

Package ‘conevol’

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Type Package

Title Analysis of Convergent Evolution

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Description Quantifies and assesses the significance of convergent evolution using multiple methods and measures as described in Stayton (2015) <[DOI:10.1111/evo.12729](https://doi.org/10.1111/evo.12729)> and Grossnickle et al. 2023. Also displays results in various ways.

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calcConv *Quantifies convergent evolution by the ratio of the current to maximum past phenotypic distance between two or more lineages, as described in Stayton (2015). Code written by Jonathan S. Mitchell for Zelditch et al. (2017).*

Description

calcConv prepares arguments for the CalcCs function

Usage

```
calcConv(phy, traits, focaltaxa, VERBOSE = FALSE)
```

Arguments

| | |
|-----------|--|
| phy | The phylogeny of interest in phylo format |
| traits | Phenotypic data for all tips |
| focaltaxa | A list consisting of the names of all putatively convergent taxa |
| VERBOSE | Whether or not to print progress |

Details

calcConv is a wrapper function which formats data, performs ancestral state reconstructions, obtains distance matrices, and determines pairwise combinations of focal taxa, which are then used as arguments for the CalcCs function, which calculates values for C1-C4 of Stayton (2015) for each pair of putatively convergent taxa.

Value

C1-C4 convergence measures for all pairs of putatively convergent taxa.

References

Stayton, C.T. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69:2140-2453.

Zelditch, M.L., J. Ye, J.S. Mitchell, and D.L. Swiderski. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71:633-649.

Examples

```
phy<-rtree(100)
traits<-fastBM(phy,nsim=3)
focaltaxa<-c("t1","t50","t100")
answer<-calcConv(phy,traits,focaltaxa,VERBOSE=FALSE)
```

| | |
|------------|---|
| calcConvCt | <i>Computes Ct-metric scores for putatively convergent tips (or groups of tips) given a set of user provided phenotypic characters and a time calibrated phylogeny.</i> |
|------------|---|

Description

calcConvCt Computes Ct-metric scores for putatively convergent tips (or groups of tips) given a set of user provided phenotypic characters and a time calibrated phylogeny.

Usage

```
calcConvCt(
  phy,
  traits,
  focaltaxa,
  groups = NULL,
  conservative = FALSE,
  VERBOSE = FALSE
)
```

Arguments

| | |
|--------------|--|
| phy | The time calibrated phylogeny of interest in phylo format |
| traits | A matrix of numeric phenotypic traits with rownames matching tip labels of phy |
| focaltaxa | A vector of tip labels for the putatively convergent taxa to be compared |
| groups | An optional vector of groups with names matching focaltaxa. Indicates the group identity of all putatively convergent taxa and limits Ct measures to intergroup comparisons only |
| conservative | Logical value indicating whether measurement of Dmax.t should be restricted to before the origin of the oldest lineage in each pairwise comparison of the focaltaxa. The origin of each convergent lineages is taken as the most recent common ancestor of tips in each user defined group. Where groups include a single tip, the parent node of the tip's subtending branch is used. Requires group object to be provided by user. |
| VERBOSE | Logical value indicating whether model information should be printed during computation |

Details

Function incorporates the optimizations introduced by Zelditch et al. (2017), which significantly improve runtimes

Reconstructions part way along branches are obtained using equation [2] of Felsenstein (1985), following code modified from the phytools (Revell, 2012) function contMap

Value

A list of the following components:

`mean` A named vector of Ct-metrics averaged from all pairwise comparisons of focal taxa. If user provided groups, this is based only on comparisons between taxa belonging to different groups.

`Cmat` A matrix of Ct-metrics for each pairwise comparison.

`path_df` A list of dataframes, one per pairwise comparison of the focal taxa, each containing information from all timepoint measurements of the two putatively convergent lineages. These provide the nodes at which comparisons were drawn, the evolutionary path along which that node fell (i.e., leading to one of two tips), the node height, reconstructed ancestral states at that node for each phenotypic trait, reconstructed ancestral values for each trait along the opposite path, and the phenotypic distance between the two lineages at that point.

`grp.mean` A matrix of Ct-metrics summarized for inter-group comparisons, returned only if user defined groups were specified. Provides overall results matching those reported in "mean", results for each unique inter-group comparison, and results averaged with equal weight given to each unique inter-group comparison (i.e., ignoring differences in the number of tips in each group).

