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Description Functions for fitting models of trait evolution on phylogenies for continuous traits. The majority of functions described in Thomas and Freckleton (2011) <doi:10.1111/j.2041-210X.2011.00132.x> and include functions that allow for tests of variation in the rates of trait evolution.

License GPL (>= 2)

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R topics documented:

addFossilToPhy	2
allCladeMembers	4
ancState	4
anolis.data	5
anolis.tree	5
as.rateData	6

as.rateMatrix	7
cladeIdentity	8
contemporaryPhy	9
dropTipPartial	10
fairProportions	11
likRatePhylo	12
likTraitPhylo	13
make.anc	14
make.likRatePhylo	15
ML.RatePhylo	16
name.check	18
node.descendants	19
nodeTimes	20
optim.likRatePhylo	20
phyloCovar	22
phyloMean	23
phyloVar	24
pic.motmot	26
plotPhylo.motmot	27
RatePhylo.allCI	29
RatePhylo.CI	31
removeNonBin	32
sampleHiddenSp	33
sliceTree	34
sortTraitData	35
timeSliceSummary	36
timeTravelPhy	37
traitData.plot	38
traitMedusaSummary	39
transformPhylo	40
transformPhylo.ll	43
transformPhylo.MCMC	46
transformPhylo.ML	48
transformPhylo.sim	53
transformRateMatrix	55

Index**57**

addFossilToPhy	<i>add a fossil to an interior branch of a time-scaled phylogeny</i>
----------------	--

Description

the function takes a time-scaled phylogeny and adds a fossil at a branch in the past

Usage

```
addFossilToPhy(phy, inGroup, fossil, fossilAge, minLength = 0.1,  
              maxLength = NULL)
```

Arguments

phy	An object of class "phylo" (see ape package).
inGroup	vector of tip labels defined as the ingroup - the fossil(s) will be placed on the stem branch leading to the 'inGroups' most recent common ancestor
fossil	tip labels for the new fossil
fossilAge	age of the fossil
minLength	minimum length leading to the fossil
maxLength	maximum length leading to the fossil. If NULL (default) then the maximum bound is half the length of the branch leading to the crown node

Value

the the time-scaled phylogeny with the fossil attached

Author(s)

Mark Puttick

References

Puttick, M. N., Kriwet, J., Wen, W., Hu, S., Thomas, G. H., & Benton, M. J. (2017). Body length of bony fishes was not a selective factor during the biggest mass extinction of all time. *Palaeontology*, 60, 727-741.

Examples

```
data(anolis.tree)  
plot(anolis.tree)  
nodelabels(214, 214)  
# add fossil to node 214  
in.groups <- node.descendants(x=214, phy=anolis.tree, tip.labels=TRUE)[[2]]  
fossilPhy <- addFossilToPhy(anolis.tree, in.groups, fossil="fakeFossil", fossilAge=60)  
plot(fossilPhy)
```

allCladeMembers	<i>allCladeMembers (internal function)</i>
-----------------	--

Description

This is an internal function to generate an allCladeMembersMatrix

Usage

```
allCladeMembers(phy)
```

Arguments

phy	phylogeny in ape phylo format
-----	-------------------------------

Value

cladeMembersMatrix

Author(s)

Gavin Thomas

ancState	<i>Estimate ancestral state (internal function)</i>
----------	---

Description

This is an internal function to estimate the character value at the root node

Usage

```
ancState(phy, y)
```

Arguments

phy	a phylogeny in APE phylo format
y	A matrix of trait data corresponding to species in phy

Author(s)

Gavin Thomas

anolis.data	<i>Anolis phenotype data</i>
-------------	------------------------------

Description

Data on anolis phenotype data from Thomas et al. 2009

Usage

```
data(anolis.data)
```

Format

An object of class "data.frame".

References

Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.data)
head(anolis.data)
```

anolis.tree	<i>Anolis phylogeny</i>
-------------	-------------------------

Description

Data on anolis phylogeny from Thomas et al. 2009

Usage

```
data(anolis.tree)
```

Format

An object of class "phylo".

References

Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
anolis.tree
```

as.rateData

*Conversion among data and phylogeny objects***Description**

Function to generate a "rateData" object containing the discrete explanatory variable, continuous response variable and set of variance co-variance matrices. It loads the trait data and removes species with missing data from the data and vcv matrix. as.rateData requires either a set of matrices in rateMatrix format created using as.rateMatrix or, if no rateMatrix object is input then it requires a phylogeny in "phylo" format. If a "phylo" object is used as.rateData will call as.rateMatrix internally. as.rateMatrix calls the "ape" function vcv.phylo multiple times and this can be slow for large phylogenies. It will often be more efficient to use as.rateMatrix first to create a "rateMatrix" object to pass to as.rateData, particularly if there are many response traits of interest to be fitted to the same phylogeny and set of reconstructed ancestral states.

Usage

```
as.rateData(y, x, rateMatrix = NULL, phy = NULL, data, meserr.col = NULL,
  meserr.propn = NULL, log.y = FALSE, report_prune = FALSE)
```

Arguments

y	The response variable - typically a continuous trait. Specified as a column name or index
x	The explanatory (discrete) variable used to define the hypothesised rate categories. Specified as a column name or index.
rateMatrix	A "rateMatrix" object or NULL
phy	An object of class "phylo" (see ape package).
data	A data frame containing (minimally) the x and y variables as columns with species names as rownames.
meserr.col	Column name or index containing measurement error for species means.
meserr.propn	Single value specifying the proportional measurement to be applied across all species.
log.y	Logical, natural log transform response variable.
report_prune	Logical. Prints a list of dropped species if TRUE

Value

rateData An object of class "rateData" which is a list containing the response (y) and explanatory (x) variable along with a list of variance-covariance matrices.

Author(s)

Gavin Thomas

References

Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

## Convert data to class rateData with a phylo object as input
anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = NULL, phy=anolis.tree, data=anolis.data, log.y=TRUE)
```

as.rateMatrix

Conversion among data and phylogeny objects

Description

Function to generate a "rateMatrix" object containing a set of variance covariance matrices. Note that as.rateMatrix calls the CAIC function `vcv.array` multiple times and this can be slow for large phylogenies (though faster than using the "ape" equivalent `vcv.phylo`).

Usage

```
as.rateMatrix(phy, x, data)
```

Arguments

phy	An object of class "phylo" (see ape package).
x	The explanatory (discrete) variable used to define the hypothesised rate categories. Can be specified as a column number or column name
data	The explanatory (discrete) variable used to define the hypothesised rate categories. Can be specified as a column number or column name

Value

rateMatrix An object of class "rateMatrix" - a list of matrices describing the expected variances and covariances of between species. Each matrix refers to the variances and covariances for a given state of x (see Thomas et al. 2006).

Author(s)

Gavin Thomas

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624.

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)

## Convert data to class rateMatrix
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)
```

cladeIdentity	<i>Identify branches (including tips) descended from a node (internal function).</i>
---------------	--

Description

Internal function to get presence absence of descendent branches from a vector of node numbers. The descendents include the branch leading to the focal node (i.e. node defines the stem group no crown group)

Usage

```
cladeIdentity(phy, nodeIDs, cladeMembersObj = NULL)
```

Arguments

phy	An object of class "phylo" (see ape package).
nodeIDs	Vector of node numbers (positive integers).
cladeMembersObj	Matrix of clade membership

Details

The function returns a matrix of unique presences given the selected node. If the selected nodes are nested then presences are only recorded for the least inclusive node.

Value

matrix Matrix of unique presences for each node id

Author(s)

Gavin Thomas

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)

cladeIdentityMatrix <- cladeIdentity(phy=anolis.tree, nodeIDs=170)
```

contemporaryPhy	<i>prune tree and data to lineages present in a time bin in the past</i>
-----------------	--

Description

the function takes a full tree and returns a pruned phylogeny with only tips and lineages found within a time bin preserved. If trait data are supplied the function will return tip states based either on the original tips found in the bin, or tip states inferred from ancestral states

Usage

```
contemporaryPhy(phy, maxBin, minBin, reScale = 0, allTraits,
  closest.min = TRUE, traits.from.tip = TRUE)
```

Arguments

phy	An object of class "phylo" (see ape package).
maxBin	the start age (older time in myr from present) of the time bin in which lineages are preserved
minBin	the final age (younger time in myr from present) of the time bin in which lineages are preserved
reScale	if the most recent tip is not from the present, the age needed to add so the phylogeny is in 'real time'
allTraits	a vector of trait data corresponding to the phy\$edge object. The trait data represent tip and internal node data for the phylogeny
closest.min	Logical. Should new tip values for lineages that span the bin be taken from the node nearest the 'minBin' age (closest.min=TRUE, default) or the 'maxBin' age (closest.min=FALSE)
traits.from.tip	Logical. Should tip values for pendant edges in the bin be taken from the original tip value or the reconstructed node value (if it is closer than the tip value)

Value

the pruned phylogeny. The object 'descendants' refers to the lineages the branch in the time bin gave rise to before it was pruned. If traits are included a vector of trait values representing species at the tips.

Author(s)

Mark Puttick

References

Puttick, M. N., Kriwet, J., Wen, W., Hu, S., Thomas, G. H., & Benton, M. J. (2017). Body length of bony fishes was not a selective factor during the biggest mass extinction of all time. *Palaeontology*, 60, 727-741.

Examples

```
## prune a random tree to taxa present between 4 and 2 units before present
# generate tree
set.seed(20)
tree <- rtree(20)
# generate traits
traits <- rnorm(20)
# plot tree and timeframe
plot(tree)
max.age <- nodeTimes(tree)[1,1]
abline(v=max.age - c(4, 2))
# prune tree to timeframe
cont.tree <- contemporaryPhy(phy=tree, maxBin=4, minBin=2, allTraits=traits)
plot(cont.tree$phy)
```

dropTipPartial

Drop tips from a phylogenetic tree while preserving deleted nodes

Description

Wrapper for the ape function `drop.tip` that preserves the number of nodes affecting each branch. For use with the `psi` and `multipsi` models.

Usage

```
dropTipPartial(phy, tip)
```

Arguments

<code>phy</code>	Phylogenetic tree in phylo format
<code>tip</code>	A vector of mode numeric or character specifying the tips to delete, to be passed to <code>drop.tip</code>

Value

Phylogenetic tree in phylo format, with an added element `Shid`, a vector of numbers of observed but "missing" speciation events per branch, in the same order as the branches in the phylo object

Author(s)

Travis Ingram

References

Ingram, T. 2011. Speciation along a depth gradient in a marine adaptive radiation. *Proc. R. Soc. B* 278: 613-618.

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)
## identify tips to drop
tips.to.go <- anolis.tree$tip.label[1:30]
dropTipPartial(phy=anolis.tree, tip=tips.to.go)
```

fairProportions

Calculate fair proportions phylogenetic diversity metric

Description

Calculate fair proportions phylogenetic diversity metric Note that `as.rateMatrix` calls the CAIC function `vcv.array` multiple times and this can be slow for large phylogenies (though faster than using the "ape" equivalent `vcv.phylo`).

