traitgram3d" uses the list control which can be supplied the same set of control parameters as phylomorphospace3d, as well as the control parameter maxit which will be passed to anc.ML.

Finally, the optional argument hold will be passed to multiple methods if supplied. It is a logical value that indicates whether or not the output to the graphical device should be held using dev.hold before plotting (defaults to hold=TRUE).

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Usage

```
fancyTree(tree, type=c("extinction","traitgram3d","droptip","densitymap",
    "contmap","phenogram95","scattergram"), ..., control=list())
phyloScattergram(tree, X=NULL, ...)
phenogram95(tree, x=NULL, ...)
```

Arguments

tree an object of class "phylo".

type the type of special plot to create. See Description.

... arguments to be passed to different methods. See Description.

control a list of control parameters, depending on type.

X in phyloScattergram, a matrix of continuous trait values. Row names in the

matrix should correspond to species names in the tree.

x in phenogram95, a named vector with values for a continuously distributed trait.

Value

This function plots different types of phylogenetic trees. For type="droptip" the function also returns the pruned tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

contMap, densityMap, drop.tip, phenogram, phylomorphospace3d, plot.phylo, plotSimmap

Examples

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```
Y < -\sin \cdot \cot x (\cot x) (\cot 
                           2,2),internal=TRUE)
B<-Y[length(tree$tip)+1:tree$Nnode,]</pre>
 Y<-Y[1:length(tree$tip),]
 fancyTree(tree,type="traitgram3d",X=Y,A=B,
                           control=list(simple.axes=TRUE,spin=FALSE))
  ## End(Not run)
 # plot with dropped tips
 tree<-pbtree(n=30)</pre>
  tips<-sample(tree$tip.label)[1:10]</pre>
 pruned<-fancyTree(tree,type="droptip",tip=tips)</pre>
  ## Not run:
 # plot 95-percent CI phenogram
  tree<-pbtree(n=30)
 x<-fastBM(tree)
 fancyTree(tree,type="phenogram95",x=x)
 ## End(Not run)
  ## reset par to defaults
 par(mar=c(5.1,4.1,4.1,2.1))
par(mfrow=c(1,1))
```

fastAnc

(Reasonably) fast estimation of ML ancestral states

Description

This function performs (reasonably) fast estimation of the ML ancestral states for a continuous trait by taking advantage of the fact that the state computed for the root node of the tree during Felsenstein's (1985) contrasts algorithm is also the MLE of the root node. Thus, the function re-roots the tree at all internal nodes and computes the contrasts state at the root each time. The function can also (optionally) compute variances or 95-percent confidence intervals on the estimates.

Usage

```
fastAnc(tree, x, vars=FALSE, CI=FALSE, ...)
```

Arguments

tree	an object of class "phylo".
X	a vector of tip values for species; names(x) should be the species names.
vars	a logical value indicating whether or not to compute variances on the ancestral state estimates. Variances are based on Equation (6) of Rohlf (2001).
CI	a logical value indicating whether or not to compute 95-percent confidence intervals on state estimates.
	optional arguments. Presently this consists of anc.states, a named vector containing ancestral states to fix. Names should correspond to node numbers in the input tree.

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Value

An object of class "fastAnc" consisting of either: a named vector containing the states at internal nodes - names are node numbers; or a list containing ancestral state estimates (ace), variances on the estimates (var), and/or 95-percent confidence intervals (CI95).

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, anc.Bayes, anc.ML, pic
```

Examples

fastBM

(Reasonably) fast quantitative trait simulation on phylogenies

Description

This function conducts (reasonably) fast quantitative trait simulation on a phylogeny under several different models: Brownian motion (default), BM with a trend (for mu!=0), bounds (for bounds!=c(-Inf, Inf)), and OU.

Usage

```
fastBM(tree, a=0, mu=0, sig2=1, bounds=c(-Inf,Inf), internal=FALSE, nsim=1,
    ...)
```

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Arguments

is a phylogenetic tree in "phylo" format. tree a value for ancestral state at the root node. an optional value for the mean of random normal changes along branches of the mu tree - can be used to simulate a trend if mu!=0. instantaneous variance of the BM process, σ^2 . sig2 bounds a vector with the lower and upper bounds (respectively) for bounded Brownian simulation - by default simulation is unbounded. internal logical value indicating whether or not to return states for internal nodes. nsim number of simulations. optional arguments alpha and theta used for OU simulation. If alpha is set then mu and bounds are ignored with a warning.

Value

A vector (for nsim=1) or matrix containing the tip states for the n species in the tree, and (optionally) the ancestral states for internal nodes.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

sim.corrs

Examples

```
## simulate 10 characters on the Anolis tree
## under Brownian motion
data(anoletree)
X<-fastBM(anoletree,nsim=10)
head(X)</pre>
```

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fastMRCA	Get the MRCA (or height above the root of the MRCA) of a pair of tip taxa

Description

This function returns the most recent common ancestor (node number) for a pair of taxa; or, in the case of fastHeight, the height above the root of the MRCA of a pair of taxa; or, in the case of fastDist, the patristic distance between a pair of taxa.

Usage

```
fastMRCA(tree, sp1, sp2)
fastHeight(tree, sp1, sp2)
fastDist(tree, sp1, sp2)
```

Arguments

tree an object of class "phylo".
sp1 species one name.
sp2 species two name.

Details

This function is mostly redundant with findMRCA (or findMRCA(..., type="height") in the case of fastHeight) but for very large trees will be considerably faster. (Also see getMRCA in the ape package.)

Value

The node number of the MRCA, the height above the root (for fastHeight), or the patristic distance between two taxa (for fastDist).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
getMRCA, findMRCA, mrca
```

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Examples

```
tree<-pbtree(n=2000)
anc<-fastMRCA(tree,"t1","t15")</pre>
```

findMRCA

Get the MRCA of a set of taxa

Description

This function returns node number of the most recent common ancestor of a set of taxa. If tips=NULL the function is redundant with mrca (for type="node") or vcv.phylo, but much slower (for type="height").

Usage

```
findMRCA(tree, tips=NULL, type=c("node","height"))
```

Arguments

tree a phylogenetic tree as an object of class "phylo".

tips a vector containing a set of tip labels.

type either "node" to return the node of the MRCA; or "height" to return the height

above the root of the MRCA of tips.

Details

If tips==NULL and type="node" (the default) it will return the result of a normal function call to mrca

If tips=NULL and type="height" it will return a matrix equal to that produced by vcv.phylo.

From phytools 0.5-66 forward findMRCA uses getMRCA in the *ape* package internally, which results in a big speed-up. Even though the two functions are thus totally redundant I have left findMRCA in the package to ensure backward compatibility.

Value

The node number of the MRCA, or a matrix of node numbers (if tips==NULL) - for type="node"; or the height of the MRCA, or a matrix of heights (if tips==NULL) - for type="height".

Author(s)

Liam Revell liam.revell@umb.edu>

References

fit.bd 75

See Also

```
findMRCA, mrca
```

Examples

fit.bd

Fits birth-death (speciation/extinction) model to reconstructed phylogeny

Description

The function fit.bd fits a birth-death model to a phylogenetic tree with edge lengths and a (potentially) incomplete sampling fraction.

The function fit.yule fits a pure-birth model with a (potentially) incomplete sampling fraction.

The function lik.bd computes the likelihood of a set of birth & death rates given the set of branching times computed for a tree and a sampling fraction.

Usage

```
fit.bd(tree, b=NULL, d=NULL, rho=1, ...)
fit.yule(tree, b=NULL, d=NULL, rho=1, ...)
lik.bd(theta, t, rho=1, N=NULL)
## S3 method for class 'fit.bd'
print(x, ...)
```

Arguments

tree	object of class "phylo".
b	birth (speciation) rate. Presently doesn't do anything as the rate cannot be fixed.
d	death (extinction) rate. Presently doesn't do anything as the rate cannot be fixed.
rho	sampling fraction.
theta	vector of b and d for likelihood function.
t	branching times for calculation of the likelihood.
N	number of tips in the tree.
X	object of class "fit.bd" for print method.
	optional arguments.

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Value

fit.bd returns an object of class "fit.bd" which can be printed. This object is a list containing the fitted model parameters, likelihood, optimization conditions, a summary of the optimization, and a likelihood function.

fit.yule returns an object of class "fit.yule". This object is a list containing the fitted model parameter, likelihood, optimization conditions, a summary of the optimization, and a likelihood function.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Nee, S., May, R. M. and Harvey, P. H. (1994) The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London B*, **344**, 305-311.

Stadler, T. (2012) How can we improve the accuracy of macroevolutionary rate estimates? *Systematic Biology*, **62**, 321-329.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

birthdeath

Examples

```
data(salamanders)
## compute sampling fraction based on 55 species of Plethodon
sampling.f<-Ntip(salamanders)/55</pre>
## fit birth-death model
bd.fit<-fit.bd(salamanders,rho=sampling.f)</pre>
print(bd.fit)
## fit Yule model
yule.fit<-fit.yule(salamanders,rho=sampling.f)</pre>
print(yule.fit)
## compare b-d and yule models
AIC(yule.fit,bd.fit)
## create a likelihood surface for b-d model
ngrid<-100
b<-seq(0.01,0.06,length.out=ngrid)
d<-seq(0.005,0.03,length.out=ngrid)</pre>
logL < -sapply(d, function(d,b) sapply(b, function(b,d))
    bd.fit$lik(c(b,d)),d=d),b=b)
contour(x=b,y=d,logL,nlevels=100,
    xlab=expression(lambda),
    ylab=expression(mu),bty="l")
title(main="Likelihood surface for plethodontid diversification",
    font.main=3)
points(bd.fit$b,bd.fit$d,cex=1.5,pch=4,
```

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```
col="blue",lwd=2)
legend("bottomright","ML solution",pch=4,col="blue",
    bg="white",pt.cex=1.5,pt.lwd=2)
```

fitBayes

Evolutionary model fitting with intraspecific variability using Bayesian MCMC

Description

This function uses Bayesian MCMC to sample terminal states (species means) as well as evolutionary parameters.

Usage

```
fitBayes(tree, x, ngen=10000, model="BM", method="reduced", control=list())
```

Arguments

tree an object of class "phylo".

x a vector of phenotypic values for individuals; names(x) should contain the

species names (not individual IDs).

ngen a integer indicating the number of generations for the MCMC.

model an evolutionary model: either "BM" or "lambda".

method a method: either "reduced" or "full".

control a list of control parameters containing the following elements: sig2: starting

value for σ^2 (BM rate); lambda: starting value for the λ parameter; a: starting for the state at the root node; xbar: starting values for the states at the tips; intV: starting value for the intraspecific variance (reduced method); or v: starting value for the vector of intraspecific variances for all species (full method); pr.mean: means for the prior distributions in the following order - sig2, lambda (if applicable), a, xbar, intV or v (if applicable), note that the prior probability distribution is exponential for sig2 and normal for a and y; pr.var: variances

on the prior distributions, same order as pr.mean.

Value

An object of class "fitBayes" that includes a matrix (mcmc) with a number of rows ngen/control\$sample+1 containing the posterior sample and likelihoods. Matrix columns are labeled by species (for species means and variances), or by the corresponding evolutionary parameter.

Author(s)

Liam Revell liam.revell@umb.edu>

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References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. and R. G. Reynolds. (2012) A new Bayesian method for fitting evolutionary models to comparative data with intraspecific variation. *Evolution*, 66, 2697-2707.

See Also

```
anc.Bayes, brownie.lite, evol.rate.mcmc
```

fitDiversityModel

Fit diversity-dependent phenotypic evolution model

Description

This function fits a diversity-dependent phenotypic evolution model (based on Mahler et al. 2010).

Usage

```
fitDiversityModel(tree, x, d=NULL, showTree=TRUE, tol=1e-6)
## S3 method for class 'fitDiversityModel'
logLik(object, ...)
## S3 method for class 'fitDiversityModel'
print(x, ...)
```

Arguments

tree	an object of class "phylo".
x	a vector with tip values for a continuously distributed trait. For print method, an object of class "fitDiversityModel".
d	a vector containing the inferred historical diversity at each node in the tree - if d=NULL (the default) function will treat the diversification as if it occurred in a single geographic area.
showTree	optional logical value indicating whether to plot the tree transformation implied by the model.
tol	some small value by which d is incremented during rescaling of psi for optimization. If R thinks your matrices are singular during optimization, try increasing tol slightly.
object	for logLik method, an object of class "fitDiversityModel".
	optional arguments for logLik and print methods. Note that for the logLik method the number of fitted parameters ("df") is assumed to be 3 for the diversity dependent model (that is, if psi is estimated) and 2 for the diversity independent model, unless otherwise specified (using the argument df).

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Value

An object of class "fitDiversityModel" consisting of the following components:

log-likelihood of the fitted model. logL

estimated starting value for the rate at the root of the tree, σ_0^2 . sig0

the estimated rate of change in the rate associated with the addition of a lineage. psi vcv

a matrix with the variances and covariance of the estimated parameters (from

the Hessian).

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Mahler, D. L, L. J. Revell, R. E. Glor, and J. B. Losos. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. Evolution, 64, 2731-2745.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol., 3, 217-223.

See Also

brownie.lite, estDiversity, evol.rate.mcmc

fitMk Fits Mk model

Description

The function fitMk fits a so-called Mk model for discrete character evolution.

plot.fitMk plots an object of class "fitMk" returned by fitMk. plot.gfit plots an object of class "gfit" from geiger's fitDiscrete function. Both plots portray the fitted model using a graph of arrows connecting states.

The function fitmultiMk fits an Mk model in which the transition rates between character states are allowed to vary depending on the mapped state of a discrete character on the tree. It can be combined with, for example, paintSubTree to test hypotheses about how the process of discrete character evolution for x varies between different parts of the tree.

The function fitpolyMk fits an Mk model to data for a discrete character with intraspecific polymorphism. Polymorphic species should be coded with the name of the two or more states recorded for the species separated by a space (e.g., A+B would indicate that both states A and B are found in the corresponding taxon). Invariably it's assumed that transitions between states must occur through a polymorphic condition, whereas transitions cannot occur directly between two incompatible polymorphic conditions. For instance, a transition between A+B and B+C would have to occur through the monomorphic state B. At time of writing, this function permits the models "ER" (equal rates 80 fitMk

for all permitted transitions), "SYM" (symmetric backward & forward rates for all permitted transitions), "ARD" (all-rates-different for permitted transitions), and a new model called "transient" in which the acquisition of polymorphism (e.g., A -> A+B) is assumed to occur at a different rate than its loss (e.g., A+B -> B). The method plot.fitpolyMk plots the fitted Mk model with intraspecific polymorphism.

Finally, the function mcmcMk runs a Bayesian MCMC version of fitMk. The shape of the prior distribution of the transition rates is Γ , with α and β via the argument prior, which takes the form of a list. The default value of α is 0.1, and β defaults to a value such tha α/β is equal to the parsimony score for x divided by the sum of the edge lengths of the tree. The shape of the proposal distribution is normal, with mean zero and a variance that can be controlled by the user via the optional argument prior.var. The argument auto.tune, if TRUE or FALSE, indicates whether or not to 'tune' the proposal variance up or down to target a particular acceptance rate (defaults to 0.5). auto.tune can also be a numeric value between 0 and 1, in which case this value will be the target acceptance ratio. The argument plot indicates whether the progress of the MCMC should be plotted (defaults to TRUE, but runs much faster when set to FALSE).

The method plot.mcmcMk plots a log-likelihood trace and a trace of the rate parameters from the MCMC. (This the samem graph that is created by setting plot=TRUE in mcmcMk.) The method density.mcmcMk computes a posterior density on the transition rates in the model from the posterior sample obtained in the MCMC, will import the package *coda* if it is available, and returns an object of class "density.mcmcMk". Finally, the method plot.density.mcmcMk creates a plot of the posterior density (or a set of plots) for the transition rates between states.

Usage

```
fitMk(tree, x, model="SYM", fixedQ=NULL, ...)
## S3 method for class 'fitMk'
plot(x, ...)
## S3 method for class 'gfit'
plot(x, ...)
fitmultiMk(tree, x, model="ER", ...)
fitpolyMk(tree, x, model="SYM", ordered=FALSE, ...)
## S3 method for class 'fitpolyMk'
plot(x, ...)
mcmcMk(tree, x, model="ER", ngen=10000, ...)
## S3 method for class 'mcmcMk'
plot(x, ...)
## S3 method for class 'mcmcMk'
density(x, ...)
## S3 method for class 'density.mcmcMk'
plot(x, ...)
```

Arguments

tree	an object of class "phylo". In the case of fitmultiMk an object of class "simmap" with a mapped discrete character.
X	a vector of tip values for species; names(x) should be the species names. In the case of plot and density methods, an object of the appropriate class.
model	model. See make.simmap or ace for details.

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fixedQ fixed value of transition matrix Q, if one is desired.

ordered for fitpolyMk, a logical value indicating whether or not the character should

be treated as ordered. For now the function assumes alphanumerical order (i.e., numbers sorted by their initial and then successive digits followed by characters

or character strings in alphabetical order).

ngen number of generations of MCMC for mcmcMk.

... optional arguments, including pi, the prior distribution at the root node (defaults

to pi="equal"). For plot method optional arguments include (but may not be limited to): signif, the number of digits for the rates to be plotted; main, a character vector of length two with the headings for each subplot; cex.main, cex.traits, and cex.rates, font sizes for the various text elements of the plot; and show.zeros, a logical argument specifying whether or not to plot arrows with the ML estimated transition rate is not different from zero (with tolerance

specified by the optional argument tol).

Details

Note that both fitMk and fitmultiMk recycle code from ace in the *ape* package for computing the likelihood. fitpolyMk and mcmcMk use fitMk internally to compute the likelihood.

Value

An object of class "fitMk", "fitmultiMk", "fitpolyMk", or "mcmcMk". In the case of density.mcmcMk an object of class "density.mcmcMk".

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, make.simmap
```

Examples

fitPagel

```
fit.ARD<-fitMk(sunfish.tree,fmode,model="ARD")
print(fit.ARD)
## compare the models
AIC(fit.ER,fit.ARD)</pre>
```

fitPagel

Function to test for correlated evolution of binary traits

Description

This function fit's Pagel's (1994) model for the correlated evolution of two binary characters. plot.fitPagel plots the fitted models using arrows.

Usage

```
fitPagel(tree, x, y, method="fitMk", model="ARD", dep.var="xy", ...)
## S3 method for class 'fitPagel'
plot(x, ...)
```

Arguments

tree	an object of class "phylo".
x	a vector of phenotypic values for a binary trait for the species in tree; or a matrix in which the rows of x give the probability of being in each column state. (The latter option is only supported for method="fitMk".) For S3 plot method, an object of class "fitPagel".
У	a second binary character for the species in tree; or a matrix in which the rows give the probability of being in each column state.
method	function to use for optimization (defaults to method="fitMk"). Other options are "ace" to use the ace function in ape for optimization, or to "fitDiscrete" (if the geiger package is installed) to use geiger's fitDiscrete for optimization.
model	model of evolution for the individual characters. Can be $model="ER"$, "SYM" (equivalent to "ER" in this case), and "ARD".
dep.var	dependent variable. If dep.var="xy" than the rate of substitution in x depends on y & vice versa. If dep.var="x" than the substitution rate in x depends on y, but not the converse. Finally, if dep.var="y" than the rate of substitution in y depends on x, but not the converse.
	optional arguments to be passed to fitMk, ace, or fitDiscrete. For plot method optional arguments include (but may not be limited to): signif, the number of digits for the rates to be plotted; main, a character vector of length two with the headings for each subplot; cex.main, cex.sub, cex.traits, and cex.rates, font sizes for the various text elements of the plot; and lwd.by.rate, a logical argument specifying whether or not to scale arrow line widths in proportion to the estimated rates.

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Value

An object of class "fitPagel" which contains the optimized matrices under an independence & a dependence model, log-likelihoods, a likelihood ratio, and a P-value for the independence model based on a chi-squared test.

plot.fitPagel creates a plot showing the different fitted models with arrows.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Pagel, M. (1994) Detecting correlated evolution on phylogenies: A general method for the comparative analysis fo discrete characters. *Proceedings of the Royal Society B*, **255**, 37-45.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, fitMk, make.simmap
```

force.ultrametric

Forces a phylogenetic tree to be ultrametric

Description

This function forces an object of class "phylo" to be ultrametric. This is achieved either by using nnls.tree from the phangorn package to compute the set of edge lengths that result in a minimized sum-of-squares distance between the patristic distance of the output and input trees (method="nnls"); or by simply extending all the external edges of the tree to match the external edge with the greatest total height (method="extend").

