

Package ‘picante’

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Author Steven W. Kembel <steve.kembel@gmail.com>, David D. Ackerly <dackerly@berkeley.edu>, Simon P. Blomberg <s.blomberg1@uq.edu.au>, Will K. Cornwell <cornwell@zoology.ubc.ca>, Peter D. Cowan <pdcc@berkeley.edu>, Matthew R. Helmus <mrhelimus@wisc.edu>, Helene Morlon <morlon.helene@gmail.com>, Campbell O. Webb <cwebb@oeb.harvard.edu>

Maintainer Steven W. Kembel <steve.kembel@gmail.com>

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Description Functions for phylocom integration, community analyses, null-models, traits and evolution. Implements numerous ecophylogenetic approaches including measures of community phylogenetic and trait diversity, phylogenetic signal, estimation of trait values for unobserved taxa, null models for community and phylogeny randomizations, and utility functions for data input/output and phylogeny plotting. A full description of package functionality and methods are provided by Kembel et al. (2010) <[doi:10.1093/bioinformatics/btq166](https://doi.org/10.1093/bioinformatics/btq166)>.

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Description

Functions for phylocom integration, community analyses, null-models, traits and evolution. Implements numerous ecophylogenetic approaches including measures of community phylogenetic and trait diversity, phylogenetic signal, estimation of trait values for unobserved taxa, null models for community and phylogeny randomizations, and utility functions for data input/output and phylogeny plotting. A full description of package functionality and methods are provided by Kembel et al. (2010) <doi:10.1093/bioinformatics/btq166>.

Details

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Author(s)

Author: Steven W. Kembel <steve.kembel@gmail.com>, David D. Ackerly <dackerly@berkeley.edu>, Simon P. Blomberg <s.blomberg1@uq.edu.au>, Will K. Cornwell <cornwell@zoology.ubc.ca>, Peter D. Cowan <pdw@berkeley.edu>, Matthew R. Helmus <mrhasmus@wisc.edu>, Helene Morlon <morlon.helene@gmail.com>, Campbell O. Webb <cwebb@oeb.harvard.edu> Maintainer: Steven W. Kembel <steve.kembel@gmail.com>

color.plot.phylo *Color tip labels based on trait*

Description

Plots a phylogeny with tip labels colored to indicate continuous or discrete trait values

Usage

```
color.plot.phylo(phylo, df, trait, taxa.names,
  num.breaks = ifelse(is.factor(df[,trait]),
    length(levels(df[,trait])), 12),
  col.names = rainbow(ifelse(length(num.breaks) > 1,
    length(num.breaks) - 1, num.breaks)),
  cut.labs = NULL,
  leg.title = NULL,
  main = trait,
  leg.cex = 1,
  tip.labs = NULL,
  ...)
```

Arguments

<code>phylo</code>	An object of class <code>phylo</code>
<code>df</code>	A dataframe containing the traits to be plotted
<code>trait</code>	A string representing the name of column in the dataframe to be plotted
<code>taxa.names</code>	A string representing the name of column in the dataframe that contains the names of the taxa
<code>num.breaks</code>	For continuous traits, the number of bins to separate the data into
<code>col.names</code>	A vector of colors to use for tip labels
<code>leg.title</code>	A title for the tip color legend
<code>main</code>	A main title for the plot
<code>cut.labs</code>	A main title for the plot
<code>leg.cex</code>	A main title for the plot
<code>tip.labs</code>	A main title for the plot
<code>...</code>	Additional argument to pass to the <code>plot.phylo</code> function

Details

If `trait` is a factor then each level of the factor is plotted with the corresponding `col.names` value (if `length(num.breaks) > length(col.names)` colors are recycled.) If `trait` is not a factor then it is assumed to be continuous and `trait` is evenly divided into `num.breaks` levels.

Value

The command is invoked for its side effect, a plot of the `phylo` with tips colored based on `trait`

Author(s)

Peter Cowan <pc@berkeley.edu>

`comdist`

Calculates inter-community mean pairwise distance

Description

Calculates MPD (mean pairwise distance) separating taxa in two communities, a measure of phylogenetic beta diversity

Usage

```
comdist(comm, dis, abundance.weighted = FALSE)
```

Arguments

`comm` Community data matrix
`dis` Interspecific distance matrix
`abundance.weighted` Should mean pairwise distances separating species in two communities be weighted by species abundances? (default = FALSE)

Details

This function calculates a measure of phylogenetic beta diversity: the expected phylogenetic distance separating two individuals or taxa drawn randomly from different communities.

Value

Distance object of MPD values separating each pair of communities.

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

C.O. Webb, D.D. Ackerly, and S.W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 18:2098-2100.

See Also

[mpd](#), [ses.mpd](#)

Examples

```
data(phylocom)
comdistnt(phylocom$sample, cophenetic(phylocom$phylo), abundance.weighted=TRUE)
```

comdistnt

Calculates inter-community mean nearest taxon distance

Description

Calculates MNTD (mean nearest taxon distance) separating taxa in two communities, a measure of phylogenetic beta diversity

Usage

```
comdistnt(comm, dis, abundance.weighted = FALSE, exclude.conspecifics = FALSE)
```

Arguments

<code>comm</code>	Community data matrix
<code>dis</code>	Interspecific distance matrix
<code>abundance.weighted</code>	Should mean nearest taxon distances from each species to species in the other community be weighted by species abundance? (default = FALSE)
<code>exclude.conspecific</code>	Should conspecific taxa in different communities be exclude from MNTD calculations? (default = FALSE)

Details

This metric has also been referred to as MNND (mean nearest neighbour distance).

This function calculates a measure of phylogenetic beta diversity: the average phylogenetic distance to the most similar taxon or individual in the other community for taxa or individuals in two communities.

Value

Distance object of MNTD values separating each pair of communities.

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

C.O. Webb, D.D. Ackerly, and S.W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 18:2098-2100.

See Also

[mntd](#), [ses.mntd](#)

Examples

```
data(phylocom)
comdistnt(phylocom$sample, cophenetic(phylocom$phylo), abundance.weighted=FALSE)
```

comm.phylo.cor *Correlations between species co-occurrence and phylogenetic distances*

Description

Calculates measures of community phylogenetic structure (correlation between co-occurrence and phylogenetic distance) to patterns expected under various null models

Usage

```
comm.phylo.cor(samp, phylo, metric = c("cij", "checkerboard", "jaccard", "doij"),
  null.model = c("sample.taxa.labels", "pool.taxa.labels",
    "frequency", "richness", "independentswap", "trialswap"), runs = 999, ...)
```

Arguments

samp	Community data matrix
phylo	Phylogenetic tree
metric	Metric of co-occurrence to use (see species.dist)
null.model	Null model to use (see Details section for description)
runs	Number of runs (randomizations)
...	Additional arguments to randomizeMatrix

Details

Currently implemented null models (arguments to null.model):

sample.taxa.labels Shuffle phylogeny tip labels (only within set of taxa present in community data)

pool.taxa.labels Shuffle phylogeny tip labels (across all taxa included in phylogenetic tree)

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

independentswap Randomize community data matrix maintaining species occurrence frequency and site richness using independent swap

trialswap Randomize community data matrix maintaining species occurrence frequency and site richness using trial swap

Value

A list with elements:

obs.corr	Observed co-occurrence/phylogenetic distance correlation
obs.corr.p	P-value of observed correlation (standard P-value for correlation coefficient, not based on comparison with randomizations)
obs.rank	Rank of observed correlation vs. random
runs	Number of runs (randomizations)
obs.rand.p	P-value of observed correlation vs. randomizations (= obs.rank / (runs + 1))
random.corr	A vector of random correlation calculated for each run

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Cavender-Bares J., D.A. Ackerly, D. Baum and F.A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities, *American Naturalist*, 163(6):823-843.

