

# Package: phyloclim (via r-universe)

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**Version** 0.9.8

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**Title** Integrating Phylogenetics and Climatic Niche Modeling

**Depends** R (>= 3.2.0), ape, raster

**Imports** methods, Rdpack, sp

**RdMacros** Rdpack

**Description** Implements some methods in phyloclimatic modeling:  
estimation of ancestral climatic niches, age-range-correlation,  
niche equivalency test and background-similarity test.

**License** GPL-3

**Encoding** UTF-8

**NeedsCompilation** no

**RoxygenNote** 7.3.1

**Repository** <https://phylotastic.r-universe.dev>

**RemoteUrl** <https://github.com/heibl/phyloclim>

**RemoteRef** HEAD

**RemoteSha** 0bd0d717d99df3697ea9749a9bef4eaababb213e

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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: 0.9.8  
Date: 2020-01-18  
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)>)

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

[ape](#)

---

 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 = 10000)
```

## 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 <a href="#">niche.overlap</a> .
tri	either "upper" or "lower", indicating which triangle of the overlap matrix to use (see <a href="#">niche.overlap</a> ).
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(PNO)

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

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

# age-range correlation
x <- age.range.correlation(phy = 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(tree)
data(PNO)

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

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

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

---

bg.similarity.test      *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 were 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 chance.

**Usage**

```
bg.similarity.test(
  p,
  env,
  n = 99,
  study.area.y = "mcp",
  conf.level = 0.95,
  app,
  dir
)

niche.equivalency.test(p, env, n = 99, app, dir)

## S3 method for class 'ntest'
plot(x, ...)

## S3 method for class 'ntest'
print(x, ...)
```

**Arguments**

p	A <a href="#">SpatialPointsDataFrame</a> or a simple data frame containing the presence points. In the latter case the first column contains the species names, the second and third column longitude and latitude (see SWD-formatted (=Samples-With-Data) files in the MAXENT tutorial).
env	An object of class <a href="#">SpatialGridDataFrame</a> containing the environmental covariates.
n	An integer giving the number of permutations of the original data (default: n = 99).
study.area.y	Defines the study area of the second species Y (see Warren et al. 2008). Can be "env" (study area corresponds to env) or "mcp" (study area is the area of a convex hull around the presence points of the second species Y).
conf.level	A real number between 0 and 1 setting the confidence level of the confidence intervals to be calculated.
app	A character string giving the path to the MAXENT application.
dir	A character string giving the name of a directory where the input and output data for MAXENT will be saved. Already existing directories will be overwritten <b>without</b> a warning. If dir is left empty the data will be written to a temporary directory, which will be deleted after execution.
x	An object of class ntest.
...	Further arguments passed to or from other methods.

**Details**

An installation of MAXENT (Phillips and Dudík 2008) is required in order to run `niche.equivalency.test` and `bg.similarity.test`. Both functions use the logistic output of MAXENT estimated using auto features.

By default, the environmental covariates given with `env` are assumed to be *continuous*. In order to use *categorical* environmental covariates, you have to prepend "cat\_" to the layer name, e.g. "cat\_landuse".

**Value**

`niche.equivalency.test` gives a list with six elements:

method	Name of the test
species	Names of the two species compared
null	Formulation of the null hypothesis
statistic	Statistics of niche overlap D based on Schoeners D and modified Hellinger distances
p.value	p-values associated with the statistics
null.distribution	Null distributions of D and I derived from randomization

`bg.similarity.test` gives a list with eight elements:

method	Name of the test
species	Names of the two species compared
null	Formulation of the null hypothesis
statistic	Statistics of niche overlap D based on Schoeners D and modified Hellinger distances
ci.x.randomY	Confidence interval for D and I based on the comparison of the first species against a set of random presence points from the study area of the second species
ci.y.randomX	Confidence interval for D and I based on the comparison of the second species against a set of random presence points from the study area of the first species
nd.x.randomY	Null distributions of D and I calculated from the comparison of the first species against a set of random presence points from the study area of the second species
nd.y.randomX	Null distributions of D and I calculated from the comparison of the second species against a set of random presence points from the study area of the first species

### Note

These functions have been tested with MAXENT 3.3.4

### References

Phillips SJ, Dudík M (2008). "Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation." *Ecography*, **31**, 161-175.

MAXENT website: [https://biodiversityinformatics.amnh.org/open\\_source/maxent/](https://biodiversityinformatics.amnh.org/open_source/maxent/)

Warren DL, Glor RE, Turelli M (2008). "Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution." *Evolution*, **62**(11), 2868–2883.

Warren DL, Seifert SN (2011). "Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria." *Ecological Applications*, **21**(1), 335–342.

### Examples