Usage

```
fairProportions(phy, nodeCount = FALSE)
```

Arguments

<code>phy</code>	An object of class "phylo" (see ape package).
<code>nodeCount</code>	Logical - should root to tip node counts be returned (default is FALSE)

Value

Returns a matrix of fair proportion for all tips in phylogeny and node counts if selected.

Author(s)

Gavin Thomas

References

- Redding, D.W. and Mooers, A.O. (2006). Incorporating evolutionary measures into conservation prioritisation. *Conservation Biology*, 20, 1670-1678.
- Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. and Baillie, J.E.M. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE*, 2, e296.

Examples

```
data(anolis.tree)

fp <- fairProportions(anolis.tree)
fpNodes <- fairProportions(anolis.tree, nodeCount=TRUE)
```

likRatePhylo

Log-likelihood rate estimation for traits and phylogenies

Description

This function calculates the log-likelihood, phylogenetic mean, and Brownian variance for a trait and a phylogeny transformed according to variation in relative rates.

Usage

```
likRatePhylo(rateData, rate = NULL, common.mean = FALSE,
  lambda.est = TRUE, lambda = 1, meserr = FALSE, sigmaScale = NULL)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=TRUE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.#'
lambda.est	Logical. Fit Pagel's lambda.
lambda	Logical. Numeric value for lambda from 0-1.
meserr	Logical. Logical. Include measurement error.
sigmaScale	Logical. Scalar for measurement error relative to tree.

Value

ll log-likelihood of the model
 mu phylogenetically corrected mean(s)
 s2 Brownian variance

Note

The means are output as treatment contrasts.

Author(s)

Gavin Thomas, Rob Freckleton

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

## Calculate phylogenetic mean, variance, log likelihood for a model where the first

# mean only
phyloMean(rateData=anolis.rateData, rate = c(1,2,0.1,1), common.mean = FALSE)

# variance only
phyloVar(rateData=anolis.rateData, rate = c(1,2,0.1,1), common.mean = FALSE)

# mean, variance and log-likelihood
likRatePhylo(rateData=anolis.rateData, rate = c(1,2,0.1,1), common.mean = FALSE)
```

likTraitPhylo

Log-likelihood rate estimation for traits and phylogenies

Description

This function calculates the log-likelihood and Brownian (co)variance for a trait(s) and a phylogeny using phylogenetically independent contrasts. Note that `as.rateMatrix` calls the `CAIC` function `vcv.array` multiple times and this can be slow for large phylogenies (though faster than using the "ape" equivalent `vcv.phylo`).

Usage

```
likTraitPhylo(y, phy, covPIC = TRUE)
```

Arguments

y	A matrix of trait data. Rownames must be included and match the taxon names in the phylogeny. Can accept single traits (calculates variance) or multiple traits (calculates variance-covariance matrix).
phy	An object of class "phylo" (see ape package).
covPIC	Logical - allow for covariance between multivariate traits (TRUE), or assume not covariance (FALSE). Only applicable to multivariate traits

Details

The "phylo" object must be rooted and fully dichotomous.

Value

brownianVariance Brownian variance (or covariance for multiple traits) given the data and phylogeny

logLikelihood The log-likelihood of the model and data

Author(s)

Gavin Thomas, Rob Freckleton

References

Felsenstein J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. Am. J. Hum. Genet. 25, 471-492. Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist 125, 1-15. Freckleton RP & Jetz W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. Proc. Roy. Soc. B 276, 21-30.

Examples

```
data(anolis.tree)
data(anolis.data)
## calculate Brownian variance log-likelihood of female SVL
female.svl <- matrix(anolis.data[, "Female_SVL"],
dimnames=list(rownames(anolis.data)))
input.data <- sortTraitData(phy=anolis.tree, y=female.svl, log.trait=TRUE)
likTraitPhylo(phy = input.data$phy, y=input.data$trait)
```

make.anc

Create design matrix (internal function)

Description

This is an internal function to generate the design matrix required to define different means for each hypothesised rate category.

Usage

```
make.anc(y, x, data = NULL, common.mean = FALSE)
```

Arguments

y	The response variable - typically a continuous trait.
x	The explanatory (discrete) variable used to define the hypothesised rate categories. Can be specified as a column number or column name.
data	A data frame containing (minimally) the x and y variables as columns with species names as rownames.
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=FALSE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates..

Value

A design matrix

Author(s)

Gavin Thomas

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

make.likRatePhylo	<i>Internal function</i>
-------------------	--------------------------

Description

Internal function. Constructor to allow fixing of rate parameters.

Usage

```
make.likRatePhylo(rateData, fixed, common.mean = FALSE, lambda.est, meserr)
```

Arguments

rateData	an object of class "rateData"
fixed	A vector stating whether each parameter should be allowed to vary (either FALSE which results in a start value of 1, or a numeric start value) or should be fixed (TRUE).
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=FALSE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates..
lambda.est	Logical - Logical. Fit Pagel's lambda.
meserr	an object of class "rateData"

Value

Returns a function to be passed to `optim.likRatePhylo`

Author(s)

Gavin Thomas

ML.RatePhylo

Maximum likelihood rate estimation for traits and phylogenies

Description

Full function for maximum likelihood estimation of rate parameters and comparison to a single rate model.

Usage

```
ML.RatePhylo(rateData, rate = NULL, fixed = NULL, pretty = TRUE,
  rateMIN = 0.001, rateMAX = 50, common.mean = FALSE, lambda.est = TRUE,
  est.CI = FALSE, meserr = FALSE, file = NULL)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.
fixed	A vector stating whether each parameter should be allowed to vary (either FALSE which results in a start value of 1, or a numeric start value) or should be fixed (TRUE).
pretty	Display the output nicely (pretty=TRUE) or as a list (pretty=FALSE)
rateMIN	Minimum value for the rate parameters.

rateMAX	Maximum value for the rate parameters
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=FALSE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
lambda.est	Logical. Estimate Pagel's lambda.
est.CI	Logical. Estimate approximate confidence intervals for rate parameters.
meserr	Logical. Incorporate measurement error.
file	File string for output. Only used if pretty=TRUE.

Value

If pretty=FALSE, returns a list containing:

MLRate Maximum likelihood estimates of the rate parameters

Lambda Maximum likelihood estimate of lambda

LCI Approximate lower confidence intervals for rate

UCI Approximate upper confidence intervals for rate parameters

means Means for each category

nParam Number of parameters in the model (how many means and rate categories)

Max.lik Maximum (log) likelihood

AIC for maximum likelihood model

AICc for maximum likelihood model

LambdaSingle Maximum likelihood estimate of lambda for the single rate model

Lik1 Likelihood of the equivalent single rate model

Likelihood ratio statistic of "Max.lik" vs "Lik1"

P P values for the LR statistic

df Degrees of freedom for the LR statistic

AIC.rate1 AIC for single rate model

AICc.rate1 AICc for single rate model

If pretty=TRUE, prints a nice version of the list to screen. If file is specified the pretty output will be sent to file, not the console.

Note

Unlike phyloMean and likRatePhylo (that use treatment contrasts), the means reported here are the actual values

Author(s)

Gavin Thomas, Rob Freckleton @examples ## Read in phylogeny and data from Thomas et al. (2009) data(anolis.tree) data(anolis.data)

```
## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree,
x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph", rateMatrix = anolis.rateMatrix,
phy=NULL, data=anolis.data, log.y=TRUE) # A model with a different rate in each of the four
groups. The 'fixed' command is used to determine # whether a particular rate is to be constrained
or not. Use '1' to fix a group and 'FALSE' to show # that the parameter is not fixed and should be
estimated. The values should be entered in the same # order as the ranking of the groups. That is,
group 0 (small islands) takes position one in the # fixed vector, group 1 (large island trunk crown
and trunk ground) takes position 2 and so on. # The default is to allow each group to take a different
mean.

ML.RatePhylo(anolis.rateData, fixed=c(1,FALSE,FALSE, FALSE), pretty=TRUE) # Run the same
model, but this time assuming a common mean across all four groups
ML.RatePhylo(anolis.rateData, fixed=c(1,FALSE,FALSE, FALSE), pretty=TRUE, common.mean=TRUE)
```

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

name.check	<i>Name check (internal function)</i>
------------	---------------------------------------

Description

This is an internal function to check if names in a trait vector or matrix match a tree

Usage

```
name.check(phy, data)
```

Arguments

phy	a phylogeny in APE phylo format
data	A matrix or vector of named trait data corresponding to species in phy

Author(s)

Gavin Thomas

node.descendants	<i>Identify nodes and tips descended from a node (internal function).</i>
------------------	---

Description

Obtains a vector of the tips and nodes subtending from a node in a phylogeny.

Usage

```
node.descendants(x, phy, tip.labels = FALSE)
```

Arguments

x	A positive integer
phy	An object of class "phylo" (see ape package).
tip.labels	Logical - output tip.labels?

Details

This function is stolen from the clade.members function in the CAIC package but returns both node and tip id's.

Value

Returns a vector of node and tip ids descended from the tip(s) "x". If tip.labels=TRUE then returns a list of node ids and tip labels.

Note

as.rateMatrix calls the CAIC function vcv.array multiple times and this can be slow for large phylogenies (though faster than using the "ape" equivalent vcv.phylo).

Author(s)

Gavin Thomas, David Orme

nodeTimes	<i>Get times for nodes and tips</i>
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Description

Produces branching and tip times for ultrametric and non-ultrametric trees

Usage

```
nodeTimes(phy)
```

Arguments

phy An object of class "phylo" (see ape package).

Value

Returns a matrix corresponding the phy "edge" matrix showing internal and external node times

Note

nodeTimes is essentially a re-written version of the "ape" `branching.times`.

Author(s)

Mark Puttick, Emmanuel Paradis

Examples

```
## Read in phylogeny from Thomas et al. (2009)
data(anolis.tree)
anolis.node.times <- nodeTimes(phy=anolis.tree)
```

optim.likRatePhylo	<i>Maximum likelihood rate estimation for traits and phylogenies</i>
--------------------	--

Description

Function for the maximum likelihood estimation of rate parameters on a trait and phylogeny.

Usage

```
optim.likRatePhylo(rateData, rate = NULL, fixed = NULL, rateMIN = 0.001,
  rateMAX = 50, common.mean = FALSE, lambda.est = TRUE, meserr = FALSE)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.
fixed	A vector stating whether each parameter should be allowed to vary (either FALSE which results in a start value of 1, or a numeric start value) or should be fixed (TRUE).
rateMIN	Minimum value for the rate parameters
rateMAX	Maximum value for the rate parameters
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=FALSE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
lambda.est	Logical. Fit Pagel's lambda.
meserr	Logical. Include measurement error.