See Also

[randomizeMatrix](#)

Examples

```
data(phylocom)
comm.phylo.cor(phylocom$sample, phylocom$phylo, metric="cij", null.model="sample.taxa.labels")
```

comm.phylo.qr	<i>Quantile regression slopes between species co-occurrence and phylogenetic distances</i>
---------------	--

Description

Calculates measures of community phylogenetic structure (quantile regression between co-occurrence and phylogenetic distance) to patterns expected under various null models

Usage

```
comm.phylo.qr(samp, phylo, metric = c("cij", "checkerboard", "jaccard", "doij"),
  null.model = c("sample.taxa.labels", "pool.taxa.labels",
    "frequency", "richness", "independentswap", "trialswap"),
  quant = 0.75, runs = 999, show.plot = FALSE, ...)
```

Arguments

samp	Community data matrix
phylo	Phylogenetic tree
metric	Metric of co-occurrence to use (see species.dist)
null.model	Null model to use (see Details section for description)
quant	Quantile of slope to be fit (using rq)
runs	Number of runs (randomizations)
show.plot	Option to display a plot of co-occurrence versus phylogenetic distance with quantile regression slope fit
...	Additional arguments to randomizeMatrix

Details

This function fits a quantile regression of co-occurrence versus phylogenetic distances separating species, and compares observed patterns to the patterns expected under some null model. The quantile regressions are fit using the [rq](#) function from the [quantreg](#) package.

Currently implemented null models (arguments to null.model):

sample.taxa.labels Shuffle phylogeny tip labels (only within set of taxa present in community data)

pool.taxa.labels Shuffle phylogeny tip labels (across all taxa included in phylogenetic tree)

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

independentswap Randomize community data matrix maintaining species occurrence frequency and site richness using independent swap

trialswap Randomize community data matrix maintaining species occurrence frequency and site richness using trial swap

Value

A list with elements:

obs.qr.intercept	Observed co-occurrence/phylogenetic distance quantile regression intercept
obs.qr.slope	Observed co-occurrence/phylogenetic distance quantile regression slope
obs.qr.slope.p	P-value of observed quantile regression slope significance versus null model (calculated based on comparison with randomizations)
obs.rank	Rank of observed quantile regression slope vs. random
runs	Number of runs (randomizations)
random.qr.slopes	A vector of quantile regression slopes calculated for each randomization

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Cavender-Bares J., D.A. Ackerly, D. Baum and F.A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities, *American Naturalist*, 163(6):823-843. Slingsby, J. A. and G. A. Verboom. 2006. Phylogenetic relatedness limits coexistence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist* 168:14-27.

See Also

[randomizeMatrix](#)

Examples

```
data(phylocom)
comm.phylo.qr(phylocom$sample, phylocom$phylo, metric="cij",
  null.model="sample.taxa.labels", runs=99)
```

cor.table

Table of correlations and P-values

Description

Table of correlations with associated P-values and df, can be used with regular or independent contrast data

Usage

```
cor.table(x, cor.method = c("pearson", "spearman"),
  cor.type=c("standard", "contrast"))
```

Arguments

x	Data frame of data points or contrasts at nodes
cor.method	Correlation method (as cor)
cor.type	Are data standard or independent contrast values?

Value

r	Correlation values
df	Degrees of freedom
P	P-values

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

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

evol.distinct	<i>Species' evolutionary distinctiveness</i>
---------------	--

Description

Calculates evolutionary distinctiveness measures for a suite of species by: a) equal splits (Redding and Mooers 2006) b) fair proportions (Isaac et al., 2007). Returns a dataframe with species identifiers and species scores.

Usage

```
evol.distinct(tree, type = c("equal.splits", "fair.proportion"),
              scale = FALSE, use.branch.lengths = TRUE)
```

Arguments

tree	an object of class phylo
type	a) equal splits (Redding and Mooers 2006) or b) fair proportions (Isaac et al., 2007)
scale	The scale option refers to whether or not the phylogeny should be scaled to a depth of 1 or, in the case of an ultrametric tree, scaled such that branch lengths are relative.
use.branch.lengths	If use.branch.lengths=FALSE, then all branch lengths are changed to 1.

Note

This function will return a vector of evolutionary distinctiveness for every species in the given tree. If only a subset of values are needed there are two, conceptually distinct options: either prune the tree first and then pass the tree in or subset the resulting vector. These two options will provide very different outputs.

Author(s)

Karen Magnuson-Ford, Will Cornwell, Arne Mooers, Mark Vellend

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.

Mark Vellend, William K. Cornwell, Karen Magnuson-Ford, and Arne Mooers. In press. Measuring phylogenetic biodiversity. In: *Biological diversity: frontiers in measurement and assessment*. Edited by Anne Magurran and Brian McGill.

expected.pd

Expected PD, PD Variance, and Edge Abundance Distribution of a phylogeny

Description

Calculates the expected phylogenetic diversity (Faith's PD) and variance of PD under binomial sampling with a fixed probability of each tip being sampled, and the Edge-length Abundance Distribution of a phylogeny.

Usage

```
expected.pd(phy)
variance.pd(phy, upper.bound=TRUE)
ead(phy)
```

Arguments

phy	phylo object
upper.bound	Calculate upper bound of PD variance? (default = TRUE)

Details

The function `expected.pd` calculates the expected phylogenetic diversity (Faith's PD - total branch length) for all subsets of a phylogeny, based on an analytic solution for expected PD.

The function `variance.pd` additionally calculates the variance of expected PD for all subsets of a phylogeny, based on an analytic solution for expected PD. If argument `upper.bound=TRUE`, a fast solution for the upper bound of the variance is returned. Otherwise, the exact solution for the variance is returned. Note that the exact solution is much slower than the upper bound solution.

The function `ead` calculates the edge abundance distribution (EAD), the length of edges with different numbers of descendant tips.

Value

n	Expected Number of tips sampled
expected.pd	Expected PD for a given n
variance.pd	Variance of PD for a given n
num.children	Number of tips descended from an edge
edge.length	Total phylogenetic edge length for a given number of tips descended from an edge

Author(s)

Steven Kembel <steve.kembel@gmail.com> and James O'Dwyer <jodwyer@santafe.edu>

References

J.P. O'Dwyer, S.W. Kembel, and J.L. Green. 2012. Phylogenetic Diversity Theory Sheds Light on the Structure of Microbial Communities. *PLoS Comput Biol* 8(12): e1002832.

See Also

[pd](#)

Examples

```
randtree <- rcoal(300)
randtree.pd.ub <- variance.pd(randtree, upper.bound=TRUE)
randtree.pd.exact <- variance.pd(randtree, upper.bound=FALSE)
plot(expected.pd(randtree), xlab="Number of tips",
      ylab="Phylogenetic diversity (PD)", type="l", log="xy")
lines(randtree.pd.exact$expected.pd+1.96*sqrt(randtree.pd.exact$variance.pd), lty=2)
lines(randtree.pd.exact$expected.pd-1.96*sqrt(randtree.pd.exact$variance.pd), lty=2)
lines(randtree.pd.ub$expected.pd+1.96*sqrt(randtree.pd.ub$variance.pd), lty=3)
lines(randtree.pd.ub$expected.pd-1.96*sqrt(randtree.pd.ub$variance.pd), lty=3)
legend("bottomright", lty=c(1,2,3), legend=c("Expected PD",
      "95 percent CI (exact)", "95 percent CI (upper bound)"))
```

IvesGodfray

Host-parasitoid food web data

Description

Data on the structure of a host-parasitoid food web from Ives & Godfray (2006). Includes information on phylogenetic covariances among 12 leaf-mining moth hosts and 27 species of parasitoid wasps.

Usage

```
data(IvesGodfray)
```

Format

A list with three elements:

- host Phylogenetic variance/covariance matrix for 12 leaf-mining moth hosts
- parasitoid Phylogenetic variance/covariance matrix for 27 species of parasitoid wasps
- interactions Matrix describing interactions between hosts and parasitoids

Source

Ives A.R. & Godfray H.C. (2006) Phylogenetic analysis of trophic associations. *The American Naturalist*, 168, E1-E14

See Also

[pblm](#)

Kcalc

K statistic of phylogenetic signal

Description

Calculates K statistic of phylogenetic signal

Usage

```
Kcalc(x, phy, checkdata=TRUE)
```

Arguments

x	Vector or data.frame of trait data (in phylo\$tip.label order)
phy	phylo object
checkdata	Check for match between trait and phylogeny taxa labels using match.phylo.data? (default=TRUE)

Value

K	K statistic
---	-------------

Author(s)

Simon Blomberg <s.blomberg1@uq.edu.au> and David Ackerly <dackerly@berkeley.edu>

References

- Blomberg, S. P., and T. Garland, Jr. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* 15:899-910.
- Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717-745.

See Also[phylosignal](#)**Examples**

```

randtree <- rcoal(20)
randtraits <- rTraitCont(randtree)
Kcalc(randtraits[randtree$tip.label], randtree)

```

match.phylo.data	<i>Match taxa in phylogeny and data</i>
------------------	---

Description

These functions compare taxa present in phylogenies with community or trait data sets, pruning and sorting the two kinds of data to match one another for subsequent analysis.