```
# path to MAXENT
# -----
maxent.exe <- file.path(system.file(package="dismo"), "java/maxent.jar")

# a data frame of coordinates where two species
# have been detected ('presence points') and
# a raster stack of environmental covariables
# -----
species <- c("enneaphylla", "laciniata")
data(sites)
samples <- sites[grep(paste(species, collapse = "|"), sites$spec), ]
data.path <- system.file("extdata", package = "phyloclim")
preds <- list.files(path = data.path, pattern = "[.]asc")
preds <- paste(data.path, preds, sep = "/")
preds <- stack(lapply(X = preds, FUN = raster))
```



```

# testing against 9 permutations of the data
# -----
reps <- 9

# run hypothesis tests
# -----
## Not run:
if (file.exists(maxent.exe)){
  net <- niche.equivalency.test(samples, preds, reps, maxent.exe)
  net; plot(net)
  bst <- bg.similarity.test(samples, preds, reps, app = maxent.exe)
  bst; plot(bst)
} else {
  message("get a copy of MAXENT (see Details)")
}

## End(Not run)

```

---

enneaphylla\_laciniata *Niche overlap for Oxalis enneaphylla and O. laciniata*

---

## Description

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

## Usage

```

data(equ)
data(sim)

```

## Format

A list containing five elements:

**method** Name of the test.

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

**statistic** Test statistics D and I of niche overlap based on Schoeners D and modified Hellinger distances.

**p.value** p-values for the test statistics (if `method = "niche equivalency test"`).

**null** Formulation of the null hypothesis.

**null.distribution** Null distributions of D and I derived from randomization (if `method = "niche equivalency test"`).

**ci.x.randomY** Confidence intervals based on null distributions (if `method = "background similarity test"`).

**ci.y.randomX** Confidence intervals based on null distributions (if method = "background similarity test").

**nd.x.randomY** Null distributions of D and I derived from randomization (if method = "background similarity test").

**nd.y.randomX** Null distributions of D and I derived from randomization (if method = "background similarity test").

### 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)
plot(equ)

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

---

niche.overlap

*Quantification of Niche Overlap*

---

### 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 stored as objects of class [SpatialGrid](#).

**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(PNO)

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

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

---

palmatifoliae

Oxalis *section* Palmatifoliae

---

**Description**

This is a data set of *Oxalis* sect. *Palmatifoliae* derived from a larger scale study by Heibl & Renner (2012). The sites data frame gives the coordinates (WGS1984) of the sites where *Oxalis* sect. *Palmatifoliae* has been collected. These were taken as presence points in distribution modeling and the list of predicted niche occupancy profiles (PNO). Finally, tree holds a phylogenetic hypothesis for the section extracted from a relaxed molecular clock model of the phylogeny of Oxalidales based approx. 7500 bp of chloroplast and nuclear markers. 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(PNO)
data(sites)
data(tree)
```

**Format**

sites a data frame representing 290 collections of *Oxalis* sect. *Palmatifoliae*.

PNO 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.

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

**Source**

Heibl, C. & S.S. Renner. Arid-adapted Distribution models and a dated phylogeny for Chilean *Oxalis* species reveal occupation of new habitats by different lineages, not rapid adaptive radiation. 2012. *Syst. Biol.* **61**(5): 823-834.