Note that neither of these should be treated as formal statistical methods for inferring an ultrametric tree. Rather, this method can be deployed when a genuinely ultrametric tree read from file fails is.ultrametric for reasons of numerical precision.

Usage

```
force.ultrametric(tree, method=c("nnls", "extend"))
```

Arguments

tree an object of class "phylo".

method the method to use to force the tree to be ultrametric. Options are "nnls" (which

uses the phangorn function nnls.tree internally), or "extend".

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Value

An ultrametric tree in an object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
is.ultrametric, nnls.tree
```

gammatest

Gamma test of Pybus & Harvey (2000)

Description

Conducts γ -test of Pybus & Harvey (2000).

Usage

```
gammatest(x)
```

Arguments

an object of class "ltt" resulting from a call of the function ltt.

Value

A an object of class "gammatest" consisting of a list that contains:

gamma a value for the γ -statistic.

p two-tailed P-value for the γ -test.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Pybus, O. G., and P. H. Harvey (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. R. Soc. Lond. B*, **267**, 2267-2272.

genSeq 85

See Also

```
1tt, mccr
```

Examples

```
tree<-pbtree(n=200)
gammatest(ltt(tree,plot=FALSE))</pre>
```

genSeq

Simulate a DNA alignment on the tree under a model

Description

Simulates DNA sequence on tree under the specified model. Uses sim.Mk internally.

Usage

```
genSeq(tree, l=1000, Q=NULL, rate=1, format="DNAbin", ...)
```

Arguments

tree	object of class "phylo".
1	length of desired sequences.
Q	transition matrix for the simulation. Row and column names (c("a","c","g","t"), although not necessarily in that order) should be provided. If NULL, a single rate is assumed.
rate	multiplier for Q, or a vector for Γ rate heterogeneity.
format	format of the output object. Can be "DNAbin", "phyDat", or "matrix".
	optional arguments.

Value

An object of class "DNAbin" or "phyDat", or a matrix of nucleotides.

Author(s)

Liam Revell liam.revell@umb.edu>

References

86 geo.legend

Examples

```
data(mammal.tree)
mammal.tree$edge.length<-mammal.tree$edge.length/
    max(nodeHeights(mammal.tree))*0.2 ## rescale tree
## simulate gamma rate heterogeneity
gg<-rgamma(n=100,shape=0.25,rate=0.25)
dna<-genSeq(mammal.tree,l=100,rate=gg)</pre>
```

geo.legend

Adds a geological (or other temporal) legend to a plotted tree

Description

The function geo. legend adds a geological (or other temporal) legend to a plotted tree.

The function geo. palette returns a geological time color palette to the user.

Usage

```
geo.legend(leg=NULL, colors=NULL, alpha=0.2, ...)
geo.palette()
```

Arguments

leg a matrix with the starting & ending point of each plotted era in rows, & names

of the time periods as rownames.

colors a vector of colors for the time periods of the rows in leg.

alpha transparency level to apply to colors.

... optional arguments.

Value

geo. legend adds a visual element to a plotted tree and invisible returns an object of class geo. legend containing the time periods and colors of the painted legend.

geo.palette simply returns a geological timescale color palette as an object of class "geo.palette".

Author(s)

Liam Revell liam.revell@umb.edu>

References

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get.treepos

Get position or node of a plotted tree interactively

Description

Both functions return the phylogenetic position of a mouse click on a plotted tree.

get. treepos returns the index of the node at the end of the selected edge, along with the branch distance to that node.

getnode simply returns the closest node to the user mouse click.

Usage

```
get.treepos(message=TRUE, ...)
getnode(...)
```

Arguments

message for get.treepos, a logical value indicating whether or not to print an instructional message.

... optional arguments.

Details

Both functions are primarily meant to be used internally by other *phytools* functions.

Value

A list for get. treepos and a node number for getnode.

Author(s)

Liam Revell liam.revell@umb.edu>

References

88 getDescendants

getCladesofSize

Get all subtrees larger than or equal to a specified size

Description

This function gets all subtrees that cannot be further subdivided into two reciprocally monophyletic subtrees of size >= clade.size.

Usage

```
getCladesofSize(tree, clade.size=2)
```

Arguments

tree is an object of class "phylo".

clade.size subtree size.

Value

An object of class "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
extract.clade, getDescendants
```

getDescendants

Get descendant node numbers

Description

getDescendants returns the set of node & tip numbers descended from node.

getParent returns the *single* parent node of a specified node number (or NULL if node is already the root).

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Usage

```
getDescendants(tree, node, curr=NULL)
getParent(tree, node)
```

Arguments

tree a phylogenetic tree as an object of class "phylo".

node an integer specifying a node number in the tree.

curr the set of previously stored node numbers - used in recursive function calls.

Value

The set of node and tip numbers for the nodes and tips descended from node in a vector, or for getParent the single node preceding node in the tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

Descendants, paintSubTree

getExtant	Returns a list of the extant or extinct lineages in a tree containing non-
	contemporaneous tips

Description

The function getExtant takes a tree as input and returns a vector containing the names of all the tips that have a height above the root that is equal (to a degree of numerical precision determined by tol) to the height of the highest tip.

getExtinct returns the complement.

Usage

```
getExtant(tree, tol=1e-8)
getExtinct(tree, tol=1e-8)
```

90 getSisters

Arguments

tree a phylogeny stored as an object of class "phylo" with some tips that are non-

contemporaneous (i.e., end before the present).

tol a tolerance value to account for numerical imprecision.

Value

A vector with the tip names of extant or extinct species in the tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

nodeHeights

getSisters

Get the sister node number, label, or set of nodes for a node or tip

Description

This function takes a tree and node or tip number of label and returns the number or label of the sister or sisters to that node or tip.

Usage

```
getSisters(tree, node, mode=c("number","label"))
```

Arguments

tree object of class "phylo".

node a node number, tip number, node label, or tip label.

mode an optional string indicating whether to return the node or tip number(s) or the

node or tip label(s), if applicable.

Value

If mode="number" this function returns an integer or vector containing the node number of numbers of the sister node or tip. If mode="label" then this function returns a list containing up to two vectors: one for the node numbers of labels of sister nodes (if applicable); and the other containing the tip labels of the sister tips.

getStates 91

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

getDescendants, Siblings

getStates

Get the states at nodes or tips from a mapped tree

Description

This function gets the states from the nodes or tips of a mapped tree (e.g., make.simmap).

Usage

```
getStates(tree, type=c("nodes","tips"))
```

Arguments

tree is a modified object of class "phylo" or "multiPhylo".

type mode indicating whether to get states at the nodes (type="nodes") or the tips

(type="tips") of the tree.

Value

A named vector (for "phylo") or matrix (for "multiPhylo").

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
describe.simmap, make.simmap, read.simmap, sim.history
```

92 labelnodes

labelnodes	Function to interactively label nodes of a plotted tree

Description

Function adds node labels to a plotted object of class "phylo". The nodes to be labels can be selected interactively by the user (i.e., by clicking on the corresponding nodes of the plotted tree).

Usage

Arguments

text text string or vector to be used as labels.

node node numbers (indices) for the labels.

interactive logical value indicating whether or not nodes should be supplied interactively. (I.e., by clicking on the nodes.)

shape shape to plot around the plotted node label(s).

optional arguments.

Value

Invisibly returns a vector of the node indices for the labeled nodes.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
cladelabels, nodelabels
```

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ladderize.simmap

Ladderize a tree with a mapped discrete character

Description

This function 'ladderizes' an object of class "phylo" with a mapped discrete character. For more information see ladderize.

Usage

```
ladderize.simmap(tree, right=TRUE)
```

Arguments

tree an object of class "simmap".

right a logical specifying how the tree should be ladderized.

Value

A ladderized object of class "simmap".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, ladderize
```

lambda.transform

 λ transformation of matrix

Description

Function multiplies the off-diagonals of a square matrix by λ . Used internally in phyl.pca and other functions.

Usage

```
lambda.transform(lambda, C)
```

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Arguments

lambda scalar, usually (but not necessarily) on the interval 0,1.

C matrix probably returned by vcv.phylo.

Value

An among-species phylogenetic variance covariance matrix (e.g., vcv.phylo) in which the off-diagonal elements have been multiplied by λ .

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

likMlambda

Likelihood for joint λ

Description

Computes the joint likelihood of Pagel's λ parameter.

Usage

```
likMlambda(lambda, X, C)
```

Arguments

scalar, usually on the interval 0,1 (although not required to be).data for various continuous character, in the form of a matrix.

C $n \times n$ matrix (for n taxa) containing the height above the root for each pair of taxa in the tree (e.g., vcv.phylo).

Details

Generally intended to be used internally by other methods that do joint optimization of λ (e.g., phyl.pca).

Value

The log-likelihood.

Author(s)

Liam Revell liam.revell@umb.edu>

linklabels 95

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

linklabels

Function to add tip labels to a plotted tree with linking lines

Description

Function adds tip labels to a plotted tree by drawing curved, bent, or straight linking lines.

Usage

Arguments

text text string or vector to be used as labels.

tips node numbers (indices) for the tips to be labeled.

link.type manner in which to draw the linking lines.

... optional arguments, including cex, lty, lwd, and col.

Details

The idea underlying this function is that the user should first plot the tree without tip labels, but set the area of the plotting device to be sufficient to accommodate the tip labels once they have been added. The function then can be called to add tip labels connected by linking lines to the tips of the plotted tree.

Value

This function annotates a plot.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
cladelabels, nodelabels, tiplabels
```

96 locate.fossil

locate.fossil

Locate a fossil lineage in a tree using continuous characters

Description

This function uses ML to place a fossil lineage into a tree using continuous traits.

Usage

```
locate.fossil(tree, X, ...)
```

Arguments

. . .

tree an object of class "phylo".

X a matrix with continuous character data.

optional arguments including time.constraint which can be a scalar (positive height above the root of the fossil or negative time before present) or a vector (age range of fossil, either positive or negative); edge.constraint, which is equivalent to constraint in locate.yeti; plot, rotate, and quiet, which have the same interpretation (and defaults) as the equivalent arguments in

locate.yeti.

Value

Optimized tree as an object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. (1981) Maximum likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics*, 25, 471-492.

Felsenstein, J. (2002) Quantitative characters, phylogenies, and morphometrics. In: MacLeod, N. and P. Forey (Eds.) *Morphology, Shape and Phylogeny* (pp. 27-44). Taylor and Francis, London.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J., D. L. Mahler, R. G. Reynolds, and G. J. Slater. (2015) Placing cryptic, recently extinct, or hypothesized taxa into an ultrametric phylogeny using continuous, character data: A case study with the lizard *Anolis roosevelti*. *Evolution*, **69**, 1027-1035.

locate.yeti 97

locate.yeti

Locate a cryptic, recently extinct, or missing taxon on a tree

Description

This function uses ML (or REML) to place a recently extinct, cryptic, or missing taxon on an ultrametric (i.e., time-calibrated) phylogeny.

Usage

```
locate.yeti(tree, X, ...)
```

Arguments

tree an object of class "phylo".

X a matrix with continuous character data.

 $. \ . \ . \ optional \ arguments \ including: \ method ("ML" \ or "REML", \ defaults \ to \ "ML"); \ search$

("heuristic" or "exhaustive", defaults to "heuristic"); constraint, a vector containing the daughter node numbers from tree\$edge for each edge to try; plot a logical argument specifying whether or not to plot the likelihood profile on edges (defaults to FALSE); rotate a logical indicating whether or not to rotate the data based on the input tree; and quiet, which is logical and has an

obvious interpretation.

Value

Optimized tree as an object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. (1981) Maximum likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics*, 25, 471-492.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J., D. L. Mahler, R. G. Reynolds, and G. J. Slater. (2015) Placing cryptic, recently extinct, or hypothesized taxa into an ultrametric phylogeny using continuous, character data: A case study with the lizard *Anolis roosevelti*. *Evolution*, **69**, 1027-1035.

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ls.tree

Least squares branch lengths for a given tree

Description

Computes the least squares branch lengths conditioned on a topology and distance matrix. Generally intended as a function to be used internally by optim.phylo.ls.

Usage

```
ls.tree(tree, D)
```

Arguments

tree phylogeny.

D distance matrix.

Value

A tree with branch lengths.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

ltt

Creates lineage-through-time plot (including extinct lineages)

Description

The function 1tt computes LTT plot with extant and extinct lineages, and optionally conducts γ -test of Pybus & Harvey (2000). The object returned by 1tt can be plotted or re-plotted using plot.

The function gtt computes the value of Pybus & Harvey's γ statistic through time by slicing the tree at various points - by default in even intervals from the time above the root at which N=3 to the present day.

The function mccr performs the MCCR test of Pybus & Harvey (2000) which takes into account incomplete taxon sampling in computing a P-value of the γ statistic.

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Usage

```
ltt(tree, plot=TRUE, drop.extinct=FALSE, log.lineages=TRUE, gamma=TRUE, ...)
gtt(tree, n=100, ...)
mccr(obj, rho=1, nsim=100, ...)
```

Arguments

tree is a phylogenetic tree in "phylo" format, or an object of class "multiPhylo"

containing a list of phylogenetic trees.

plot a logical value indicating whether or not to create LTT plot.

drop.extinct logical value indicating whether or not to drop extinct tips from the tree.

log.lineages logical value indicating whether LTT plot should be on log-linear (default) or

linear-linear scale.

gamma logical value indicating whether or not to compute γ from Pybus & Harvey

(2000; Proc. Roy. Soc. B).

n for gtt the number of time intervals to use to track γ through time.

obj for mccr an object of class "ltt".

rho for mccr sampling fraction.

nsim for mccr number of simulations to use for the MCCR test.

... other arguments to be passed to plotting methods. See plot.default.

Details

Although it is calculated here, it's unclear how to interpret the γ -statistic if not all the tips in the tree are contemporaneous.

Value

1tt returns an object of class "1tt" which includes the following components:

times a vector of branching times.

1tt a vector of linages.

gamma optionally, a value for the γ -statistic.

p two-tailed P-value for the γ -test.

If tree is an object of class "multiPhylo", then an object of class "multiLtt" is returned consisting of a list of object of class "ltt".

gtt returns an object of class "gtt".

mccr returns of object of class "mccr".

Author(s)

Liam Revell liam.revell@umb.edu>

100 ltt95

References

Pybus, O. G., and P. H. Harvey (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. R. Soc. Lond. B*, **267**, 2267-2272.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
gammatest, 1tt95
```

Examples

```
## LTT plots
set.seed(99)
trees<-pbtree(n=100, scale=100, nsim=10)
obj<-ltt(trees,plot=FALSE)
plot(obj,log="y",log.lineages=FALSE,
    bty="1")
title(main="LTT plots for 10 pure-birth trees",
    font.main=3)
tree<-pbtree(b=1,d=0.25,t=4)
obj<-ltt(tree,gamma=FALSE,show.tree=TRUE,
    bty="1")
title(main="LTT plot with superimposed tree",
    font.main=3)
obj
## GTT plot
data(anoletree)
anole.gtt<-gtt(anoletree,n=40)</pre>
plot(anole.gtt)
```

1tt95

Creates a $(1-\alpha)$ -percent CI for a set of LTTs

Description

This function computes LTT plots for a set of trees & plots a $(1-\alpha)$ -percent CI by various methods.

Usage

```
ltt95(trees, alpha=0.05, log=FALSE, method=c("lineages","times"),
    mode=c("median","mean"), ...)
## S3 method for class 'ltt95'
plot(x, ...)
```

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Arguments

is an object of class "multiPhylo" containing a list of phylogenetic trees. trees confidence level. Defaults to alpha=0.05. alpha=0 will mean that the interval alpha around all trees in the set will be plotted. log logical value indicating whether or not to plot on the semi-log scale. method plot the CI on the number of lineages given time ("lineages"); or on times given a number of lineages ("times").

plot the median or mean LTT.

mode

object of class "1tt95" for plotting method. Χ

> optional arguments to be used by 1tt95 or the plotting method. So far: res gives the number of time-steps (defaults to res=100); xaxis ("standard", "negative", or "flipped") determines the scale (time from the root, time back from the present, or time from the present) of the x-axis of the plot; lend determines the line end type (as in par); shaded determines whether to plot the $(1-\alpha)$ -percent CI using dotted lines (if FALSE) or shading (if TRUE); and bg is the

background color for shading if shaded=TRUE.

Details

This function creates a plot and invisibly returns an object of class "1tt95".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol., 3, 217-223.

See Also

ltt

make.era.map	Create "era" map on a phylogenetic tree	

Description

This function creates a temporal map on the tree based on limits provided by the user.

Usage

```
make.era.map(tree, limits, ...)
```

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Arguments

tree an object of class "phylo".

limits a vector containing the temporal limits, in time since the root node of the tree,

for the mappings. The first number should be 0, and each subsequent number should be the start of each subsequent regime or era to be mapped on the tree.

... optional arguments.

Value

An object of class "simmap" with the specified eras mapped as different regimes.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap, plotSimmap
```

Examples

```
tree<-pbtree(n=1000,scale=100)
tree<-make.era.map(tree,c(0,25,50,75))
plot(tree,ftype="off",lwd=1)
par(mar=c(5.1,4.1,4.1,2.1)) ## reset margins to default</pre>
```

make.simmap

Simulate stochastic character maps on a phylogenetic tree or trees

Description

This function performs stochastic mapping using several different alternative methods.

For Q="empirical", make.simmap first fits a continuous-time reversible Markov model for the evolution of x and then simulates stochastic character histories using that model and the tip states on the tree. This is the same procedure that is described in Bollback (2006), except that simulation is performed using a fixed value of the transition matrix, Q, instead of by sampling Q from its posterior distribution.

For Q="mcmc", make. simmap first samples Q nsim times from the posterior probability distribution of Q using MCMC, then it simulates nsim stochastic maps conditioned on each sampled value of Q.

For Q set to a matrix, make.simmap samples stochastic mappings conditioned on the fixed input matrix.

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Usage

```
make.simmap(tree, x, model="SYM", nsim=1, ...)
```

Arguments

tree

a phylogenetic tree as an object of class "phylo", or a list of trees as an object of class "multiPhylo".