Usage

```

match.phylo.comm(phy, comm)
match.phylo.data(phy, data)
match.comm.dist(comm, dis)

```

Arguments

phy	A phylogeny object of class phylo
comm	Community data matrix
data	A data object - a vector (with names matching phy) or a data.frame or matrix (with row names matching phy)
dis	A distance matrix - a dist or matrix object

Details

A common pitfall in comparative analyses in R is that taxa labels are assumed to match between phylogenetic and other data sets. These functions prune a phylogeny and community or trait data set to match one another, reporting taxa that are missing from one data set or the other.

Taxa names for phylogeny objects are taken from the phylogeny's tip labels. Taxa names for community data are taken from the column names. Taxa names for trait data are taken from the element names (vector) or row names (data.frame or matrix). Taxa names for distance data are taken from column/row names of the distance matrix/dist object.

If community data lack taxa names, the function will issue a warning and no result will be returned, since the community-phylogenetic analyses in `picante` require named taxa in the community data set.

If trait data or distance matrix lack names, a warning is issued and the data are assumed to be sorted in the same order as the phylogeny's tip labels or community's column labels.

These utility functions are used by several functions that assume taxa labels in phylogeny and data match, including [kcalc](#), [phylosignal](#), and [raoD](#).

Value

A list containing the following elements, pruned and sorted to match one another:

phy	A phylogeny object of class phylo
comm	Community data matrix
data	A data object (vector, data.frame or matrix)
dist	A distance matrix - a dist or matrix object

Author(s)

Steven Kembel <steve.kembel@gmail.com>

See Also

[prune.missing](#), [prune.sample](#)

Examples

```
data(phylocom)
match.phylo.comm(phylocom$phylo, phylocom$sample)
match.phylo.data(phylocom$phylo, phylocom$traits[1:10,])
```

matrix2sample

Convert community data matrix to Phylocom sample

Description

Converts a community data matrix to a Phylocom database-format community sample

Usage

```
matrix2sample(z)
```

Arguments

z Community data matrix

Value

Phylocom database-format community sample

Author(s)

Steven Kembel <steve.kembel@gmail.com> and Cam Webb <cwebb@oeb.harvard.edu>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

Examples

```
data(phylocom)
matrix2sample(phylocom$sample)
```

mntd

Mean nearest taxon distance

Description

Calculates MNTD (mean nearest taxon distance) for taxa in a community

Usage

```
mntd(samp, dis, abundance.weighted=FALSE)
```

Arguments

samp	Community data matrix
dis	Interspecific distance matrix
abundance.weighted	Should mean nearest taxon distances for each species be weighted by species abundance? (default = FALSE)

Details

This metric has also been referred to as MNND (mean nearest neighbour distance), and the function was named mnnd in picante versions < 0.7.

Value

Vector of MNTD values for each community.

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Webb, C., D. Ackerly, M. McPeck, and M. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475-505.

See Also[ses.mntd](#)**Examples**

```
data(phylocom)
mntd(phylocom$sample, cophenetic(phylocom$phylo), abundance.weighted=TRUE)
```

mpd

Mean pairwise distance

Description

Calculates mean pairwise distance separating taxa in a community

Usage

```
mpd(samp, dis, abundance.weighted=FALSE)
```

Arguments

samp	Community data matrix
dis	Interspecific distance matrix
abundance.weighted	Should mean pairwise distances be weighted by species abundance? (default = FALSE)

Value

Vector of MPD values for each community

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Webb, C., D. Ackerly, M. McPeck, and M. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475-505.

See Also[ses.mpd](#)**Examples**

```
data(phylocom)
mpd(phylocom$sample, cophenetic(phylocom$phylo), abundance.weighted=TRUE)
```

multiPhylosignal	<i>Calculates phylogenetic signal for data.frame of traits</i>
------------------	--

Description

Calculates phylogenetic signal for data.frame of traits. Traits may have missing values in which case the tree will be pruned prior to calculating phylogenetic signal for each trait.

Usage

```
multiPhylosignal(x, phy, checkdata=TRUE, ...)
```

Arguments

x	Data frame of trait data (traits in columns) with row names corresponding to tip.labels
phy	phylo object
checkdata	Check for match between trait and phylogeny taxa labels using match.phylo.data? (default=TRUE)
...	Additional arguments to phylosignal

Value

Returns a data frame with phylogenetic signal results for each trait

Author(s)

Steven Kembel <steve.kembel@gmail.com>

pblm	<i>Phylogenetic Bipartite Linear Model</i>
------	--

Description

Fits a linear model to the association strengths of a bipartite data set with or without phylogenetic correlation among the interacting species

Usage

```
pblm(assocs, tree1=NULL, tree2=NULL, covars1=NULL, covars2=NULL, bootstrap=FALSE,
     nreps=10, maxit=10000, pstart=c(.5,.5))
pblmpredict(x, tree1.w.novel=NULL, tree2.w.novel=NULL, predict.originals=FALSE)
```

Arguments

assoc	A matrix of association strengths among two sets of interacting species
tree1	A phylo tree object or a phylogenetic covariance matrix for the rows of assoc
tree2	A phylo tree object or a phylogenetic covariance matrix for the columns of assoc
covars1	A matrix of covariates (e.g., traits) for the row species of assoc
covars2	A matrix of covariates (e.g., traits) for the column species of assoc
bootstrap	logical, bootstrap confidence intervals of the parameter estimates
nreps	Number of bootstrap replicated data sets to estimate parameter CIs
maxit	as in <code>optim</code>
pstart	starting values of the two phylogenetic signal strength parameters passed to <code>optim</code>
x	object of class <code>pblm</code>
tree1.w.novel	A phylo tree object or a phylogenetic covariance matrix which corresponds to tree1 of x with species to predict associations
tree2.w.novel	A phylo tree object or a phylogenetic covariance matrix which corresponds to tree2 of x with species to predict associations
predict.originals	if TRUE then the associations of each original species in the two phylogenies is predicted

Details

Fit a linear model with covariates using estimated generalized least squares to the association strengths between two sets of interacting species. Associations can be either binary or continuous. If phylogenies of the two sets of interacting species are supplied, two *phylogenetic signal strength* parameters ($d1$ and $d2$), one for each species set, based on an Ornstein-Uhlenbeck model of evolution with stabilizing selection are estimated. Values of $d=1$ indicate no stabilizing selection and correspond to the Brownian motion model of evolution; $0 < d < 1$ represents stabilizing selection; $d=0$ depicts the absence of phylogenetic correlation (i.e., a star phylogeny); and $d > 1$ corresponds to disruptive selection where phylogenetic signal is amplified. Confidence intervals for these and the other parameters can be estimated with bootstrapping.

The function `pblmpredict` predicts the associations of novel species following the methods given in appendix B of Ives and Godfray (2006).

Value

MSE	total, full (each d estimated), star ($d=0$), and base ($d=1$) mean squared errors
signal.strength	two estimates of phylogenetic signal strength
coefficients	estimated intercept and covariate coefficients with approximate 95 percent CIs for the three model types (full, star, base)
CI.boot	95 percent CIs for all parameters

variates	matrix of model variates (can be used for plotting)
residuals	matrix of residuals from the three models (full, star and base)
predicted	predicted associations
bootvalues	matrix of parameters estimated from the nreps bootstrap replicated data sets used to calculate CIs
phylocovs	phylogenetic covariance matrices scaled by the estimated d1 and d2
cors.1	correlations among predicted and observed associations for species of tree1, NA if predict.originals=FALSE
cors.2	correlations among predicted and observed associations for species of tree2, NA if predict.originals=FALSE
pred.novels1	predicted associations for the novel speices of tree1
pred.novels2	predicted associations for the novel speices of tree2

Note

Covariates that apply to both species sets (e.g., sampling site) should be supplied in the covariate matrix of the set with the most species.

Bootstrapping CIs is slow due to the function `optim` used to estimate the model parameters. See appendix A in Ives and Godfray (2006) for a discussion about this bootstrapping procedure

If `pblmpredict=TRUE` the function does not first remove each species in turn when predicting the associations of the original species as is done in Ives and Godfray (2006).

