

# Package ‘phyloclim’

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**Author** Christoph Heibl

**Maintainer** Christoph Heibl <christoph.heibl@gmx.net>

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**Description** This package implements some recently developed methods in phyloclimatic modeling.

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phyloclim-package      *Phyloclimatic data analysis*

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### Description

This package implements some recently developed methods in phyloclimatic modeling.

### Details

Package: phyloclim  
Type: Package  
Version: 0.8.1  
Date: 2011-01-21  
License: GPL (>= 2)

phyloclim is intended to provide methods for the quantification of niche occupancy and niche overlap and combine this data with phylogenetic trees. Niche overlap can be quantified either from profiles of environmental suitability for a given environmental variable (PNO or predicted niche occupancy profiles, see [pno](#)) or from two-dimensional suitability surfaces (environmental niche models (ENMs) or species distribution models (SDMs)) with [niche.overlap](#). Randomization tests for testing the significance of niche overlap in terms of niche identity and niche similarity are available in [niche.equivalency.test](#) and [bg.similarity.test](#). Phylogenetic data can be integrated into comparative methods such as [age.range.correlation](#) and the estimation of ancestral environmental tolerances ([anc.clim](#)), which is a non-parametric approach based on resampling of PNO profiles. The functions in phyloclim are in an early stage of development, so they should be used with care! Any feedback is welcome!

### Author(s)

Maintainer: Christoph Heibl <[christoph.heibl@gmx.net](mailto:christoph.heibl@gmx.net)>

### See Also

[ape](#)

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adenophylla\_arenaria      *Niche overlap for Oxalis adenophylla and O. arenaria*

---

### Description

Objects `equ` and `sim` contain the results of the [niche.equivalency.test](#) and the [bg.similarity.test](#) (Warren et al. 2008) for *Oxalis adenophylla* and *O. arenaria* from section *Palmatifoliae*.

### Usage

```
data(equ)
data(equ)
```

### Format

A list containing five elements:

**test** Name of the test.

**spec** Names of the two species compared.

**D** Measure of niche overlap D based on Schoeners D together with p-values.

**I** Measure of niche overlap I based on Hellinger distances together with p-values.

**null.distribution** Null distributions of D and I derived from randomization.

### Source

C. Heibl, unpublished data.

### References

Warren, D., R.E. Glor, & M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. **62**: 2868-2883.

### Examples

```
# plot results of niche equivalency test
data(equ)
plotNicheEquivalency(equ)

# plot results of background similarity test
data(sim)
plotBackgroundSimilarity(sim)
```

---

age.range.correlation *Age-Range Correlation*

---

### Description

This function can be used to test for phylogenetic signal in patterns of niche overlap (Warren et al., 2008) based on the age-range correlation (ARC) as implemented by Turelli & Fitzpatrick (2006).

### Usage

```
age.range.correlation(phy, overlap, tri = "upper", n = 1000)
```

**Arguments**

phy	An object of class "phylo", which must be ultrametric.
overlap	A matrix of class "niolap", containing pairwise measures of niche overlap as produced by <code>niche.overlap</code> .
tri	Either "upper" or "lower", indicating which triangle of the overlap matrix to use (see <code>niche.overlap</code> ).
n	An integer giving the number of iterations for the Monte Carlo resampling procedure.

**Details**

In age-range correlation (ARC; *sensu* Fitzpatrick & Turelli 2006), phylogenetic relationships are taken into account when computing average range (or niche) overlap between two clades at node  $i$  by

$$\bar{o}_i = \sum_{j \in \text{Clade1}} \sum_{k \in \text{Clade2}} \left(\frac{1}{2}\right)^{n_{jk}-1} o_{jk}$$

where the double sum is over all species in the two clades,  $o(jk)$  denotes the overlap between species  $j$  and  $k$ , and  $n(jk)$  is the number of nodes separating the two species on the phylogeny. Plotting  $\bar{o}_i$  against node ages depicts the ARC for a given clade. Slopes and intercept derived from a linear model can be used to characterize speciation mode (allopatric versus sympatric) or niche evolution (conservatism versus flexibility) in the clade (see Fitzpatrick & Turelli [2006] and Warren et al. [2008], respectively).

The significance of the ARC is assessed via Monte Carlo simulation by random permutation of the overlap matrix to estimate the distribution of slope and intercept under the null hypothesis of no phylogenetic signal.