Х

a vector containing the tip states for a discretely valued character, or a matrix containing the prior probabilities of tip states in rows and character states as column names. The names (if x is a vector) or row names (if x is a matrix) should match the tip labels of the tree. The vector can be of class "factor", "character", or "numeric" (although in the lattermost case its content should obviously be only integer values).

model

a character string containing the model or a transition model specified in the form of a matrix. See ace for more details.

nsim

number of simulations. If tree is an object of class "multiPhylo", then nsim simulations will be conducted per input tree.

. . .

optional arguments. So far, pi gives the prior distribution on the root node of the tree. Acceptable values for pi are "equal", "estimated", or a vector with the frequencies. If pi="estimated" then the stationary distribution is estimated by numerically solving pi*Q=0 for pi, and this is used as a prior on the root. The function defaults to pi="equal" which results in the root node being sampled from the conditional scaled likelihood distribution at the root. message tells whether or not to print a message containing the rate matrix, Q and state frequencies. message defaults to TRUE. For optional argument Q="mcmc" (see below) the mean value of Q from the posterior sample is printed. tol gives the tolerance for zero elements in Q. (Elements less then tol will be reset to tol). Optional argument Q can be a string ("empirical" or "mcmc"), or a fixed value of the transition matrix, Q. If "empirical" than a single value of Q, the most likely value, is used for all simulations. If "mcmc", then nsim values of Q are first obtained from the posterior distribution for Q using Bayesian MCMC, then a simulated stochastic character map is generated for each sampled value of Q. Optional argument vQ can consist of a single numeric value or a vector containing the variances of the (normal) proposal distributions for the MCMC. The order of vQ is assumed to be in the order of the index.matrix in ace for the chosen model. prior is a list containing alpha and beta parameters for the Γ prior distribution on the transition rates in Q. Note that alpha and beta can be single values or vectors, if different priors are desired for each value in the transition matrix Q. As for vQ, the order of prior is assumed to correspond with the order of index. matrix as in ace, prior can also be given the optional logical value use.empirical which tells the function whether or not to give the prior distribution the empirical mean for O. If TRUE then only prior\$beta is used and prior\$alpha is set equal to prior\$beta times the empirical mean of Q. burnin and samplefreq are burn-in and sample frequency for the MCMC, respectively.

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Details

make.simmap uses code modified from ace (by Paradis et al.) to perform Felsenstein's pruning algorithm to compute the likelihood.

As of *phytools* $>= 0.2-33 \times \text{can}$ be a vector of states or a matrix containing the prior probabilities of tip states in rows. In this case the column names of x should contain the states, and the row names should contain the tip names.

Note that there was a small (but potentially significant) bug in how node states were simulated by make.simmap in versions of *phytools* <= 0.2-26. Between *phytools* 0.2-26 and 0.2-36 there was also a bug for asymmetric models of character change (e.g., model="ARD"). Finally, between *phytools* 0.2-33 and *phytools* 0.2-47 there was an error in use of the conditional likelihoods for the root node, which caused the root node of the tree to be sampled incorrectly. These issues should be fixed in all later versions.

Q="mcmc" and Q set to a fixed value were introduced to phytools \geq 0.2-53.

If tree is an object of class "multiPhylo" then nsim stochastic maps are generated for each input tree.

Value

A object of class "simmap" or "multiSimmap" which consists of an object of class "phylo" (or a list of such objects with class "multiPhylo"), with the following additional elements:

maps a list of named vectors containing the times spent in each state on each branch,

in the order in which they occur.

mapped.edge a matrix containing the total time spent in each state along each edge of the tree.

Q the assumed or sampled value of Q.

logL the log-likelihood of the assumed or sampled Q.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Bollback, J. P. (2006) Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, **7**, 88.

Huelsenbeck, J. P., R. Neilsen, and J. P. Bollback (2003) Stochastic mapping of morphological characters. *Systematic Biology*, **52**, 131-138.

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

brownie.lite, brownieREML, countSimmap, describe.simmap, evol.vcv, plotSimmap, read.simmap,
write.simmap

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Examples

```
## load tree and data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## extract discrete character (feeding mode)
fmode<-setNames(sunfish.data$feeding.mode,</pre>
    rownames(sunfish.data))
## do stochastic mapping
smap.trees<-make.simmap(sunfish.tree,fmode,model="ER",</pre>
     nsim=100)
## print a summary of the stochastic mapping
summary(smap.trees)
## plot a posterior probabilities of ancestral states
cols<-setNames(c("blue","red"),levels(fmode))</pre>
plot(summary(smap.trees), colors=cols, ftype="i")
legend("topleft",c("non-piscivorous","piscivorous"),
   pch=21,pt.bg=cols,pt.cex=2)
par(mar=c(5.1,4.1,4.1,2.1))
## plot posterior density on the number of changes
plot(density(smap.trees),bty="1")
title(main="Posterior distribution of changes of each type",
    font.main=3)
```

map.overlap

Proportional overlap between two mapped character histories on a tree

Description

This function computes the fraction of a stochastic character mapping that is shared between two differently mapped trees. In map.overlap it will compute a single quantity giving the overall similarity of the maps, consequently this measure only makes sense of some or all of the states are shared between the two mapped tress. In Map.Overlap what is computed instead is a matrix in which the rows correspond to the states observed in tree1 and the columns give the states for tree2, with the numerical values of the matrix showing the total overlap between each pair of mapped states on the two trees.

Usage

```
map.overlap(tree1, tree2, tol=1e-6, ...)
Map.Overlap(tree1, tree2, tol=1e-06, standardize=TRUE, ...)
```

Arguments

```
tree1 an object of class "simmap".
tree2 an object of class "simmap".
tol an optional tolerance value.
```

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standardize for Map.Overlap, a logical value indicating whether or not to standardize over-

lap by dividing by the summed branch length of the tree.

optional arguments, such as check.equal, a logical value indicating whether or not to check if tree1 and tree2 match in underlying topology and branch lengths (they should). This value is TRUE by default, but can be set to FALSE if

tree1 and tree2 are known to be equal to speed up calculation.

Value

A numerical value on the interval (0, 1), for map. overlap; or a matrix whose elements should sum to 1.0 (Map.Overlap).

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap
```

map.to.singleton

Converts a tree without singletons to a tree with singleton nodes

Description

The function map.to.singleton takes an object of class "simmap" with a mapped discrete character and converts it to a tree with singleton nodes, in which edge has only one state. The states for each edge are stored in names(tree\$edge.length). In a sense this is just an alternative way to use the general structure of the "phylo" object to encode a tree with a mapped character.

plotTree.singletons plots a tree with singleton nodes. Note that plotTree and plot.phylo now have no trouble graphing trees with singleton nodes - but they do this by just ignoring the singletons. plotTree.singletons marks the singletons as nodes on the plotted phylogeny.

drop.tip.singleton drops tips from the tree leaving ancestral nodes for all remaining tips as singletons.

Finally, rootedge.to.singleton converts a tree with a root edge to a tree with a singleton node instead.

Usage

```
map.to.singleton(tree)
plotTree.singletons(tree)
drop.tip.singleton(tree, tip)
rootedge.to.singleton(tree)
```

mapped.states 107

Arguments

tree an object of class "simmap" (for map.to.singleton, or a tree with one or

more singleton nodes (for plotTree.singletons, drop.tip.singleton, and

rootedge.to.singleton).

tip for drop. tip. singleton, a tip label or vector of tip labels.

Value

An object of class "phylo" with singleton nodes. plotTree.singletons graphs a tree in which the singleton nodes are shown.

If names (tree\$edge.length)!=NULL plotTree.singletons will use a different color from palette for each mapped state.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
collapse.singles, drop.tip, make.simmap
```

mapped.states	Returns a vector, matrix, or list of the mapped states on a tree or set of
	trees

Description

Computes and orders a vector, matrix, or list of the unique mapped states on a tree or state of trees of class "simmap" or "multiSimmap".

Usage

```
mapped.states(tree, ...)
```

Arguments

tree a single tree or a set of trees as an object of class "simmap" or "multiSimmap",

respectively.

... optional arguments.

Value

A vector, matrix, or list.

108 markChanges

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

markChanges

Add marked changes to a plotted tree with mapped discrete character

Description

This function adds the reconstructed changes to a plotted tree with a stochastically mapped discrete character.

Usage

```
markChanges(tree, colors=NULL, cex=1, lwd=2, plot=TRUE)
```

Arguments

tree an object of class "simmap".

colors a named vector of colors used to plot the stochastically mapped character on the

tree.

cex expansion factor for line height.

lwd line width.

plot logical value indicating whether the changes should be plotted or not.

Value

This function returns (invisibly) a matrix containing the x & y coordinates of the marked changes on the plotted tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

 ${\tt plotSimmap}$

matchNodes 109

matchNodes	Matches nodes between two trees	

Description

This function returns a matrix in which the first column contains *all* of the internal nodes of tr1 and the second column contains the matching nodes from tr2, inasmuch as they can be identified.

For method="descendants", pairs of matching nodes are defined by sharing all descendant leaves in common.

For method="distances", nodes are considered to matched if the share the same set of distances (or proportional distances, for optional argument corr=TRUE) to all tips.

matchLabels is functionally equivalent but matches node (tip) indices based on identifying matching in the labels only.

Usage

```
matchNodes(tr1, tr2, method=c("descendants", "distances"), ...) matchLabels(tr1, tr2)
```

Arguments

tr1	first tree.
tr2	second tree.
method	method to use to match nodes between trees. "descendants" uses the tip species descended from each node; "distances" uses the distances from the nodes to the tips. Any umambiguous shortening of "descendants" or "distances" is also permitted.
	optional arguments which may or may not be used depending on the value of method. tol is a tolerance value for the difference from exact matching that is allowed for method="distances". corr, which is FALSE by default, indicates whether to match nodes under method="distances" using the correlation

Value

A matrix in which the first column contains the nodes of tr1 with the second column containing matching nodes in tr2, with the criterion for matching defined by method.

(corr=TRUE) or the absolute similarity of distances.

Author(s)

Liam Revell liam.revell@umb.edu>

References

110 mergeMappedStates

mergeMappedStates

Merge two or more mapped states into one state

Description

This function merges two or mapped states on the tree to get one new state.

For instance, one could merge the states "C", "G", and "T" and define the new the state "not-A".

Usage

```
mergeMappedStates(tree, old.states, new.state)
```

Arguments

tree an object of class "simmap" or "multiSimmap" containing one or more phylo-

genetic trees with a mapped discrete character.

old.states states to merge.

new.state name for new state.

Value

An object of class "simmap" or "multiSimmap".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap
```

midpoint.root 111

midpoint.root

Midpoint root a phylogeny

Description

This function midpoint roots a rooted or unrooted tree (Farris 1972).

Usage

```
midpoint.root(tree)
```

Arguments

tree

an object of class "phylo".

Details

Midpoint rooting involves locating the midpoint of the longest path between any two tips and putting the root in that location.

This function performs the same operation as midpoint in the phangorn package, but uses no phangorn code internally.

Value

An object of class "phylo" containing a rooted phylogenetic tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Farris, J. (1972) Estimating phylogenetic trees from distance matrices. *American Naturalist*, **106**, 645-667.

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
midpoint, reroot, root
```

112 minRotate

minRotate	Rotates all nodes of the tree to minimize the difference in order with a vector

Description

This function rotates all the nodes of the tree to try and minimize the different between the order of the tips and the rank-order of a numeric vector x or (in the case of tipRotate the actual integer vector, x.

Usage

```
minRotate(tree, x, ...)
tipRotate(tree, x, ...)
```

Arguments

. . .

tree tree.
x numeric vector.

optional arguments to be used by tipRotate. Presently optional arguments can be fn, function to be used to compute the distance between the order of the tip labels in tree and the numeric vector x (presently fn=function(x) x^2 by default); methods, the method or methods of tree traversal (can be "pre", "post", or c("pre", "post"), for pre-, post-, or both pre- and post-order tree traversal); rotate.multi, whether to rotate multifurcations in all possible ways using rotate.multi (defaults to FALSE); and print, a logical argument specifying whether to print the search progress or to behave quietly. Only the option print is available for minRotate.

Details

Both functions are designed primarily to be used internally by other *phytools* functions and particularly by phylo.to.map (in the case of minRotate) and by cophylo (in the case of tipRotate).

Value

A node-rotated object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

minSplit 113

minSplit	Finding the minimum (median) split in the posterior sample

Description

This function takes a phylogenetic tree and a list of splits and identifies the split with the smallest summed or summed squared distances to all the other splits.

Usage

```
minSplit(tree, split.list, method="sum", printD=FALSE)
```

Arguments

tree an object of class "phylo".

split.list either a matrix with two named columns, "node" and "bp"; a \$mcmc matrix from

evol.rate.mcmc(); or the entire raw output from evol.rate.mcmc().

method an optional string indicating the criterion to minimize: options are "sum" and

"sumsq".

printD logical specifying whether to print distances to screen (FALSE by default).

Value

A list with the following components:

node node for the minimum split.

bp location on the branch leading to node of the minimum split.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J., D. L. Mahler, P. Peres-Neto, and B. D. Redelings (2012) A new method for identifying exceptional phenotypic diversification. *Evolution*, **66**, 135-146.

See Also

```
evol.rate.mcmc, posterior.evolrate
```

114 modified.Grafen

modified.Grafen

Computes modified Grafen edge lengths

Description

This function computes modified Grafen edge lengths in which the length of the edge is determined not by the number of descendant leaves, but instead by the maximum number of node lengths in the path from the node to any leaf.

node.paths is used internally by modified.Grafen and computes the set of paths from a node to all tips descended from that node.

Usage

```
modified.Grafen(tree, power=2)
node.paths(tree, node)
```

Arguments

tree object of class "phylo".

power power to raise the depths of each node (in nodes).

node number for node.paths.

Value

An object of class "phylo" with edge lengths.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
compute.brlen
```

mrp.supertree 115

mrp.supertree	Matrix representation parsimony supertree estimation

Description

This function estimates the MRP (matrix representation parsimony) supertree from a set of input trees (Baum 1992; Ragan 1992).

Usage

```
mrp.supertree(trees, method=c("pratchet","optim.parsimony"), ...)
compute.mr(trees, type=c("phyDat","matrix"))
```

Arguments

trees	an object of class "multiPhylo" that consists of a list of phylogenetic trees.
method	an argument specifying whether to optimize the tree using the <i>phangorn</i> parsimony optimizer pratchet or optim.parsimony.
type	for compute.mr, the type of object to return (e.g., "phyDat" or "matrix").
	optional arguments - mostly to be passed to pratchet or optim.parsimony.

Details

mrp. supertree uses pratchet or optim.parsimony from the *phangorn* package (Schliep, 2011) for optimization, and prop.part from *ape* package (Paradis et al. 2004).

See pratchet or optim.parsimony for optional arguments, which vary slightly depending on the method. All optional arguments of these methods are available to the user with one exception. The argument tree in optim.parsimony is supplied instead as start. In addition to being an object of class "phylo", start can also be assigned the string values of "NJ" or "random", in which case either a neighbor-joining or random tree will be used as the starting tree for optimization.

The function compute.mr computes the matrix-representation matrix of the input trees. It is used internally by mrp.supertree, but can also be used to export an object that can be written to file if desired.

Value

```
An object of class "phylo" or "multiPhylo" that is the MP or set of MP MRP trees. In the case of compute.mr, an object of class "phyDat" or a matrix.
```

Author(s)

```
Liam Revell liam.revell@umb.edu>
```

116 multi.mantel

References

Baum, B. R., (1992) Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon*, **41**, 3-10.

Felsenstein, J. (2004) Inferring Phylogenies. Sinauer.

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Ragan, M. A. (1992) Phylogenetic inference based on matrix representation of trees. *Molecular Phylogenetics and Evolution*, 1, 53-58.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Schliep, K. P. (2011) phangorn: phylogenetic analysis in R. Bioinformatics, 27, 592-593.

See Also

exhaustiveMP, optim.parsimony, pratchet

multi.mantel

Multiple matrix regression (partial Mantel test)

Description

This function conducting a multiple matrix regression (partial Mantel test) and uses Mantel (1967) permutations to test the significance of the model and individual coefficients. It also returns the residual and predicted matrices.

Usage

```
multi.mantel(Y, X, nperm=1000)
```

Arguments

Υ	single "dependent" square matrix. Can be either a symmetric matrix of class "matrix" or a distance matrix of class "dist".
X	a single independent matrix or multiple independent matrices in a list. As with Y can be a object of class "matrix" or class "dist", or a list of such objects.
nperm	number of Mantel permutations to be used to compute a P-value of the test.

Details

Printing the object to screen will result in a summary of the analysis similar to summary.1m, but with p-values derived from Mantel permutations.

Methods residuals and fitted can be used to return residual and fitted matrices, respectively.

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Value

An object of class "multi.mantel" consisting of the following elements:

r. squared multiple R-squared.

coefficients model coefficients, including intercept.
tstatistic t-statistics for model coefficients.
fstatistic F-statistic for the overall model.

probt vector of probabilities, based on permutations, for tstatistic.

probF probability of F, based on Mantel permutations.

residuals matrix of residuals.

predicted matrix of predicted values.

nperm tne number of permutations used.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

multiC

Returns a list with phylogenetic VCV matrix for each mapped state

Description

This function takes a modified "phylo" object as input and returns a set of so-called phylogenetic covariance matrices (e.g., see vcv.phylo) as a list: one for each mapped state.

Usage

```
multiC(tree, internal=FALSE)
```

Arguments

tree an object of class "simmap" consisting of a phylogeny with a mapped discrete

character.

internal logical value indicating whether or not internal nodes should be returned.

Value

A list of matrices.

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Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
evolvcv.lite, read.simmap, vcvPhylo, vcv.phylo
```

multiRF

Computes Robinson-Foulds distance between a set of trees

Description

Computes the Robinson-Foulds (Robinson & Foulds 1981) distance between a set of trees in an object of class "multiPhylo".

Usage

```
multiRF(trees,quiet=FALSE,multi2di=FALSE)
```

Arguments

trees	object of class "multiPhylo" consisting of two or more fully bifurcating, un-

rooted trees. If trees are rooted, they will be unrooted.

quiet logical argument indicating whether or not to run quietly. (Defaults to FALSE.)
multi2di logical argumenet indicating whether or not to resolve multifurcating trees. (De-

faults to FALSE.)

Details

Computes the Robinson-Foulds distance between all phylogenies in an object of class "multiPhylo". Uses prop.part internally for most of the heavy lifting.

Value

A matrix containing distances.

Author(s)

Liam Revell liam.revell@umb.edu>

nodeHeights 119

References

Robinson, D. R., Foulds, L. R. (1981) Comparison of phylogenetic trees. *Mathematical Biosciences*, **53**, 131-147.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

nodeHeights

Compute the heights above the root of each node

Description

nodeHeights computes the height above the root for all nodes in the tree. nodeheight computes the height above the root for a single node.

Usage

```
nodeHeights(tree, ...)
nodeheight(tree, node, ...)
```

Arguments

tree a phylogeny as an object of class "phylo".

node for nodeheight, the node for which we want to compute a height above the root

(or including the root edge, for root.edge=TRUE).

... optional arguments - presently only root.edge, a logical value indicating whether

or not to include the root edge length in the calculation of node heights.

Details

The function nodeHeights also gives a handy way to get the total length of the tree from the root to the heighest tip which will be given by max(nodeHeights(tree)). Generally speaking, nodeHeights will be faster if the heights of all or a large proportion of nodes is needed, wherease nodeheight will be faster if the height of one or a small number of nodes are needed.