Value

MLRate Maximum likelihood estimates of the rate parameters
 Max.lik Maximum (log) likelihood
 AIC AIC for maximum likelihood model
 AICc AICc for maximum likelihood model
 convergence convergence value from optim
 n.parameters Number of parameters in the model (how many means and rate categories)

Author(s)

Gavin Thomas

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)
```

```
# A model with a different rate in each of the four groups. The 'fixed' command is used to determine
# whether a particular rate is to be constrained or not. Use '1' to fix a group and 'FALSE' to show
# that the parameter is not fixed and should be estimated. The values should be entered in the same
# order as the ranking of the groups. That is, group 0 (small islands) takes position one in the
# fixed vector, group 1 (large island trunk crown and trunk ground) takes position 2 and so on.
# The default is to allow each group to take a different mean.
```

```
optim.likRatePhylo(anolis.rateData, rate=c(1,1,1,1), common.mean=TRUE, lambda.est=FALSE)
```

phyloCovar

Calculation of Brownian (co)variance using independent contrasts.

Description

Calculates the Brownian variance (single trait) or variance-covariance matrix (multiple traits) using phylogenetically independent contrasts.

Usage

```
phyloCovar(x, phy, estimator = "unbiased")
```

Arguments

x	A continuous trait
phy	An object of class "phylo" (see ape package).
estimator	Should Brownian variance (or covariance) be based on the unbiased ("unbiased" - default) or maximum likelihood ("ML") estimator.

Value

brownianVariance Brownian variance (or covariance for multiple traits) given the data and phylogeny

Author(s)

Gavin Thomas, Rob Freckleton

References

Felsenstein J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. *Am. J. Hum. Genet.* 25, 471-492. Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* 125, 1-15. Freckleton RP & Jetz W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. Roy. Soc. B* 276, 21-30.

Examples

```
data(anolis.tree)
data(anolis.data)
## calculate Brownian variance of female SVL
female.svl <- matrix(anolis.data[, "Female_SVL"],
  dimnames=list(rownames(anolis.data)))
input.data <- sortTraitData(phy=anolis.tree, y=female.svl, log.trait=TRUE)
phyloCovar(x=input.data$trait, phy = input.data$phy)
```

phyloMean

Calculation of phylogenetically corrected mean.

Description

This function calculates the phylogenetic mean of the data given the tree and model of evolution

Usage

```
phyloMean(rateData, rate = NULL, common.mean = FALSE, lambda.est = TRUE,
  lambda = 1, meserr = FALSE)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=TRUE) or all categories should have the same mean (common.mean=FALSE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
lambda.est	Logical. Fit Pagel's lambda.
lambda	Numeric value for lambda from 0-1.
meserr	Logical. Include measurement error.

Value

mu phylogenetically corrected mean

Note

The means are output as treatment contrasts.

Author(s)

Gavin Thomas, Rob Freckleton

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

# A model with a different rate in each of the four groups. The 'fixed' command is used to determine
# whether a particular rate is to be constrained or not. Use '1' to fix a group and 'FALSE' to show
# that the parameter is not fixed and should be estimated. The values should be entered in the same
# order as the ranking of the groups. That is, group 0 (small islands) takes position one in the
# fixed vector, group 1 (large island trunk crown and trunk ground) takes position 2 and so on.
# The default is to allow each group to take a different mean.

phyloMean(anolis.rateData, rate=c(1,1,1,1), common.mean=FALSE)
# common mean for all groups
phyloMean(anolis.rateData, rate=c(1,1,1,1), common.mean=TRUE)
```

phyloVar

Calculation of Brownian variance.

Description

This function calculates the phylogenetic variance (Brownian variance, or rate) of the data given the tree and model of evolution

Usage

```
phyloVar(rateData, rate = NULL, common.mean = FALSE, lambda.est = TRUE,
lambda = 1, meserr = FALSE)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.

<code>common.mean</code>	a logical specifying whether each rate category should have its own mean (<code>common.mean=FALSE</code>) or all categories should have the same mean (<code>common.mean=TRUE</code>). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
<code>lambda.est</code>	Logical. Fit Pagel's lambda.
<code>lambda</code>	Numeric value for lambda from 0-1.
<code>meserr</code>	Logical. Include measurement error.

Value

phylo.var phylogenetic variance (Brownian variance)

Author(s)

Gavin Thomas, Rob Freckleton

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
## Read in phylogeny and data from Thomas et al. (2009)
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

# A model with a different rate in each of the four groups. The 'fixed' command is used to determine
# whether a particular rate is to be constrained or not. Use '1' to fix a group and 'FALSE' to show
# that the parameter is not fixed and should be estimated. The values should be entered in the same
# order as the ranking of the groups. That is, group 0 (small islands) takes position one in the
# fixed vector, group 1 (large island trunk crown and trunk ground) takes position 2 and so on.
# The default is to allow each group to take a different mean.

phyloVar(anolis.rateData, rate=c(1,2,1,1), common.mean=FALSE)
# common mean for all groups
phyloVar(anolis.rateData, rate=c(1,2,1,1), common.mean=TRUE)
```

pic.motmot	<i>Phylogenetically independent contrasts (internal)</i>
------------	--

Description

Calculates phylogenetically independent contrasts.

Usage

```
pic.motmot(x, phy)
```

Arguments

x	A matrix of trait values with taxon names as rownames.
phy	An object of class "phylo" (see ape package).

Details

Extracts values for contrasts, expected variances using contrasts by calling pic.

Value

contr A matrix with two columns containing raw contrasts in the first column and their expected variances in the second column.

root.v Expected variances of branches either side of root

V Expected variance at the root

Author(s)

Gavin Thomas, Rob Freckleton, Emmanuel Paradis

References

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

plotPhylo.motmot	<i>Tree plotting for rates Plots trees with colours based on rates of trait evolution. Also provides simple coloured plotting for trait values using the "ace" function in the ape library.</i>
------------------	---

Description

Tree plotting for rates Plots trees with colours based on rates of trait evolution. Also provides simple coloured plotting for trait values using the "ace" function in the ape library.

Usage

```
plotPhylo.motmot(phy, x = NULL, traitMedusaObject = NULL,
  reconType = "rates", type = "phylogram", use.edge.length = TRUE,
  show.tip.label = TRUE, show.node.label = FALSE, edge.color = "black",
  edge.width = 1, edge.lty = 1, font = 3, cex = par("cex"),
  adj = NULL, srt = 0, no.margin = FALSE, root.edge = FALSE,
  label.offset = 0.5, underscore = FALSE, x.lim = NULL, y.lim = NULL,
  direction = "rightwards", lab4ut = "horizontal", tip.color = "black",
  palette = "hotspot.colors")
```

Arguments

phy	An object of class "phylo" (see ape package).
x	A matrix of trait values.
traitMedusaObject	Output from traitMedusaSummary.
reconType	Colour branches according to rate shifts ("rates" - requires traitMedusaObject) or ancestral state reconstruction ("picReconstruction" - requires x).
type	a character string specifying the type of phylogeny to be drawn; it must be one of "phylogram" (the default), "cladogram", "fan", "unrooted", "radial" or any unambiguous abbreviation of these.
use.edge.length	a logical indicating whether to use the edge lengths of the phylogeny to draw the branches (the default) or not (if FALSE). This option has no effect if the object of class "phylo" has no 'edge.length' element.
show.tip.label	a logical indicating whether to show the tip labels on the phylogeny (defaults to TRUE, i.e. the labels are shown).
show.node.label	a logical indicating whether to show the node labels on the phylogeny (defaults to FALSE, i.e. the labels are not shown).
edge.color	a vector of mode character giving the colours used to draw the branches of the plotted phylogeny. These are taken to be in the same order than the component edge of phy. If fewer colours are given than the length of edge, then the colours are recycled.

<code>edge.width</code>	a numeric vector giving the width of the branches of the plotted phylogeny. These are taken to be in the same order than the component <code>edge</code> of <code>phy</code> . If fewer widths are given than the length of <code>edge</code> , then these are recycled.
<code>edge.lty</code>	same than the previous argument but for line types; 1: plain, 2: dashed, 3: dotted, 4: dotdash, 5: longdash, 6: twodash.
<code>font</code>	an integer specifying the type of font for the labels: 1 (plain text), 2 (bold), 3 (italic, the default), or 4 (bold italic).
<code>cex</code>	a numeric value giving the factor scaling of the tip and node labels (Character EXpansion). The default is to take the current value from the graphical parameters.
<code>srt</code>	a numeric giving how much the labels are rotated in degrees (negative values are allowed resulting in clock-like rotation); the value has an effect respectively to the value of <code>direction</code> (see Examples). This option has no effect if <code>type = "unrooted"</code> .
<code>no.margin</code>	a logical. If TRUE, the margins are set to zero and the plot uses all the space of the device (note that this was the behaviour of <code>plot.phylo</code> up to version 0.2-1 of 'ape' with no way to modify it by the user, at least easily).
<code>root.edge</code>	a logical indicating whether to draw the root edge (defaults to FALSE); this has no effect if ' <code>use.edge.length = FALSE</code> ' or if ' <code>type = "unrooted"</code> '.
<code>label.offset</code>	a numeric giving the space between the nodes and the tips of the phylogeny and their corresponding labels. This option has no effect if <code>type = "unrooted"</code> .
<code>underscore</code>	a logical specifying whether the underscores in tip labels should be written as spaces (the default) or left as are (if TRUE).
<code>x.lim</code>	a numeric vector of length one or two giving the limit(s) of the x-axis. If NULL, this is computed with respect to various parameters such as the string lengths of the labels and the branch lengths. If a single value is given, this is taken as the upper limit.
<code>y.lim</code>	same than above for the y-axis.
<code>direction</code>	a character string specifying the direction of the tree. Four values are possible: "rightwards" (the default), "leftwards", "upwards", and "downwards".
<code>lab4ut</code>	(= labels for unrooted trees) a character string specifying the display of tip labels for unrooted trees: either "horizontal" where all labels are horizontal (the default), or "axial" where the labels are displayed in the axis of the corresponding terminal branches. This option has an effect only if <code>type = "unrooted"</code> .
<code>tip.color</code>	the colours used for the tip labels, eventually recycled (see examples).
<code>palette</code>	Defines the colour scheme with four options: <code>hotspot.colors</code> (red to blue), <code>heat.colors</code> (yellow to red), <code>cool.colors</code> (blues), <code>combi.colors</code> (yellows to reds and blues)
<code>adj</code>	anumeric specifying the justification of the text strings of the labels: 0 (left-justification), 0.5 (centering), or 1 (right-justification). This option has no effect if <code>type = "unrooted"</code> . If NULL (the default) the value is set with respect of <code>direction</code> (see details).

Value

Returns a data frame of colours used in plot along with rate (or ancestral state) range for each colour.

Author(s)

Gavin Thomas

Examples