**Examples**

```
# 290 collections of Palmatifoliae
# -----
data(sites)
plot(sites$long, sites$lat,
     xlab = "Longitude", ylab = "Latitude")

## PNO profiles along 19 bioclimatic variables
## -----
data(PNO); names(PNO)
temp <- names(PNO)[1]
plotPNO(PNO[[temp]], xlab = temp)

## phylogenetic hypothesis for Palmatifoliae
## -----
data(tree)
plot(tree)
```

---

plotAncClim

*Chronograms with Climatic Data on the Y-Axis*


---

**Description**

Plot the history of climatic tolerance for a clade *sensu* Evans et al. (2009).

**Usage**

```
plotAncClim(
  x,
  layer,
  clades = NULL,
  col,
  density = TRUE,
  tipmode = 1,
  nchar = 3,
  cex,
  tipspace,
  cladespace = 1,
  lwd,
  ylab = ""
)
```

**Arguments**

x	A list with elements tree, data, and (optional) central.density (see details).
layer	<i>Do not use.</i>
clades	A list containing vectors of tip labels which define the clades to highlight.
col	A vector containing colors for different clades (see Examples).
density	Logical, if TRUE, the central density intervals for recent species are plotted.
tipmode	Integer: tipmode = 0 means no tiplabels (and no central density intervals) are plotted; values 1, 2, and 3 define different ways of plotting the tiplabels (see Examples).
nchar	An integer giving the number of characters to which the tiplabels are truncated.
cex	Numeric character <b>expansion</b> factor for tiplabels; multiplied by <code>par("cex")</code> yields the final character size. NULL is are equivalent to 1.0.
tipspace	The fraction of the x-axis that is reserved for tiplabel plotting. If no value is given (default), plotAncClim calculates the fraction as $1 - (4 / nbtips)$ , but this can be overridden by specifying a fixed value for tipspace in <code>[0, 1]</code> .
cladespace	A positive reel number; <b>tentative</b> : a factor controlling the space between tiplabels of different clades.
lwd	The line width, a positive number, defaulting to 1.
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.

## References

Evans MEK, Smith SA, Flynn RS, Donoghue MJ (2009). “Climate, niche evolution, and diversification of the “bird-cage” evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*.” *American Naturalist*, **173**(2), 225–240.

## See Also

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

## Examples

```
# load phylogeny and PNOs of Oxalis sect. Palmatifoliae
data(tree)
data(PNO)

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

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

# visualize results with default branch coloration
plotAncClim(ac)

# alternative clade colors are given according to the order
# in which tip labels appear from left to right
plotAncClim(ac, col = c("red", "purple", "blue"))

# the 'tipmode' argument
plotAncClim(ac, tipmode = 0)
plotAncClim(ac, tipmode = 1)
plotAncClim(ac, tipmode = 2, nchar = 5)
plotAncClim(ac, tipmode = 3, nchar = 4)
```

---

plotPNO

*Plot Predicted Niche Occupancy Profiles*

---

## Description

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",
legend.cex = 1
)

```

### 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	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.
legend.cex	Numeric controlling the size of the legend.

### References

Evans MEK, Smith SA, Flynn RS, Donoghue MJ (2009). "Climate, niche evolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*)." *American Naturalist*, **173**(2), 225–240.

### See Also

[pno](#)

### Examples

```

# load PNOs for Oxalis sect. Palmatifoliae
data(PNO)

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

# same plot, but with weighted means added
plotPNO(x = 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) variable 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	A character string, giving the path to an ASCII raster map with environmental data (bioclimatic layer) and ArcGIS-compatible header (see Details).
path_model	A character string, giving the path to the <b>directory</b> , where MAXENT probability surfaces are stored as ASCII raster maps with ArcGIS-compatible header (see Details).
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 argument path\_model points to the directory where the MAXENT probability distributions must be stored as ASCII maps with an **ArcGIS-compatible** header (as obtained with MAXENT output filetype: **asc**).

An example for an ArcGIS-compatible 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.



**References**

Evans MEK, Smith SA, Flynn RS, Donoghue MJ (2009). "Climate, niche evolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*)." *American Naturalist*, **173**(2), 225–240.

**See Also**

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

---

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

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**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)**

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**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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