Value

Either a matrix of the same dimensions as tree\$edge containing the height above the root of each node in edge (for nodeHeights); or a single positive number (for nodeHeight).

Author(s)

Liam Revell liam.revell@umb.edu>

References

120 nodelabels.cophylo

See Also

```
vcvPhylo
```

Examples

```
tree<-rtree(10)
X<-nodeHeights(tree)</pre>
```

nodelabels.cophylo

Add labels to a plotted "cophylo" object

Description

This function adds node, edge, or tip labels to the plotted trees of a "cophylo" object.

Usage

```
nodelabels.cophylo(..., which=c("left","right"))
edgelabels.cophylo(..., which=c("left","right"))
tiplabels.cophylo(..., which=c("left","right"))
```

Arguments

... arguments to be passed to nodelabels, edgelabels, or tiplabels.

which argument indicated which of the two plotted trees (the "left" or "right" tree)

to be used.

Details

Note that the order of tips, edges, and nodes may be different in the object of class "cophylo" than they are in the original input trees, particularly if cophylo(...,rotate=TRUE) was used.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
cophylo, edgelabels, nodelabels, tiplabels
```

optim.phylo.ls 121

optim.phylo.ls	Phylogeny inference using the least squares method	
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Description

This function performs phylogeny inference using least-squares.

Usage

```
optim.phylo.ls(D, stree=NULL, set.neg.to.zero=TRUE, fixed=FALSE,
    tol=1e-10, collapse=TRUE)
```

Arguments

D a distance matrix.

stree an optional starting tree for the optimization.

set.neg.to.zero

a logical value indicating whether to set negative branch lengths to zero (default

TRUE).

fixed a logical value indicating whether to estimate the topology - if TRUE only the

branch lengths will be computed.

tol a tolerance value used to assess whether the optimization has converged.

collapse a logical indicating whether to collapse branches with zero length.

Details

Function uses nni from the *phangorn* package (Schliep 2011) to conduct NNIs for topology estimation. Since topology optimization is performed using NNIs, convergence to the true least-squares topology is not guaranteed. It is consequently probably wise to start with a very good tree - such as a NJ tree.

Value

An object of class "phylo" that (may be) the least-squares tree with branch lengths; also returns the sum of squares in attr(tree, "Q-score").

Author(s)

Liam Revell liam.revell@umb.edu>

References

Cavalli-Sforza, L. L., and A. W. F. Edwards. (1967) Phylogenetic analysis: Modesl and estimation procedures. *American Journal of Human Genetics*, **19**, 233-257.

Felsenstein, J. (2004) Inferring Phylogenies. Sinauer.

122 orderMappedEdge

Paradis, E., J. Claude, and K. Strimmer. (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Schliep, K. P. (2011) phangorn: phylogenetic analysis in R. Bioinformatics, 27, 592-593.

See Also

exhaustiveMP, nni

orderMappedEdge

Order the columns of mapped.edge to match across trees

Description

This function takes a modified object of class "multiPhylo" with a mapped discrete character (e.g., see read.simmap and sorts the columns of each tree\$mapped.edge to have the same state ordering. This is handy if we want to, for instance, run brownie.lite on a set of mapped trees, and then average the fitted parameter values across trees. The function also works for a single tree.

Usage

orderMappedEdge(trees, ordering=NULL)

Arguments

trees object of class "phylo" or "multiPhylo".

ordering ordering for the columns of \$mapped.edge. If NULL, then an alphabetical or-

der is assumed. Options are "alphabetical", "numerical", or any specific

ordering of the mapped traits (e.g., c("A", "B", "C").

Value

A modified object of class "phylo" or "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

paintSubTree 123

paintSubTree	Paint sub-trees with a discrete character

Description

This function maps or "paints" an arbitrary, i.e., user-specified, discrete character history on the tree. paintSubTree paints the clade downstream of node with a particular state; whereas paintBranches paints only a specified branch.

Usage

```
paintSubTree(tree, node, state, anc.state="1", stem=FALSE)
paintBranches(tree, edge, state, anc.state="1")
```

Arguments

tree	a phylogenetic tree as an object of class "phylo" or a modified object with mapped character traits.
node	an integer specifying the node number tipward of which the function should paint the derived state.
edge	an integer or vector of integers specifying the node or tip numbers of the edges that should be painted in paintBranches.
state	a string (or numeric value) specifying the state to paint on the tree tipward of node.
anc.state	the ancestral state to use; will only be applied if there are presently no character values mapped on the tree.
stem	logical or numeric value indicating whether to use the derived state on the stem leading to node (or not, if stem=FALSE), or, alternatively, what fraction of the stem should be assigned to the derived clade. Note that for tip clades stem=FALSE is not allowed.

Value

An object of class "simmap" that contains the specified paintings as a mapped discrete character.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap, plotSimmap, sim.history
```

paste.tree

paste.tree

Paste two trees together

Description

Primarily internal function for posterior.evolrate; can be used to graft a clade into a receptor tree, at the "sticky tip" labeled with "NA".

Usage

```
paste.tree(tr1, tr2)
```

Arguments

tr1 receptor tree. tr2 donor clade.

Details

The donor clade needs to have a root edge, even if it is zero length.

Value

A tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
tr1<-rtree(10)
tr2<-rtree(10)
tr1$tip.label[1]<-"NA"
tr2$root.edge<-0
tr3<-paste.tree(tr1,tr2)</pre>
```

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pbtree

Simulate pure-birth or birth-death stochastic tree or trees

Description

This function simulates stochastic birth-death trees. Simulation can be performed conditioning on n, on t, or on both simultaneously. If the both, then (for optional argument method="rejection") rejection sampling is performed whereby trees are simulated given b and t until a tree containing n taxa is found. The giving-up point can be set using the optional argument max. count. Simulations can also be performed in continuous time (the default) or discrete time; the difference being that wait times in the continuous-time simulation come from the exponential distribution; whereas waiting times in discrete-time simulations come from the geometric distribution. In addition, discrete-time simulations allow for the possibility that multiple speciation events can occur at (exactly) the same time, so long as they are on separate branches. Finally, sometimes for stopping criterion n in discrete-time there will be a number of tips different from n. This indicates that the last event contained more than one speciation event, and a warning is printed.

method="direct" is presently experimental. It does not really perform direct sampling; however waiting times & birth or death events are sampled first - with only wait-times consistent with n and t being retained. This rejection sampling occurs one layer earlier than for method="rejection". This results in a significant (several-fold) speed-up of the code and enables sampling conditioned on n and t simultaneously for much higher b and d. At the present time, extant.only=TRUE does not work for this mode, nor does type="discrete".

Note that if ape=FALSE, then the function will run faster, and the tree is theoretically compatible with the ape "phylo" standard; however some downstream errors with functions such as bind. tree have been observed.

Usage

```
pbtree(b=1, d=0, n=NULL, t=NULL, scale=NULL, nsim=1, type=c("continuous",
   "discrete"), ...)
```

Arguments

b	birth rate or speciation rate for type="continuous"; the probability of speciating per time-step for type="discrete".
d	death rate or extinction rate for type="continuous"; the probability of going extinct per time-step for type="discrete".
n	desired number of species (i.e., taxa-stop criterion).
t	total time for simulation (i.e., time-stop criterion).
scale	if set, rescales tree to have total length scale.
nsim	number of simulated trees to return.
type	string to indicate whether to simulate trees in continuous or discrete time. If the former, then wait times between speciation events are drawn from an exponential distribution; whereas if the latter then wait times comes from a geometric distribution.

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. . .

optional arguments including ape, a logical value indicating whether to return nodes in a 'ape' compatible ordering (default is TRUE); extant.only a logical value indicating whether or not to return only extant species (defaults to FALSE); max.count a numeric value indicating the maximum number of iterations to run is sampling conditioned on both n and t (defaults to 1e5); method gives the method used for simultaneously conditioning on n and t - options are "rejection" and "direct"; tip.label, a vector of tip labels (only works for n!=NULL); and, finally, quiet, a logical value indicating whether or not to suppress certain message (defaults to FALSE).

Value

A tree or list of trees as an object of class "phylo" or "multiPhylo", respectively.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
# simulate a pure-birth tree with 400 tips, scaled to a length of 1.0
tree<-pbtree(n=400,scale=1)
# simulate a pure-birth tree conditioning on n & t
tt<-log(50)-log(2)
tree<-pbtree(n=50,t=tt)</pre>
```

pgls.Ives

Phylogenetic regression with intraspecific sampling error

Description

This function fits the phylogenetic regression model with within-species sampling error following Ives et al. (2007).

pgls. SEy fits a simpler model in which only sampling error in y is taken into account. This function uses gls from the nlme package internally for optimization and returns an object of class "gls" that is compatible with all methods for that object class.

Usage

```
pgls.Ives(tree, X, y, Vx=NULL, Vy=NULL, Cxy=NULL, lower=c(1e-8,1e-8),
fixed.b1=NULL)
pgls.SEy(model, data, corClass=corBrownian, tree=tree,
    se=NULL, method=c("REML","ML"), interval=c(0,1000), ...)
```

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Arguments

tree	a phylogeny as an object of class "phylo".
X	a named vector containing a <i>single</i> independent variable (multiple independent variables to be added in future). X can contain the species means, or a single long vector containing the sample of values for each species. In the latter case the names (X) will be repeating - all samples from the same species should have the same name.
у	vector the dependent variable. Can be species means or individual values, as for X .
Vx	sampling variances for X. If NULL, then the within-species variance is computed from the data assuming that individual samples, not species means, have been provided in X.
Vy	sampling variances for y. If NULL, then the within-species variance is computed from the data assuming that individual samples, not species means, have been provided in y.
Сху	sampling covariances between X and y. This will also be computed from the data if Cxy==NULL. Note than in this case - but not for the calculation of Vx and Vy, the same number of observations and the same ordering must be provided for X and y. If this is not the case, then it is assumed that different individuals have been sampled for X and y and thus Cxy is assumed to be zero for all species.
lower	vector specifying the lower bounds for estimation for σ_x^2 and σ_y^2 , respectively. (Must be $>$ 0.)
fixed.b1	fixed regression slope, β . Usually set to zero for null hypothesis testing.
model	model to fit. (For pgls. SEy.)
data	data frame. (For pgls. SEy.)
corClass	correlation structure. (For pgls.SEy.)
se	vector of standard errors in y. (For pgls. SEy.)
method	optimization method. (For pgls.SEy.)
interval	interval over which to perform optimization. (For pgls.SEy.)
•••	optional arguments. (For pgls. SEy.)

Details

In the case of pgls. Ives, only the bivariate regression model is implemented. Note that some problems have been reported with the optimization algorithm for this model, which is simple and thus may fail to find the ML solution.

In the case of pgls. SEy the user can (theoretically) specify any class of linear model permitted by gls.

Value

In the case of pgls. Ives, an object of class "pgls. Ives" with the following components:

beta a vector or matrix of regression coefficients.

phenogram phenogram

sig2x	fitted BM rate for X.
sig2y	fitted BM rate for y.

a fitted ancestral states for X and y.

logL log-likelihood.

convergence a value for convergence. convergence=0 is good; see optim for more details.

message a message for convergence.

In the case of pgls. SEy, an object of class "gls".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Ives, A. R., P. E. Midford, and T. Garland Jr. (2007) Within-species measurement error in phylogenetic comparative methods. *Systematic Biology*, **56**, 252-270.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
brownie.lite, phylosig, phyl.resid
```

Description

Function plots a traitgram (Evans et al. 2009), that is, a projection of the phylogenetic tree in a space defined by phenotype (on the y axis) and time (on the x). If a discrete character is mapped on the tree this will also be plotted.

Usage

```
phenogram(tree, x, fsize=1.0, ftype="reg", colors=NULL, axes=list(),
   add=FALSE, ...)
```

Arguments

tree	an object of class "phylo", with or without a mapped discrete character.
x	a vector containing the states at the tips or the states at all the tips and the internal nodes of the tree.
fsize	relative font size for tip labels.
ftype	font type - options are "reg", "i" (italics), "b" (bold), or "bi" (bold-italics).

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colors colors for plotting the mapped character (if available) in tree. If no character

is mapped on the tree, then a single color for all the branches of the tree can be

provided.

axes list of axis dimensions. Items are time and trait.

add optional logical value indicating whether to add to an open plot. If TRUE, then

new axes will not be plotted.

set to quiet=TRUE.

optional arguments including xlim, ylim, log, main, sub, xlab, ylab, asp, type, lty, lwd, offset, and digits are as in plot.default or par. Note that axes overrides xlim and ylim. spread.labels is a logical value indicating whether or not to minimize tip label overlap (default is TRUE); spread.cost is a numeric vector indicating the relative penalty to be used for label overlap and deviance, respectively (if spread.labels=TRUE); spread.range is the range over which to (potentially) spread the labels - note that if labels do not overlap, not all of that range will be used; finally, link is a numeric value by which to offset the tip labels, linking them to the tips with a dashed line (default is 0, if spread.labels=FALSE, or 10-percent of the total tree length otherwise). The optional argument offsetFudge "fudges" the computation of label offset in scaling xlim. It is 1.37, which is the correct fudge in the Windows R GUI, but this may need to be changed in other systems. hold indicates whether (or not) the output to the graphical device should be held using dev.hold before plotting (defaults to hold=TRUE). quiet suppresses some system messages if

Details

For spread.labels=TRUE numerical optimization is performed to optimize the distribution of the labels vertically, where the solution depends on the vector spread.cost containing the cost of overlap (first) and the cost of deviation from the vertical position of the tip. Note that because this is done via numerical optimization, plotting may hang briefly while the best solution is found (especially for large trees).

Value

Plots a traitgram, optionally with a mapped discrete character, and (invisibly) returns a matrix containing the coordinates of the plotted tip labels.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Evans, M. E. K., Smith, S. A., Flynn, R. S., Donoghue, M. J. (2009) Climate, niche evolution, and diversification of the "bird-cage" evening primroses (Oenothera, sections Anogra and Kleinia). *American Naturalist*, **173**, 225-240.

phyl.cca

Examples

```
## load data from Garland et al. (1992)
data(mammal.tree)
data(mammal.data)
## extract character of interest
ln.bodyMass<-log(setNames(mammal.data$bodyMass,
    rownames(mammal.data)))
## plot traitgram
phenogram(mammal.tree,ln.bodyMass,ftype="i",
    spread.cost=c(1,0),fsize=0.7,xlab="time (ma)",
    ylab="log(body mass)")</pre>
```

phyl.cca

Phylogenetic canonical correlation analysis

Description

This function performs phylogenetic canonical correlation analysis (e.g., Revell & Harrison 2008; *Bioinformatics*).

Usage

```
phyl.cca(tree, X, Y, lambda=1.0, fixed=TRUE)
```

Arguments

tree a phylogenetic tree in "phylo" format.

X a data matrix with traits in columns.

Y data matrix with traits in columns, to be correlated with X.

lambda optionally, a (fixed) value for λ .

fixed optionally, a logical value indicating whether or not to estimate λ using likeli-

hood.

Details

(Optional) joint optimization of λ is performed using optimize on the interval (0,1).

Value

An object of class "phyl.cca" containing the following components:

cor canonical correlations.

xcoef coefficients for the canonical variables for X.
ycoef coefficients for the canonical variables for Y.
xscores matrix with the canonical scores for X.
yscores matrix with the canonical scores for Y.

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chisq vector of χ^2 values.

p P-values for the hypothesis test that the *i*th and all subsequent correlations are

zero.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J., Harrison, A. S. (2008) PCCA: A program for phylogenetic canonical correlation analysis. *Bioinformatics*, **24**, 1018-1020.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
phyl.pca
```

phyl.pairedttest

Phylogenetic paired t-test

Description

This function conducts a phylogenetic paired t-test, roughly following Lindenfors et al. (2010; *J. Evol. Biol.*). This is not a phylogenetic ANOVA, in which we want to compare the means of different sets of species on the tree. Instead, we are interested in the difference between two characters, or two measures of a character within a species, and we want to know if this difference is significantly different from zero controlling for the phylogenetic non-independence of species.

Usage

```
phyl.pairedttest(tree, x1, x2=NULL, se1=NULL, se2=NULL, lambda=1.0, h0=0.0,
    fixed=FALSE, ...)
```

Arguments

tree	a phylogeny as an object of class "phylo".
x1	data vector for first trait, or matrix with two traits in columns.
x2	data vector for second trait (or null if x1 is a matrix).
se1	standard errors for x1.
se2	standard errors for x2.
lambda	starting value for Pagel's λ (or fixed value, if fixed=TRUE).
h0	null hypothesis (to be tested) for the mean difference between $x1$ and $x2$.
fixed	logical value specifying whether or not to optimize λ .
	optional arguments.

phyl.pca

Details

Likelihood optimization is performed using optim with method="L-BFGS-B" with box constraints on λ (0,1).

Value

An object of class "phyl.pairedttest" with the following components:

dbar phylogenetic mean difference.

se standard error of dbar.

sig2 estimated evolutionary variance (of the difference).

lambda fitted (or fixed) value of λ .

logL log-likelihood of the fitted model.

t.dbar t-value ((dbar-h0)/se where se is computed from the Hessian).

P. dbar P-value.

df the degrees of freedom.

h0 the null hypothesis that was tested.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Lindenfors, P., L. J. Revell, and C. L. Nunn (2010) Sexual dimorphism in primate aerobic capacity: A phylogenetic test. *J. Evol. Biol.*, **23**, 1183-1194.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

phyl.pca

Phylogenetic principal components analysis

Description

This function performs phylogenetic PCA (e.g., Revell 2009; Evolution).

Usage

```
phyl.pca(tree, Y, method="BM", mode="cov", ...)
## S3 method for class 'phyl.pca'
biplot(x, ...)
scores(object, ...)
## S3 method for class 'phyl.pca'
scores(object, ...)
```

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Arguments

tree phylogeny as an object of class "phylo".

Y data matrix with traits in columns.

method method to obtain the correlation structure: can be "BM" or "lambda".

mode is the mode for the PCA: can be "cov" or "corr".

x object of class "phyl.pca" for biplot method.
object of class "phyl.pca" for scores method.

... for S3 plotting method biplot.phyl.pca, other arguments to be passed to

biplot.

Details

If method="lambda" then λ will be optimized on the interval (0,1) using optimize. Optimization method can be set using the option opt which can take values "ML", "REML", or "fixed". If the last of these is selected than the user should also specify a value of λ to use via the argument lambda.

S3 methods (print, summary, and biplot) are modified from code provided by Joan Maspons and are based on the same methods for objects of class "prcomp". Function biplot now permits the argument choices to be supplied, which should be a vector of length two indicated the two PC axes to be plotted.

S3 method scores extracts or computes (for a matrix of newdata) PC scores given an object of class "phyl.pca".

Value

An object of class "phyl.pca" consisting of a list with some or all of the following components:

Eval diagonal matrix of eigenvalues.

Evec matrix with eigenvectors in columns.

S matrix with scores.
L matrix with loadings.

lambda fitted value of λ (method="lambda" only).

logL log-likelihood for λ model (method="logL" only).

Author(s)

Liam Revell liam.revell@umb.edu>, Joan Maspons

References

Revell, L. J. (2009) Size-correction and principal components for interspecific comparative studies. *Evolution*, **63**, 3258-3268.

phyl.resid

See Also

```
phyl.cca, phyl.resid
```

Examples

```
## load data from Mahler et al. (2010)
data(anoletree)
data(anole.data)
## run phylogenetic PCA
anole.pca<-phyl.pca(anoletree,anole.data)
print(anole.pca)
## plot results
plot(anole.pca)
biplot(anole.pca)</pre>
```

phyl.resid

Phylogenetic size-correction via GLS regression

Description

This function fits one or multiple phylogenetic regressions (depending on the number of columns in Y) and computes the residuals. Designed for phylogenetic size correction using GLS regression (e.g., Revell 2009; *Evolution*).