```
# Data and phylogeny
data(anolis.tree)
data(anolis.data)

# female SVL data
female.svl <- matrix(anolis.data[, "Female_SVL"],
  dimnames=list(rownames(anolis.data)))
input.data <- sortTraitData(phy=anolis.tree, y=female.svl, log.trait=TRUE)

# arbitrarily reduce data size for speed in this example
phy.clade <- extract.clade(input.data[[1]], 182)
male.length.clade <- as.matrix(input.data[[2]][match(input.data[[1]]$tip.label,
  rownames(input.data[[2]])),])
# Identify rate shifts and print and plot results with up to one rate shifts
# and minimum clade size of 10.
anolisSVL_MEDUSA <- transformPhylo.ML(male.length.clade, phy=phy.clade,
  model="tm1", minCladeSize=10, nSplits=1)
anolisSVL_MEDUSA_out <- traitMedusaSummary(anolisSVL_MEDUSA,
  cutoff=1, AICc=FALSE)
colours <- plotPhylo.motmot(phy=phy.clade, traitMedusaObject = anolisSVL_MEDUSA_out,
  reconType = "rates", type = "fan", cex=0.6, edge.width=3)
```

RatePhylo.allCI

*Confidence intervals for rate parameters***Description**

Calculates approximate confidence intervals for all rate parameters. CIs are estimated for one rate parameters while fixing others at a given value (usually the maximum likelihood estimate).

These are reliable (given the asymptotic assumptions of the chi-square distribution) if only two groups are being compared but should be regarded only as a rough approximation for ≥ 3 different rate categories. If the rates are correlated the CIs may be underestimated.

Usage

```
RatePhylo.allCI(rateData, MLrate = NULL, fixed = NULL, rateMIN = 0.001,
  rateMAX = 50, common.mean = FALSE, lambda.est = TRUE)
```

Arguments

rateData	an object of class "rateData"
MLrate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal. Normally these will be the maximum likelihood rate estimates.

<code>fixed</code>	A vector stating whether each parameter should be allowed to vary (either FALSE which results in a start value of 1, or a numeric start value) or should be fixed (TRUE).
<code>rateMIN</code>	Minimum value for the rate parameters
<code>rateMAX</code>	Maximum value for the rate parameters
<code>common.mean</code>	a logical specifying whether each rate category should have its own mean (<code>common.mean=FALSE</code>) or all categories should have the same mean (<code>common.mean=FALSE</code>). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
<code>lambda.est</code>	Logical. Estimate Pagel's lambda.

Value

`rateLci` Lower confidence interval for rate estimate
`rateUci` Upper confidence interval for rate estimate

Author(s)

Gavin Thomas, Rob Freckleton

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.data)
data(anolis.tree)
## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)

anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

# A model with a different rate in each of the four groups. The 'fixed' command is used to determine
# whether a particular rate is to be constrained or not. Use '1' to fix a group and 'FALSE' to show
# that the parameter is not fixed and should be estimated. The values should be entered in the same
# order as the ranking of the groups. That is, group 0 (small islands) takes position one in the
# fixed vector, group 1 (large island trunk crown and trunk ground) takes position 2 and so on. The
# default is to allow each group to take a different mean.

anole.ML <- optim.likRatePhylo(rateData=anolis.rateData, rate=NULL,
fixed=c(FALSE,FALSE,FALSE, FALSE),
common.mean=FALSE, lambda.est=FALSE)

# Confidence intervals for the first two parameters
```

```
RatePhylo.CI(rateData=anolis.rateData, MLrate = anole.ML$MLRate,
fixed=c(FALSE, TRUE, TRUE, TRUE), rateMIN = 0.001, rateMAX = 50,
common.mean = FALSE)
```

RatePhylo.CI

*Confidence intervals for rate parameters***Description**

Calculates approximate confidence intervals for all rate parameters. CIs are estimated for one rate parameters while fixing others at a given value (usually the maximum likelihood estimate).

These are reliable (given the asymptotic assumptions of the chi-square distribution) if only two groups are being compared but should be regarded only as a rough approximation for ≥ 3 different rate categories. If the rates are correlated the CIs may be underestimated.

Usage

```
RatePhylo.CI(rateData, MLrate = NULL, fixed, rateMIN = 0.001,
rateMAX = 50, common.mean = FALSE, lambda.est = TRUE)
```

Arguments

rateData	an object of class "rateData"
MLrate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal. Normally these will be the maximum likelihood rate estimates.
fixed	A vector stating whether each parameter should be allowed to vary (either FALSE which results in a start value of 1, or a numeric start value) or should be fixed (TRUE).
rateMIN	Minimum value for the rate parameters
rateMAX	Maximum value for the rate parameters
common.mean	a logical specifying whether each rate category should have its own mean (common.mean=FALSE) or all categories should have the same mean (common.mean=TRUE). See Thomas et al. (2009) for a discussion on the impact of assumptions about mean on rate estimates.
lambda.est	Logical. Estimate Pagel's lambda.

Value

rateLci Lower confidence interval for rate estimate
rateUci Upper confidence interval for rate estimate

Author(s)

Gavin Thomas, Rob Freckleton

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624.

Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in *Anolis*: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
data(anolis.data)

## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)
anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

# A model with a different rate in each of the four groups. The 'fixed' command is used to determine
# determine whether a particular rate is to be constrained or not. Use '1' to fix a group and
# 'FALSE' to show that the parameter is not fixed and should be estimated. The values
# should be entered in the same order as the ranking of the groups. That is, group
# 0 (small islands) takes position one in the fixed vector, group 1 (large island trunk crown
# and trunk ground) takes position 2 and so on. The default is to allow each group
# to take a different mean.

anole.ML <- optim.likRatePhylo(rateData=anolis.rateData, rate=NULL,
fixed=c(FALSE,FALSE,FALSE, FALSE), common.mean=FALSE, lambda.est=FALSE) # ML estimates

# Confidence intervals for the first parameters

RatePhylo.CI(rateData=anolis.rateData, MLrate = anole.ML$MLRate,
fixed=c(FALSE, TRUE, TRUE, TRUE), rateMIN = 0.001, rateMAX = 50,
common.mean = FALSE)
```

removeNonBin

remove species occurring before time in the past (internal function)

Description

removes tips and lineages after a time in the past

Usage

```
removeNonBin(phy, traitData, keepByTime = 0, tol = 1e-08)
```


Arguments

phy	An object of class "phylo" (see ape package).
traitData	data associated with the species
keepByTime	an age at which to keep preserve tips before the present (time = 0)
tol	edge length precision in time cut (default = 1e-08)

Value

a list with the prunedPhylogeny and a prunedData

Author(s)

Mark Puttick

References

Puttick, M. N., Kriwet, J., Wen, W., Hu, S., Thomas, G. H., & Benton, M. J. (2017). Body length of bony fishes was not a selective factor during the biggest mass extinction of all time. *Palaeontology*, 60, 727-741.

sampleHiddenSp	<i>Sample hidden speciation events along branches of a tree (internal function)</i>
----------------	---

Description

Uses estimated speciation and extinction rates to sample the number of speciation events 'hidden' by subsequent extinction on each branch of a tree following Bokma (2008). For use with the psi and multipsi models.

Usage

```
sampleHiddenSp(phy, lambda.sp = NULL, mu.ext = NULL, useMean = FALSE)
```

Arguments

phy	Phylogenetic tree in phylo format
lambda.sp	Estimate of the rate of speciation "lambda"
mu.ext	Estimate of the rate of extinction "mu"
useMean	A logical indicating whether to output the average or expected number of hidden speciation events per branch, which may be non-integer (if TRUE), or to sample an integer number on each branch from a Poisson distribution (if FALSE, the default)

Details

The expected number of hidden speciation events are calculated for each branch given its start and end times, and estimates of lambda and mu which are assumed to be constant across the tree. To properly account for uncertainty in the effect of extinction on the number of nodes affecting each branch of a tree, it may be appropriate to repeat model-fitting on many realizations of Sobs on the tree of interest (similar to evaluating phylogenetic uncertainty)

Value

Phylogenetic tree in phylo format, with an added element Sobs, a vector of numbers of hidden speciation events per branch, in the same order as the branches in the phylo object

Author(s)

Travis Ingram

References

Bokma, F. 2008. Detection of "punctuated equilibrium" by Bayesian estimation of speciation and extinction rates, ancestral character states, and rates of anagenetic and cladogenetic evolution on a molecular phylogeny. *Evolution* 62: 2718-2726.

Ingram, T. 2011. Speciation along a depth gradient in a marine adaptive radiation. *Proc. R. Soc. B* 278: 613-618.

sliceTree	<i>Slice tree (internal function)</i>
-----------	---------------------------------------

Description

Split tree for the time slice function

Usage

```
sliceTree(phy, splitTime)
```

Arguments

phy	Phylogenetic tree in phylo format
splitTime	Split time in the past

Value

Branch lengths of sliced tree

Author(s)

Mark Puttick

sortTraitData	<i>Sort data and remove missing entries for tree and trait data</i>
---------------	---

Description

Plots a phylogeny with lines representing the value of a continuous trait

Usage

```
sortTraitData(phy, y, log.trait = TRUE)
```

Arguments

phy	An object of class "phylo" or "multiPhylo" (see ape package).
y	A matrix of trait values with taxon names as rownames. Missing values should be NA
log.trait	Logical. If TRUE, data are log-transformed

Value

phy Tree with missing data pruned
trait Rearranged data with missing species removed

Author(s)

Mark Puttick

Examples

```
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
any(is.na(male.length[,1]))
data.sorted <- sortTraitData(anolis.tree, male.length)
phy <- data.sorted[[1]]
male.length <- data.sorted[[2]]
```

timeSliceSummary	<i>Identify shifts in the rate of trait diversification through time</i>
------------------	--

Description

Summarises phenotypic rate variation on phylogenies through

Usage

