Package ‘metacom’

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Description Functions to analyze coherence, boundary clumping, and turnover following the pattern-based metacommunity analysis of Leibold and Mikkelson 2002 <doi:10.1034/j.1600-0706.2002.970210.x>. The package also includes functions to visualize ecological networks, and to calculate modularity as a replacement to boundary clumping.
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Description

‘metacom’ provides functions for the analysis of the elements of metacommunity structure (coherence, boundary clumping, & turnover), following the pattern-based metacommunity framework of Leibold & Mikkelsen 2002 and Presley et al. 2010. This package is designed to allow the user to distinguish between several idealized patterns of metacommunity structure (Presley et al. 2010) utilizing any number of null model algorithms for the randomization procedure. However, these metrics can also be used in isolation, and without ordination via reciprocal averaging, and instead, ordering along some biological gradient.

A metacommunity is a set of sites (e.g. plants in plant-pollinator networks) associated through interactions (e.g. insect species (columns) interact with plant species (rows) in plant-pollinator networks). The pattern-based metacommunity concept, proposed by Leibold & Mikkelsen 2002 and expounded on by Presley et al. 2010, allows for the evaluation of metacommunity structure by using randomization techniques to discern between 10 patterns of metacommunity structure. This is performed by ordinating site-by-species interaction matrices and calculating three metrics; coherence, boundary clumping & turnover.

The metacom package calculates these three metrics; coherence is calculated using the function Coherence(), boundary clumping with BoundaryClump(), and turnover (from either species or range perspective) using the Turnover() function. These functions are consolidated in the Metacommunity() function, which can be used to calculate all three metrics. In order to interpret the output of these functions, it will be helpful to read Leibold & Mikkelsen 2002 and Presley et al. 2010, but to also read Ulrich and Gotelli 2013, as this paper outlines the difficulty seemingly inherent with investigating community structure. Also, these functions do not have to be used strictly in the Leibold and Mikkelsen 2002 framework.

I caution the user to be aware that the creation of null matrices can be performed to allow (or not allow) sites to be empty, or species to not exist at any site (i.e. column sums and/or row sums are allowed to be zero). This is controlled by the logical argument ‘allow.empty’ in the Metacommunity(), NullMaker(), Coherence(), and Turnover() functions. Restricting nulls to not allow empty rows or columns may be biologically realistic, but it also reduces the number of unique null matrices that can be built, which will impact computation time, making it infeasible or impossible in some situations. These situations occur when you have a very sparse interaction matrix, and is also influenced by null model algorithm (‘method’) that you choose.

The ‘metacom’ package is partially adapted from previous Matlab code written by Christopher Higgins (available at http://www.tarleton.edu/Faculty/higgins/EMS.htm) and relies on many functions in the ‘vegan’ package (Oksanen et al. 2012)
BoundaryClump

Author(s)
Tad Dallas

References


BoundaryClump

Determines boundary clumping

Description
'BoundaryClump' calculates the Morisita’s Index (Morisita 1962) for presence-absence interaction matrices, using a chi-squared test to assess significance.

Usage
BoundaryClump(comm, order = TRUE, scores = 1, binary = TRUE, fill = TRUE)

Arguments
comm community data in the form of a presence absence matrix
order logical argument indicating whether to ordinate the interaction matrix or not. See details.
scores axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
BoundaryClump

binary logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.

fill should embedded absences be filled before the statistic is calculated? (default is TRUE)

Details

This statistic is not based on randomization methods, so the function only requires a presence-absence interaction matrix and two arguments regarding the ordination of the empirical matrix.

The default is the range perspective, meaning that the analyses of boundary clumping and species turnover compare the distribution of species among sites. If the 'community' perspective is desired, transpose the matrix before analysis using the transpose function ('t()'). However, the author cautions against misinterpretation of the community perspective, as the biological meaning of turnover and boundary clumping differ between perspectives.

Boundary clumping, quantified by the Morisita’s index, is a measure of the degree to which species range boundaries overlap. This measure, and species turnover, cannot be interpreted unless the network is significantly coherent (see 'Coherence()').

If 'order' is FALSE, the interaction matrix is not ordinated, allowing the user to order the matrix based on site characteristics or other biologically relevant characteristics.

Value

'BoundaryClump' returns a data frame containing the calculated Morisita’s index ('index'), the corresponding p-value ('P'), and the degrees of freedom ('df').

The p-value is based on a chi-squared test comparing the Morisita’s index to a value of 1. If the Morisita's index is less than 1, a left-tailed test is performed (less clumping than expected by chance).