Usage

```
phyl.resid(tree, x, Y, method="BM")
```

Arguments

tree	a phylogenetic tree in "phylo" format.
X	vector containing the single independent variable (e.g., size), or matrix with multiple independent variables in columns.
Υ	vector or matrix with one or multiple dependent variables in columns.
method	method to obtain the correlation structure: can be "BM" or "lambda".

Details

Optionally fits λ for each regression model. Likelihood optimization of λ is performed for method= "lambda" using optimize on the interval (0,1). This function is theoretically redundant with residuals applied to a "gls" object class in which the correlation structure is based on corBrownian or corPagel; however some users may find this method simpler, and it provides a good way to cross-check your results & make sure that you are using gls correctly.

phyl.RMA

Value

A list with the following components:

beta a vector or matrix of regression coefficients. resid a vector or matrix of residuals for species. lambda a vector of λ values (method="lambda" only). logL a vector of log-likelihoods (method="lambda" only).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2009) Size-correction and principal components for interspecific comparative studies. *Evolution*, **63**, 3258-3268.

Revell, L. J. (2010) Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, **1**, 319-329.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
phyl.pca, gls
```

phyl.RMA

Phylogenetic reduced major axis (RMA) regression

Description

This function performs phylogenetic RMA regression.

Usage

```
phyl.RMA(x, y, tree, method="BM", lambda=NULL, fixed=FALSE, h0=1.0)
## S3 method for class 'phyl.RMA'
coef(object, ...)
## S3 method for class 'phyl.RMA'
plot(x, ...)
```

phyl.RMA

Arguments

x vector with names. In the case of the S3 plot method x is an object of class

"phyl.RMA".

y vector with names.

tree a phylogenetic tree in "phylo" format.

method method to obtain the correlation structure: can be "BM" or "lambda".

lambda value of lambda for fixed λ .

fixed logical value indicating whether or not λ should be optimized using likelihood.

h0 null hypothesis for β . Defaults to 1.0. Note that a null hypothesis of 0.0 is not

allowed.

object for coef method, an object of class "phyl.RMA".

... optional arguments for S3 methods.

Details

Optionally jointly estimates λ if method="lambda". Likelihood optimization of λ is performed using optimize on the interval (0,1). Note that some statistician think there is *never* a condition in which a reduced-major-axis regression should be used.

The statistical hypothesis testing is based on Clarke (1980; reviewed in McArdle 1988), which differs from some other implementations of non-phylogenetic major axis regression in R.

Value

An object of class "phyl.RMA" consisting of a list with the following components:

RMA. beta a vector of RMA regression coefficients.

V a VCV matrix for the traits.

lambda fitted value of λ (method="lambda" only). logL log-likelihood (method="lambda" only).

test a vector containing results for hypothesis tests on β .

resid a vector of residuals for y given x.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Clarke, M. R. B. (1980) The reduced major axis of a bivariate sample. *Biometrika*, 67, 441-446.

McArdle, B. H. (1988) The structural relationship: Regression in biology. *Can. J. Zool.*, **66**, 2329-2339.

phyl.vcv 137

See Also

```
phyl.cca, phyl.pca, phyl.resid
```

phyl.vcv

Compute evolutionary VCV matrix for a tree & dataset

Description

Primarily an internal function for phyl.pca; this can be used to compute the phylogenetic trait variance-covariance matrix given a phylogenetic VCV, λ , and a data matrix.

This function should not be confused with vcv.phylo in the ape package (although one of the objects returned is the output of vcv.phylo).

Usage

```
phyl.vcv(X, C, lambda)
```

Arguments

lambda value for λ transformation.

X data matrix.

C matrix containing the height above the root of each pair of species in the tree.

Typically this will have been produced by calling vcv.phylo.

Value

A list containing three elements, as follows: C, the matrix vcv.phylo transformed by lambda; R, the among trait variance-covariance matrix for the data in X; and alpha, a vector of ancestral states at the root node of the tree.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

phylANOVA

phylANOVA	Phylogenetic ANOVA and post-hoc tests	

Description

This function performs the simulation-based phylogenetic ANOVA of Garland et al. (1993) and (optionally) conducts all posthoc comparisons of means among groups (also obtaining the P-values by phylogenetic simulation).

Usage

```
phylANOVA(tree, x, y, nsim=1000, posthoc=TRUE, p.adj="holm")
```

Arguments

tree	a phylogenetic tree in "phylo" format.
x	a vector containing the groups.
у	a vector containing the response variable (continuously valued).
nsim	an integer specifying the number of simulations (including the observed data).
posthoc	a logical value indicating whether or not to conduct posthoc tests to compare the mean among groups.
p.adj	method to adjust P-values for the posthoc tests to account for multiple testing. Options same as p.adjust.

Details

This function uses a little bit of code from both phy. anova in the geiger package and pairwise.t.test.

Value

An object of class "phylANOVA" containing the following elements:

F F from observed data.

Pf P-value for F from simulation.

T matrix of t-values.

Pt matrix of multiple test corrected P-values from posthoc t-tests.

Author(s)

Liam Revell liam.revell@umb.edu>

phylo.heatmap 139

References

Garland, T., Jr., A. W. Dickerman, C. M. Janis, & J. A. Jones. (1993) Phylogenetic analysis of covariance by computer simulation. *Systematic Biology*, **42**, 265-292.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, W. Challenger. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics*, 24, 129-131.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
anova, pairwise.t.test
```

phvlo	.heatm	ap

Creates a phylogenetic heat map

Description

Functions creates a multivariate phylogenetic heatmap.

Usage

```
phylo.heatmap(tree, X, fsize=1, colors=NULL, standardize=FALSE, ...)
```

Arguments

tree	an object of class "phylo".
X	a matrix containing data for multiple continuous characters in which rownames correspond to the tip labels of the tree.
fsize	an integer or vector of length 3 containing the font size for the tip labels, the trait labels, and the legend text. (If a single integer is supplied, then the value will be recycled.)
colors	a vector of colors to be passed to image. Can be a function call (e.g., heat.colors(n=200)[200:1]).
standardize	a logical value indicating whether or not to standardize each column of X to have the same variance & mean prior to analysis.
	optional arguments. So far these include: legend, a logical value indicating whether or not to plot a figure legend (defaults to legend=TRUE); labels, a logical value indicating whether or not to plot trait labels (defaults to labels=TRUE); split, a numeric vector indicating the fraction of the horizontal dimension to use for the tree & heatmap, respectively (defaults to split=c(0.5,0.5)); xlim, ylim, & mar, defined as in par; and ftype, lwd, and pts as defined in plotSimmap.

Value

Function creates a plot.

phylo.impute

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
## load data
data(anoletree)
data(anole.data)
## compute phylogenetic residuals
anole.data<-as.matrix(anole.data)
anole.resids<-cbind(anole.data[,1],
    phyl.resid(anoletree,anole.data[,1,drop=FALSE],
    anole.data[,2:ncol(anole.data)])$resid)
colnames(anole.resids)[1]<-"SVL"
## plot phylogenetic heatmap
phylo.heatmap(anoletree,anole.resids,
    split=c(0.7,0.3),fsize=c(0.4,0.8,0.8),
    standardize=TRUE)
par(mar=c(5.1,4.1,4.1,2.1)) ## reset margins to default</pre>
```

phylo.impute

Phylogenetic imputation for multivariate continuous character data

Description

This function performs phylogenetic imputation using Maximum Likelihood.

Usage

```
phylo.impute(tree, X, ...)
```

Arguments

tree an object of class "phylo".

X data matrix with species names as row labels. Missing data to be imputed should be coded NA.

... optional arguments.

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Details

This function performs phylogenetic imputation in which the evolution of the characters in X is assumed to have occured by correlation multivariate Brownian motion. Missing values are imputed by maximizing their likelihood jointly with the parameters of the Brownian model. The function evol.vcv is used internally to compute the likelihood. Note that the *Rphylopars* package (https://CRAN.R-project.org/package=Rphylopars) also does phylogenetic imputation for multivariate trait data and it seems to be much faster.

Value

An object of class "phylo.impute" consisting of a complete data frame with missing values imputed.

Since optimization is performed numerically using likelihood, a summary of the optimization can be seen by evaluating attr(object, "optim"), in which object is of class "phylo.impute".

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
evol.vcv
```

phylo.to.map

Plot tree with tips linked to geographic coordinates

Description

phylo.to.map creates an object of class "phylo.to.map" and (optionally) plots that object. plot.phylo.to.map plots an object of class "phylo.to.map" in which the tips of the tree point to coordinates on a geographic map.

Usage

```
phylo.to.map(tree, coords, rotate=TRUE, ...)
## S3 method for class 'phylo.to.map'
plot(x, type=c("phylogram", "direct"), ...)
```

phylo.to.map

Arguments

tree an object of class "phylo".

coords a matrix containing the latitude (in column 1) and the longitude of all tip species

in the tree. The row names should be the same as tree\$tip.label; however, more than one set of coordinates per species can be supplied by duplicating

some row names.

rotate a logical value indicating whether or not to rotate nodes of the tree to better

match longitudinal positions.

x for plot.phylo.to.map, an object of class "phylo.to.map".

type a string indicating whether to map the tips of the tree onto a geographic map

from a square phylogram (type="phylogram") or to project the tree directly

onto the map (type="direct").

.. various optional arguments. For the function phylo.to.map, which first cre-

ates an object of the special class "phylo.to.map" and then (optionally) plots this object, arguments include: database and regions (see map), as well as any arguments that should be passed to plot.phylo.to.map internally. For phylo.to.map, optional arguments xlim and ylim, which control the plot area for the map; fsize for the font size of plot labels and ftype for the font type (following plotSimmap; split which controls the proportion of vertical (or horizontal) space for the tree (first) and map, in a vector; psize the size of the plotted points on the map - or cex.points, a vector contain the size of the tip points and geographic coordinate points, respectively; from.tip a logical value indicating whether to plot the linking lines from the tips (if TRUE) or from the end of the tip label, the default; colors, a single value or a vector of point types; lwd and lty for the linking lines; and pts a logical value indicating whether or

not to plot points at the tips of the tree. mar and asp are as in par.

Value

phylo.to.map creates an object of class "phylo.to.map" and (if plot=TRUE) plots a phylogeny projected onto a geographic map.

plot.phylo.to.map plots on object of class "phylo.to.map".

Author(s)

Liam Revell liam.revell@umb.edu>

References

phylo.toBackbone 143

phylo.toBackbone

Converts tree to backbone or vice versa

Description

Converts between "phylo" and "backbonePhylo".

Usage

```
phylo.toBackbone(x, trans, ...)
backbone.toPhylo(x)
```

Arguments

x an object of class "phylo" (for the function phylo.toBackbone), or an object

of the special class "backbonePhylo" (for backbone.toPhylo).

trans data frame containing the attributes necessary to translate a backbone tree to an

object of class "backbonePhylo". The data frame should contain the following variables: tip.label: the tip labels in the input tree (not all need be included); clade.label: labels for the unobserved subtrees; N: number of species in each subtree; and depth: desired depth of each subtree. depth for each terminal taxon in x cannot be greater than the terminal edge length for that taxon.

.. optional arguments.

Value

Either an object of class "phylo" or an object of class "backbonePhylo", depending on the method.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
plot.backbonePhylo
```

144 phylomorphospace

phyloDesign

Compute design matrix for least squares analyses

Description

Primarily an internal function for optim.phylo.ls, this function creates a design matrix for least squares phylogenetic analysis.

Usage

```
phyloDesign(tree)
```

Arguments

tree

phylogenetic tree.

Details

This function returns a matrix containing the edges in the tree (in columns) and pairs of tip node numbers (in rows). Values in the matrix are either 1 if the edge is on the shortest path between the two tips; and 0 otherwise. Probably do not use unless you know what you're doing.

Value

A matrix.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

phylomorphospace

Creates phylomorphospace plot

Description

This function creates a phylomorphospace plot (a projection of the tree into morphospace) for two characters following Sidlauskas (2008; *Evolution*). It will also plot a discrete character mapped on tree.

project.phylomorphospace animates the phylomorphospace projection.

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Usage

```
phylomorphospace(tree, X, A=NULL, label=c("radial","horizontal","off"),
    control=list(), ...)
project.phylomorphospace(tree, X, nsteps=200, sleep=0,
direction=c("to","from","both"), ...)
```

Arguments

tree a phylogenetic tree in "phylo" format, or a modified "phylo" object with a

mapped discrete character.

X an n x 2 matrix of tip values for two characters in n species.

A an optional m x 2 matrix (for m nodes) of values for two taits at internal nodes in

the tree - if not supplied, these values will be estimated using fastAnc.

label string indicating whether to plot the tip labels in the same direction as the ter-

minal edge (label="radial"), horizontally label="horizontal", or not at all "off". label=TRUE and label=FALSE are also acceptable, for compatibility

with phytools $\leq 0.3-03$.

control a list containing the following optional control parameters: col.edge: a vector

of edge colors; and col. node: a vector of node colors.

nsteps for project.phylomorphospace the number of frames in the animation be-

tween the phylogeny & the phylomorphospace or *vice versa*.

sleep for project.phylomorphospace the time between frames.

direction for project.phylomorphospace whether to morph "to" a phylomorphospace,

"from" a phylomorphospace, or there & back again ("both").

... optional arguments for plotting, including xlim, ylim, xlab, ylab, lwd, colors,

fsize, and node.by.map. colors is only used when there is a mapped discrete character on the tree, in which case control\$col.edge is ignored. fsize is relative to the default, which is textxy(...,cx=0.75). node.by.map is a logical value (defaults to FALSE which tells the function whether or not to plot the node colors using the colors of the mapped discrete character. Setting this option to TRUE will cause control\$col.node to be ignored. node.size is a vector containing the point size relative to the default (see par for plotted internal nodes and tips, respectively. Defaults to node.size=c(1,1.3). If only one number is provided it will be recycled. axes is a logical value indicating whether or not axes should be plotted (see plot.default. Finally, add indicates whether to

add the phylmorphospace to the current plot.

Value

This function creates a phylomorphospace plot

Author(s)

Liam Revell liam.revell@umb.edu>

References

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-90.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Sidlauskas, B. (2008) Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. *Evolution*, **62**, 3135-3156.

Examples

```
## load tree & data from Revell & Collar (2009)
data(sunfish.tree)
data(sunfish.data)
## set colors for mapped discrete character
cols<-setNames(c("blue","red"),
    levels(sunfish.data$feeding.mode))
phylomorphospace(sunfish.tree,sunfish.data[,3:2],
    colors=cols,bty="1",ftype="off",node.by.map=TRUE,
    node.size=c(0,1.2),xlab="relative buccal length",
    ylab="relative gape width")
title(main="Phylomorphospace of buccal morphology in Centrarchidae",
    font.main=3)</pre>
```

phylomorphospace3d

Creates tree-dimensional phylomorphospace plot

Description

This function creates a phylomorphospace plot for three characters using the 3D visualization package, 'rgl'.

Usage

```
phylomorphospace3d(tree, X, A=NULL, label=TRUE, control=list(),
    method=c("dynamic","static"), ...)
```

Arguments

tree	a phylogenetic tree in "phylo" format.
X	an n x 3 matrix of tip values for two characters in n species.
A	an optional m x 3 matrix (for m nodes) of values for two taits at internal nodes in the tree - if not supplied, these values will be estimated using anc.ML.
label	logical value indicating whether to print tip labels next to terminal nodes in the plot (presently doesn't do anything, but labels can be dropped using control).

control	a list containing the following optional control parameters: spin: a logical value indicating whether to animate the plot when created; axes: a logical indicating whether to plot the axes; box: a logical value indicating whether to plot in box; simple.axes: logical value indicating whether to replace box and axes with simpler axes; lwd: line widths; ftype: font type ("off" turns off labels altogether); col.edge a vector of colors of length nrow(tree\$edge).
method	a string either "dynamic" for a dynamic (animated) plot created using rgl; or "static" for a flat 3D plot created using scatterplot3d and base graphics. The latter has the advantage of being very easy to export in standard format.
	optional arguments to be passed to scatterplot3d. Most options not available. angle is an important option that does work here.

Value

This function creates a three dimensional phylomorphospace plot. The function returns a function from spin3d (for method="dynamic"); or a series of functions from scatterplot3d (for method="static").

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Sidlauskas, B. (2008) Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. *Evolution*, **62**, 3135-3156.

See Also

fancyTree, phenogram, phylomorphospace

Examples

148 phylosig

phylosig	Compute phylogenetic signal with two methods	

Description

This function computes phylogenetic signal using two different methods. It can also conduct the hypothesis tests for significant phylogenetic signal, and estimate phylogenetic signal incorporating sampling error following Ives et al. (2007).

Usage

```
phylosig(tree, x, method="K", test=FALSE, nsim=1000, se=NULL, start=NULL,
    control=list())
## S3 method for class 'phylosig'
plot(x, ...)
```

Arguments

tree	a phylogenetic tree in "phylo" format.
X	vector containing values for a single continuously distributed trait. In the case of the plot method, x is an object of class "phylosig".
method	method to compute signal: can be "K" or "lambda".
test	logical indicating whether or not to conduct a hypothesis test of "K" or "lambda".
nsim	for method="K", number of simulations in randomization test.
se	named vector containing the standard errors for each species.
start	vector of starting values for optimization of (respectively) σ^2 and λ . Only used in method="lambda" and se!=NULL.
control	list of control parameters for multidimensional optimization, implemented in optim. Only used in method="lambda" and se!=NULL.
	optional arguments for plot method.

Details

 λ optimization is performed using optimize with the range of λ set between 0 and the theoretical upper limit of λ (determined by the relative height of the most recent internal node on the tree). plot.phylosig creates either a plot of the null distribution of K or a likelihood surface, depending on the value of method.

Value

The function returns an object of class "phylosig". With default arguments (method="K", test=FALSE, and se=NULL), this will be a single numeric value. Otherwise, if (method="K"), it will consist of a list with up to the following components:

```
K value of the K-statistic.
```

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rate of evolution, σ^2 , for estimation with sampling error. logL log-likelihood, for estimation with sampling error. P optionally, the P-value from the randomization test.

If (method="lambda"), it will be a list with up to the following components:

lambda fitted value of λ .

sig2 rate of evolution, σ^2 , for estimation with sampling error.

logL log-likelihood.

logL0 log-likelihood for $\lambda = 0$.

P P-value of the likelihood ratio test.

convergence value for convergence, for estimation with sampling error only. (See optim).

message from optim, for estimation with sampling error only.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

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

Ives, A. R., P. E. Midford, T. Garland Jr. (2007) Within-species variation and measurement error in phylogenetic comparative biology. *Systematic Biology*, **56**, 252-270.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, 401, 877-884.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Examples

```
## load data from Garland et al. (1992)
data(mammal.tree)
data(mammal.data)
## extract characters of interest
ln.bodyMass<-log(setNames(mammal.data$bodyMass,</pre>
    rownames(mammal.data)))
ln.homeRange<-log(setNames(mammal.data$homeRange,</pre>
    rownames(mammal.data)))
## compute phylogenetic signal K
K.bodyMass<-phylosig(mammal.tree,ln.bodyMass,</pre>
    test=TRUE)
print(K.bodyMass)
plot(K.bodyMass)
K.homeRange<-phylosig(mammal.tree,ln.homeRange,</pre>
    test=TRUE)
print(K.homeRange)
plot(K.homeRange)
## compute phylogenetic signal lambda
```

150 plot.backbonePhylo

```
lambda.bodyMass<-phylosig(mammal.tree,ln.bodyMass,
    method="lambda",test=TRUE)
print(lambda.bodyMass)
plot(lambda.bodyMass)
lambda.homeRange<-phylosig(mammal.tree,ln.homeRange,
    method="lambda",test=TRUE)
print(lambda.homeRange)
plot(lambda.homeRange)</pre>
```

plot.backbonePhylo

Plots backbone tree with triangles as clades

Description

Function plots a backbone tree (stored as an object of class "backbonePhylo") with triangles as subtrees.

Usage

```
## S3 method for class 'backbonePhylo' plot(x, ...)
```

Arguments

Х

an object of class "backbonePhylo".

. . .

optional arguments. Includes vscale (to rescale the vertical dimension in plotting), fixed.height (logical value to fix the plotted height of subtree triangles), print.clade.size (logical), fixed.n1 (logical value indicating whether or not to use the fixed triangle height for subtrees containing only one taxon, or to plot as a leaf - defaults to FALSE), and col (a single value, or a vector with names, giving the clade colors), as well as xlim, ylim, and lwd (as well as perhaps other standard plotting arguments).

Value

Plots a tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
phylo.toBackbone
```

plotBranchbyTrait 151

Examples

```
## first create our backbone tree with
## random subtree diversities
tree<-phytools:::lambdaTree(pbtree(n=10),lambda=0.5)
## create a translation table
## leaving a couple of single-taxon clades for fun
tip.label<-sample(tree$tip.label,8)</pre>
clade.label<-LETTERS[1:8]</pre>
N<-ceiling(runif(n=8,min=1,max=20))
## set crown node depth to 1/2 the maximum depth
depth<-sapply(tip.label,function(x,y)</pre>
0.5*y$edge.length[which(tree$edge[,2]==
which(y$tip.label==x))],y=tree)
trans<-data.frame(tip.label,clade.label,N,depth)</pre>
rownames(trans)<-NULL</pre>
rm(tip.label,clade.label,N,depth)
## here's what trans looks like
trans
## convert
obj<-phylo.toBackbone(tree,trans)</pre>
## plot
plot(obj)
```

stead of estimated.

plotBranchbyTrait

Plot branch colors by a quantitative trait or value

Description

Function plots a tree with branches colored by the value for a quantitative trait or probability, by various methods. Unlike most other tree plotting functions in phytools, this function calls plot.phylo (not plotSimmap) internally.