```
timeSliceSummary(timeSliceObject, cutoff = 4, AICc = TRUE,
  lowerBound = 1e-08, upperBound = 1000, plot.phylo = TRUE, cex.tip = 1,
  tip.offset = 1, phylo.width = 1, tip.colour = "grey50",
  colour.ramp = c("blue", "red"))
```

Arguments

timeSliceObject	Output of a timeSlice analysis in transformPhylo.ML
cutoff	Cutoff value for differences in AIC scores when comparing models. More complex models with an AIC score more than this number of units lower than simpler models are retained (as per runMedusa in the geiger package).
AICc	If true, AICc is used instead of AIC.
lowerBound	Minimum value for parameter estimates.
upperBound	Maximum value for parameter estimates.
plot.phylo	Logical. If TRUE, the phylogeny is plotted
cex.tip	The character size of tip labels
tip.offset	the distance tip labels should be printed from pendant edges
phylo.width	The width of edges on the phylogeny
tip.colour	Colour of species' tip labels
colour.ramp	The colours signifying different rates from low (first colour) to high (second colour)

Details

This functions summarises the output of a "timeSlice" model in transformPhylo.ML (see below). The best overall model is chosen based on AIC (or AICc if AICc=TRUE). The cut-off point for improvement in AIC score between successively more complex models can be defined using cutoff. The default cutoff is 4 but this is somewhat arbitrary and a "good" cut-off may well vary between data sets so it may well be worth exploring different cutoffs.

Value

ModelFit Summary of the best optimal rate shift model.
 Rates Summary of the rate parameters from the best rate shift model.
 optimalTree A phylo object with branch lengths scaled relative to rate.

Author(s)

Mark Puttick

References

To Add

Examples

```
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
sortedData <- sortTraitData(anolis.tree, male.length)
phy <- sortedData$phy
male.length <- sortedData$trait
phy.clade <- extract.clade(phy, 182)
male.length.clade <- as.matrix(male.length[match(phy.clade$tip.label,
rownames(male.length)),])
timeSlice.10.ml <- transformPhylo.ML(y=male.length.clade, phy=phy.clade, model="timeSlice",
splitTime=c(10))
outputSummary <- timeSliceSummary(timeSlice.10.ml, cutoff=0.001, cex.tip=0.5,
phylo.width=2, colour.ramp=c("blue", "red"))
```

timeTravelPhy

timeTravelPhy (internal function)

Description

removes tips and lineages after a time in the past

Usage

```
timeTravelPhy(phy, node, nodeEstimate, timeCut, traits = TRUE)
```

Arguments

phy	An object of class "phylo" (see ape package).
node	nodes arising more recently than the cut time
nodeEstimate	trait the number of descendants arising from the nodes
timeCut	position at which to cut the phylogeny
traits	Logical. Include trait values in the output tree

Value

the pruned phylogeny and a 'tipObject' of the number of lineages found in the pruned branches

Author(s)

Mark Puttick

References

Puttick, M. N., Kriwet, J., Wen, W., Hu, S., Thomas, G. H., & Benton, M. J. (2017). Body length of bony fishes was not a selective factor during the biggest mass extinction of all time. *Palaeontology*, 60, 727-741.

traitData.plot

plot a univariate continuous trait data on a phylogeny

Description

Plots a phylogeny with lines representing the value of a continuous trait

Usage

```
traitData.plot(y, phy, col.label = "red", col.tree = "black",
  cex.plot = 0.7, include.hist = F)
```

Arguments

y	A matrix of trait values with taxon names as rownames.
phy	An object of class "phylo" (see ape package).
col.label	colour labels for the traits at the tips and in the histogram
col.tree	colour for the edge labels on the tree
cex.plot	Numeric. The size of labels for the histogram axis labels
include.hist	Logical. Include a histogram alongside the plot of the tree?

Value

A plot with the trait values shown at the tips, and a histogram of the trait values

Author(s)

Mark Puttick

Examples

```
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
sortedData <- sortTraitData(anolis.tree, male.length)
phy <- sortedData$phy
male.length <- sortedData$trait
traitData.plot(y=male.length, phy)
```

traitMedusaSummary	<i>Identify shifts in the rate of trait diversification</i>
--------------------	---

Description

Summarises phenotypic rate variation on phylogenies.

Usage

```
traitMedusaSummary(traitMedusaObject = NULL, cutoff = 4, AICc = TRUE,  
  lowerBound = 1e-08, upperBound = 200)
```

Arguments

traitMedusaObject	Output of a medusa analysis in transformPhylo.ML
cutoff	Cutoff value for differences in AIC scores when comparing models. More complex models with an AIC score more than this number of units lower than simpler models are retained (as per runMedusa in the geiger package).
AICc	If true, AICc is used instead of AIC.
lowerBound	Minimum value for parameter estimates.
upperBound	Maximum value for parameter estimates.

Details

This functions summarises the output of a "medusa" model in transformPhylo.ML (see below). The best overall model is chosen based on AIC (or AICc if AICc=TRUE). The cut-off point for improvement in AIC score between successively more complex models can be defined using cutoff. The default cutoff is 4 but this is somewhat arbitrary and a "good" cut-off may well vary between data sets so it may well be worth exploring different cutoffs. Summarises fits of "medusa" models ("clade" models generated without any a priori assertion of the location of phenotypic diversification rate shifts). It uses the same approach as the runMedusa function in the geiger package (runMedusa tests for shifts in the rate of lineage diversification). The algorithm first fits a constant-rate Brownian model to the data, it then works iteratively through the phylogeny fitting a two-rate model at each node in turn. Each two-rate model is compared to the constant rate model and the best two-rate model is retained. Keeping the location of this rate shift intact, it then repeats the procedure for a three-rate model and so on. The maximum number of rate shifts can be specified a priori using nSplits. Limits can also be applied to the size (species richness) of clades on which to infer new rate shifts using minCladeSize. This can be useful to enable large trees to be handled but should be used cautiously since specifying a large minimum clade size may result in biologically interesting nested rate shifts being missed. Equally, very small clade sizes may provide poor estimates of rate that may not be informative.

Value

ModelFit Summary of the best optimal rate shift model.

Rates Summary of the rate parameters from the best rate shift model.

optimalTree A phylo object with branch lengths scaled relative to rate.

Author(s)

Gavin Thomas

References

Alfaro ME, Santini F, Brock CD, Alamillo H, Dornburg A, Carnevale G, Rabosky D & Harmon LJ. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. PNAS 106, 13410-13414. O'Meara BC, Ane C, Sanderson MJ & Wainwright PC. 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution 60, 922-933 Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. Evolution 63, 2017-2030.

Examples

```
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
sortedData <- sortTraitData(anolis.tree, male.length)
phy <- sortedData$phy
male.length <- sortedData$trait
phy.clade <- extract.clade(phy, 182)
male.length.clade <- as.matrix(male.length[match(phy.clade$tip.label, rownames(male.length)),])
tm1 <- transformPhylo.ML(male.length.clade, phy=phy.clade, model="tm1", minCladeSize=10, nSplits=1)
tm1_out <- traitMedusaSummary(tm1, cutoff=1)
```

transformPhylo

Phylogenetic tree transformations

Description

Transforms the branch lengths of a phylo object according to a model of trait evolution (see details).

Usage

```
transformPhylo(phy, model = NULL, y = NULL, meserr = NULL,
  sigmaScale = NULL, kappa = NULL, lambda = NULL, delta = NULL,
  alpha = NULL, psi = NULL, lambda.sp = NULL, nodeIDs = NULL,
  rateType = NULL, branchRates = NULL, cladeRates = NULL,
  splitTime = NULL, timeRates = NULL, acdcRate = NULL,
  branchLabels = NULL)
```


Arguments

phy	An object of class "phylo" (see ape package).
model	The model of trait evolution (see details).
y	A matrix of trait values.
meserr	A vector (or matrix) of measurement error for each tip. This is only applicable to univariate analyses. Largely untested - please use cautiously
sigmaScale	If meserr is included, a scaling factor for the amount of error that is added
kappa	Value of kappa transform.
lambda	Value of lambda transform.
delta	Value of delta transform.
alpha	Value of alpha (OU) transform.
psi	Value of psi transform.
lambda.sp	Estimate of speciation (lambda) for the psi models
nodeIDs	Integer - ancestral nodes of clades.
rateType	If model="clade", a vector specifying if rate shift occurs in a clade ("clade") or on the single branch leading to a clade ("branch").
branchRates	Numeric vector specifying relative rates for individual branches
cladeRates	Numeric vector specifying relative rates for clades.
splitTime	A split time (measured from the present, or most recent species) at which a shift in the rate occurs for the "timeSlice" model
timeRates	The rates (from ancient to recent) for the timeSlice model
acdcRate	Value of ACDC transform.
branchLabels	A vector of length equal to the number of internal branches, signifying the which "multiPsi" class it belongs to

Details

Transforms the branch lengths of a phylo object according to one of the following models:

- model="bm" - Brownian motion (constant rates random walk)
- model="kappa" - fits Pagel's kappa by raising all branch lengths to the power kappa. As kappa approaches zero, trait change becomes focused at branching events. For complete phylogenies, if kappa approaches zero this infers speciation trait change.
- model="lambda" - fits Pagel's lambda to estimate phylogenetic signal by multiplying all internal branches of the tree by lambda, leaving tip branches as their original length (root to tip distances are unchanged);
- model="delta" - fits Pagel's delta by raising all node depths to the power delta. If delta < 1, trait evolution is concentrated early in the tree whereas if delta > 1 trait evolution is concentrated towards the tips. Values of delta above one can be difficult to fit reliably.
- model="free" - fits Mooer's et al's (1999) free model where each branch has its own rate of trait evolution. This can be a useful exploratory analysis but it is slow due to the number of parameters, particularly for large trees.

- `model="clade"` - fits a model where particular clades are a priori hypothesised to have different rates of trait evolution (see O'Meara et al. 2006; Thomas et al. 2006, 2009). Clades are specified using nodeIDs and are defined as the mrca node. Unique rates for each clade are specified using `cladeRates`. `rateType` specifies whether the rate shift occurs in the stem clade or on the single branch leading to the clade.
- `model="OU"` - fits an Ornstein-Uhlenbeck model - a random walk with a central tendency proportional to α . High values of α can be interpreted as evidence of evolutionary constraints, stabilising selection or weak phylogenetic signal.
- `model="psi"` - fits a model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate (Ingram 2010). Note that 'original nodes' from the full phylogeny can be included as an element on the phylogeny (e.g., `phy$orig.node`) as well as estimates of 'hidden' speciation (e.g., `phy$hidden.speciation`) if estimates of extinction (μ) are > 0 .
- `model="multiPsi"` fits a acceleration-deacceleration model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate but allows separate values of ψ fitted to separate branches (Ingram 2010; Ingram et al. 2016). Note that 'original nodes' from the full phylogeny can be included as an element on the phylogeny (e.g., `phy$orig.node`) as well as estimates of 'hidden' speciation (e.g., `phy$hidden.speciation`) if estimates of extinction (μ) are > 0 .
- `model="ACDC"` fits a model to in which rates can exponentially increased or decrease through time (Blomberg et al. 2003). If the upper bound is < 0 , the model is equivalent to the 'Early Burst' model of Harmon et al. 2010. If a `nodeIDs` is supplied, the model will fit a ACDC model nested within a clade, with a BM fit to the rest of the tree.
- `model="timeSlice"` A model in which all branch rates change at time(s) in the past.

Value

phy A phylo object

Author(s)

Gavin Thomas, Mark Puttick

References

- Ingram T. 2011. Speciation along a depth gradient in a marine adaptive radiation. *Proc. Roy. Soc. B.* 278, 613-618.
- Ingram T, Harrison AD, Mahler L, Castaneda MdR, Glor RE, Herrel A, Stuart YE, and Losos JB. Comparative tests of the role of dewlap size in *Anolis* lizard speciation. *Proc. Roy. Soc. B.* 283, 20162199. # @references Mooers AO, Vamossi S, & Schluter D. 1999. Using phylogenies to test macroevolutionary models of trait evolution: sexual selection and speciation in *Cranes* (Gruinae). *American Naturalist* 154, 249-259.
- O'Meara BC, Ane C, Sanderson MJ & Wainwright PC. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* 60, 922-933
- Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26, 331-348.
- Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* 401, 877-884.

Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
anolis.treeDelta <- transformPhylo(phy=anolis.tree, model="delta", delta=0.5)
```