If the Morisita’s index is greater than 1, a right-tailed test is performed (more clumping than expected by chance).

Author(s)

Tad Dallas

References


Examples

data(TestMatrices)
intmat <- TestMatrices[[1]]
bound.test <- BoundaryClump(intmat, order=TRUE, scores=1, binary=TRUE, fill=TRUE)
bound.test
### Coherence

**Determines coherence**

**Description**

This function determines the number of embedded absences in an interaction matrix, and compares this value against null simulated matrices. Species ranges should be coherent along the ordination axis, as this axis represents a latent environmental gradient. A negative value of coherence (empirical matrix has more embedded absences than null matrices) indicates a 'checkerboard' pattern (Leibold & Mikkelson 2002). Nonsignificance has been historically interpreted as being indicative of a 'random' pattern, though this may be seen as accepting the null hypothesis, as nonsignificance cannot be used to infer a process.

**Usage**

```r
Coherence(comm, method = "r1", sims = 1000L, scores = 1L, order = TRUE,
          allow.empty = FALSEL, binary = TRUEL, verbose = FALSEL, seed = 1I)
```

**Arguments**

- **comm**: community data in the form of a presence absence matrix
- **method**: null model randomization method used by 'nullmaker'. See details below (and the help file of function 'nullmaker') for more information.
- **sims**: number of simulated null matrices to use in analysis
- **scores**: axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
- **order**: logical argument indicating whether to ordinate the interaction matrix or not. See details.
- **allow.empty**: logical argument indicating whether to allow null matrices to have empty rows or columns
- **binary**: logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.
- **verbose**: Logical. Prints a graphical progress bar that tracks the creation of null matrices. Useful for conservative null models on large and/or sparse data.
- **seed**: seed for simulating the null model. Null matrices should be repeatable.

**Details**

'method' is an argument handed to functions in the 'vegan' package. Leibold & Mikkelson advocated the use of equiprobable rows and columns (provided that rows and columns had at least one entry). This method is called 'r00'. Methods maintaining row (site) frequencies include 'r0', 'r1' & 'r2'. The default method argument is 'r1', which maintains the species richness of a site (row totals) and fills species ranges (columns) based on their marginal probabilities. Arguably the most conservative null algorithm is the fixed row - fixed column total null, which is implemented as 'fixedfixed'. See the help file for 'commsimulator' or Wright et al. 1998 for more information.
Imagine

If 'order' is FALSE, the interaction matrix is not ordinated, allowing the user to order the matrix based on site characteristics or other biologically relevant characteristics.

This function can either be used as a standalone, or can be used through the 'metacommunity()' function, which determines all 3 elements of metacommunity structure (coherence, boundary clumping, & turnover) (Leibold & Mikkelson 2002)

Value

A vector containing the number of embedded absences (embAbs), z-score (z), p-value (pval), mean (simulatedMean) and variance (simulatedVariance) of simulations, and null model randomization method (method).

Author(s)

Tad Dallas

References


Examples

```r
# define an interaction matrix
data(TestMatrices)
intmat=TestMatrices[[7]]

# determine coherence of interaction matrix
coh.intmat <- Coherence(intmat, method='r1', sims=100,
                        scores=1, order=TRUE, binary=TRUE)

# return results
coh.intmat
```

Imagine

Plotting of site-by-species interaction matrices

Description

'Imagine' produces an image plot, grid of small rectangles representing species occurrences in sites, of a given interaction matrix.
Imagine

Usage

Imagine(comm, col = c(0, 1), order = TRUE, scores = 1, fill = TRUE, xlab = "Species", ylab = "Site", yline = 2, xline = 2, sitenames = rownames(comm), speciesnames = colnames(comm), binary = TRUE)

Arguments

- **comm**: community data in the form of a presence absence matrix
- **col**: colors used to plot interactions. First value is the background color (no interaction) and the second color indicates an interaction.
- **order**: logical. Should the interaction matrix be ordered based on reciprocal averaging scores before plotting?
- **scores**: axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
- **fill**: logical. Should species ranges be made coherent before plotting?
- **xlab**: name of the x axis
- **ylab**: name of the y axis
- **yline**: line that the y-axis label is plotted on.
- **xline**: line that the x-axis label is plotted on.
- **sitenames**: names for each row in the interaction matrix. Default is to not plot names.
- **speciesnames**: names for each site in the interaction matrix. Default is to not plot names.
- **binary**: logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.

Value

Produces an image plot of the interaction matrix. The code is very simple, and may need to be modified if you have long site or species names, or wish to make it prettier than I have the ability to.