Usage

```
plotBranchbyTrait(tree, x, mode=c("edges","tips","nodes"), palette="rainbow",
    legend=TRUE, xlims=NULL, ...)
```

Arguments

tree	an object of class "phylo".
X	either a vector of states for the edges, tips, or nodes of the tree (for mode="edges", "tips", and "nodes", respectively).
mode	string indicating plotting mode. mode="edges", the default, requires that the mapping state of each edge in the tree should be provided. mode="tips" takes the tip values and estimates the state at each internal node. The mapped character value along each branch is the average of the nodes subtending that branch. mode="nodes" similar to "tips", except that the node values are provided in-

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palette color palette to translate character values to color. Options are presently "rainbow"

(the default), "heat.colors", and "gray". palette can also be a function pro-

duced by colorRampPalette.

legend can be a logical value (TRUE or FALSE) or a numeric value greater than 0. In the

latter case the numeric value gives the length of the plotted legend, which also

acts as a scale bar for the branch lengths of the tree.

xlims range for the translation map between trait values and the color map. Should be

inclusive of all the values in x.

... other optional arguments to be passed to plot.phylo - pretty much all argu-

ments are available. In addition, there plotBranchbyTrait has the following additional optional arguments: tol a small tolerance value to be added to the range of x; prompt for legend=TRUE, a logical value indicating whether to prompt for the position of the legend (or not) - the default is to put the legend in the lower left hand size of the plot; title for legend=TRUE, the title of the legend; and digits for legend=TRUE, the number of digits in the quantitative scale of the legend. Finally, cex can be supplied as either a single numeric value, or as a vector of two different values. If the latter is true than the second element of cex will be passed internally to the function add.color.bar.

Details

Note that if prompt=TRUE, the function will prompt for the position of the legend.

Value

Plots a phylogeny.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

plotSimmap Plot stochastic character mapped tree

Description

Function plots one or multiple stochastic character mapped trees.

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Usage

```
plotSimmap(tree, colors=NULL, fsize=1.0, ftype="reg", lwd=2, pts=FALSE,
    node.numbers=FALSE, mar=NULL, add=FALSE, offset=NULL,
    direction="rightwards", type="phylogram", setEnv=TRUE, part=1.0,
    xlim=NULL, ylim=NULL, nodes="intermediate", tips=NULL, maxY=NULL,
    hold=TRUE, split.vertical=FALSE,
    lend=2, asp=NA, outline=FALSE, plot=TRUE)
## S3 method for class 'simmap'
plot(x, ...)
## S3 method for class 'multiSimmap'
plot(x, ...)
```

Arguments

tree	a modified object of class "phylo" or "multiPhylo" containing a stochastic mapping or set of mappings (e.g., see read.simmap & make.simmap).
colors	a vector with names translating the mapped states to colors - see Examples.
fsize	relative font size for tip labels.
ftype	font type - options are "reg", "i" (italics), "b" (bold), or "bi" (bold-italics).
lwd	line width for plotting.
pts	logical value indicating whether or not to plot filled circles at each vertex of the tree, as well as at transition points between mapped states. Default is FALSE.
node.numbers	a logical value indicating whether or not node numbers should be plotted.
mar	vector containing the margins for the plot to be passed to par. If not specified, the default margins are [0.1,0.1,0.1].
add	a logical value indicating whether or not to add the plotted tree to the current plot (TRUE) or create a new plot (FALSE, the default).
offset	offset for the tip labels in character widths.
direction	plotting direction. Options are "rightwards" (the default), "leftwards", "upwards" or "downwards". For method="fan" direction is ignored.
type	plot type. Can be "phylogram", "fan", or "cladogram". Only a subset of options are presently available for type="fan".
setEnv	logical value indicating whether or not to set the environment .PlotPhyloEnv. Setting this to TRUE (the default) will allow compatibility with ape labeling functions such as nodelabels.
part	value between 0 and 1 for type="fan" indicating what fraction of the full circular tree to use as plotting area. For instance, part=0.5 will plot a half fan phylogeny. It also affects the axis scaling used.
xlim	x-limits for the plot.
ylim	y-limits for the plot.
nodes	node placement following Felsenstein (2004; pp. 574-576). Can be "intermediate", "centered", "weighted", or "inner". So far only works for type="phylogram".

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labeled vector containing the vertical position of tips. Normally this will be 1:N tips for N tips in the tree. maxY maximum value of y to use before rotating a tree into fan configuration. This will only make a difference if different from Ntip(tree). hold logical argument indicating whether or not to hold the output to the graphical device before plotting. Defaults to hold=TRUE. split.vertical split the color of the vertically plotted edges by the state of the daughter edges. Only applies if the edge state changes exactly at a node. lend line end style. See par. aspect ratio. See plot.window. asp logical value indicating whether or not to draw a black outline around the plotted outline edges of the tree.

logical value indicating whether or not to actually plot the tree. (See equivalent

argument in plot.phylo.)

x for S3 plotting method, object of class "simmap" or "multiSimmap".

... for S3 plotting method, other arguments to be passed to plotSimmap.

Details

plot

The underscore character "_" is automatically swapped for a space in tip labels, as in plot.phylo.

Value

Plots a tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Bollback, J. P. (2006) Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Felsenstein, J. (2004) Inferring Phylogenies. Sinauer.

Huelsenbeck, J. P., R. Neilsen, and J. P. Bollback. (2003) Stochastic mapping of morphological characters. *Systematic Biology*, **52**, 131-138.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

densityMap, make.simmap, read.simmap

plotThresh 155

Examples

plotThresh

Tree plotting with posterior probabilities of ancestral states from the threshold model

Description

This function uses the object returned by ancThresh to plot the posterior probabilities of ancestral states under the threshold model. It is also called internally by ancThresh.

Usage

Arguments

tree	phylogenetic tree.
x	a named vector containing discrete character states; or a matrix containing the tip species, in rows, and probabilities of being in each state, in columns.
mcmc	list object returned by ancThresh.
burnin	number of generations (not samples) to exclude as burn in; if NULL then 20 percent of generations are excluded as burn-in.
piecol	a named vector containing the colors for the posterior probabilities plotted as pie charts at internal nodes.
tipcol	a string indicating whether the tip colors should be based on the input data ("input") or sampled tip liabilities ("estimated"). These will only differ if there is uncertainty in the tip states.
legend	logical value or text to be plotted in the legend.
•••	other arguments to be passed to plot.phylo - label.offset should be >0 so that tip labels and species names do not overlap.

plotTree

Value

Plots a tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, bold68, 743-759.

See Also

```
ancThresh, plot.phylo
```

plotTree

Plots rooted phylogenetic tree

Description

This function plots a rooted phylogram. Arguments in ... are passed to plotSimmap, with the exception of optional argument color which is used to determine the plotted color of the branch lengths of the tree.

Usage

```
plotTree(tree, ...)
```

Arguments

tree a phylogenetic tree in "phylo" format; or multiple trees as an object of class

"multiPhylo".

... optional arguments.

Value

This function plots a rooted phylogram.

Author(s)

Liam Revell liam.revell@umb.edu>

plotTree.datamatrix 157

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
plot.phylo, plotSimmap
```

Examples

```
tree<-pbtree(n=25)
plotTree(tree,color="blue",ftype="i")</pre>
```

plotTree.datamatrix

Plot a tree with a discrete character data matrix at the tips

Description

Function plots a phylogeny next to a matrix of discrete character data.

Usage

```
plotTree.datamatrix(tree, X, ...)
```

Arguments

tree an object of class "phylo".

X a data frame with columns as factors.

... optional arguments.

Value

Invisibly returns a list containing the font size, a list of the colors used for each column of the plotted data matrix, and the x-coordinate of the rightmost edge of the matrix.

Author(s)

```
Liam Revell liam.revell@umb.edu>
```

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
{\tt dotTree}, {\tt phylo.heatmap}
```

plotTree.errorbars

plotTree.errorbars

Plot a tree with error bars around divergence dates

Description

Plots a tree with error bars around divergence times (nodes).

Usage

```
plotTree.errorbars(tree, CI, ...)
```

Arguments

tree an object of class "phylo".

CI confidence intervals around internal nodes of the tree, measured in time since

the present.

.. optional arguments to be passed to plotTree.

Details

The matrix CI show contain (in rows) the lower & upper confidence bounds in time since the present.

Optional arguments specific to the error bar plot include gridlines, bar.lwd,cex (for the points plotted at nodes), and bar.col.

Value

Plots a tree with error bars around internal nodes..

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ltt, plotTree
```

plotTree.wBars 159

plotTree.wBars	Plot a tree with bars at the tips	

Description

plotTree.wbars plots a phylogeny in phylogram or fan style with bars at the tips representing the values for a phenotypic trait.

plotTree.barplot creates a split plot in which a right-facing phylogram is on the left, and a bar plot is shown on the right.

plotTree.boxplot creates a split plot in which a right-facing phylogram is on the left, and a box plot is shown on the right.

Usage

Arguments

tree	an object of class "phylo".
X	a named vector or matrix of trait values. For plotTree.boxplot, the names should repeat for multiple observations per species. For plotTree.boxplot x can also be supplied as a formula, though in that case the factor levels need to be provided in a valid cladewise order of the tips in tree. This order doesn't need to correspond with the current order of the tip labels. For plotTree.barplot x can be a matrix (or a data frame) in which columns are the values of multiple traits to be simultaneously plotted on the tree.
scale	scaling factor for the tip bars (relative to the total tree height). If left as NULL a reasonable scaling factor is computed automatically.
width	width of the tip bars.
type	plot type. Can be "phylogram" or "fan".
method	plotting method to use. Can be "plotTree" (for plotTree) or "plotSimmap" (for plotSimmap).
tip.labels	argument indicating whether or not tip labels should be plotted. Defaults to tip.labels=FALSE.
col	colors of the plotted bars. Can be a single value or a vector with length equal to the number of tips in the tree.
border	single value specifying the color of the border for the plotted bars. Defaults to border=NULL, which means that black borders will be plotted.
args.plotTree	in plotTree.barplot, arguments to be passed to plotTree.

plotTree.wBars

```
    in plotTree.barplot, arguments to be passed to barplot.
    in plotTree.boxplot, arguments to be passed to boxplot.
    optional arguments to be passed to plotTree or plotSimmap in the case of plotTree.wBars. For plotTree.barplot, the only optional argument is add. Generally this should not be used; however it can be used to tell the function to draw the tree & barplot, respectively, in the next two open plotting devices rather than creating a table of figures in the current plotting device.
```

Value

Plots a tree with an associated bar plot for a continuously valued character at the tips.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

barplot, dotTree, plotSimmap, plotTree

Examples

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posterior.evolrate

Analysis of the posterior sample from evol.rate.mcmc

Description

This function takes a phylogenetic tree, an average split position, and a raw MCMC output from evol.rate.mcmc and returns a posterior sample of evolutionary rates rootward (σ_1^2) and tipward (σ_2^2) from the average split.

Usage

```
posterior.evolrate(tree, ave.shift, mcmc, tips, showTree=FALSE)
```

Arguments

tree a phylogenetic tree in "phylo" format.

ave.shift mean or median shift-point from the posterior sample (see minSplit.

mcmc matrix \$mcmc from evol.rate.mcmc (probably with burnin excluded).

tips list of stips in state σ_1^2 for each sampled generation of MCMC.

showTree optional logical value indicating whether or not to plot the stretched and shrunken

tree generated by the pre-processing algorithm implemented in this function (de-

fault is FALSE).

Value

A matrix containing the posterior sample of evolutionary rates and shift-points between rates.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J., D. L. Mahler, P. Peres-Neto, and B. D. Redelings (2012) A new method for identifying exceptional phenotypic diversification. *Evolution*, **66**, 135-146.

See Also

```
evol.rate.mcmc, minSplit
```

print.backbonePhylo

posthoc

Generic post-hoc test

Description

This function conducts posthoc test.

Usage

```
posthoc(x, ...)
```

Arguments

x an object on which to conduct a post-hoc test.

... optional arguments to be passed to method.

Details

So far is only implemented for object class "ratebytree".

Value

An object.

Author(s)

Liam Revell liam.revell@umb.edu>

See Also

ratebytree

print.backbonePhylo

Print method for backbone phylogeny

Description

Print method for an object of class "backbonePhylo".

Usage

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

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Arguments

x an object of class "backbonePhylo".

... optional arguments.

Value

Prints to screen.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
phylo.toBackbone
```

ratebystate	Method for investigating the rate of one trait as a function of the state
	of another

Description

This function attempts to ask if the rate of a continuous character, y, depends on the state of a separate continuous trait, x. This is accomplished by regressing the squared contrasts in y on the branch or node ancestral estimates of x.

Usage

```
ratebystate(tree, x, y, nsim=100, corr=c("pearson", "spearman"), ...)
```

Arguments

tree	phylogenetic tree.
x	a continuous character - the dependent variable in the model.
у	a second continuous trait - the response variable.
nsim	number of simulations for hypothesis testing.
corr	correlation method to use. Same as in cor.

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. . .

optional arguments which include sim.method ("fastBM" or "sim.corrs"; see fastBM and sim.corrs); method ("by.node" or "by.branch" indicating whether to assume the rate varies as a function of the node state or the mean branch state); message - a logical value indicating whether or not to return corr and method; finally logarithm - indicating whether or not to fit a model in which the variance of Brownian evolution in y changes as a multiplicative function of x. The default is logarithm=FALSE.

Value

This function returns an object of class "ratebystate" with up to the following four elements:

beta value of the regression coefficient for square of the contrasts in y regressed on

the ancestral or branch-wise estimated states for x.

r correlation coefficient for corr=corr.

corr string giving the value of corr.
method string giving the value of method.

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

fastAnc, pic

ratebytree

Likelihood test for rate variation among trees, clades, or traits

Description

This function essentially implements three different methods for comparing the rate or process of evolution between trees: one for continuously-valued traits, a second for discrete characters, and a third for the rate of diversification (speciation & extinction).

In all cases, the function takes an object of class "multiPhylo" containing two or more phylogenies (trees), and (for the first two analyses) a list of trait vectors (x).

For continuous traits, the function then proceeds to fit two models: one in which the rate (or regime, for models "OU" and "EB") of trait evolution is equal among all trees; and a second in which the rates or regimes can differ between trees.

The latter model corresponds to an extension of the *censored* approach of O'Meara et al. (2006; Revell et al. 2018) and should also be related to the method of Adams (2012) for comparing rates

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among traits. See brownie.lite for a different implementation of the *noncensored* approach of O'Meara et al. (2006).

For discrete traits, the function instead proceeds to fit two variants of the Mk model (Lewis 2001): one in which the parameters values (transition rates) of the process are free to vary between trees, and a second in which they are fixed to be the same.

For diversification alone, the function fits two different diversification (speciation & extinction) models (Nee et al. 1994; Stadler 2012): one in which the birth (speciation) and death (extinction) rates are identical between the trees, and a second in which they are permitted to differ in various ways depending on the value of "model" (Revell 2018).

The method posthoc conducts a post-hoc comparison of parameter estimates between trees in the multi-rate or multi-process model. The parameter that is compared depends on the fitted model. For instance, in model="BM" posthoc comparison is made of sig2; if model="OU" fitted values of alpha are compared; and so on. The argument p.adjust.method can be used to specify a method for adjusting P-values for multiple tests following p.adjust (defaults to p.adjust.method="none".

Usage

```
ratebytree(trees, x, ...)
## S3 method for class 'ratebytree'
posthoc(x, ...)
```

Arguments

trees	an object of class "multiPhylo". If x consists of a list of different traits to be compared, then trees could also be a simple set of duplicates of the same tree, e.g., rep(tree,length(x)).
Х	a list of trait vectors for a continuous trait in which the names of each vectors correspond to the tip labels of trees. This is not used if type="diversification". In the case of posthoc.ratebytree, an object of class "ratebytree".
	optional arguments, including the argument type ("continuous", "discrete", or "diversification"), which, if not specified, the function will attempt to ascertain. See Details for more information.

Details

At present it is not possible to specify different models to fit for the different trees - although if (for instance) character evolution on tree 1 proceeded by a strong *OU* process while character evolution on tree 2 was by *BM*, we would probably reject a constant-process model and tree 2 should show a very low value of alpha.

To compute the standard errors for each fitted paramater value, the function computes the negative inverse of the Hessian matrix at the MLEs; however, if this matrix is computationally singular the generalized inverse (ginv) will be used instead without warning.

The function also conducts a likelihood-ratio test to compare the two models.

For continuous character, optional arguments presently include the following: model, the model of continuous trait evolution (options are "BM", the default, "OU", and "EB"). tol, used as a minimum value for the fitting rates, to prevent problems in optimization. trace, a logical value indicating whether or not to report progress in the optimization. test, the method for hypothesis testing

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(options are "chisq" and "simulation"). quiet, a logical value indicating whether or not to run perfectly quietly. Finally, se, a list of vectors containing the standard errors for each value of x.