References

Grossnickle DM, Brightly WH, Weaver LN, Stanchak KE, Roston RA, Pevsner SK, Stayton CT, Polly PD, Law CJ. 2022. A cautionary note on quantitative measures of phenotypic convergence. in revision
 Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71: 633-649
 Stayton CT. 2015. The definition, recognition, and interpretation of convergent evolution and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69(8): 2140-2153.
 Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217-223.
 Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125, 1-15.

Examples

```
# create time calibrated tree
mytree<-rtree(100)
mycalibration <- makeChronosCalib(mytree, node="root", age.max=50)
phy <- chronos(mytree, calibration = mycalibration, control = chronos.control() )
class(phy)<-"phylo"

# create three normally distributed phenotypic traits
traits <- cbind(rnorm(Ntip(phy)),rnorm(Ntip(phy)),rnorm(Ntip(phy)))
rownames(traits) <- phy$tip.label
focaltaxa <- sample(phy$tip.label, 5)

system.time(run <- calcConvCt(phy, traits, focaltaxa))
```

| | |
|--------|---|
| calcCs | <i>Calculates the C1-C4 measures of convergent evolution between two lineages as described in Stayton (2015). All measures quantify convergence by the ratio of current to maximum past phenotypic distance between lineages. Can be used as-is but more often will be used within the calcConv script. Code written by Jonathan S. Mitchell for Zelditch et al. (2017)</i> |
|--------|---|

Description

calcCs calculates the C1-C4 measures of convergent evolution

Usage

```
calcCs(tips, ancList, allDists, phy, VERBOSE = FALSE)
```

Arguments

| | |
|----------|--|
| tips | Two putatively convergent tips |
| ancList | A list of ancestors of all tips. Most often obtained from calcConv |
| allDists | A matrix of phenotypic distances between all nodes (tips and ancestors). Most often obtained from calcConv |
| phy | The phylogeny of interest |
| VERBOSE | Whether or not to print progress |

Details

calcCs calculates values of C1-C4, all of which are fundamentally based on comparing the current phenotypic distance between two tips to the maximum past distances between the ancestors of those tips. Higher values indicate a greater amount of past phenotypic distance which has been "closed" by subsequent evolution, and thus greater convergence. C1 is the ratio of tip to maximum ancestral distance. C2 is the difference of those two values. C3 scales C2 by the total amount of evolution that has occurred in the two lineages. C4 scales C2 by the total amount of evolution that has occurred in the entire phylogeny. The arguments for this function will usually be obtained from the calcConv script in `conevol` - this allows certain computationally-intensive steps (e.g., calculating ancestral states) to only be performed once, thus saving a great deal of time. This script also corrects an error in the calculation of C4 of previous versions of `conevol`.

Value

C1-C4 convergence measures for all pairs of putatively convergent taxa.

References

Stayton, C.T. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69:2140-2453.

Zelditch, M.L., J. Ye, J.S. Mitchell, and D.L. Swiderski. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71:633-649.

calcCsCt

Computes Ct values for a pair of tips. Internal, called in calcConv.

Description

calcCsCt Computes Ct values for a pair of tips. Internal, called in calcConv.

Usage

```
calcCsCt(
  tips,
  ancList,
  allDists,
  phy,
  VERBOSE = FALSE,
  allVals,
  edge,
  lim.height = NULL
)
```

Arguments

| | |
|------------|--|
| tips | vector of two tips |
| ancList | list of node paths for all tips in the user provided phylogeny |
| allDists | matrix of phenotypic distances between all exterior and interior node pairs |
| phy | The time calibrated phylogeny of interest in phylo format |
| VERBOSE | logical value indicating whether model information should be printed during computation |
| allVals | a matrix of observed and reconstructed phenotypes for all user supplied traits at interior and exterior nodes |
| edge | a list of data frames, each including the edge matrix of user supplied phylogeny, along with node heights and reconstructed phenotype for each of the user supplied traits |
| lim.height | an optional tree height used to limit Dmax.t, passed only if groups are defined and a conservative test is run (see calcConv) |

Details

Function incorporates the optimizations introduced by Zelditch et al. (2017), which significantly improve runtimes

Reconstructions part way along branches are obtained using equation [2] of Felsenstein (1985), following code modified from the phytools (Revell, 2012) function contMap

Value

A list of the Ct values

References

Grossnickle DM, Brightly WH, Weaver LN, Stanchak KE, Roston RA, Pevsner SK, Stayton CT, Polly PD, Law CJ. 2022. A cautionary note on quantitative measures of phenotypic convergence. in revision Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71: 633-649 Stayton CT. 2015. The definition, recognition, and interpretation of convergent evolution and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69(8): 2140-2153. Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217-223. Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125, 1-15.

convnum

Quantify convergence by the number of convergent events

Description

This program takes in a set of taxa that are already suspected to be convergent in a particular area of morphospace. It then counts the number of times that a lineage has invaded that region of morphospace.