**Value**

A list of four elements:

age.range.correlation	A matrix with age and average overlap for each node.
linear.regression	A linear model of mean niche (or range)overlap versus node age.
sig	Significance of intercept and slope derived by randomization. $f$ is the fraction of randomized datasets with intercept and slopes greater than the observed data. p-values are calculated as $2 * \min(f, 1 - f)$ .
MonteCarlo.replicates	A matrix containing intercepts and slopes of randomized datasets.

**Author(s)**

Christoph Heibl

## References

Fitzpatrick, B.M & Turelli, M. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* **60**: 601-615.

Warren, D., R.E. Glor, & M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**: 2868-2883.

## See Also

[niche.overlap](#)

## Examples

```
# load PNOs for Oxalis sect. Palmatifoliae ...
data(palmatifoliae_pno)

# ... and calculate niche overlap between species
no <- niche.overlap(palmatifoliae_pno$AnnualMeanTemperature)

# load phylogeny and PNOs of Oxalis sect. Palmatifoliae
data(palmatifoliae_tree)

# age-range correlation
x <- age.range.correlation(phy = palmatifoliae_tree, overlap = no,
n = 100)

# plot average niche overlap versus node age
plot(x$age.range.correlation)

# add a regression line
abline(x$linear.regression$coefficients)

# add regression lines from Monte Carlo randomization
apply(x$MonteCarlo.replicates, 1, abline, lwd = 0.2, col = "grey50")
```

---

anc.clim

*Estimation of Ancestral Climatic Tolerances*

---

## Description

This function implements a nonparametric approach to estimate ancestral climatic tolerances proposed by Evans et al. (2009), using [ace](#) from the ape package.

## Usage

```
anc.clim(target, posterior = NULL, pno, n = 100, method = "GLS")
```

**Arguments**

target	An object of class "phylo"; a best estimate (e.g., ML estimate) of topology on which to summarize mean estimated climatic tolerances, must be ultrametric.
posterior	An object of class "multiPhylo" containing a sample of ultrametric trees from the posterior distribution of a Bayesian tree search to be used for reconstruction of ancestral climatic tolerances. posterior = NULL (the default) means that reconstruction uses target instead.
pno	A data frame containing predicted niche occupancy (PNO) profiles, produced e.g. with <a href="#">pno</a> .
n	An integer: The PNO profile given by pno argument will be resamples n times.
method	A character string specifying the method used for estimation. Two choices are possible: "ML" or "GLS" (see <a href="#">ace</a> for details).

**Value**

A list containing three elements:

tree	An object of class "phylo", the target tree used in the estimation.
means	A vector containing the means of estimated ancestral climatic tolerances. The elements of means are in the same order as node numbers in element tree.
central.density	A matrix, which for each of the terminal nodes in tree contains the minimum and the maximum of the 80 percent density interval of climatic tolerances (as sampled from the PNO).

**Author(s)**

Christoph Heibl

**References**

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*). *Am. Nat.* **173**: 225-240.

**See Also**

[pno](#), [plotAncClim](#)

**Examples**

```
# load phylogeny and PNOs of Oxalis sect. Palmatifoliae
data(palmatifoliae_tree)
data(palmatifoliae_pno)

# choose summer precipitation for analysis
clim <- palmatifoliae_pno$PrecipitationWarmestQuarter
```

```
# estimate ancestral tolerances
ac <- anc.clim(target = palmatifoliae_tree, pno = clim, n = 100)

# visualize results
plotAncClim(ac, ylab = "Precipitation of warmest quarter (mm)")
```

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descendants

*descendants*


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### Description

This is an internal function not be called by the user.

---

hypothesis.testing

*Niche equivalency and background similarity test*


---

### Description

Hypothesis testing as proposed by Warren et al. (2008) based on the generation of pseudoreplicate datasets. The niche equivalency (or identity) test asks whether the ecological niche models (ENMs) of two species are more different than expected if they are drawn from the same underlying distribution. The background similarity test asks whether ENMs drawn from populations with partially or entirely non-overlapping distributions are any more different from one another than expected by random chance.

### Usage

```
niche.equivalency.test(spec, n, maxent, mx = 2000)
```

```
bg.similarity.test(spec, n, maxent, mx = 2000)
```

### Arguments

spec	A vector of mode character and length = 2 that corresponds to two species names in the sample file (see details).
n	An integer given the number of permutations of the original data.
maxent	A list containing the location of the MAXENT application and its input files (see details).
mx	An integer giving the number of megabytes of memory made available to JAVA.