transformPhylo.ll	<i>Log-likelihood for models of trait evolution.</i>
-------------------	--

Description

Fits likelihood models for various models of continuous character evolution.

Usage

```
transformPhylo.ll(y = NULL, phy, model = NULL, meserr = NULL,
  kappa = NULL, lambda = NULL, delta = NULL, alpha = NULL, psi = NULL,
  lambda.sp = NULL, nodeIDs = NULL, rateType = NULL, branchRates = NULL,
  cladeRates = NULL, timeRates = NULL, splitTime = NULL,
  branchLabels = NULL, acdcRate = NULL, covPIC = TRUE)
```

Arguments

y	A matrix of trait values.
phy	An object of class "phylo" (see ape package).
model	The model of trait evolution (see details).
meserr	A vector (or matrix) of measurement error for each tip. This is only applicable to univariate analyses.
kappa	Value of kappa transform.
lambda	Value of lambda transform.
delta	Value of delta transform.
alpha	Value of alpha (OU) transform.
psi	Value of psi transform.
lambda.sp	Speciation rate estimate for the tree.
nodeIDs	Integer - ancestral nodes of clades.
rateType	If model="clade", a vector specifying if rate shift occurs in a clade ("clade") or on the single branch leading to a clade ("branch").
branchRates	Numeric vector specifying relative rates for individual branches
cladeRates	Numeric vector specifying relative rates for clades.
timeRates	The rates (from ancient to recent) for the timeSlice model

splitTime	A split time (measured from the present, or most recent species) at which a shift in the rate occurs for the "timeSlice" model
branchLabels	Branches on which different psi parameters are estimated in the "multipsi" model.
acdcRate	Value of ACDC transform.
covPIC	Logical. For multivariate analyses, allow for co-variance between traits rates (TRUE) or no covariance in trait rates (FALSE). If FALSE, only the trait variances not co-variances are used.

Details

This function fits likelihood models (see below) for continuous character evolution where the parameter values are set a priori. The function returns the log-likelihood and the Brownian variance (or variance covariance matrix). model="bm"- Brownian motion (constant rates random walk) model="kappa" - fits Pagel's kappa by raising all branch lengths to the power kappa. As kappa approaches zero, trait change becomes focused at branching events. For complete phylogenies, if kappa approaches zero this infers speciation trait change. model="lambda" - fits Pagel's lambda to estimate phylogenetic signal by multiplying all internal branches of the tree by lambda, leaving tip branches as their original length (root to tip distances are unchanged); model="delta" - fits Pagel's delta by raising all node depths to the power delta. If delta <1, trait evolution is concentrated early in the tree whereas if delta >1 trait evolution is concentrated towards the tips. Values of delta above one can be difficult to fit reliably. model="free" - fits Mooer's et al's free model where each branch has its own rate of trait evolution. This can be a useful exploratory analysis but it is slow due to the number of parameters, particularly for large trees. model="clade" - fits a model where particular clades are a priori hypothesised to have different rates of trait evolution (see O'Meara et al. 2006; Thomas et al. 2006, 2009). Clades are specified using nodeIDs and are defined as the mrca node. Unique rates for each clade are specified using cladeRates. rateType specifies whether the rate shift occurs in the stem clade or on the single branch leading to the clade. model="OU" - fits an Ornstein-Uhlenbeck model - a random walk with a central tendency proportional to alpha. High values of alpha can be interpreted as evidence of evolutionary constraints, stabilising selection or weak phylogenetic signal. model="psi" - fits a model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate (Ingram 2010).

Value

brownianVariance Brownian variance (or covariance for multiple traits) given the data and phylogeny

logLikelihood The log-likelihood of the model and data

Author(s)

Gavin Thomas, Mark Puttick

References

Felsenstein J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. *Am. J. Hum. Genet.* 25, 471-492. Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* 125, 1-15. Freckleton RP & Jetz W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. Roy. Soc. B* 276, 21-30.

Ingram T. 2011. Speciation along a depth gradient in a marine adaptive radiation. *Proc. Roy. Soc. B.* 278, 613-618.

Ingram T, Harrison AD, Mahler L, Castaneda MdR, Glor RE, Herrel A, Stuart YE, and Losos JB. 2016. Comparative tests of the role of dewlap size in *Anolis* lizard speciation. *Proc. Roy. Soc. B.* 283, 20162199. # Mooers AO, Vamosi S, & Schluter D. 1999. Using phylogenies to test macroevolutionary models of trait evolution: sexual selection and speciation in *Cranes* (Gruinae). *American Naturalist* 154, 249-259. O'Meara BC, Ane C, Sanderson MJ & Wainwright PC. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* 60, 922-933. Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26, 331-348. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* 401, 877-884. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in *Anolis*: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
# Data and phylogeny
data(anolis.tree)
data(anolis.data)

# anolis.data is not matrix and contains missing data so put together matrix of
# relevant traits (here female and male snout vent lengths) and remove species
# with missing data from the matrix and phylogeny
anolisSVL <- data.matrix(anolis.data)[,c(5,6)]
anolisSVL[,1] <- log(anolisSVL[,1])
anolisSVL[,2] <- log(anolisSVL[,2])

tree <- drop.tip(anolis.tree, names(attr(na.omit(anolisSVL), "na.action")))
anolisSVL <- na.omit(anolisSVL)

# log likelihood of kappa = 0.1 or 1
transformPhylo.ll(anolisSVL, phy=tree, model="kappa", kappa=0.1)
transformPhylo.ll(anolisSVL, phy=tree, model="kappa", kappa=1)

# log likelihood of lambda = 0.01 or 1
transformPhylo.ll(anolisSVL, phy=tree, model="lambda", lambda=0.01)
transformPhylo.ll(anolisSVL, phy=tree, model="lambda", lambda=1)

# log likelihood of delta = 1.5 or 1
transformPhylo.ll(anolisSVL, phy=tree, model="delta", delta=1.5)
transformPhylo.ll(anolisSVL, phy=tree, model="delta", delta=1)

# log likelihood of alpha = 0.001 or 2
transformPhylo.ll(anolisSVL, phy=tree, model="OU", alpha=0.001)
transformPhylo.ll(anolisSVL, phy=tree, model="OU", alpha=2)

# log likelihood of psi = 0 (gradual) or 1 (speciational)
phy.bd <- birthdeath(tree)
mu_over_lambda <- phy.bd[[4]][1]
lambda_minus_mu <- phy.bd[[4]][2]
lambda.sp <- as.numeric(lambda_minus_mu / (1 - mu_over_lambda))
transformPhylo.ll(anolisSVL, phy=tree, model="psi", psi=0, lambda.sp=lambda.sp)
```

```
transformPhylo.ll(anolisSVL, phy=tree, model="psi", psi=1, lambda.sp=lambda.sp)
```

transformPhylo.MCMC *Bayesian MCMC for models of trait evolution*

Description

Fits Bayesian models for various models of continuous character evolution using a Metropolis-Hastings Markov Chain Monte Carlo (MCMC) approach

Usage