Author(s)

Matthew Helmus <mrhelmus@gmail.com>

References

Ives A.R. & Godfray H.C. (2006) Phylogenetic analysis of trophic associations. *The American Naturalist*, 168, E1-E14

Blomberg S.P., Garland T.J. & Ives A.R. (2003) Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717-745

Examples

```
#load example data from Ives & Godfray (2006)
data(IvesGodfray)

#net attack rate of parasitoid on host eq.4 in Ives and Godfray
A<-(-1*log(1-IvesGodfray$interactions[,-28]/t(IvesGodfray$interactions[28])))

# Make tips of the phylogenetic trees contemporaneous by extending tips
p<-dim(IvesGodfray$host)[1]
q<-dim(IvesGodfray$parasitoid)[1]
host.cov.scaled<-IvesGodfray$host
```

```

para.cov.scaled<-IvesGodfray$parasitoid
for (i in 1:p)
{
  host.cov.scaled[i,i]<-max(host.cov.scaled)
}
for (i in 1:q)
{
  para.cov.scaled[i,i]<-max(para.cov.scaled)
}

# scale covariance matrices (this reduces numerical problems caused by
# determinants going to infinity or zero)
host.cov.scaled<-host.cov.scaled/(det(as.matrix(host.cov.scaled))^(1/p))
para.cov.scaled<-para.cov.scaled/(det(as.matrix(para.cov.scaled))^(1/q))

pblm.A <- pblm(sqrt(A),tree1=host.cov.scaled,tree2=para.cov.scaled)
pblm.A$signal.strength #compare to Ives and Godfray (2006) Table 1 Line 1
pblm.A$MSE

```

pcd

Phylogenetic Community Dissimilarity

Description

Pairwise dissimilarity in phylogenetic community composition that is partitioned into a nonphylogenetic and a phylogenetic component.

Usage

```
pcd(comm, tree, PSVmncd=NULL, PSVpool=NULL, reps=10^4)
```

Arguments

comm	Community data matrix
tree	Object of class phylo or a phylogenetic covariance matrix
PSVmncd	Vector of null mean conditional <i>phylogenetic species variability</i> (<i>PSV</i>) values
PSVpool	The standard, unconditional <i>PSV</i> calculated for the species pool
reps	The number of random draws from the species pool used to produce PSVmncd

Details

Phylogenetic community dissimilarity (*PCD*) is the pairwise differences between communities derived by asking how much of the variance among species in the values of a hypothetical nonselected trait in one community can be predicted by the known trait values of species in another community. *PCD* is partitioned into a nonphylogenetic component that reflects shared species between communities (*PCDc*) and a phylogenetic component that reflects the evolutionary relationships among nonshared species (*PCDp*). In order to compare communities that vary in species richness, the

metric is standardized under the assumption that the species in communities are selected at random from the species pool. The analyses here define the species pool as the list of all species in the set of communities in `comm`, but the species pool can be defined under any hypothesis of community assembly either by manipulating the code or inputting a user defined `PSVmncd` and `PSVpool`.

Value

The function returns a list with items:

<code>PCD</code>	A square matrix of <i>PCD</i> values
<code>PCDc</code>	A square matrix of <i>PCDc</i> values
<code>PCDp</code>	A square matrix of <i>PCDp</i> values
<code>PSVmncd</code>	A vector of null mean conditional <i>PSV</i> values used to calculate <i>PCD</i>
<code>PSVpool</code>	The unconditional <i>PSV</i> of the species pool used to calculate <i>PCD</i>

Note

The sampling procedure used to standardize *PCD* and produce `PSVmncd` and `PSVpool` can be slow.

Author(s)

Anthony Ives <arives@wisc.edu> and Matthew Helmus <mrhelmus@gmail.com>

References

Ives A.R. & Helmus M.R. (2010). Phylogenetic metrics of community similarity. *The American Naturalist*, 176, E128-E142.

See Also

[psv](#), [phylosor](#), [unifrac](#)

Examples

```
data(phylocom)
pcd(phylocom$sample, phylocom$phylo)
```

pd *Calculate Faith's Phylogenetic Diversity*

Description

Calculate the sum of the total phylogenetic branch length for one or multiple samples.

Usage

```
pd(samp, tree, include.root=TRUE)
```

Arguments

samp	Community data matrix
tree	A phylo tree object
include.root	Should the root node be included in all PD calculations (default = TRUE)

Value

Returns a dataframe of the PD and species richness (SR) values for all samples

Warning

If the root is to be included in all calculations (`include.root=TRUE`), the PD of all samples will include the branch length connecting taxa in those samples and the root node of the supplied tree. The root of the supplied tree may not be spanned by any taxa in the sample. If you want the root of your tree to correspond to the most recent ancestor of the taxa actually present in your sample, you should prune the tree before running `pd`:

```
prunedTree <- prune.sample(sample, tree)
```

Note

The data sets need not be species-community data sets but may be any sample data set with an associated phylogeny. PD is not statistically independent of species richness, it positively correlates with species richness across samples. The function [ses.pd](#) compares observed PD to the values expected under various randomizations and allows a way to standardize for unequal richness across samples.

If the root is to be included in all calculations of PD (`include.root=TRUE`), the tree must be rooted. Single-species samples will be assigned a PD value equal to the distance from the root to the present.

If the root is not included in all calculations by default (`include.root=FALSE`), the tree need not be rooted, but in the case of single-species samples the PD will be equal to NA and a warning will be issued.

Author(s)

Matthew Helmus <mrhasmus@gmail.com>, Jonathan Davies <davies@nceas.ucsb.edu>, Steven Kembel <steve.kembel@gmail.com>

References

Faith D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1-10.

See Also

[psr](#), [ses.pd](#)

Examples

```
data(phylocom)
pd(phylocom$sample, phylocom$phylo)
```

phyEstimate

Phylogenetic estimation of traits for unobserved taxa

Description

Uses phylogenetic ancestral state reconstruction to estimate trait values for unobserved taxa.

Usage

```
phyEstimate(phy, trait, method="pic", ...)
phyEstimateDisc(phy, trait, best.state=TRUE, cutoff=0.5, ...)
```

Arguments

phy	phylo object
trait	vector or data.frame containing trait values
method	ancestral state estimation method used by ace (default="pic")
best.state	estimate best-supported trait state for discrete variables? (default=TRUE)
cutoff	support cutoff required to declare a best.state
...	Additional arguments passed to ace

Details

These functions use phylogenetic ancestral state estimation to infer trait values for novel taxa on a phylogenetic tree, for continuous (`phyEstimate`) and discrete (`phyEstimateDisc`) traits.

The required input is a phylogenetic tree object plus a vector or data.frame containing estimated trait values for a subset of the taxa in the phylogenetic tree. Trait values for taxa that are present in the tree but not the trait data will be estimated using ancestral state estimation (Garland and Ives 2000). Briefly, for each taxon present in the tree but not the trait data, the phylogeny is rerooted at the most recent common ancestor of the novel taxon and the rest of the phylogeny, and the trait value of the novel taxon is estimated from the reconstructed trait value at the root of the rerooted phylogeny.

For `phyEstimateDisc`, the state with the highest support will be reported if argument `best.state=TRUE`. If the best-supported state's support is less than the specified `cutoff`, no best state is reported and a NA value will be returned.

Value

phyEstimate produces a data frame with columns:

est Estimated trait value
se Standard error of estimated trait value

phyEstimateDisc produces a data frame with columns:

states 1..N A column with statistical support is produced for each discrete trait state
estimated.state If best.state=TRUE, a column with the state with the highest support
estimated.state.support Statistical support for the state with the highest support

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

T. Garland Jr., and A.R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155:346364.

S.W. Kembel, M. Wu, J.A. Eisen, and J.L. Green. 2012. Incorporating 16S gene copy number information improves estimates of microbial diversity and abundance. *PLoS Computational Biology* 8(10):e1002743.

Examples

```
#generate random phylogeny
randtree <- rcoal(50)
#simulate trait evolution for a subset of taxa on phylogeny
randtraits <- sample(rTraitCont(randtree, sigma=10, root.value=100), 40)
#estimate trait values for "missing" taxa using PIC method
phyEstimate(randtree, randtraits, method="pic")
```

phylocom

Phylocom default data

Description

Phylogeny, community and trait data from the Phylocom 4.0 distribution

Usage

data(phylocom)

Format

A list with three elements:

- phylo Phylogenetic tree (an object of class phylo)
- sample Community data (a data.frame with samples in rows and species in columns)
- traits Trait data (a data.frame with species in rows and traits in columns)

Source

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

phylosignal	<i>Measure phylogenetic signal</i>
-------------	------------------------------------

Description

Calculates K statistic of phylogenetic signal as well as P-value based on variance of phylogenetically independent contrasts relative to tip shuffling randomization.