**Details**

An installation of MAXENT (Phillips et al., 2006; <http://www.cs.princeton.edu/~schapire/maxent/>) is required in order to run `niche.equivalency.test` and `bg.similarity.test`. The `maxent` argument of both functions is a list of four elements:

**app** The path to the MAXENT application.

**samples** The path to a SWD-formatted file with sample points.

**background** The path to a SWD-formatted file with background points.

**projections** The path to a folder containing environmental GIS layers to be used for projection of the MAXENT models.

For an explanation of SWD-formatted (=Samples-With-Data) files and model projection see the MAXENT tutorial.

**Value**

A list containing five elements:

<code>test</code>	Name of the test.
<code>spec</code>	Names of the two species compared.
<code>D</code>	Measure of niche overlap D based on Schoeners D together with p-values.
<code>I</code>	Measure of niche overlap I based on Hellinger distances together with p-values.
<code>null.distribution</code>	Null distributions of D and I derived from randomization.

**Note**

These functions have been developed with MAXENT version 3.3.1. and subsequently updated to work with versions 3.3.2 and 3.3.3

**Author(s)**

Christoph Heibl

**References**

- Phillips, S.J, M. Dudik, & R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* **190**: 231-259.
- Warren, D., R.E. Glor, & M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. **62**: 2868-2883.

**See Also**

[niche.overlap](#)

---

internalFunctions	<i>PHYLOCLIM Internal Functions</i>
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### Description

This is an internal function in PHYLOCHLIM and not intended to be called by the user.

---

niche.overlap	<i>Quantification of Niche Overlap</i>
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---

### Description

This function quantifies the degree of niche overlap using the statistics D and I (as proposed by Warren et al., 2008) based on Schoeners D (Schoener, 1968) and Hellinger Distances (van der Vaart, 1998). Niche overlap can be calculated either from the probability surfaces of entire ecological niche models (Warren et al., 2008) or from single dimensions of the climatic niches (Evans et al., 2009).

### Usage

```
niche.overlap(x)
```

### Arguments

x                    Might take one of the following forms: (1) a data frame containing predicted niche occupancy (PNO) profiles, e.g., as derived by [pno](#); (2) a vector of file-names referencing to probability surfaces saved in ASCII-format with an ArcGIS-compatible header; (3) a list containing probability surfaces of class "asc" (see [import.asc](#)).

### Value

A matrix of class "niolap". The upper triangle contains pairwise comparisons of niche overlap in terms of D, whereas the lower triangle contains values of I.

### Author(s)

Christoph Heibl

## References

- 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*). *Am. Nat.* **173**: 225-240.
- Schoener, T.W. 1968. Anolis lizards in Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704-726.
- Van der Vaart, A.W. 1998. Asymptotic statistics. Cambridge University Press, U.K.
- Warren, D. L., R. E. Glor, & M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**: 2868-2883.

## See Also

[pno](#), [niche.equivalency.test](#), [bg.similarity.test](#), [age.range.correlation](#)

## Examples

```
# load PNOs for Oxalis sect. Palmatifoliae
data(palmatifoliae_pno)

# niche overlap on a annual precipitation gradient:
no <- niche.overlap(palmatifoliae_pno$AnnualPrecipitation)

# upper triangle: based on Schoeners D
# lower triangle: based on Hellinger distances
print(no)
```

---

palmatifoliae\_pno      *PNOs for Oxalis sect. Palmatifoliae*

---

## Description

For 19 bioclimatic variables summarizing temperature and precipitation and five species of *Oxalis*, the suitability or probability of occurrence is given along the environmental gradients.

## Usage

```
data(palmatifoliae_pno)
```

## Format

A list consisting of 19 matrixes. Each matrix corresponds to an environmental variable and contains the predicted niche occupancy profile (PNO) for each species of *Oxalis* sect. *Palmatifoliae*, whereby column 1 of each matrix gives the values of the environmental variable and columns 2-6 give probabilities of occurrence of each species along the environmental gradient in column 1.