Usage

```
convnum(  
  phy,  
  phendata,  
  convtips,  
  plot = TRUE,  
  ellipse = NULL,  
  plotellipse = NULL  
)
```

Arguments

| | |
|-------------|--|
| phy | The phylogeny of interest in phylo format |
| phendata | Phenotypic data for all tips |
| convtips | A list consisting of the names of all convergent taxa |
| plot | Whether or not to plot a phylomorphospace with lineages that cross into the region of interest highlighted as red arrows. Default=TRUE |
| ellipse | Optional. An ellipse defining the region of interest, into which groups may or may not converge. |
| plotellipse | Optional. The ellipse defining the region of interest in the first two dimensions. |

Details

This function will construct an ellipse around all convergent taxa. Then it will reconstruct ancestral states throughout the phylogeny, and use those to determine how many lineages have crossed into this ellipse from the outside.

Value

The number of lineages that have crossed into the region of trait space occupied by the convergent taxa.

References

- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K.(2013). cluster: Cluster Analysis Basics and Extensions. R package version 1.14.4.
- Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. Bioinformatics, 20, 289-290.
- Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3 217-223.

Examples

```
phy<-rtree(10)
phendata<-fastBM(phy,nsim=2)
convtips<-c("t1","t2","t3")
answer<-convnum(phy,phendata,convtips,plot=TRUE,ellipse=NULL,plotellipse=NULL)
```

| | |
|------------|---|
| convnumsig | <i>Assess the significance of convergent evolution using simulations and the convnum metric</i> |
|------------|---|

Description

Simulates evolution along a given phylogeny, using parameters derived from observed data, and calculates the convnum metric for each simulation for a set of user-defined taxa. Then compares the observed convnum value to the simulated values to assess the significance of the observed levels of convergent evolution.

Usage

```
convnumsig(
  phy,
  phendata,
  convtips,
  nsim,
  ellipse = NULL,
  plot = FALSE,
  plotellipse = NULL
)
```

Arguments

| | |
|-------------|--|
| phy | The phylogeny of interest in phylo format |
| phendata | Phenotypic data for all tips |
| convtips | A list consisting of the names of all convergent taxa |
| nsim | The number of simulations to conduct |
| ellipse | Optional. An ellipse defining the region of interest, into which groups may or may not converge. |
| plot | Optional. Describes whether or not to show phylomorphospaces for all of the simulations. |
| plotellipse | Optional. The ellipse defining the region of interest in the first two dimensions. |

Details

None

Value

A list, consisting first of the p-value for the observed convnum, and second of a vector containing all of the simulated convnum values. Also displays a histogram of all of the simulated convnum values.

References

- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K.(2013). cluster: Cluster Analysis Basics and Extensions. R package version 1.14.4.
- Paradis, E., J. Claude, and K. Strimmer (2004) APE: Analyses of phylogenetics and evolution in R language. Bioinformatics, 20, 289-290.
- Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3 217-223.

Examples

```

phy<-rtree(10)
phendata<-fastBM(phy,nsim=2)
convtips<-c("t1","t2","t3")
answer<-convnumsig(phy,phendata,convtips,10,plot=FALSE,ellipse=NULL,plotellipse=NULL)

```

| | |
|---------|--|
| convSig | <i>Uses simulations to assess the significance of C1-C4 measures of convergent evolution as described in Stayton (2015). Code written by Jonathan S. Mitchell for Zelditch et al. (2017)</i> |
|---------|--|

Description

convSig calculates the significance of measures of convergent evolution.