```
transformPhylo.MCMC(y, phy, model, mcmc.iteration = 1000, burn.in = 0.1,
  hiddenSpeciation = FALSE, full.phy = NULL, lowerBound = NULL,
  upperBound = NULL, opt.accept.rate = TRUE, acceptance.sd = NULL,
  opt.prop = 0.25, fine.tune.bound = 0.05, fine.tune.n = 30,
  useMean = FALSE, random.start = TRUE)
```

Arguments

y	A matrix of trait values.
phy	An object of class "phylo" (see ape package).
model	The model of trait evolution (see details).
mcmc.iteration	Integer - the number of generations for which to run the MCMC chain
burn.in	The proportion of the chain (as given by mcmc.iteration) which to discard as 'burn-in'
hiddenSpeciation	Logical. If TRUE the psi model will include nodes that are on the 'full.phy' but not the tree pruned of trait data
full.phy	The full phylogeny containing the species that do not contain trait data so are not included in 'phy'
lowerBound	Minimum value for parameter estimates
upperBound	Maximum value for parameter estimates
opt.accept.rate	Logical. Perform a pre-run optimisation to achieve an acceptance rate close to 0.44?
acceptance.sd	Numeric. The starting standard deviation for the proposal distribution
opt.prop	The proportion of the mcmc.iteration with which to optimise the acceptance rate.
fine.tune.bound	The distance (+/-) from the optimal acceptance rate of 0.44 at which the fine-tune algorithm will stop. Default = 0.05.
fine.tune.n	The number of iterations with which to optimise the acceptance rate.

useMean	Logical. Use the branch-based estimates of extinction of mean (TRUE, default) for the "psi" and "multispi" models only applicable if "hiddenSpeciation" = TRUE
random.start	Use a random starting value for the MCMC run (TRUE), or use the environment set.seed() value

Details

fine.tune.n The method estimates posterior probabilities using a Metropolis-Hastings MCMC approach. To aide convergence, the model will attempt to reach an acceptable proposal ratio (~0.44) when **opt.accept.rate=TRUE**. These initial fine-tune repetitions only save the standard deviation for the truncated normal distribution that is used for the proposal mechanism. The chain is discarded. Posterior probabilities and MCMC diagnostics come from the separate output chain that commences after this fine-tune procedure. The MCMC model will estimate the posterior probability for the following models.

- **model="kappa"** fits Pagel's kappa by raising all branch lengths to the power kappa. As kappa approaches zero, trait change becomes focused at branching events. For complete phylogenies, if kappa approaches zero this infers speciation trait change. Default bounds from ~0 - 1.
- **model="lambda"** fits Pagel's lambda to estimate phylogenetic signal by multiplying all internal branches of the tree by lambda, leaving tip branches as their original length (root to tip distances are unchanged). Default bounds from ~0 - 1.
- **model="delta"** fits Pagel's delta by raising all node depths to the power delta. If delta < 1, trait evolution is concentrated early in the tree whereas if delta > 1 trait evolution is concentrated towards the tips. Values of delta above one can be difficult to fit reliably. Default bounds from ~0 - 5.
- **model="OU"** fits an Ornstein-Uhlenbeck model - a random walk with a central tendency proportional to alpha. High values of alpha can be interpreted as evidence of evolutionary constraints, stabilising selection or weak phylogenetic signal. It is often difficult to distinguish among these possibilities. Default bounds from ~0 - 10.
- **model="psi"** fits a acceleration-deacceleration model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate (Ingram 2010).
- **model="ACDC"** fits a model to in which rates can exponentially increased or decrease through time (Blomberg et al. 2003). If the upper bound is < 0, the model is equivalent to the 'Early Burst' model of Harmon et al. 2010. Default rate parameter bounds from $\ln(1e-10) \sim \ln(20)$ divided by the root age.

Value

median The median estimate of the posterior for the parameter

95.HPD The 95 percent Highest Posterior Density for the parameter

ESS Effective Sample Size for the posterior

acceptance.rate The ratio for which new proposals were accepted during the MCMC chain

mcmc.chain Full MCMC chain containing all iterations (including burn-in)

Author(s)

Mark Puttick, Gavin Thomas

Examples

```
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
sortedData <- sortTraitData(anolis.tree, male.length)
phy <- sortedData$phy
male.length <- sortedData$trait
phy.clade <- extract.clade(phy, 182)
male.length.clade <- as.matrix(male.length[match(phy.clade$tip.label, rownames(male.length)),])
## please note, this model will be need to run for longer to achieve convergence
lambda.mcmc <- transformPhylo.MCMC(y=male.length.clade, phy=phy.clade,
model="lambda", mcmc.iteration=1000, burn.in=0.1)
```

transformPhylo.ML

Maximum likelihood for models of trait evoluion

Description

Fits likelihood models for various models of continuous character evolution. Model fitting is based on maximum-likelihood evaluation using phylogenetically independent contrasts. This is exactly equivalent to, but substantially faster than, GLS approaches.

Usage

```
transformPhylo.ML(y, phy, model = NULL, modelCIs = TRUE, nodeIDs = NULL,
rateType = NULL, minCladeSize = 1, nSplits = 2, splitTime = NULL,
boundaryAge = 10, testAge = 1, restrictNode = NULL, lambdaEst = FALSE,
acdcScalar = FALSE, branchLabels = NULL, hiddenSpeciation = FALSE,
full.phy = NULL, useMean = FALSE, profilePlot = FALSE,
lowerBound = NULL, upperBound = NULL, covPIC = TRUE, n.cores = 1,
tol = NULL, meserr = NULL, controlList = c(fnscale = -1, maxit = 100,
factr = 1e-07, pgtol = 0, type = 2, lmm = 5), returnPhy = FALSE)
```

Arguments

y	A matrix of trait values.
phy	An object of class "phylo" (see ape package).
model	The model of trait evolution (see details).
modelCIs	Logical - estimate confidence intervals for parameter estimates.
nodeIDs	Integer - ancestral nodes of clades applicable to rate heterogenous and nested models of evolution (see details)

rateType	If model="clade", a vector specifying if rate shift occurs in a clade ("clade") or on the single branch leading to a clade ("branch").
minCladeSize	Integer - minimum clade size for inferred rate shift (where model="medusa").
nSplits	Integer - number of rate shifts to apply for model="medusa" and "timeSlice".
splitTime	A split time (measured from the present, or most recent species) at which a shift in the rate occurs for the "timeSlice" model. If splitTime = NULL, then all ages between 1 million year intervals from the root age - 10 Ma to the present + 10 Ma will be included in the search. The best model will be retained in each search, and will be used as a fixed age in the next search. The model will calculate the likelihood for the number of shifts defined by 'nSplits'.
boundaryAge	Only applicable if splitTime = NULL, the age distance from the tips and and youngest tip for which to search for rate shifts. For example, if boundaryAge = 10, only ages between the root age - 10 and the latest tip + 10 will be included in the search. Set to zero to allow testing of all ages.
testAge	If splitTime = NULL, the interval between ages to be tested. For example, if testAge = 1, all 1 Ma ages between the ages defined by 'boundaryAge' will be tested.
restrictNode	List defining monophyletic groups within which no further rate shifts are searched.
lambdaEst	Logical. Estimate lambda alongside parameter estimates to reduce data noise. Only applicable for models "kappa", "delta", "OU", "psi", "multispi", and "ACDC". Default=FALSE.
acdcScalar	Logical. For nested EB rate model, simultaneously estimated a rate scalar alongside EB model. Default=FALSE.
branchLabels	Branches on which different psi parameters are estimated in the "multispi" model
hiddenSpeciation	Logical. If TRUE the psi model will include nodes that are on the 'full.phy' but not the tree pruned of trait data
full.phy	The full phylogeny containing the species that do not contain trait data so are not included in 'phy'
useMean	Logical. Use the branch-based estimates of extinction of mean (TRUE, default) for the "psi" and "multispi" models only applicable if "hiddenSpeciation" = TRUE
profilePlot	Logical. For the single parameter models "kappa", "lambda", "delta", "OU", "psi", "multispi", and "ACDC", plot the profile of the likelihood.
lowerBound	Minimum value for parameter estimates
upperBound	Maximum value for parameter estimates
covPIC	Logical. For multivariate analyses, allow for co-variance between traits rates (TRUE) or no covariance in trait rates (FALSE). If FALSE, only the trait variances not co-variances are used.
n.cores	Integer. Set number of computing cores when running model="traitMedusa" (tm1 and tm2 models)
tol	Tolerance (minimum branch length) to exclude branches from trait MEDUSA search. Primarily intended to prevent inference of rate shifts at randomly resolved polytomies.

meserr	A vector (or matrix) of measurement error for each tip. This is only applicable to univariate analyses. Largely untested - please use cautiously
controlList	List. Specify fine-tune parameters for the optim likelihood search
returnPhy	Logical. In TRUE the phylogeny with branch lengths transformed by the ML model parameters is returned

Details

This function finds the maximum likelihood parameter values for continuous character evolution. For "kappa", "delta", "OU", "multipsi", and "ACDC" it is possible to fit a 'nested' model of evolution in which the ancestral rate of BM swiches to a different node, as specified by nodeIDs or branchLabels for multipsi. The function returns the maximum-likelihood parameter estimates for the following models.

- model="bm" Brownian motion (constant rates random walk).
- model="kappa" fits Pagel's kappa by raising all branch lengths to the power kappa. As kappa approaches zero, trait change becomes focused at branching events. For complete phylogenies, if kappa approaches zero this infers speciation trait change. Default bounds from ~0 - 1.
- model="lambda" fits Pagel's lambda to estimate phylogenetic signal by multiplying all internal branches of the tree by lambda, leaving tip branches as their original length (root to tip distances are unchanged). Default bounds from ~0 - 1.
- model="delta" fits Pagel's delta by raising all node depths to the power delta. If delta < 1, trait evolution is concentrated early in the tree whereas if delta > 1 trait evolution is concentrated towards the tips. Values of delta above one can be difficult to fit reliably. If a nodeIDs is supplied, the model will fit a delta model nested within a clade, with a BM fit to the rest of the tree. Default bounds from ~0 - 5.
- model="OU" fits an Ornstein-Uhlenbeck model - a random walk with a central tendency proportional to alpha. High values of alpha can be interpreted as evidence of evolutionary constraints, stabilising selection or weak phylogenetic signal. It is often difficult to distinguish among these possibilities. If a nodeIDs is supplied, the model will fit a OU model nested within a clade, with a BM fit to the rest of the tree. For OU models, alternative optimisation are performed with different starting values (1e-8, 0.01, 0.1, 1, 5). Default bounds from ~0 - 10.
- model="ACDC" fits a model to in which rates can exponentially increased or decrease through time (Blomberg et al. 2003). If the upper bound is < 0, the model is equivalent to the 'Early Burst' model of Harmon et al. 2010. If a nodeIDs is supplied, the model will fit a ACDC model nested within a clade, with a BM fit to the rest of the tree. Default rate parameter bounds from $\ln(1e-10) \sim \ln(20)$ divided by the root age. Note this process starts on the stem branch leading to the MRCA of the common node, unlike the other methods that start at the common node.
- model="psi" fits a acceleration-deacceleration model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate (Ingram 2010). Note that the algorithm will automatically estimate speciation and extinction estimates, and will incorporate estimates of 'hidden' speciation if death estimates are greater than 0.

- `model="multiPsi"` fits a acceleration-deacceleration model to assess to the relative contributions of speciation and gradual evolution to a trait's evolutionary rate but allows separate values of `psi` fitted to separate branches (Ingram 2010; Ingram et al. 2016). Note that the algorithm will automatically estimate speciation and extinction estimates, and will incorporate estimates of 'hidden' speciation if death estimates are greater than 0.
- `model="free"` fits Mooers et al's free model where each branch has its own rate of trait evolution. This can be a useful exploratory analysis but it is slow due to the number of parameters, particularly for large trees. Default rate parameter bounds from ~ 0 - 200.
- `model="clade"` fits a model where particular clades are a priori hypothesised to have different rates of trait evolution (see O'Meara et al. 2006; Thomas et al. 2006, 2009). Clades are specified using nodeIDs and are defined as the mrca node. Default rate parameter bounds from ~ 0 - 200.
- `model="tm1"` fits "clade" models without any a priori assertion of the location of phenotypic diversification rate shifts. It uses the same AIC approach as the `runMedusa` function in the `geiger` package (`runMedusa` tests for shifts in the rate of lineage diversification). The algorithm first fits a constant-rate Brownian model to the data, it then works iteratively through the phylogeny fitting a two-rate model at each node in turn. Each two-rate model is compared to the constant rate model and the best two-rate model is retained. Keeping the location of this rate shift intact, it then repeats the procedure for a three-rate model and so on. The maximum number of rate shifts can be specified a priori using `nSplits`. Limits can be applied to the size (species richness) of clades on which to infer new rate shifts using `minCladeSize`. This can be useful to enable large trees to be handled but should be used cautiously since specifying a large minimum clade size may result in biologically interesting nested rate shifts being missed. Equally, very small clade sizes may provide poor estimates of rate that may not be informative. Limits on the search can also be placed using `restrictNode`. This requires a list where each element of the list is a vector of tip names that define monophyletic groups. Rate shifts will not be searched for within any of the defined groups. Default rate parameter bounds from ~ 0 - 1000.
- `model="tm2"` this model is similar to "tm1", however, at each node it assesses the fit of two models. The first model is exactly as per "tm1". The second model infers a rate shift on the single branch descending directly from a node but not on any of the descending branches thereafter. Only the best fitting single-branch or whole clade model is retained for the next iteration. If a single-branch shift is favoured, this infers either that there was a rapid shift in trait value along the stem leading to the crown group, or that the members of the clade have undergone parallel shifts. In either case, this can be considered as a change in mean, though separating a single early shift from a clade-parallel shift is not possible with this method.
- `model="timeSlice"` A model in which all branch rates change at a time or times set a priori by the user. If Default rate parameter bounds from ~ 0 - 1000. If `splitTime=NULL`, all 1 Ma (as defined by `test Age`) intervals from the root of the tree - 10 and the youngest tip + 10 will be included in the search. The ± 10 Ma age can be modified using the argument `boundaryAge`. At each stage the best fitting model will be stored, and the search will continue until `n` shifts, with `n` shifts defined by `nSplits`. If a single value or vector is used for `splitTime`, only these ages are included in the search.

Value

Returns the maximum log-likelihood and parameter estimates (with 95 percent confidence intervals if specified). If `model="bm"` instead returns the Brownian (co)variance and log-likelihood.

traitMedusaObject A list in which the first element contains a matrix summarising the parameter estimates and node ids, log-likelihoods, number of parameters (k), AIC and AICc for the best one-rate model, two-rate model, three rate model and so on. The second element is a sub-list where the first element contains all two-rate models, the second element contains all three-rate models and so on. This can be summarised using traitMedusaSummary. The third element is the input trait data. The fourth element is the input phylogeny.

Note

Confidence intervals are based on the assumption of an asymptotic Chi-square distribution. For multi-parameter models (e.g. rate shift models with more than two rates) the confidence intervals are approximate and are calculated for each parameter in turn while holding all other parameters at their maximum likelihood value.

Author(s)

Gavin Thomas, Mark Puttick

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Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
# Data and phylogeny
data(anolis.tree)
data(anolis.data)
attach(anolis.data)
male.length <- matrix(Male_SVL, dimnames=list(rownames(anolis.data)))
sortedData <- sortTraitData(anolis.tree, male.length)
phy <- sortedData$phy
male.length <- sortedData$trait
phy.clade <- extract.clade(phy, 182)
male.length.clade <- as.matrix(male.length[match(phy.clade$tip.label, rownames(male.length)),])

# Brownian motion model
transformPhylo.ML(male.length.clade , phy=phy.clade, model="bm")

# Delta
transformPhylo.ML(male.length.clade , phy=phy.clade, model="delta", upperBound=2)

# The upper confidence interval for kappa is outside the bounds so try increasing
# the upper bound

transformPhylo.ML(male.length.clade , phy=phy.clade, model="delta", upperBound=5)

# Test for different rates in different clades - here with 2 hypothesised
# unusual rates compared to the background

# This fits the non-censored model of O'Meara et al. (2006)
phy.clade$node.label[which(phy.clade$node.label == "3")] <- 2
transformPhylo.ML(male.length.clade, phy=phy.clade, model="clade", nodeIDs=c(49, 54))

# Identify rate shifts and print and plot results with upto three rate shifts
# and minimum clade size of 20.
anolisSVL_MEDUSA <- transformPhylo.ML(male.length.clade, phy=phy.clade, model="tm1",
minCladeSize=10, nSplits=2)
```