Usage

```
phylosignal(x, phy, reps = 999, checkdata=TRUE, ...)
```

Arguments

x	Trait vector (same order as phy\$tip.label)
phy	phylo object
reps	Number of randomizations
checkdata	Check for match between trait and phylogeny taxa labels using match.phylo.data? (default=TRUE)
...	Additional arguments passed to pic

Value

Data frame with columns:

K	K statistic
PIC.variance	Mean observed PIC variance
PIC.variance.P	P-value of observed vs. random variance of PICs
PIC.variance.z	Z-score of observed vs. random variance of PICs

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Blomberg, S. P., and T. Garland, Jr. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* 15:899-910.

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

See Also

[Kcalc](#)

Examples

```
randtree <- rcoal(20)
randtraits <- rTraitCont(randtree)
phylosignal(randtraits[randtree$tip.label],randtree)
```

phylosor

Phylogenetic index of beta-diversity PhyloSor

Description

Fraction of branch-length shared between two communities

Usage

```
phylosor(samp, tree)
```

Arguments

samp	Community data matrix
tree	Object of class phylo - a rooted phylogeny

Value

A distance object of the PhyloSor index of similarity between communities, the fraction of PD (branch-length) shared between two samples

Warning

The phylosor of all samples will include the branch length connecting taxa in those samples and the root of the supplied tree. The root of the supplied tree may not be spanned by any taxa in the sample. If you want the root of your tree to correspond to the most recent ancestor of the taxa actually present in your sample, you should prune the tree before running phylosor:

```
prunedTree <- prune.sample(sample, tree)
```

Note

The root of the supplied tree is included in calculations of PhyloSor. The supplied tree must be rooted. Single-species samples will be assigned a PD value equal to the distance from the root to the present.

Author(s)

Helene Morlon <morlon.helene@gmail.com> and Steven Kembel <steve.kembel@gmail.com>

References

Bryant, J.B., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J., Green, J.L. 2008. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences 105 Supplement 1: 11505-11511

See Also

[phylosor.rnd, pd](#)

Examples

```
data(phylocom)
phylosor(phylocom$sample, phylocom$phylo)
```

phylosor.rnd	<i>Null PhyloSor values of phylogenetic beta-diversity</i>
--------------	--

Description

PhyloSor values obtained by randomization for different choices of null models

Usage

```
phylosor.rnd(samp, tree, cstSor=TRUE, null.model=c("taxa.labels",
  "frequency", "richness", "independentswap", "trialswap"),
  runs=999, iterations=1000)
```

Arguments

samp	Community data matrix
tree	Object of class phylo - a rooted phylogeny
cstSor	TRUE if the Sorensen similarity should be kept constant across communities. FALSE otherwise
null.model	Null model to use (see Details section)
runs	Number of randomizations
iterations	Number of iterations to use for each randomization (for independent swap and trial null models)

Details

Currently implemented null models (arguments to null.model):

taxa.labels Shuffle community data matrix labels. Maintains species richness in each community and species shared between communities. Should be used with cstSor=TRUE

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency). Does not maintain species richness in communities nor species shared between communities. Can only be used with cstSor=FALSE

richness With cstSor=TRUE: For each pair of community, maintains species richness in each community and species shared between communities. Sample in the species pool with equal probability; With cstSor=FALSE: Maintains species richness in each community, does not maintain species shared between communities. Sample in the species pool with equal probability

independentswap Randomize community data matrix with the independent swap algorithm (Gotelli 2000) maintaining species occurrence frequency and sample species richness. Can only be used with cstSor=FALSE

trialswap Randomize community data matrix with the trial-swap algorithm (Miklos & Podani 2004) maintaining species occurrence frequency and sample species richness. Can only be used with cstSor=FALSE

Value

A list of length the number of runs. Each element of the list is a distance matrix containing the PhyloSor values of phylogenetic beta-diversity obtained by randomization

Author(s)

Helene Morlon <morlon.helene@gmail.com> and Steven Kembel <steve.kembel@gmail.com>

References

Bryant, J.B., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J., Green, J.L. 2008. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences 105 Supplement 1: 11505-11511

See Also

[phylosor](#), [randomizeMatrix](#)

Examples

```
data(phylocom)
phylosor.rnd(phylocom$sample,phylocom$phylo,cstSor=TRUE,null.model="richness",runs=5)
```

phylostruct	<i>Permutations to Test for Phylogenetic Signal in Community Composition</i>
-------------	--

Description

Randomize sample/community data matrices to create null distributions of given metrics

Usage

```
phylostruct(samp, tree, env=NULL, metric=c("psv", "psr", "pse", "psc", "sppregs"),
  null.model=c("frequency", "richness", "independentswap", "trialswap"),
  runs=100, it=1000, alpha=0.05, fam="binomial")
```

Arguments

samp	community data matrix, species as columns, communities as rows
tree	phylo tree object or a phylogenetic covariance matrix
env	environmental data matrix
metric	if metric="psv", "psr", "pse", or "psc" compares the observed mean of the respective metric to a null distribution at a given alpha; if metric="sppregs" compares the three correlations produced by sppregs to null distributions
null.model	permutation procedure used to create the null distribution, see randomizeMatrix
runs	the number of permutations to create the distribution, a rule of thumb is (number of communities)/alpha
it	the number of swaps for the independent and trial-swap null models, see randomizeMatrix
alpha	probability value to compare the observed mean/correlations to a null distribution
fam	as in sppregs

Details

The function creates null distributions for the [psd](#) set of metrics and for the correlations of [sppregs](#) from observed community data sets.

Value

metric	metric used
null.model	permutation used
runs	number of permutations
it	number of swaps if applicable
obs	observed mean value of a particular metric or the three observed correlations from sppregs

mean.null mean(s) of the null distribution(s)

quantiles.null quantiles of the null distribution(s) to compare to obs; determined by alpha

phylo.structure
 if obs less than (alpha/2), phylo.structure="underdispersed"; if obs greater
 than (1-alpha/2), phylo.structure="overdispersed"; otherwise phylo.structure="random"
 and NULL if metric="sppregs"

nulls null values of the distribution(s)

Author(s)

Matthew Helmus <mrhelmus@gmail.com>

References

Helmus M.R., Bland T.J., Williams C.K. & Ives A.R. (2007a) Phylogenetic measures of biodiversity. *American Naturalist*, 169, E68-E83

Helmus M.R., Savage K., Diebel M.W., Maxted J.T. & Ives A.R. (2007b) Separating the determinants of phylogenetic community structure. *Ecology Letters*, 10, 917-925

Gotelli N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, 81, 2606-2621

See Also

[psd](#), [sppregs](#), [randomizeMatrix](#)

prune.sample

Prune tree to match community data or trait data

Description

Prune a phylogenetic tree to include only species present in a community data set or with non-missing trait data

Usage

```
prune.sample(samp, phylo)
prune.missing(x, phylo)
```

Arguments

phylo	phylo object
samp	Community data matrix
x	Vector of trait data

Value

Returns a pruned phylo object

Author(s)

Steven Kembel <steve.kembel@gmail.com>

 psd

Phylogenetic Species Diversity Metrics

Description

Calculate the bounded phylogenetic biodiversity metrics: phylogenetic species variability, richness, evenness and clustering for one or multiple samples.

Usage

```
psv(samp, tree, compute.var=TRUE, scale.vcv=TRUE)
psr(samp, tree, compute.var=TRUE, scale.vcv=TRUE)
pse(samp, tree, scale.vcv=TRUE)
psc(samp, tree, scale.vcv=TRUE)
psd(samp, tree, compute.var=TRUE, scale.vcv=TRUE)
psv.spp(samp, tree)
```

Arguments

samp	Community data matrix
tree	A phylo tree object or a phylogenetic covariance matrix
compute.var	Computes the expected variances for PSV and PSR for each community
scale.vcv	Scale the phylogenetic covariance matrix to bound the metric between 0 and 1

Details

Phylogenetic species variability (PSV) quantifies how phylogenetic relatedness decreases the variance of a hypothetical unselected/neutral trait shared by all species in a community. The expected value of PSV is statistically independent of species richness, is one when all species in a sample are unrelated (i.e., a star phylogeny) and approaches zero as species become more related. PSV is directly related to mean phylogenetic distance, except except calculated on a scaled phylogenetic covariance matrix. The expected variance around PSV for any sample of a particular species richness can be approximated. To address how individual species contribute to the mean PSV of a data set, the function `psv.spp` gives signed proportions of the total deviation from the mean PSV that occurs when all species are removed from the data set one at a time. The absolute values of these “species effects” tend to positively correlate with species prevalence.