## Source

C. Heibl, unpublished data.

**Examples**

```
data(palmatifoliae_pno)
## a list of 19 bioclimatic variables:
names(palmatifoliae_pno)

## minimum temperature during coldest month
mintemp <- palmatifoliae_pno$MinTemperatureColdestMonth

## minimum temperate range occupied by Oxalis sect. Palmatifoliae
range(mintemp[, 1])

## plot PNO profile for minimum temperature
plotPNO(mintemp)
```

---

palmatifoliae\_tree      *Phylogeny of Oxalis sect. Palmatifoliae*

---

**Description**

This is a phylogenetic hypothesis for *Oxalis* sect. *Palmatifoliae* extracted from a relaxed molecular clock model of the phylogeny of Oxalidales based approx. 7500 bp of chloroplast and nuclear markers.

**Usage**

```
data(palmatifoliae_tree)
```

**Format**

object of class "phylo" (see Value section of [read.tree](#))

**Source**

Heibl, C., G. Bahnweg, & S.S. Renner. Arid-adapted *Oxalis* diversity predates environmental heterogeneity in the South American southern cone. Submitted.

**Examples**

```
data(palmatifoliae_tree)

## plot phylogeny
plot(palmatifoliae_tree)
```

---

plotAncClim

*Chronograms with climatic data on the y-axis*


---

### Description

This function can be used to plot the history of climatic tolerance for a clade *sensu* Evans et al. (2009).

### Usage

```
plotAncClim(x, clades = NULL, col, density = TRUE, lwd = 1,
            xspace = c(0, 0.1), ylab = "")
```

### Arguments

x	A list with elements tree, data, and (optional) central.density (see details).
clades	A list containing vectors of tip labels which define the clades to highlight.
col	A vector containing colors for different clades.
density	Logical, if TRUE, the central density intervals for recent species are plotted.
lwd	The line width, a positive number, defaulting to 1.
xspace	A vector of mode numeric; the first element controls the space between tiplabels of different clades, the second element sets the spaces between tiplabels within clades.
ylab	A character string, giving a label for the y-axis, i.e., for the bioclimatic dimension of the plot.

### Details

The main argument x is a list consisting of at least the first two of the following elements: (1) tree is an ultrametric phylogenetic tree stored as object of class phylo; (2) data is an object of class matrix; its columns correspond to bioclimatic variables and its rows correspond to node numbers such as defined by class phylo objects; (3) central.density must only be included if density = TRUE – it is a list, which for every bioclimatic variable, contains a matrix that contains the some minimum and maximum quantile of the respective bioclimatic variable for every tip in the tree.

### Author(s)

Christoph Heibl

### References

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*). *Am. Nat.* **173**: 225-240.

**See Also**

[pno](#), [pno.weighted.mean](#), [anc.clim](#)

**Examples**

```
# load phylogeny and PNOs of Oxalis sect. Palmatifoliae
data(palmatifoliae_tree)
data(palmatifoliae_pno)

# choose summer precipitation for analysis
clim <- palmatifoliae_pno$PrecipitationWarmestQuarter

# estimate ancestral tolerances
ac <- anc.clim(target = palmatifoliae_tree, pno = clim, n = 100)

# visualize results
plotAncClim(ac)
```

---

plotNicheEquivalency *Visualize results of niche equivalency and background similarity tests.*

---

**Description**

This functions plot the estimates of niche overlap D and I together with their expected null distribution based on randomization.

**Usage**

```
plotNicheEquivalency(x)

plotBackgroundSimilarity(x)
```

**Arguments**

x A list with five elements: (1) type of test, (2) species names, (3) D, (4) I, and (5) null distributions as produced by [niche.equivalency.test](#) and [bg.similarity.test](#).

**Author(s)**

Christoph Heibl

**See Also**

[niche.equivalency.test](#), [bg.similarity.test](#), [niche.overlap](#)

**Examples**

```
# plot results of niche equivalency test
data(equ)
plotNicheEquivalency(equ)

# plot results of background similarity test
data(sim)
plotBackgroundSimilarity(sim)

# These results suggest that O. adenophylla and O. arenaria
# differ significantly in their climatic niches, but their niches
# are neither more nor less similar than expected by chance.
```

---

plotPNO

*Plot Predicted Niche Occupancy Profiles*


---

**Description**

This function can be used to plot predicted niche occupancy profiles (PNOs). PNOs can be obtained in a geographical information system by summing the cumulative probabilities of each climatical value for a species distribution model (SDM).