transformPhylo.sim	<i>Phylogenetic tree transformations</i>
--------------------	--

Description

Transforms the branch lengths of a phylo object according to a model of trait evolution (see details).

Usage

```
transformPhylo.sim(phy, n = 1, x = NULL, model = NULL, kappa = NULL,
  lambda = NULL, delta = NULL, alpha = NULL, psi = NULL,
```

```

acdcRate = NULL, lambda.sp = NULL, nodeIDs = NULL, rateType = NULL,
cladeRates = NULL, branchRates = NULL, rate = NULL,
group.means = NULL, splitTime = NULL, timeRates = NULL,
branchLabels = NULL)

```

Arguments

<code>phy</code>	An object of class "phylo" (see ape package).
<code>n</code>	Number of simulations
<code>x</code>	Vector, matrix or data.frame (with taxon names as names or rownames) of categories for each species. Only applicable if model="mixedRate"
<code>model</code>	The model of trait evolution (see details).
<code>kappa</code>	Value of kappa transform.
<code>lambda</code>	Value of lambda transform.
<code>delta</code>	Value of delta transform.
<code>alpha</code>	Value of alpha (OU) transform.
<code>psi</code>	Value of psi transform. Note that 'original nodes' from the full phylogeny can be included as an element on the phylogeny (e.g., <code>phy\$orig.node</code>) as well as estimates of 'hidden' speciation (e.g., <code>phy\$hidden.speciation</code>) if estimates of extinction (μ) are > 0 .
<code>acdcRate</code>	Value of ACDC transform.
<code>lambda.sp</code>	Estimate of speciation (lambda) for the psi models
<code>nodeIDs</code>	Integer - ancestral nodes of clades.
<code>rateType</code>	If model="clade", a vector specifying if rate shift occurs in a clade ("clade") or on the single branch leading to a clade ("branch").
<code>cladeRates</code>	Numeric vector specifying relative rates for clades.
<code>branchRates</code>	Numeric vector specifying relative rates for individual branches
<code>rate</code>	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated.
<code>group.means</code>	a vector of the relative difference in means between rate categories, expressed as a scalar applied to the expected standard deviation (see Ricklefs 2006)
<code>splitTime</code>	A split time (measured from the present, or most recent species) at which a shift in the rate occurs for the "timeSlice" model
<code>timeRates</code>	The rates (from ancient to recent) for the timeSlice model
<code>branchLabels</code>	Branches on which different psi parameters are estimated in the "multipsi" model.

Value

Returns a matrix of simulated dated with taxon names as rownames (number of columns=n).

Author(s)

Gavin Thomas, Mark Puttick

References

Ricklefs RE. 2006. Time, species, and the generation of trait variation in clades. *Systematic Biology* 55, 151-159.

Ricklefs RE. 2006. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030

Examples

```
data(anolis.tree)
data(anolis.data)

# Simulate 10 sets of data with kappa=0.1 using the anolis tree
sim.dat1 <- transformPhylo.sim(phy=anolis.tree, n=10, model="kappa", kappa=0.1)

# Simulate 10 sets of data where rates and means differ between to the categories defined by "x"
x <- anolis.data$geo_ecomorph
names(x) <- rownames(anolis.data)
sim.dat2 <- transformPhylo.sim(phy=anolis.tree, n=10, x=x, model="mixedRate", rate=c(1,1,2,4),
group.means=c(0,5,0,0))
```

transformRateMatrix	<i>Conversion among data and phylogeny objects</i>
---------------------	--

Description

Transforms the expected variance and covariances among species according to hypotheses of rate variation between lineages.

Usage

```
transformRateMatrix(rateData, rate = NULL)
```

Arguments

rateData	an object of class "rateData"
rate	a vector of relative rate parameters. The length of the vector is equal to the number of rates being estimated. If rate=NULL then rates are equal.

Value

retMat Rate-transformed variance covariance matrix

Author(s)

Gavin Thomas

References

Thomas GH, Freckleton RP, & Szekely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273, 1619-1624. Thomas GH, Meiri S, & Phillimore AB. 2009. Body size diversification in Anolis: novel environments and island effects. *Evolution* 63, 2017-2030.

Examples

```
data(anolis.tree)
data(anolis.data)
## Convert data to class rateData with a rateMatrix object as input
anolis.rateMatrix <- as.rateMatrix(phy=anolis.tree, x="geo_ecomorph", data=anolis.data)
anolis.rateData <- as.rateData(y="Female_SVL", x="geo_ecomorph",
rateMatrix = anolis.rateMatrix, phy=NULL, data=anolis.data, log.y=TRUE)

# Tranform the expected variance covariance matrix so that the rates in the first and last
# categories are equal (both 1) whereas the rate in the second category is twice as fast (2) and
# the rate in the third category is ten times slower.

trans.anolis.rateData <- transformRateMatrix(rateData=anolis.rateData, rate = c(1,2,0.1,1))
```


Index

*Topic **datasets**

anolis.data, [5](#)
anolis.tree, [5](#)

addFossilToPhy, [2](#)
allCladeMembers, [4](#)
ancState, [4](#)
anolis.data, [5](#)
anolis.tree, [5](#)
as.rateData, [6](#)
as.rateMatrix, [7](#)

cladeIdentity, [8](#)
contemporaryPhy, [9](#)

dropTipPartial, [10](#)

fairProportions, [11](#)

likRatePhylo, [12](#)
likTraitPhylo, [13](#)

make.anc, [14](#)
make.likRatePhylo, [15](#)
ML.RatePhylo, [16](#)

name.check, [18](#)
node.descendants, [19](#)
nodeTimes, [20](#)

optim.likRatePhylo, [20](#)

phyloCovar, [22](#)
phyloMean, [23](#)
phyloVar, [24](#)
pic.motmot, [26](#)
plotPhylo.motmot, [27](#)

RatePhylo.allCI, [29](#)
RatePhylo.CI, [31](#)
removeNonBin, [32](#)

sampleHiddenSp, [33](#)
sliceTree, [34](#)
sortTraitData, [35](#)

timeSliceSummary, [36](#)
timeTravelPhy, [37](#)
traitData.plot, [38](#)
traitMedusaSummary, [39](#)
transformPhylo, [40](#)
transformPhylo.ll, [43](#)
transformPhylo.MCMC, [46](#)
transformPhylo.ML, [48](#)
transformPhylo.sim, [53](#)
transformRateMatrix, [55](#)