Phylogenetic species richness (PSR) is the number of species in a sample multiplied by PSV. It can be considered the species richness of a sample after discounting by species relatedness. The

value is maximum at the species richness of the sample, and decreases towards zero as relatedness increases. The expected variance around PSR for any sample of a particular species richness can be approximated.

Phylogenetic species evenness (PSE) is the metric PSV modified to incorporate relative species abundances. The maximum attainable value of PSE (i.e., 1) occurs only if species abundances are equal and species phylogeny is a star. PSE essentially grafts each individual of a species onto the tip of the phylogeny of its species with branch lengths of zero.

Phylogenetic species clustering (PSC) is a metric of the branch tip clustering of species across a sample's phylogeny. As PSC increases to 1, species are less related to one another the tips of the phylogeny. PSC is directly related to mean nearest neighbor distance.

Value

Returns a dataframe of the respective phylogenetic species diversity metric values

Note

These metrics are bounded either between zero and one (PSV, PSE, PSC) or zero and species richness (PSR); but the metrics asymptotically approach zero as relatedness increases. Zero can be assigned to communities with less than two species, but conclusions drawn from assigning communities zero values need be carefully explored for any data set. The data sets need not be species-community data sets but may be any sample data set with an associated phylogeny.

Author(s)

Matthew Helmus <mrhelmus@gmail.com>

References

Helmus M.R., Bland T.J., Williams C.K. & Ives A.R. (2007) Phylogenetic measures of biodiversity. *American Naturalist*, 169, E68-E83

See Also

[mpd](#), [mnnd](#), [specaccum](#), [psr](#)

Examples

```
data(phylocom)
psd(phylocom$sample, phylocom$phylo)
```

randomizeMatrix	<i>Null models for community data matrix randomization</i>
-----------------	--

Description

Various null models for randomizing community data matrices

Usage

```
randomizeMatrix(samp, null.model = c("frequency", "richness",  
  "independentswap", "trialswap"), iterations = 1000)
```

Arguments

samp	Community data matrix
null.model	Null model to use (see Details section for description)
iterations	Number of independent or trial-swaps to perform

Details

Currently implemented null models (arguments to null.model):

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

independentswap Randomize community data matrix with the independent swap algorithm (Gotelli 2000) maintaining species occurrence frequency and sample species richness

trialswap Randomize community data matrix with the trial-swap algorithm (Miklos & Podani 2004) maintaining species occurrence frequency and sample species richness

Value

Randomized community data matrix

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621
Miklos I. & Podani J. 2004. Randomization of presence-absence matrices: Comments and new algorithms. *Ecology* 85: 86-92.

Examples

```
data(phylocom)
randomizeMatrix(phylocom$sample, null.model="richness")
```

raoD	<i>Rao's quadratic entropy</i>
------	--------------------------------

Description

Calculates Rao's quadratic entropy, a measure of within- and among-community diversity taking species dissimilarities into account

Usage

```
raoD(comm, phy=NULL)
```

Arguments

comm	Community data matrix
phy	Object of class phylo - an ultrametric phylogenetic tree (optional)

Details

Rao's quadratic entropy (Rao 1982) is a measure of diversity in ecological communities that can optionally take species differences (e.g. phylogenetic dissimilarity) into account. This method is conceptually similar to analyses of genetic diversity among populations (Nei 1973), but instead of diversity of alleles among populations, it measures diversity of species among communities.

If no phylogeny is supplied, Dkk is equivalent to Simpson's diversity (probability that two individuals drawn from a community are from different taxa), Dkl is a beta-diversity equivalent of Simpson's diversity (probability that individuals drawn from each of two communities belong to different taxa), and H is Dkl standardized to account for within-community diversity.

If an ultrametric phylogeny is supplied, Dkk is equivalent to the mean pairwise phylogenetic distance (distance to MRCA) between two individuals drawn from a community, Dkl is the mean pairwise phylogenetic distance between individuals drawn from each of two communities, and H is Dkl standardized to account for within-community diversity.

$$D[kl] = \text{sum}(t[ij] * x[ki] * x[lj])$$

where $x[ki]$ is the relative abundance of taxon i in community k and $t[ij]$ is a matrix of weights for all pairs of taxa i,j . Without a phylogeny, when $i=j$, $t[ij]=0$, otherwise $t[ij]=1$. With a phylogeny, $t[ij]$ is the phylogenetic distance to MRCA for taxa i,j .

$$H[kl] = D[kl] - (D[kk] + D[l]) / 2$$

Alpha, beta and total measure the average diversity within, among, and across all communities based on Dkk and H values taking variation in number of individuals per community into account. A Fst-like measure is calculated by dividing beta by the total diversity across all samples.

Value

A list of results

Dkk	Within-community diversity
Dk1	Among-community diversity
H	Among-community diversities excluding within-community diversity
total	Total diversity across all samples
alpha	Alpha diversity - average within-community diversity
beta	Beta diversity - average among-community diversity
Fst	Beta diversity / total diversity

Warning

Alpha, beta, and total diversity components and Fst should not be interpreted as a measure of relative differentiation among versus within communities. See Jost (2007) for a detailed description of this problem. Hardy and Jost (2008) suggest Fst can be interpreted as 'local species identity excess' or 'local phylogenetic similarity excess' rather than as a measure of among-community differentiation.

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

- Hardy, O.J., and Jost. L. 2008. Interpreting and estimating measures of community phylogenetic structuring. *J. Ecol.* 96:849-852.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427-2439.
- Nei, M. 1973. Analysis of gene diversity in sub-divided populations. *Proceedings of the National Academy of Sciences of the USA* 70:3321-3323.
- Rao, C.R. 1982. Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* 21:2443.
- Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

See Also

[mpd](#), [comdist](#)

Examples

```
data(phylocom)
raoD(phylocom$sample)
raoD(phylocom$sample, phylocom$phylo)
```

readsample	<i>Read Phylocom sample</i>
------------	-----------------------------

Description

Reads a Phylocom sample file and converts to a community data matrix

Usage

```
readsample(filename = "")
```

Arguments

filename	Phylocom sample file path
----------	---------------------------

Value

Community data matrix

Author(s)

Steven Kembel <skembel> and Cam Webb <cwebb@oeb.harvard.edu>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

sample2matrix	<i>Convert Phylocom sample to community data matrix</i>
---------------	---

Description

Convert a Phylocom database-format sample to community data matrix.

Usage

```
sample2matrix(x)
```

Arguments

x	Phylocom sample formatted data frame, a data frame with three columns: <ul style="list-style-type: none">• Column 1 Community name• Column 2 Species abundance• Column 3 Species name
---	---

Author(s)

Steven Kembel <steve.kembel@gmail.com> and Cam Webb <cwebb@oeb.harvard.edu>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

 ses.mntd

Standardized effect size of MNTD

Description

Standardized effect size of mean nearest taxon distances in communities. When used with a phylogenetic distance matrix, equivalent to -1 times the Nearest Taxon Index (NTI).

Usage

```
ses.mntd(samp, dis, null.model = c("taxa.labels", "richness", "frequency",
  "sample.pool", "phylogeny.pool", "independentswap", "trialswap"),
  abundance.weighted=FALSE, runs = 999, iterations = 1000)
```

Arguments

samp	Community data matrix
dis	Distance matrix (generally a phylogenetic distance matrix)
null.model	Null model to use (see Details section for description)
abundance.weighted	Should mean nearest taxon distances for each species be weighted by species abundance? (default = FALSE)
runs	Number of randomizations
iterations	Number of iterations to use for each randomization (for independent swap and trial null models)

Details

The metric used by this function has also been referred to as MNND (mean nearest neighbour distance), and the function was named `ses.mnnd` in *picante* versions < 0.7.