For type="discrete" the optional arguments are slightly different. The argument model can be used, but it must assume the values "ER", "SYM", "ARD", or a numeric matrix following ace.

Finally, for type="diversification" models are so far "birth-death", "equal-extinction", and "equal-specation", and "Yule". It is also important to consider supplying the sampling fractions, rho, which is a vector of values between 0 and 1 of the same length as trees. If not provided the method will assume a sampling fraction of 1.0 for all trees - which is seldom true of empirical studies.

Value

An object of class "ratebytree" or an object of class "posthoc.ratebytree" in the case of the method posthoc.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Adams, D. C. (2012) Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Syst. Biol.*, **62**, 181-192.

Lewis, P. O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, **50**, 913-925.

Nee, S., May, R. M. and Harvey, P. H. (1994) The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London B*, **344**, 305-311.

O'Meara, B. C., C. Ane, M. J. Sanderson, and P. C. Wainwright. (2006) Testing for different rates of continuous trait evolution using likelihood. *Evolution*, **60**, 922-933.

Stadler, T. (2012) How can we improve the accuracy of macroevolutionary rate estimates? *Systematic Biology*, **62**, 321-329.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2018) Comparing the rates of speciation and extinction between phylogenetic trees. emphEcology and Evolution, **8**, 5303-5312.

Revell, L. J., Gonzalez-Valenzuela, L. E., Alfonso, A., Castellanos-Garcia, L. A., Guarnizo, C. E., and Crawford, A. J. (2018) Comparing evolutionary rates between trees, clades, & traits. *Methods Ecol. Evol.*, **9**, 994-1005.

See Also

brownie.lite, fitMk

rateshift 167

rateshift	Find the temporal position of one or more rate shifts
racesiirit	Tha the temporal position of one of more rate shifts

Description

Function finds the location of one or more rate shifts. likSurface.rateshift plots the likelihood surface (which is sometimes quite rugged).

Usage

```
rateshift(tree, x, nrates=1, niter=10, method="ML", ...)
## S3 method for class 'rateshift'
plot(x, ...)
likSurface.rateshift(tree, x, nrates=2, shift.range=NULL,
    density=20, plot=TRUE, ...)
```

Arguments

tree	object of class "phylo".
x	vector of phenotypic trait values for species. names(x) should contain the species names and match tree\$tip.label. For plot method, x is an object of class "rateshift".
nrates	number of rates.
niter	number of iterations of optimization routine to ensure convergence.
method	optimization method. Can be "ML" (maximum likelihood) or "REML" (restricted maximum likelihood).
	optional arguments. In the case of the plot method, these will be passed to plotSimmap. For rateshift, optional arguments include: tol, tolerance; plot & print, logical values indicating whether to plot or print the progress of the optimization (default to FALSE); quiet, logical argument indicating whether to suppress all notifications (defaults to FALSE); minL, numeric value; and fixed.shift, either a vector of fixed shift points, or a logical value.
shift.range	for likSurface.rateshift.
density	for likSurface.rateshift.
plot	logical argument for likSurface.rateshift. If plot=FALSE then the surface is returned.

Value

A fitted object of class "rateshift", or, in the case of likSurface.rateshift, a likelihood surface for the shift points.

Author(s)

Liam Revell liam.revell@umb.edu>

168 read.newick

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
brownie.lite
```

read.newick

Robust Newick style tree reader

Description

This function reads a Newick style tree from file.

Usage

```
read.newick(file="", text, ...)
```

Arguments

file name of text file with single Newick style tree or multiple trees, one per line.

text character string containing tree.

optional arguments to be passed to scan. Note that if the arguments sep or what are supplied this could generate an error. Useful optional arguments might

what are supplied this could generate an error. Useful optional arguments might include skip (number of lines to skip) and nlines (number of lines to read).

Details

This function is almost completely redundant with read. tree; however it is 'robust' in that it does not fail if the tree contains so-called 'singles' (nodes with only one descendant).

Value

An object of class "phylo", possibly containing singles (see collapse.singles).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
read.tree, read.nexus
```

read.simmap 169

Examples

```
tree<-"((Human,Chimp),Gorilla),Monkey);"
phy<-read.newick(text=tree)</pre>
```

read.simmap

Read SIMMAP style trees from file

Description

This reads one or multiple SIMMAP style trees from file.

Usage

```
read.simmap(file="", text, format="nexus", rev.order=TRUE, version=1)
```

Arguments

file name of text file with one or multiple SIMMAP v1.0 or v1.5 style trees.

text character string containing the tree. If version=1.5 this argument is ignored. (This format tree can only be read from file in the present version.)

format format of the trees: either "phylip" or "nexus" - the latter is the default output from SIMMAP. If version=1.5 this argument is ignored.

rev.order a logical value indicating whether the states and times along each branch is given (from root to tip) in right-to-left order (if TRUE) or in left-to-right order. If version=1.5 this argument is ignored.

version version of SIMMAP for input tree. If the tree(s) was/were simulated in SIMMAP v1.0 or written to file by link{make.simmap} then version=1.0; if the tree(s)

Details

This function now accepts trees in both SIMMAP v1.0 and SIMMAP v1.5 format. In addition, it can read a more flexible format than is produced by SIMMAP (for instance, multi-character mapped states and more than 7 mapped states). Uses some modified code from read.nexus from the "ape" package to read the NEXUS block created by SIMMAP. Also creates the attribute "map.order" which indicates whether the stochastic map was read in from left to right or right to left. This attribute is used by default by write.simmap to write the tree in the same order.

was/were simulated using SIMMAP v1.5 then version=1.5.

Value

A modified object of class "phylo" (or list of class "multiPhylo") with the following additional elements:

maps a list of named vectors containing the times spent in each state on each branch,

in the order in which they occur.

mapped.edge a matrix containing the total time spent in each state along each edge of the tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Bollback, J. P. (2006) Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
brownie.lite, evol.vcv, read.tree, read.nexus
```

reorder.backbonePhylo Reorders a backbone phylogeny

Description

Function reorders an object of class "backbonePhylo".

Usage

```
## S3 method for class 'backbonePhylo'
reorder(x, order="cladewise", ...)
```

Arguments

```
x an object of class "backbonePhylo".order order. See reorder.phylo for possible orderings.optional arguments.
```

Value

An object of class "backbonePhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

reorderSimmap 171

See Also

```
phylo.toBackbone
```

reorderSimmap

Reorder edges of a simmap tree

Description

Function returns a reordered modified "phylo" object by using reorder.phylo but then sorting the additional elements \$mapped.edge and \$maps to have the same order as \$edge.

Usage

```
reorderSimmap(tree, order="cladewise", index.only=FALSE, ...)
```

Arguments

```
tree a modified object of class "phylo".

order either "cladewise" or "pruningwise" (see reorder.phylo).

index.only logical value indicating whether only an index should be returned.

other arguments.
```

Value

A modified object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
reorder.phylo, plotSimmap
```

rep.phylo

rep.phylo

Replicate a tree or set of trees

Description

S3 method rep for object of class "phylo" or "multiPhylo". repPhylo is just an alias for rep.phylo and rep.multiPhylo.

Usage

```
## S3 method for class 'phylo'
rep(x, ...)
## S3 method for class 'multiPhylo'
rep(x, ...)
repPhylo(tree, times)
```

Arguments

tree object of class "phylo".
times number of times to replicate tree.
x for S3 method an object of class "phylo" or "multiPhylo".
... other arguments for rep (specifically, times).

Value

An object of class "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
c.phylo, rep
```

Examples

```
tree<-pbtree(n=100)
trees<-rep(tree,100)</pre>
```

reroot 173

reroot	Re-root a tree along an edge	
--------	------------------------------	--

Description

This function re-roots a phylogenetic tree at an arbitrary position along an edge.

Usage

```
reroot(tree, node.number, position=NULL, interactive=FALSE, ...)
```

Arguments

tree	a phylogenetic tree in "phylo" format.
node.number	number of the node descending from the target branch in tree\$edge - this can also be a tip in which case the node number is the index number of the tip in tree\$tip.label.
position	position along the target edge at which to re-root the tree. If not supplied, then the tree will be re-rooted <i>at</i> the node or tip.
interactive	logical value indicating whether to use interactive mode (defaults to interactive=FALSE).
	arguments to be passed to plotTree for interactive=TRUE only.

Details

This function had an error for rootings along edges descended from the root node for phytools<=0.2-47. This should be fixed in the present version. Now uses paste.tree, root, and splitTree internally. Earlier versions also had an error related to node labels. This should be fixed in phytools>=0.4-47.

Value

A phylogenetic tree in "phylo" format.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
splitTree, paste.tree, root
```

174 rerootingMethod

rerootingMethod	Get marginal ancestral state	e reconstructions by re-rooting
-----------------	------------------------------	---------------------------------

Description

This function uses the re-rooting method of Yang et al. (1995) to get the marginal ancestral state estimates for each internal node of the tree using likelihood. This method get the conditional scaled likelihoods for the root node (which is the same as the marginal ancestral state reconstruction for that node) and successively moves the root to each node in the tree. The function can also return the posterior probabilities for the tip nodes of the tree.

Usage

```
rerootingMethod(tree, x, model=c("ER", "SYM"), ...)
```

Arguments

tree	an object of class "phylo".
x	a vector of tip values for species, or a matrix containing the prior probability
	that the tip is in each state. If x is a vector, then names(x) should be the species
	names. If x is a matrix of prior probabilities, then rownames should be species
	names, column names should be states for the discrete character, and rows of

the matrix should sum to 1.0.

model any revsersible model. model=c("ER", "SYM") recommended.

optional arguments. Presently the logical argument tips. If tips=TRUE, then the function will also compute the empirical Bayes posterior probabilities of the tips following Yang (2006). Note that ... is passed internally to fitMk, but should be used in this way with caution because any arguments that conflict with the default arguments of the method will cause the function execution to fail. The most practical use of this would be to force a particular value of the

transition matrix, Q, via the argument fixedQ.

Details

This function calls fitMk internally. fitMk uses some code adapted from ace in the ape package. print and plot methods are now available for the object class.

Value

An object of class "rerootingMethod" containing at least the following elements:

loglik the log-likelihood.

Q the fitted transition matrix between states.

marginal.anc the marginal ancestral state reconstructions for each node (and, optionally, each

tip).

rescaleSimmap 175

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Yang, Z., Kumar, S., Nei, M. (1995) A new method of inference of ancestral nucleotide and amino acid sequences. *Genetics*, **141**, 1641-1650.

See Also

```
ace, fitMk, make.simmap
```

 ${\tt rescaleSimmap}$

Rescale SIMMAP style tree

Description

This function scales a tree with a mapped discrete character to an arbitrary total height, preserving the relative time spent in each state along each edge.

Usage

```
rescaleSimmap(tree, ...)
```

Arguments

tree

a phylogenetic tree in modified "phylo" format with a discrete character mapping (e.g., see read.simmap or make.simmap).

... other arguments, such as depth.

Details

Replaces rescaleTree (now rescale.phylo) in the 'geiger' package for SIMMAP style trees.

Value

A phylogenetic tree in modified "phylo" format.

Author(s)

Liam Revell liam.revell@umb.edu>

176 resolveNode

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap
```

resolveNode

Compute all possible resolutions of a node or all nodes in a multifurcating tree

Description

This functions resolves a single multifurcation or all multifurcations in a tree in all possible ways. If the input tree has edge lengths, then the resolutions will use internal edges of zero length.

Usage

```
resolveNode(tree,node)
resolveAllNodes(tree)
```

Arguments

tree an object of class "phylo".

node for resolveNode, the node with a polytomy to resolve.

Details

For resolveNode applied to a multifurcation with n descendants, the number of resolved trees will be equal to the number of possible rooted trees of n taxa. (For instance, three for a trifurcation, 15 for a quadrifurcation, and so on.)

For resolveAllNodes the number of fully resolved trees will be equal to the product of numbers for resolveNode applied to each multifurcation separately. (For instance, 45 for a tree containing one trifurcation and one quadrifurcation.)

Value

An object of class "multiPhylo" - or, if the input tree is already fully resolved, an object of class "phylo" indentical to tree.

Author(s)

Liam Revell < liam.revell@umb.edu>

rotateNodes 177

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

multi2di

rotateNodes

Rotates a node or set of nodes in a phylogenetic tree

Description

The function rotateNodes is a simple wrapper for rotate which rotates a set of nodes or all nodes.

The function rotate.multi finds all possible rotations around a multifurcating node, given by node. This will be an object of class "multiPhylo", assuming that the node specified is indeed a multifurcation.

The function allRotations computes all possible rotated trees for a given input phylogeny. For a binary tree, this is generally two raised to the power of the number of internal nodes (so a very large number, if *N* is even modest in size).

Usage

```
rotateNodes(tree, nodes, polytom=c(1,2), ...)
rotate.multi(tree, node)
allRotations(tree)
```

Arguments

tree object of class "phylo".

nodes either a single node number to rotate, a vector of node numbers, or the string "all".

polytom a vector of mode numeric and length two specifying the two clades that should be exchanged in a polytomy (see rotate).

node a single node to rotate (in the case of rotate.multi).

optional arguments.

Details

All three functions also address the problem that the product of multiple rotations from rotate can be non-compliant with the implicit "phylo" standard because the tip numbers in tree\$edge are not in numerical order 1:n for n tips.

178 roundBranches

Value

An object of class "phylo" (i.e., a phylogenetic tree), in the case of rotateNodes, or an object of class "multiPhylo" for rotate.multi or allRotations.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

roundBranches

Rounds the branch lengths of a tree

Description

This function rounds the branch lengths of a tree or trees and reconciles any mappings for objects of class "simmap" or "multiSimmap".

Usage

```
roundBranches(tree, digits)
```

Arguments

tree an object of class "phylo", "multiPhylo", "simmap", or "multiSimmap".

digits number of digits for rounding. Passed to round.

Value

An object of class "phylo", "multiPhylo", "simmap", or "multiSimmap", with rounded edge lengths.

Author(s)

Liam Revell liam.revell@umb.edu>

References

roundPhylogram 179

roundPhylogram	Plot a round phylogram	

Description

Function plots one or multiple round phylograms.

Usage

```
roundPhylogram(tree, fsize=1.0, ftype="reg", lwd=2, mar=NULL, offset=NULL,
    direction="rightwards", type="phylogram", xlim=NULL, ylim=NULL, ...)
```

Arguments

tree	an object of class "phylo" or "multiPhylo" containing one or multiple phylogenies.
fsize	relative font size for tip labels.
ftype	font type - options are "reg", "i" (italics), "b" (bold), or "bi" (bold-italics).
lwd	line width for plotting.
mar	vector containing the margins for the plot to be passed to par. If not specified, the default margins are $[0.1,0.1,0.1,0.1]$.
offset	offset for the tip labels.
direction	plotting direction. Only the option direction="rightwards" is presently supported.
type	plot type. Can be "phylogram" or "cladogram". If type="cladogram" then the branch lengths are not necessary (and, indeed, are not used).
xlim	x-limits for the plot.
ylim	y-limits for the plot.
	optional arguments.

Details

The underscore character "_" is automatically swapped for a space in tip labels, as in plotSimmap.

Value

Plots a tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

180 rstate

See Also

```
plotSimmap, plotTree
```

Examples

```
data(mammal.tree)
roundPhylogram(compute.brlen(mammal.tree),
   fsize=0.8,ftype="i")
par(mar=c(5.1,4.1,4.1,2.1)) ## reset margin to default
```

rstate

Pick a random state according to a vector of probabilities

Description

Primarily an internal function for make.simmap.

Usage

```
rstate(y)
```

Arguments

У

vector of probabilities. Must have names & should probably add to 1.0.

Details

This function picks a random element in a vector according to the probability assigned that element. It returns the name. Uses rmultinom.

Value

A character or string.

Author(s)

Liam Revell liam.revell@umb.edu>

References

sampleFrom 181

sa	ampleFrom	Sample from a set of distributions

Description

Function samples from a set of normal distributions with parameters given in xbar and xvar.

Usage

```
sampleFrom(xbar=0, xvar=1, n=1, randn=NULL, type="norm")
```

Arguments

xbar a named vector of means.

xvar a named vector of variances.

n a vector containing the sample sizes of each species.

randn a range of sample sizes are to be random.

type "norm" is the only distribution implemented so far.

Value

A vector, with labels.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

setMap	Set color map for various phylogenetic objects of classes	

Description

Function to change the color map (ramp) in an object of class "contMap", "densityMap", or "phyloScattergram".

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Usage

```
setMap(x, ...)
## S3 method for class 'contMap'
setMap(x, ...)
## S3 method for class 'densityMap'
setMap(x, ...)
## S3 method for class 'phyloScattergram'
setMap(x, ...)
```

Arguments

```
x an object of class "contMap", "densityMap", or "phyloScattergram".
... arguments to be passed to colorRampPalette. Also, the argument invert which (if invert=TRUE) will just flip the current color ramp.
```

Value

An object of class "contMap", "densityMap", or "phyloScattergram".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. 2013. Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, **4**, 754-759.

See Also

```
contMap, densityMap
```

sim.corrs

Multivariate Brownian simulation with multiple correlations and rates

Description

This function conducts BM simulation on a tree with multiple rates and/or multiple evolutionary correlations between characters. If vcv is a single matrix, instead of a list of matrices, sim.corrs will simulate multivariate BM with a single rate matrix.

Usage

```
sim.corrs(tree, vcv, anc=NULL, internal=FALSE)
```

sim.history 183

Arguments

tree	is a phylogenetic tree in 'phylo' format; or a modified 'phylo' tree with a mapped discrete character.
vcv	is a square covariance matrix or named list of matrices (one for each mapped state on the tree).
anc	optional vector of values for the root state.
internal	logical value indicating whether to return states at internal nodes.

Value

A matrix containing the multivariate tip states for the n species in the tree (and nodes if internal= TRUE).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J., and D. C. Collar (2009) Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution*, **63**, 1090-1100.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
fastBM, make.simmap, read.simmap, sim.history, sim.rates
```

sim.history	Simulate character history or a discrete character at the tips of the tree under some model

Description

The function sim.history simulates a stochastic character history for a discretely valued character trait on the tree. The resultant tree is stored as a modified "phylo" object in stochastic character map (e.g., make.simmap) format.

The function sim. Mk simulates the states for a discrete character at the tips of the tree only.

Finally, the function sim.multiMk is the same as sim.Mk except that it permits the user to simulate under different values of Q in different parts of the tree.

Usage

```
sim.history(tree, Q, anc=NULL, nsim=1, direction=c("column_to_row",
"row_to_column"), ...)
sim.Mk(tree, Q, anc=NULL, nsim=1, ...)
sim.multiMk(tree, Q, anc=NULL, nsim=1, ...)
```

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Arguments

tree a phylogenetic tree as an object of class "phylo". For the case of sim.multiMk

tree should be an object of class "simmap" in which the regimes for simulation

have been mapped onto the tree.