**Usage**

```
plotPNO(x, subset = NULL, thinning = NULL, xlab = NULL,
tail_threshold = 0, wm = FALSE, legend.pos = "topleft")
```

**Arguments**

x	A data frame or matrix with columns corresponding to species and rows corresponding to values along an environmental gradient. The first column contains the environmental variable, the remaining columns probabilities of suitability.
subset	A vector of mode "character" which can be used to restrict the calculation of weighted means to those columns in x whose column names match subset; defaults to NULL.
thinning	An integer that can be used to thin fuzzy PNOs prior to plotting; defaults to NULL.
xlab	A character string given the label for the x-axis.
tail_threshold	A numeric that can be used to cut long tails of PNOs; defaults to 0.
wm	A logical indicating if weighted mean should be added for each species.
legend.pos	Controls the position of the legend. Might either be a list object containing x and y coordinates (such as e.g. returned by <a href="#">locator</a> ) of the <b>topleft corner</b> of the legend box or one of the following: "topleft" (default), "bottomleft", "topright", or "bottomright". If legend.pos == NULL the plotting of the legend is suppressed.

**Author(s)**

Christoph Heibl

**References**

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*). *Am. Nat.* **173**: 225-240.

**See Also**

[pno](#)

**Examples**

```
# load PNOs for Oxalis sect. Palmatifoliae
data(palmatifoliae_pno)

# plot predicted niche occupancy for annual mean temperature
plotPNO(x = palmatifoliae_pno$AnnualMeanTemperature,
        xlab = "Annual Mean Temperature (degree C)")

# same plot, but with weighted means added
plotPNO(x = palmatifoliae_pno$AnnualMeanTemperature,
        xlab = "Annual Mean Temperature (degree C)", wm = TRUE)
```

---

pno

*Predicted Niche Occupancy Profiles*

---

**Description**

Following the approach of Evans et al. (2009), pno integrates species probability (suitability) distributions (e.g. derived with MAXENT) with respect to single climatic (or other environmental) variables in order to get predicted niche occupancy (PNO) profiles for each species and environmental variable.

**Usage**

```
pno(path_bioclim, path_model, subset = NULL,
    bin_width = 1, bin_number = NULL)
```

**Arguments**

path_bioclim	The path leading to an ASCII raster map with environmental data (bioclimatic layer) and ArcGIS-compatible header.
path_model	The path leading to the directory, where MAXENT probability surfaces are stored as ASCII raster maps with ArcGIS-compatible header.

subset	A vector of mode 'character' giving taxon names if only a subset of the species ENMs in path_model is to be used
bin_width	A numeric, giving the bin interval.
bin_number	An integer, giving the number of bins used.

### Details

The path arguments path\_bioclim and path\_model point to the directories where the environmental data and the MAXENT probability distributions must be stored as ASCII maps with an **ArcGIS-compatible** header (as obtained with MAXENT output filetype: **asc**). An example header:

```
ncols      958
nrows     376
xllcorner -73.440304
yllcorner -55.27622
cellsize  0.0166
NODATA_value -9999
```

### Value

A data frame of cumulative probabilities of suitability for each value on an environmental gradient (rows) for the a set of studied taxa (rows). The first column gives the mean of each category.

### Author(s)

Christoph Heibl

### References

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*). *Am. Nat.* **173**: 225-240.

### See Also

[pno.weighted.mean](#), [niche.overlap](#), [anc.clim](#)

---

`pno.weighted.mean`      *Weighted means of niche dimensions*

---

### Description

This function calculates the mean of an environmental variable weighted by the cumulative probability of each value of the environmental gradient extracted from a species distribution model (e.g. MAXENT)

**Usage**

```
pno.weighted.mean(x, subset = NULL, normalize = TRUE)
```

**Arguments**

x	A data frame or matrix with columns corresponding to species and rows corresponding to values along an environmental gradient. The first column contains the environmental variable, the remaining columns probabilities of suitability.
subset	A vector of mode "character" which can be used to restrict the calculation of weighted means to those columns in x whose column names match subset; defaults to NULL.
normalize	A logical, indicating whether to normalize PNOs prior to calculation of weighted means.

**Value**

A vector of weighted means corresponding to the columns in x.

**Author(s)**

Christoph Heibl

**References**

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*) *Am. Nat.* **173**: 225-240.

**See Also**

[pno](#), [anc.clim](#), [plotAncClim](#)

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