Author(s)

Tad Dallas

Examples

```r
# define an interaction matrix
data(TestMatrices)
pres3c=TestMatrices[[6]]

# plot interaction matrix
Imagine(pres3c, col=c('white','blue'), order=TRUE, fill=FALSE)
```
Metacommunity

Analysis of the Elements of Metacommunity Structure

Description

'Metacommunity' is a wrapper for the analysis of the three elements of metacommunity structure (coherence, boundary clumping, & turnover) following the framework of Leibold & Mikkelson 2002. It is important to note here that the results of boundary clumping and turnover are only relevant if the matrix is significantly positively coherent (i.e. empirical matrix has fewer embedded absences than null matrices).

Usage

```r
Metacommunity(comm, scores = 1, method = "r1", sims = 1000,
            order = TRUE, allowEmpty = FALSE, binary = TRUE, verbose = FALSE,
            seed = 1)
```

Arguments

- **comm**: community data in the form of a presence absence matrix
- **scores**: Axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores. See Details.
- **method**: null model randomization method used by 'nullmaker'. See details.
- **sims**: number of simulated null matrices to use in analysis
- **order**: logical argument indicating whether to ordinate the interaction matrix or not. See details.
- **allowEmpty**: logical argument indicating whether to allow null matrices to have empty rows or columns
- **binary**: logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.
- **verbose**: Logical. Prints a graphical progress bar that tracks the creation of null matrices. Useful for conservative null models on large and/or sparse data.
- **seed**: seed for simulating the null model. Null matrices should be repeatable.

Details

'method' is an argument handed to functions in the 'vegan' package. Leibold & Mikkelson advocated the use of equiprobable rows and columns (provided that rows and columns had at least one entry). This method is called 'r00'. Methods maintaining row (site) frequencies include 'r0','r1' & 'r2'. The default method argument is 'r1', which maintains the species richness of a site (row totals) and fills species ranges (columns) based on their marginal probabilities. Arguably the most conservative null algorithm is the fixed row - fixed column total null, which can be attained using many of swap algorithms described in the vegan package (sequential methods like 'tswap', 'swap', and non-sequential 'quasiswap' and 'backtracking'). See the help file for 'commsim' or Wright et al. 1998 for more information.
If ‘order’ is FALSE, the interaction matrix is not ordinated, allowing the user to order the matrix based on site characteristics or other biologically relevant characteristics.

**Value**

A list of length 4, containing:
- **Comm** – ordinated matrix used to calculate coherence, boundary clumping & turnover
- **Coherence** – output of the Coherence() function, giving information on the number of embedded absences and the significance relative to simulated null matrices
- **Turnover** – output of the Turnover() function, testing the number of species replacements relative to simulated null matrices
- **Boundary** – output of the BoundaryClump() function, which calculates the Morisita’s index, assessing significance using a chi-squared test

**Note**

This function may take awhile to finish as a result of the creation of null matrices. If you are running multiple interaction matrices, the code can be parallelized using the ‘snow’ package.

**Author(s)**

Tad Dallas

**References**


**Examples**

```r
# define an interaction matrix
data(TestMatrices)
intmat <- TestMatrices[[7]]

# determines the elements of metacommunity structure
ems.test <- MetaCommunity(intmat, method='r1', sims=100, scores=1)
```
Modularity

Calculates Barber’s Bipartite Modularity

Description

Modularity, community formation, boundary clumping. Call it what you want, there is a fair amount of overlap in definition here. As such, we posit that modularity statistics may be able to detect boundary clumping better than Morisita’s index. We offer a function here to calculate modularity. Specifically, this function calculates Barber’s Q statistic, and compares it relative to null model randomizations.

Usage

```r
Modularity(comm, method = "tswap", sims = 1000, scores = 1,
order = TRUE, c = length(comm), nstarts = 100, returnModules = FALSE)
```

Arguments

- `comm`: community data in the form of a presence absence matrix
- `method`: null model randomization method used by Nullmaker. See details below (and the help file of function Nullmaker) for more information.
- `sims`: number of simulated null matrices to use in analysis
- `scores`: axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
- `order`: logical argument indicating whether to ordinate the interaction matrix or not. See details.
- `c`: starting guess for the number of modules present. Defaults to the maximum number of modules possible.
- `nstarts`: number of starts. Default is 100. More will both slow the function down, and increase the likelihood of converging on the true modularity value.
- `returnModules`: logical argument indicating whether to return a vector of module IDs

Details

`method` is an argument handed to functions in the vegan package. Leibold & Mikkelson advocated the use of equiprobable rows and columns (provided that rows and columns had at least one entry). This method is called `r00`. Methods maintaining row (site) frequencies include `r0`, `r1`, and `r2`. The default method argument is `r1`, which maintains the species richness of a site (row totals) and fills species ranges (columns) based on their marginal probabilities. Arguably the most conservative null algorithm is the fixed row - fixed column total null, which can be attained using many of swap algorithms described in the vegan package (sequential methods like `tswap`, `swap`, and non-sequential `quasiswap` and `backtracking`). See the help file for `commsim` or Wright et al. 1998 for more information.