Currently implemented null models (arguments to `null.model`):

taxa.labels Shuffle distance matrix labels (across all taxa included in distance matrix)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

- frequency** Randomize community data matrix abundances within species (maintains species occurrence frequency)
- sample.pool** Randomize community data matrix by drawing species from pool of species occurring in at least one community (sample pool) with equal probability
- phylogeny.pool** Randomize community data matrix by drawing species from pool of species occurring in the distance matrix (phylogeny pool) with equal probability
- independentswap** Randomize community data matrix with the independent swap algorithm (Gotelli 2000) maintaining species occurrence frequency and sample species richness
- trialswap** Randomize community data matrix with the trial-swap algorithm (Miklos & Podani 2004) maintaining species occurrence frequency and sample species richness

Value

A data frame of results for each community

ntaxa	Number of taxa in community
mntd.obs	Observed MNTD in community
mntd.rand.mean	Mean MNTD in null communities
mntd.rand.sd	Standard deviation of MNTD in null communities
mntd.obs.rank	Rank of observed MNTD vs. null communities
mntd.obs.z	Standardized effect size of MNTD vs. null communities (= (mntd.obs - mntd.rand.mean) / mntd.rand.sd, equivalent to -NTI)
mntd.obs.p	P-value (quantile) of observed MNTD vs. null communities (= mntd.obs.rank / runs + 1)
runs	Number of randomizations

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

See Also

[mntd](#), [randomizeMatrix](#)

Examples

```
data(phylocom)
ses.mntd(phylocom$sample, cophenetic(phylocom$phylo), null.model="taxa.labels")
```

ses.mpd

*Standardized effect size of MPD***Description**

Standardized effect size of mean pairwise distances in communities. When used with a phylogenetic distance matrix, equivalent to -1 times the Nearest Relative Index (NRI).

Usage

```
ses.mpd(samp, dis, null.model = c("taxa.labels", "richness", "frequency", "sample.pool",
    "phylogeny.pool", "independentswap", "trialswap"),
    abundance.weighted = FALSE, runs = 999, iterations = 1000)
```

Arguments

samp	Community data matrix
dis	Distance matrix (generally a phylogenetic distance matrix)
null.model	Null model to use (see Details section for description)
abundance.weighted	Should mean nearest taxon distances for each species be weighted by species abundance? (default = FALSE)
runs	Number of randomizations
iterations	Number of iterations to use for each randomization (for independent swap and trial null models)

Details

Currently implemented null models (arguments to null.model):

taxa.labels Shuffle distance matrix labels (across all taxa included in distance matrix)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency)

sample.pool Randomize community data matrix by drawing species from pool of species occurring in at least one community (sample pool) with equal probability

phylogeny.pool Randomize community data matrix by drawing species from pool of species occurring in the distance matrix (phylogeny pool) with equal probability

independentswap Randomize community data matrix with the independent swap algorithm (Gotelli 2000) maintaining species occurrence frequency and sample species richness

trialswap Randomize community data matrix with the trial-swap algorithm (Miklos & Podani 2004) maintaining species occurrence frequency and sample species richness

Value

A data frame of results for each community

ntaxa	Number of taxa in community
mpd.obs	Observed mpd in community
mpd.rand.mean	Mean mpd in null communities
mpd.rand.sd	Standard deviation of mpd in null communities
mpd.obs.rank	Rank of observed mpd vs. null communities
mpd.obs.z	Standardized effect size of mpd vs. null communities (= (mpd.obs - mpd.rand.mean) / mpd.rand.sd, equivalent to -NRI)
mpd.obs.p	P-value (quantile) of observed mpd vs. null communities (= mpd.obs.rank / runs + 1)
runs	Number of randomizations

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

See Also

[mpd, randomizeMatrix](#)

Examples

```
data(phylocom)
ses.mpd(phylocom$sample, cophenetic(phylocom$phylo), null.model="taxa.labels")
```

ses.pd

Standardized effect size of PD

Description

Standardized effect size of phylogenetic diversity (Faith's PD) in communities.

Usage

```
ses.pd(samp, tree, null.model = c("taxa.labels", "richness", "frequency",
  "sample.pool", "phylogeny.pool", "independentswap", "trialswap"),
  runs = 999, iterations = 1000, include.root=TRUE)
```

Arguments

samp	Community data matrix
tree	Phylogeny (phylo object)
null.model	Null model to use (see Details section for description)
runs	Number of randomizations
iterations	Number of iterations to use for each randomization (for independent swap and trial null models)
include.root	Include distance to root node in calculation of PD (see documentation in pd function)

Details

Currently implemented null models (arguments to null.model):

taxa.labels Shuffle taxa labels across tips of phylogeny (across all taxa included in phylogeny)

richness Randomize community data matrix abundances within samples (maintains sample species richness)

frequency Randomize community data matrix abundances within species (maintains species occurrence frequency)

sample.pool Randomize community data matrix by drawing species from pool of species occurring in at least one community (sample pool) with equal probability

phylogeny.pool Randomize community data matrix by drawing species from pool of species occurring in the phylogeny (phylogeny pool) with equal probability

independentswap Randomize community data matrix with the independent swap algorithm (Gotelli 2000) maintaining species occurrence frequency and sample species richness

trialswap Randomize community data matrix with the trial-swap algorithm (Miklos & Podani 2004) maintaining species occurrence frequency and sample species richness

Value

A data frame of results for each community

ntaxa	Number of taxa in community
pd.obs	Observed PD in community
pd.rand.mean	Mean PD in null communities
pd.rand.sd	Standard deviation of PD in null communities
pd.obs.rank	Rank of observed PD vs. null communities
pd.obs.z	Standardized effect size of PD vs. null communities (= (pd.obs - pd.rand.mean) / pd.rand.sd)
pd.obs.p	P-value (quantile) of observed PD vs. null communities (= mpd.obs.rank / runs + 1)
runs	Number of randomizations

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

Proches, S., Wilson, J.R.U. and Cowling, R.M. 2006. How much evolutionary history in a 10 x 10m plot? Proceedings of Royal Society of London B, Biological Sciences 273:1143-1148.

See Also

[pd](#), [randomizeMatrix](#)

Examples

```
data(phylocom)
ses.pd(phylocom$sample, phylocom$phylo, null.model="taxa.labels", runs=99)
```

specaccum.psr

Phylogenetic Species Richness Sample-Based Rarefaction Curve

Description

Finds a sample-based rarefaction curve for phylogenetic species richness for a set of samples.

Usage

```
specaccum.psr(samp, tree, permutations = 100, method = "random", ...)
```

Arguments

samp	Community data matrix
tree	A phylo tree object or a phylogenetic covariance matrix
permutations	Number of permutations with method method= "random"
method	Species accumulation method, currently only "random" is supported which adds samples in random order.
...	Other parameters to functions

Value

The function returns an object of class "specaccum" with items:

call	Function call.
method	Accumulator method.
sites	Number of sites/samples.
richness	The mean phylogenetic species richness corresponding to number of sites/samples.
sd	The standard deviation of phylogenetic species accumulation curve (or its standard error) estimated from permutations in method = "random".
perm	Permutation results with method = "random" and NULL in other cases. Each column in perm holds one permutation.

Author(s)

Matthew Helmus <mrhasmus@gmail.com> based on the vegan package [specaccum](#) function by Roeland Kindt and Jari Oksanen.

References

Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391

Helmus M.R., Bland T.J., Williams C.K. & Ives A.R. (2007) Phylogenetic measures of biodiversity. *American Naturalist*, 169, E68-E83

See Also

[psr](#), [specaccum](#)

Examples

```
data(phylocom)
accum.sr<-specaccum(phylocom$sample, permutations = 100, method = "random")
plot(accum.sr, col="blue")
points(accum.sr$sites, accum.sr$richness, pch=19, col="blue")

accum.psr<-specaccum.psr(phylocom$sample, phylocom$phylo, permutations = 100, method = "random")
plot(accum.psr, add=TRUE, col = "red")
points(accum.psr$sites, accum.psr$richness, pch=19, col="red")

legend(5,5,legend=c("SR", "PSR"),pch=c(19,19),col=c("blue","red"))
```

species.dist	<i>Species co-occurrence distances</i>
--------------	--

Description

Compute interspecific distances based on patterns of species co-occurrence in communities.

Usage

```
species.dist(x, metric = c("cij", "jaccard", "checkerboard", "doij"))
```

Arguments

x	Community data matrix
metric	Co-occurrence metric to use (see Details section for description)

Details

Currently implemented co-occurrence measures (arguments to metric):

cij Schoener's index of co-occurrence

jaccard Jaccard index of co-occurrence

checkerboard Checkerboard index of co-occurrence

doij DOij index of co-occurrence

Value

A dist object with co-occurrences among all species pairs

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Hardy, O.J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96:914-926.