Usage

```
convSig(phy, traits, focaltaxa, nsim = 1000)
```

Arguments

| | |
|-----------|--|
| phy | The phylogeny of interest in phylo format |
| traits | Phenotypic data for all tips |
| focaltaxa | A list consisting of the names of all putatively convergent taxa |
| nsim | The number of simulations to use to assess significance |

Details

This script simulates data according to a Brownian motion model of evolution, and then assesses convergence on that simulated data. The number of times that the simulated data produces greater convergence than that observed in the empirical data is used to calculate a P-value.

Value

C1-C4 convergence measures for all pairs of putatively convergent taxa and their associated p-values.

References

Stayton, C.T. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69:2140-2453.

Zelditch, M.L., J. Ye, J.S. Mitchell, and D.L. Swiderski. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71:633-649.

Examples

```
phy<-rtree(100)
traits<-fastBM(phy,nsim=3)
focaltaxa<-c("t1","t50","t100")
answer<-convSig(phy,traits,focaltaxa,nsim=10)
```

| | |
|-----------|--|
| convSigCt | <i>Computes and conducts significance tests on Ct-metric scores for putatively convergent tips (or groups of tips) given a set of user provided phenotypic characters and a time calibrated phylogeny.</i> |
|-----------|--|

Description

convSigCt Computes and conducts significance tests on Ct-metric scores for putatively convergent tips (or groups of tips) given a set of user provided phenotypic characters and a time calibrated phylogeny.

Usage

```
convSigCt(phy, traits, focaltaxa, groups = NULL, nsim = 1000, ...)
```

Arguments

| | |
|-----------|---|
| phy | The time calibrated phylogeny of interest in phylo format |
| traits | a matrix of numeric phenotypic traits with rownames matching tip labels of phy |
| focaltaxa | a vector of tip labels for the putatively convergent taxa to be compared |
| groups | an optional vector of groups with names matching focaltaxa. Indicates the group identity of all putatively convergent taxa and limits Ct measures to intergroup comparisons only |
| nsim | number of simulated (Brownian motion) datasets used to build the null distribution |
| ... | optional arguments to be passed to calcConv. If convservative is TRUE, Dmax.t is restricted to before the origin of the oldest lineage in each pairwise comparison of the focal taxa. The origin of convergent lineages is taken as the most recent common ancestors of each user defined group. Where these groups include a single tip, the parent node of its subtending branch is used. Requires user |

to provide groups. If VERBOSE is TRUE, model information will be printed during computation, including time limits imposed on Dmax.t if the conservative option is chosen.

Details

Function incorporates the optimizations introduced by Zelditch et al. (2017), which significantly improve runtimes

Reconstructions part way along branches are obtained using equation [2] of Felsenstein (1985), following code modified from the phytools (Revell, 2012) function contMap

Value

A list of the following components:

pvals a matrix containing Ct1 - Ct4 and p-values from significance tests for each

meas.Cmat a matrix of Ct values for each pairwise comparison of focaltaxa

meas.path a list of dataframes, one per pairwise comparison of focaltaxa, each containing information from all timepoint measurements of the two putatively convergent lineages. These provide the nodes at which comparisons were drawn, the evolutionary path along which that node fell (i.e., leading to one of two tips), the node height, reconstructed ancestral states at that node for each phenotypic trait, reconstructed ancestral values for each trait along the opposite path, and the phenotypic distance between the two lineages at that point.

sim.avg average Ct values from all pairwise comparisons between focaltaxa using simulated Brownian motion traits, number of columns corresponds to the user provided number of simulations

sim.path a list of dataframes as in meas.path, but obtained using simulated data. Length of object determined by number of pairwise comparisons multiplied by the number of simulated datasets.

grp.mean a matrix of Ct-metrics summarized for inter-group comparisons, returned only if user defined groups were specified. Provides overall results matching those reported in "mean", results for each unique inter-group comparison, and results averaged with equal weight given to each unique inter-group comparison (i.e., ignoring differences in the number of tips in each group).

grp.pvals a matrix of p-values associated with Ct values in grp.mean object. Returned only if user defined groups were specified.

References

Grossnickle DM, Brightly WH, Weaver LN, Stanchak KE, Roston RA, Pevsner SK, Stayton CT, Polly PD, Law CJ. 2022. A cautionary note on quantitative measures of phenotypic convergence. in revision Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71: 633-649 Stayton CT. 2015. The definition, recognition, and interpretation of convergent evolution and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69(8): 2140-2153. Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217-223. Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125, 1-15.