If `order` is `FALSE`, the interaction matrix is not ordinated, allowing the user to order the matrix based on site characteristics or other biologically relevant characteristics.
Value

A vector containing Barber’s modularity statistic (Q), the z statistic comparing observed modularity against null matrices (z), p-value (pval), and mean (simulatedMean) and variance (simulatedVariance) from null model simulations.

Author(s)

Tomlin Pulliam and Tad Dallas

References


Examples

# define an interaction matrix
data(TestMatrices)
intmat <- TestMatrices[[3]]

# determine Barber’s modularity
mod.intmat <- Modularity(intmat, method="r1", sims=5,
scores=1, order=TRUE, nstarts=10)

# return results
mod.intmat

---

NullMaker  

Null matrix creator

Description

Creates null matrices based on the constraints of the null model algorithm ('method'). Also allows for null matrices with a species that occurs at no sites, or a site without any species to be removed from the suite of simulated null matrices. This function borrows heavily from the commsimulator() function in the 'vegan' package, but also allows for the fixed-fixed null model.

Usage

NullMaker(comm, sims = 1000, method = "r1", ordinate = TRUE, scores = 1,
allowEmpty = FALSE, verbose = FALSE, seed = 1)
**Arguments**

- **comm**: community data in the form of a presence absence matrix
- **sims**: number of simulated null matrices to use in analysis
- **method**: null model randomization method. See details below.
- **ordinate**: logical. Would you like to ordinate the null matrices? Default is TRUE.
- **scores**: Axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores. See Details.
- **allowEmpty**: logical argument indicating whether to allow null matrices to have empty rows or columns
- **verbose**: Logical. Prints a graphical progress bar that tracks the creation of null matrices. Useful for conservative null models on large and/or sparse data.
- **seed**: seed for simulating the null model. Null matrices should be repeatable.

**Details**

'method' is the null model algorithm used to create the null matrices. The choice of a null algorithm is nontrivial. Leibold & Mikkelson advocated the use of equiprobable rows and columns (provided that rows and columns had at least one entry). This method is called 'r00'. Methods maintaining row (site) frequencies include 'r0','r1' & 'r2', whereas species (column) occurrences are preserved with fixed column methods such as 'c0'. The default method argument is 'r1', which maintains the species richness of a site (row totals) and fills species ranges (columns) based on their marginal probabilities. Arguably the most conservative null algorithm is the fixed row - fixed column total null, which can be attained using many of swap algorithms described in the vegan package (sequential methods like 'tswap', 'swap', and non-sequential 'quasiswap' and 'backtracking'). Other randomization methods are also available. See the help file for 'commsim', or Wright et al. 1998 for more information.

**Value**

- **rmats** – A list of length(sim) containing the null matrices

**Author(s)**

Tad Dallas and John Lefcheck

**References**


**See Also**

- nullmodel(), permatfull(), commsim()
Examples

```r
# define an interaction matrix
data(TestMatrices)
intmat <- TestMatrices[[7]]

# creation of the null matrices
nulls <- NullMaker(intmat, sims=100, method='r1')
```

---

**Description**

'OrderMatrix' ordinates an interaction matrix scores derived from reciprocal averaging (Gauch et al. 1977). These scores represent a latent environmental gradient along which species distributions are structured.

**Usage**

```r
OrderMatrix(comm, scores = 1, outputScores = FALSE, binary = TRUE)
```

**Arguments**

- **comm**: community data in the form of a presence absence matrix
- **scores**: axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
- **outputScores**: logical. Default is to return the ordinated matrix. If 'outputScores' is TRUE, the function returns the site and species scores.
- **binary**: logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.

**Value**

'OrderMatrix' returns either an ordinated matrix (outputScores = FALSE) or the site and species scores (outputScores = TRUE) obtained from reciprocal averaging. This function is already contained within functions calculating coherence, species turnover & boundary clumping, but may be useful for visualizations or for hypothesis testing concerning the important variables associated with the site or species scores.