Q a matrix containing the instantaneous transition rates between states. Note that

for sim.history by default (i.e., when direction="column_to_row", see below) normally this is the transpose of the matrix produced by fitDiscrete in the geiger package or make.simmap in phytools; that is to say the transition rate from i -> j should be given by Q[j,i]. However, if your matrix is properly conformed (i.e., rows or columns sum to 0), then sim.history will attempt to transpose your matrix correctly & will return an informative message (if message=TRUE, see below). For sim.Mk and sim.multiMk this matrix has the same conformation as in fitContinuous and make.simmap. For sim.multiMk Q should be a list of transition matrices with names that correspond to the states

mapped onto the tree.

and an optional value for the state at the root node; if NULL, a random state will

be assigned. anc can be a vector of states, in which one of the states will be chosen randomly for each simulation. For sim.history anc can be a vector of probabilities with names, in which case a state will be chosen in proportion to

the given probabilities.

nsim number of simulations.

direction row/column direction of the input transition matrix, Q. direction="column_to_row"

indicates that the transition rate from $i \rightarrow j$ should be given by Q[j, i], while

direction="row_to_column" indicates the converse.

... other optional arguments. Currently only message, a logical value indicating

whether or not to turn on informational messages (defaults to message=TRUE).

Value

sim.history returns an object of class "simmap" (a tree with a mapped discrete character) or "multiSimmap" for <code>nsim</code> greater than one.

sim.Mk and sim.multiMk return a factor with the states of our discrete character at the tips of the tree only.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

fitMk, fitmultiMk, make.simmap, read.simmap, plotSimmap, sim.rates

sim.ratebystate 185

sim.ratebystate Conduct simulation of state dependent rate variation	
--	--

Description

This function attempts to simulate two characters under a model in which the rate of evolution for the second (y) depends on the states for the first (x). See ratebystate for more details.

Usage

```
sim.ratebystate(tree, sig2x=1, sig2y=1, beta=c(0,1), ...)
```

Arguments

tree	phylogenetic tree.
sig2x	variance of the Brownian process of evolution for x , σ_x^2 .
sig2y	variance of the Brownian process of evolution for y when $x-min(x)==1$ (for logarithm=FALSE) or $x==0$ (for logarithm=TRUE).
beta	intercept and slope of the relationship between the value of x and the Brownian rate in y .
	optional arguments which include method ("by.node" or "by.branch" indicating whether to assume the rate varies as a function of the node state or the mean branch state); plot, a logical value indicating whether or not to plot a phenogram with the branches used for simulation of y after rescaling by the state of x; and logarithm, a logical value indicating whether or not simulate changes in the variance of Brownian evolution for y as an additive logarithm=FALSE or multiplicative function of x. The default is logarithm=FALSE.

Value

This function returns a matrix.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

fastBM, ratebystate

186 sim.rates

S11	m	ra	tes	٠

Brownian or OU simulation with multiple evolutionary regimes

Description

The function sim.rates conducts BM simulation on a tree with multiple rates.

The function multiOU conducts multi-regime OU simulations on the tree under a range of conditions.

Usage

```
sim.rates(tree, sig2, anc=0, nsim=1, internal=FALSE, plot=FALSE)
multiOU(tree, alpha, sig2, theta=NULL, a0=NULL, nsim=1, internal=FALSE, ...)
```

Arguments

tree	is a stochastic map format phylogenetic tree in modified "phylo" format (e.g., see make.simmap).
sig2	a named vector containing the rates for each state; names should be states in mtree.
anc	optional value for the root state.
nsim	number of simulations.
internal	logical value indicating whether to return states at internal nodes.
plot	logical value indicating whether or not to visual the rate heterogeneity (default value is FALSE.
alpha	single value or vector of values of the OU α parameter.
theta	single value or vector of values of the OU θ parameter.
a0	optional value of the root state. Defaults to zero.
	optional arguments.

Details

multiOU uses a difference equation approximation of the OU process.

Value

A vector (for nsim=1) or matrix containing the tip states for the n species in the tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

simBMphylo 187

See Also

fastBM, make.simmap, read.simmap, sim.history

SimbMphylo Creates a graphical illustration of Brownian motion evolution on a phylogeny	simBMphylo	Creates a graphical illustration of Brownian motion evolution on a phylogeny
---	------------	--

Description

The function simulates a discrete-time pure-birth phylogeny (for fixed *N* and *t* using rejection sampling) and then discrete-time Brownian motion on that tree. It then proceeds to generating a plot of the results.

Usage

```
simBMphylo(n, t, sig2, plot=TRUE, ...)
## S3 method for class 'simBMphylo'
plot(x, ...)
```

Arguments

n	number of taxa to simulate in the output tree.
t	total time for the simulation.
sig2	the rate of evolution under Brownian motion, σ^2 , or a vector of rates. If the latter the length of the vector must exactly match t, otherwise the first element of sig2 will just be duplicated t times.
plot	optional logical value indicating whether or not the simulated object should be plotted.
	optional arguments to be passed to the plot method.
x	in plot method, object of class "simBMphylo".

Value

An object of class "simBMphylo" or a plot.

Author(s)

```
Liam Revell liam.revell@umb.edu>
```

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
bmPlot, fastBM, pbtree
```

188 skewers

Examples

```
set.seed(777)
simBMphylo(n=6,t=100,sig2=0.01)
## reset par to defaults
par(mfrow=c(1,1))
par(mar=c(5.1,4.1,4.1,2.1))
```

skewers

Matrix comparison using the method of random skewers

Description

This function performs the random skewers matrix comparison method of Cheverud (1996; also see Cheverud & Marroig 2007 for more details). In addition, it includes a more robust hypothesis test in which random covariance matrices are simulated under a variety of models, and then the mean correlation between response vectors to random skewers are computed.

Usage

```
skewers(X, Y, nsim=100, method=NULL)
```

Arguments

X covariance matrix.Y covariance matrix.

nsim number of random vectors.

method method to generate a null distribution of the random skewers correlation be-

tween matrices. If method=NULL then the correlation will be compared to the correlation between random vectors; however this test has type I error substantially above the nominal level for ostensibly random matrices. Other values of method will be passed as covMethod to genPositiveDefMat for a more robust hypothesis test (see below). Recommended values include "unifcorrmat".

Value

A list with the following components:

r mean random skewers correlation.

p p-value from simulation.

Author(s)

Liam Revell liam.revell@umb.edu>

splitEdgeColor 189

References

Cheverud, J. M. (1996) Quantitative genetic analysis of cranial morphology in the cotton-top (Saguinus oedipus) and saddle-back (S. fuscicollis) tamarins. *J. Evol. Biol.*, **9**, 5–42.

Cheverud, J. M. & Marroig, G. (2007) Comparing covariance matrices: Random skewers method compared to the common principal components model. *Genetics & Molecular Biology*, **30**, 461–469.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

splitEdgeColor

Split edge colors when descendant edges have different mapped states

Description

This function splits the vertical line colors to match the daughter edges when the daughters have different states. Mostly to be used with trees generated using paintBranches or paintSubTree. Also used internally by plotSimmap.

Usage

```
splitEdgeColor(tree,colors,lwd=2)
```

Arguments

tree object of class "simmap".

colors named vector of colors to be used for plotting.

1wd width of the plotted lines.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

plotSimmap

splitplotTree

splitplotTree	Plots a phylogeny in two columns

Description

Function plots a tree in two columns or windows.

Usage

```
splitplotTree(tree, fsize=1.0, ftype="reg", lwd=2, split=NULL, new.window=FALSE)
plotTree.splits(tree, splits=NULL, file=NULL, fn=NULL, ...)
```

Arguments

tree	an object of class "phylo".
fsize	relative font size for tip labels.
ftype	font type - options are "reg", "i" (italics), "b" (bold), or "bi" (bold-italics).
lwd	line width for plotting.
split	relative vertical position for splitting the tree (between 0 & 1).
new.window	whether or not to plot the split tree in a new window. If FALSE then the tree will be plotted in two columns within the same plotting window.
splits	for plotTree.splits relative positions (from 0 to 1) to split the tree across pages or devices.
file	filename if saving to a PDF file is desired. Otherwise will plot to the default plotting device.
fn	function to be executed on each plotted page. For instance, might be: function() cladelabels() if clade labels are desired.
	other arguments to be passed to plotTree.

Value

Plots a tree.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
plotTree, plotSimmap
```

splitTree 191

|--|

Description

Primarily an internal function for posterior.evolrate, this function splits the tree at a given point, and returns the two subtrees as an object of class "multiPhylo".

Usage

```
splitTree(tree, split)
```

Arguments

tree phylogenetic tree.

split split encoded as a list with two elements: node: the node number tipward of the

split; and bp: the position along the branch to break the tree, measured from the

rootward end of the edge.

Details

Probably do not use this unless you can figure out what you are doing.

Value

Two trees in a list.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

192 starTree

starTree

Create star phylogeny

Description

This function creates a star phylogeny.

Usage

```
starTree(species, branch.lengths=NULL)
```

Arguments

```
species a list of species.
```

branch.lengths an optional list of branch lengths in the same order as species.

Details

Creates a star phylogeny with (optionally) user specified branch lengths.

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

stree

strahlerNumber 193

strahlerNumber	Computes Strahler number for trees and nodes

Description

The function strahlerNumber computes the Strahler number of all nodes and tips in the tree. For more information about Strahler numbers see http://en.wikipedia.org/wiki/Strahler_number. The function extract.strahlerNumber extracts all of the most inclusive clades of Strahler number i.

Usage

```
strahlerNumber(tree, plot=TRUE)
extract.strahlerNumber(tree, i, plot=TRUE)
```

Arguments

tree an object of class "phylo".

i order of Strahler number to extract for extract.strahlerNumber.

plot logical value indicating whether to plot the tree with Strahler numbers for node

labels.

Value

Either a vector with the Strahler number for each tip and internal node; or (for extract.strahlerNumber the set of (most inclusive) subtrees with Strahler number i as an object of class "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

194 threshBayes

threshBayes Threshold model using Bayesian MCMC	shold model using Bayesian MCMC	
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Description

This function uses Bayesian MCMC to fit the quantitative genetics threshold model (Felsenstein 2012) to data for two discrete characters or one discrete and one continuous character.

Usage

```
threshBayes(tree, X, types=NULL, ngen=10000, control=list(), ...)
```

Arguments

tree an object of class "phylo". Χ a matrix or data frame containing values for a discrete character and a continuous character; or two discrete characters. The row names of X should be species a vector of length ncol(X) containing the data types for each column of X, for types instance c("discrete", "continuous"). a integer indicating the number of generations for the MCMC. ngen a list of control parameters for the MCMC. Control parameters include: sample, control the sampling interval for the MCMC; propvar, a vector containing (in this order) proposal variances for the two rates (if the type is "discrete" this will be ignored), the two ancestral states, and the correlation; propliab, a single proposal variance for the liabilities; pr.mean, a vector for the mean of the prior probability distributions for each parameter, in the same order as propvar; pr.liab, currently ignored; pr.var, a vector with variances for the prior densities for each parameter, in the same order as pr. mean - note that for the rates we use an exponential distribution so the first two means are currently ignored; and pr.vliab currently ignored.

.. other optional arguments. The argument auto. tune adjusts the proposal distribution to target an proposal acceptance rate (of 0.234, by default).

Details

The plot method for the object class can be used to generate a three panel plot showing the likelihood profile, the mean acceptance rates (using a sliding window), and a profile plot for the correlation coefficient, r.

The density method for the object can be used to plot a posterior density of the correlation coefficient, *r*. This posterior density is of class "density.threshBayes" which can also be plotted using an plot method.

Discrete characters must be binary, but can be coded as any factor.

threshDIC 195

Value

This function returns an object of class "threshBayes" consisting of a list with at least the following two elements: par a matrix containing the posterior sample for the model parameters (evolutionary rates, ancestral states, and correlation); liab a matrix containing the posterior sample of the liabilities. For continuous characters, the liabilities are treated as known and so the posterior samples are just the observed values.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Felsenstein, J. (2012) A comparative method for both discrete and continuous characters using the threshold model. *American Naturalist*, **179**, 145-156.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, **68**, 743-759.

See Also

```
anc.Bayes, bmPlot, evol.rate.mcmc
```

+h	res	hг	TC
τn	res	nι	JΙC

Deviance Information Criterion from the threshold model

Description

This function computes the Deviance Information Criterion from the MCMC object returned by ancThresh.

Usage

```
threshDIC(tree, x, mcmc, burnin=NULL, sequence=NULL, method="pD")
```

Arguments

tree	phylogenetic tree.
x	a named vector containing discrete character states; or a matrix containing the tip species, in rows, and probabilities of being in each state, in columns.
mcmc	list object returned by ancThresh.
burnin	number of generations (not samples) to exclude as burn in; if not supplied then 20 percent of generations are excluded.

196 threshState

sequence assumed ordering of the discrete character state. If not supplied and x is a vector

then numerical-alphabetical order is assumed; if not supplied and x is a matrix,

then the column order of x is used.

method method for computing the effective number of parameters (options are "pD" and

"pV").

Value

A vector containing the mean deviance and deviance for the parameter means, the effective number of parameters, and the DIC.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, **68**, 743-759.

See Also

ancThresh

threshState	Computes value for a threshold character from a liability and thresh-
	olds

Description

Primarily to be used internally by ancThresh; can also be used to simulate threshold traits.

Usage

```
threshState(x, thresholds)
```

Arguments

x liability.

thresholds a named vector containing the thresholds.

Value

A discrete character value.

to.matrix 197

Author(s)

Liam Revell < liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Revell, L. J. (2014) Ancestral character estimation under the threshold model from quantitative genetics. *Evolution*, **68**, 743-759.

See Also

ancThresh, threshDIC

to.matrix

Convert a character vector to a binary matrix

Description

This function takes a vector of characters and computes a binary matrix. Primarily to be used internally by make.simmap and rerootingMethod.

Usage

```
to.matrix(x, seq)
```

Arguments

x a vector of characters.

seq the sequence for the columns in the output matrix.

Value

A binary matrix of dimensions length(x) by length(seq).

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

198 tree.grow

tree.grow

Creates an animation of a tree growing from left-to-right or upwards

Description

This function simulates a birth-death tree under user-defined conditions and then creates an animation of that tree growing from left-to-right in the plotting device, or upwards.

Usage

```
tree.grow(..., res=200, direction="rightwards", ladderize=TRUE)
```

Arguments

... arguments to pass to pbtree.

res number of steps (the resolution of the animation). This also corresponds to the

number of frames that will be created if the animation is to be converted to a .gif

file.

direction the direction to plot the tree. Only direction="rightwards" (the default) and

direction="upwards" are supported.

ladderize logical value indicating whether or not to 'ladderize' the plotted tree. (Defaults

to TRUE.)

Value

An object of class "phylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

pbtree

Examples

```
## Not run:
## to create a .gif with ImageMagick installed
png(file="pbtree-
tree.grow(b=0.06,d=0.02,t=100)
dev.off()
system("ImageMagick convert -delay 5 -loop 0 *.png pbtree-anim.gif")
## End(Not run)
```

treeSlice 199

treeSlice	Slices the tree at a particular point and returns all subtrees, or the tree rootward of the point

Description

This function slices a tree at a particular height above the root and returns all subtrees or all non-trivial subtrees (i.e., subtrees with more than 1 taxon). Uses extract.clade in the "ape" package.

It can also be used to crop the terminal fraction of a tree for orientation="rootwards".

Usage

```
treeSlice(tree, slice, trivial=FALSE, prompt=FALSE, ...)
```

Arguments

+ ===	is a phylogopatic troc in "phylo" format
tree	is a phylogenetic tree in "phylo" format.
slice	a real number indicating the height above the root at which to slice the tree.
trivial	a logical value indicating whether or not to return subtrees with a number of tips less than two (default is FALSE).
prompt	logical value indicating whether or not the height of the slice should be given interactively.
	for prompt=TRUE, other arguments to be passed to plotTree. In addition, the argument orientation can be used to specify whether the "tipwards" subtrees or the "rootwards" phylogeny are/is to be returned by the function call (using those two argument values, respectively).

Value

An object of class "phylo" or "multiPhylo".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
extract.clade
```

200 vcvPhylo

untangle

Attempts to untangle crossing branches for plotting

Description

This function attempts to untangle the branches of a tree that are tangled in plotting with plot.phylo, plotTree, or plotSimmap.

Usage

```
untangle(tree, method=c("reorder", "read.tree"))
```

Arguments

tree as an object of class "phylo" or "simmap".

method method to use to attempt to untangle branches. method="reorder" uses two

calls of reorder.phylo or reorderSimmap; method="read.tree" writes the tree to a text string and then reads it back into memory using read.tree.

Value

An object of class "phylo" or "simmap".

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

vcvPhylo

Calculates cophenetic (i.e., phylogenetic VCV) matrix

Description

This function returns a so-called *phylogenetic variance covariance matrix* (e.g., see vcv.phylo), but (optionally) including ancestral nodes and under different evolutionary models.

Usage

```
vcvPhylo(tree, anc.nodes=TRUE, ...)
```

write.simmap 201

Arguments

tree object of class "phylo".

anc.nodes logical value indicating whether or not to include ancestral nodes.

... optional arguments including internal (synonym of anc.nodes) and model

(can be "BM", "OU", or "lambda".

Value

A matrix.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

write.simmap

Write a stochastic character mapped tree to file

Description

This function writes stochastic character mapped trees to file in multiple SIMMAP formats (Bollback 2006).

Usage

```
write.simmap(tree, file=NULL, append=FALSE, map.order=NULL, quiet=FALSE,
format="phylip", version=1.0)
```

Arguments

tree an object of class "simmap" or "multiSimmap".

file an optional filename.

append a logical value indicating whether to append to file.

map.order a optional value specifying whether to write the map in left-to-right or right-to-

left order. Acceptable values are "left-to-right" or "right-to-left" or some abbreviation of either. If not provided, write.simmap will use attr(tree, "map.order")

if available.

quiet logical value indicating whether or not to print a warning message when map.order

is neither specified by a function argument or as an attribute of tree.

format file format for output.

version version of SIMMAP. Note that the options are 1.0 and 1.5. version=1.5 is

generally recommended because in this format the tree can also be parsed by

typical tree readers, but absent its mapped trait.

202 writeAncestors

Value

A file.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Bollback, J. P. (2006) Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Huelsenbeck, J. P., R. Neilsen, and J. P. Bollback (2003) Stochastic mapping of morphological characters. *Systematic Biology*, **52**, 131-138.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
make.simmap, read.simmap, plotSimmap
```

writeAncestors

Write a tree to file with ancestral states and (optionally) CIs at nodes

Description

This function writes a tree to file with ancestral character states and (optionally) 95-percent confidence intervals stored as node value..

Usage

Arguments

tree	a phylogenetic tree or set of trees as an object of class "phylo" or "multiPhylo".
Anc	a vector of ancestral states, a list containing the ancestral states and 95-percent confidence intervals (as from fastAnc or ace, or a list of such results.
file	an optional string with the filename for output.
digits	an integer indicating the number of digits to print for branch lengths and ancestral character values.
format	a string indicating whether to output the result in simple Newick (i.e., "phylip") or Nexus format.
	additional arguments including x: a vector of character values, in which case ancestral states are estimated internally using fastAnc; and CI: a logical value indicating whether or not to estimate 95-percent confidence intervals.

writeNexus 203

Value

A file, string, or vector of strings.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
ace, fastAnc, write.tree
```

writeNexus

Write a tree to file in Nexus format

Description

This function writes one or multiple phylogenetic trees to file in NEXUS format. Redundant with ape::write.nexus.

Usage

```
writeNexus(tree, file="")
```

Arguments

tree object of class "phylo" or "multiPhylo".

file file name for output.

Value

Trees written to file.

Author(s)

Liam Revell liam.revell@umb.edu>

References

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

See Also

```
write.simmap, write.nexus
```

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