Examples

```
# create time calibrated tree
mytree<-rtree(50)
mycalibration <- makeChronosCalib(mytree, node="root", age.max=50)
phy <- chronos(mytree, calibration = mycalibration, control = chronos.control() )
class(phy)<-"phylo"

# create three normally distributed phenotypic traits
traits <- cbind(rnorm(Ntip(phy)),rnorm(Ntip(phy)),rnorm(Ntip(phy)))
rownames(traits) <- phy$tip.label
focaltaxa <- sample(phy$tip.label, 5)

system.time(run2 <- convSigCt(phy, traits, focaltaxa, nsim=10))
```

multianc

Reconstructs ancestral states for multiple characters

Description

Uses fastAnc to reconstruct ancestral states for multiple phenotypic characters

Usage

```
multianc(phy, phendata)
```

Arguments

| | |
|----------|---|
| phy | The phylogeny of interest in phylo format |
| phendata | Phenotypic data for all tips |

Details

None

Value

A matrix with the tips data in the first n rows and the ancestral data in the remaining n-1 rows.

References

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

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

Examples

```

phy<-rtree(10)

phendata<-fastBM(phy,nsim=2)

ancs<-multianc(phy,phendata)

```

plotCt *Plots calcConv or convSig output.*

Description

plotCt Plots calcConv or convSig output.

Usage

```

plotCt(
  output,
  phy,
  focaltaxa,
  nsim = 25,
  col = c("black", "forest green", "dodgerblue2", "firebrick1", "purple", "orange",
    "salmon", "goldenrod", "springgreen2", "plum1"),
  groups = NULL,
  ...
)

```

Arguments

| | |
|-----------|---|
| output | object containing calcConv or convSig output |
| phy | The time calibrated phylogeny of interest in phylo format |
| focaltaxa | a vector of tip labels for the putatively convergent taxa to be compared |
| nsim | number of null simulations to plot |
| col | vector of colors to use for all unique intergroup comparisons a default option is given usable with up to five groups. If number of groups is 1 or less than length of col, not all colors will be used |
| groups | an optional vector of groups with names matching focaltaxa, indicating the group identity of all focaltaxa |
| ... | optional arguments to be passed to tiplabels |

Details

Creates a plot that shows the phenotypic distances between pairs of putatively convergent lineages over time. When these distances decrease, convergence has occurred. When more than two putatively convergent taxa are analyzed, all pairs are plotted.

Value

A plot identifying putatively convergent taxa in the provided phylogeny and tracking the change in phenotypic distance between taxa since their most recent common ancestor

References

Grossnickle DM, Brightly WH, Weaver LN, Stanchak KE, Roston RA, Pevsner SK, Stayton CT, Polly PD, Law CJ. 2022. A cautionary note on quantitative measures of phenotypic convergence. in revision Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71: 633-649 Stayton CT. 2015. The definition, recognition, and interpretation of convergent evolution and two new measures for quantifying and assessing the significance of convergence. *Evolution* 69(8): 2140-2153. Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217-223. Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125, 1-15.

plotellipse

Plots an ellipse

Description

Plots a minimum ellipse around a set of data

Usage

```
plotellipse(ellipse)
```

Arguments

ellipse Gives the parameters of the ellipse - output from the ellipsoidhull function in cluster.

Details

Routine adapted from a suggestion made on CrossValidated: <http://stats.stackexchange.com/questions/9898/how-to-plot-an-ellipse-from-eigenvalues-and-eigenvectors-in-r>

Value

Nothing - just plots the ellipse.

References

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K.(2013). cluster: Cluster Analysis Basics and Extensions. R package version 1.14.4.

pullNodeSeq *Extracts a vector of ancestors for a given taxon. Code written by Jonathan S. Mitchell for Zelditch et al. (2017)*

Description

pullNodeSeq Extracts a vector of all ancestors of a given taxon in a phylogeny.

Usage

```
pullNodeSeq(phy, tip)
```

Arguments

| | |
|-----|---|
| phy | The phylogeny of interest in phylo format |
| tip | The tip of interest |

Value

A vector of ancestors

References

Zelditch, M.L., J. Ye, J.S. Mitchell, and D.L. Swiderski. 2017. Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* 71:633-649.

Examples

```
phylogeny<-rtree(100)  
answer<-pullNodeSeq(phy=phylogeny, tip="t1")
```


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