**Note**

'OrderMatrix', like many of these functions, relies heavily on the 'vegan' package.

**Author(s)**

Tad Dallas
References


Examples

# define an interaction matrix
data(TestMatrices)
presSc <- TestMatrices[[6]]

# obtain an ordinated interaction matrix
OrderMatrix(presSc, scores = 1, outputScores = FALSE)

# obtain site and species scores from reciprocal averaging
OrderMatrix(presSc, scores = 1, outputScores = TRUE)

---

TestMatrices  Test matrices used to evaluate metacommunity functions

Description

A list of 7 test matrices from two of the foundational papers on the Elements of Metacomunity Structure analysis (Leibold & Mikkelson 2002 and Presley et al. 2010)

Format

A list containing interaction matrices from Leibold & Mikkelson 2002 and Presley et al. 2010:

1) dim=(20 x 20) Randomly generated matrix (‘rbinom(400,1,0.4)’)
2) dim=(10 x 10) Leibold & Mikkelson 2002 Figure 1b
3) dim=(10 x 10) Leibold & Mikkelson 2002 Figure 2a
4) dim=(10 x 10) Leibold & Mikkelson 2002 Figure 2b
5) dim=(15 x 10) Leibold & Mikkelson 2002 Figure 3c
6) dim=(20 x 20) Presley et al. Figure 3c
7) dim(20 x 20) Presley et al. Figure 4a
**Turnover**

**Source**

**Examples**

```r
#load list containing interaction matrices
data(TestMatrices)

length(TestMatrices)
names(TestMatrices)

#image plot of interaction matrix, using the Imagine() function
test <- TestMatrices[[6]]
Imagine(test, fill=FALSE, order=TRUE)
```

---

**Description**

'Turnover' is a function that assesses species turnover from the range perspective (traditional method).

**Usage**

```r
Turnover(comm, method = "r1", sims = 1000, scores = 1, order = TRUE,
         allowEmpty = FALSE, binary = TRUE, verbose = FALSE, seed = 1,
         fill = TRUE)
```

**Arguments**

- **comm**: community data in the form of a presence absence matrix
- **method**: null model randomization method used by 'nullmaker'. See details.
- **sims**: number of simulated null matrices to use in analysis
- **scores**: axis scores to ordinate matrix. 1: primary axis scores (default) 2: secondary axis scores
- **order**: logical argument indicating whether to ordinate the interaction matrix or not. See details.
- **allowEmpty**: logical argument indicating whether to allow null matrices to have empty rows or columns
**binary** logical argument indicating whether to ordinate the community matrix based on abundance or binary (default) data.

**verbose** Logical. Prints a graphical progress bar that tracks the creation of null matrices. Useful for conservative null models on large and/or sparse data.

**seed** seed for simulating the null model. Null matrices should be repeatable.

**fill** should embedded absences be filled before the statistic is calculated? (default is TRUE)

**Details**

If the ‘community’ perspective is desired, simply transpose the matrix before analysis using the transpose function (‘t()’), but make sure you understand the implications of this action, as the interpretation of the output changes dramatically.

‘method’ is an argument handed to functions in the ‘vegan’ package. Leibold & Mikkelson advocated the use of equiprobable rows and columns (provided that rows and columns had at least one entry). This method is called ‘r00’. Methods maintaining row (site) frequencies include ‘r0’, ‘r1’ & ‘r2’. The default method argument is ‘r1’, which maintains the species richness of a site (row totals) and fills species ranges (columns) based on their marginal probabilities. Arguably the most conservative null algorithm is the fixed row - fixed column total null, which is implemented as ‘fixedfixed’. See the help file for ‘commsimulator’ or Wright et al. 1998 for more information.

If ‘order’ is FALSE, the interaction matrix is not ordinated, allowing the user to order the matrix based on site characteristics or other biologically relevant characteristics.

This function can either be used as a standalone, or can be used through the 'metacommunity()' function, which determines all 3 elements of metacommunity structure (coherence, boundary clumping, & turnover) (Leibold & Mikkelson 2002). The turnover metric used here is equivalent to the number of checkerboard units community with species ranges (range perspective) filled in

**Value**

A data.frame containing the test statistic (turnover), z-value (z), p-value (pval), mean (simulated-Mean) and variance (simulatedVariance) of simulations, and randomization method (method)

**Author(s)**

Tad Dallas

**References**


Examples

```r
# define an interaction matrix
data(TestMatrices)
intmat <- TestMatrices[[3]]

# determine species turnover
turnover.intmat <- Turnover(intmat, method='r1', sims=100, scores=1, binary=TRUE)
```
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