See Also

[vegdist](#)

sppregs

*Regressions to Separate Phylogenetic Attraction and Repulsion***Description**

Fit regressions on species abundance or presence/absence across communities and calculate phylogenetic correlations

Usage

```
sppregs(samp, env, tree=NULL, fam="gaussian")
sppregs.plot(sppreg, rows=c(1,3), cex.mag=1, x.label="phylogenetic correlations",
             y.label=c("occurrence correlations w/ env", "occurrence correlations wo/ env",
                       "change in correlations"))
```

Arguments

samp	community data matrix, species as columns, communities as rows
env	environmental data matrix
tree	phylo tree object or a phylogenetic covariance matrix
fam	with fam = "gaussian" fits with glm ; with fam = "binomial" fit logistic regressions with Firth's bias-reduction using brglm
sppreg	object from function sppregs
rows	rows = c(1, 3) plots in a row; rows = c(3, 1) in a column
cex.mag	value for cex in par
x.label	x axis labels
y.label	y axis labels

Details

For each species in `samp`, the function fits regressions of species presence/absence or abundances on the environmental variables supplied in `env`; and calculates the $(n^2-n)/2$ pairwise species correlations between the residuals of these fits and pairwise species phylogenetic correlations. The residuals can be thought of as the presence/absence of species across sites/communities after accounting for how species respond to environmental variation across sites. Each set of coefficients can be tested for phylogenetic signal with, for example, the function [phylosignal](#).

The function `sppregs.plot` produces a set of three plots of the correlations of pairwise species phylogenetic correlations versus: the observed pairwise correlations of species across communities, the residual correlations, and the pairwise differences between (i.e., the change in species co-occurrence once the environmental variables are taken into account). The significance of these correlations can be tested via permutation with the function [phylostruct](#).

Value

family	the regression error distribution
residuals	the residuals from each species regression
coefficients	the estimated coefficients from each species regression
std.errors	the standard errors of the coefficients
correlations	correlations of pairwise species phylogenetic correlations between: the observed pairwise correlations of species across communities, the residual correlations, and the pairwise differences between the two
cors.pa	the observed pairwise correlations of species across communities
cors.resid	the residual pairwise correlations of species across communities
cors.phylo	the phylogenetic pairwise correlations among species

Note

The function requires the library [brglm](#) to perform logistic regressions

Author(s)

Matthew Helmus <mrhelmus@gmail.com>

References

Helmus M.R., Savage K., Diebel M.W., Maxted J.T. & Ives A.R. (2007) Separating the determinants of phylogenetic community structure. *Ecology Letters*, 10, 917-925

See Also

[phylostruct](#), [phylosignal](#)

tax.distinctiveness *Taxonomic distinctiveness sensu Vane-Wright or May*

Description

Taxic diversity: Vane-Wright et al., 1991 and May 1990 which accounts for polytomies by counting the number of branches descending from each node that lies on the path from a spp tip to the root (not just counting the number of nodes).

Usage

```
tax.distinctiveness(tree, type = c("Vane-Wright", "May"))
```

Arguments

tree	an object of class phylo
type	specify "Vane-Wright" or "May"

Author(s)

Karen Magnuson-Ford, Will Cornwell, Arne Mooers, Mark Vellend

References

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991). What to protect? - Systematics and the agony of choice. *Biological Conservation*, 55, 235-254.

May, R.M. (1990). Taxonomy as destiny. *Nature*, 347, 129-130.

Mark Vellend, William K. Cornwell, Karen Magnuson-Ford, and Arne Mooers. In press. Measuring phylogenetic biodiversity In: *Biological diversity: frontiers in measurement and assessment*. Edited by Anne Magurran and Brian McGill.

 traitgram

Draw phylogeny with nodes at trait positions

Description

Draws a phylogeny where x position of nodes and tips corresponds to value of a continuous trait variable, and y position corresponds to node depth (i.e. age).

Usage

```
traitgram(x, phy, xaxt = 's', underscore = FALSE, show.names = TRUE,
          show.xaxis.values = TRUE, method = c('ML', 'pic'), ...)
```

Arguments

x	Trait vector (same order as phy\$tip.label, or with taxon names in names)
phy	phylo object
xaxt	x axis default type
underscore	if FALSE remove underscore from taxonomic names
show.names	if TRUE show taxon names across tips of phylogeny
show.xaxis.values	if TRUE show values for trait on x=axis
method	method for calculation of internal trait values. 'ML' = maximum likelihood method; 'pic' = independent contrasts method. pic option can be used when ML fails to converge or otherwise seems to fail to correctly reconstruct ancestral values
...	Additional arguments passed to plot

Value

Plots a traitgram, no values returned.

Author(s)

David Ackerly <dackerly@berkeley.edu>

References

Ackerly, D. D. 2009. Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences USA* 106:19699-19706. doi: 10.1073/pnas.0901635106.

Evans, M. E. K., S. A. Smith, R. S. Flynn, and M. J. Donoghue. 2009. Climate, Niche Evolution, and Diversification of the "bird-cage" Evening Primroses (Oenothera, Sections Anogra and Kleinia). *American Naturalist* 173:225-240.

Examples

```
randtree <- rcoal(20)
randtraits <- rTraitCont(randtree)
traitgram(randtraits,randtree)
traitgram(randtraits,randtree,method='pic')
```

unifrac

Unweighted UniFrac distance between communities

Description

Calculates unweighted UniFrac, a phylogenetic beta diversity metric of the the unique (non-shared) fraction of total phylogenetic diversity (branch-length) between two communities.

Usage

```
unifrac(comm, tree)
```

Arguments

comm	Community data matrix
tree	Object of class phylo - a rooted phylogeny

Value

A dist object of the unweighted UniFrac distances between communities (the unique (non-shared) fraction of total phylogenetic diversity (branch-length) between two communities).

Warning

The UniFrac distance between samples will include the branch length connecting taxa in those samples and the root of the supplied tree. The root of the supplied tree may not be spanned by any taxa in the sample. If you want the root of your tree to correspond to the most recent ancestor of the taxa actually present in your samples, you should prune the tree before running unifrac: `prunedTree <- prune.sample(sample, tree)`

Note

The supplied tree must be rooted. Single-species samples will be assigned a PD value equal to the distance from the root to the present.

Author(s)

Steven Kembel <steve.kembel@gmail.com>

References

Lozupone, C., Hamady, M., and Knight, R. 2006. UniFrac - an online tool for comparing microbial community diversity in a phylogenetic context. *BMC Bioinformatics* 7:371.

See Also

[pd](#)

Examples

```
data(phylocom)
unifrac(phylocom$sample, phylocom$phylo)
```

utility

Picante utility functions

Description

Picante utility functions for tree and data manipulation

Usage

```
df2vec(x, colID=1)
internal2tips(phy, int.node, return.names = FALSE)
node.age(phy)
pic.variance(x, phy, scaled = TRUE)
sortColumns(x)
sortRows(x)
taxaShuffle(x)
tipShuffle(phy)
```

Arguments

phy	phylo object
x	A data.frame, matrix or dist object
colID	Numeric or character ID of column to include
int.node	internal node number
return.names	TRUE or FALSE
scaled	Scale contrasts by branch length

Details

Various utility functions for manipulating trees, data, etc.

Value

df2vec	A named vector
internal2tips	Vector of tips descended from a node
node.age	Phylo object with phylo\$ages vector of node ages corresponding to phylo\$edge
pic.variance	Variance of independent contrasts
sortColumns	A data.frame or matrix with columns sorted by name
sortRows	A data.frame or matrix with rows sorted by name
taxaShuffle	Matrix with taxa names shuffled
tipShuffle	Phylo object with taxa names shuffled

Author(s)

Steven Kembel <steve.kembel@gmail.com>, Peter Cowan <cdc@berkeley.edu>, David Ackerly <dackerly@berkeley.edu>

writesample

Write a Phylocom community sample file

Description

Write a community data matrix to a Phylocom community sample file

Usage

```
writesample(community, filename = "")
```

Arguments

community	Community data matrix
filename	Filename path

Author(s)

Steven Kembel <steve.kembel@gmail.com> and Cam Webb <cwebb@oeb.harvard.edu>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

`writetraits`*Write a Phylocom traits formatted file*

Description

Write a Phylocom traits formatted file

Usage

```
writetraits(trt, file = "", bin = NULL, sigd = 3)
```

Arguments

<code>trt</code>	Data frame containing trait data
<code>file</code>	Filename path
<code>bin</code>	Vector index of trait columns to be treated as binary
<code>sigd</code>	Significant digits for output

Author(s)

David Ackerly <dackerly@berkeley.edu> and Steven Kembel <steve.kembel@gmail.com>

References

Webb, C.O., Ackerly, D.D., and Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.

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