Calculating species association and niche overlap using the spaa R package

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Ecological niche refers to resource allocation (Jintun Zhang, 2004), and is important in many aspects, for example, ordination analysis, community assembly etc. At the community scale, niche is usually quantified by the occurrence and co-occurrence of species. Although a great number of studies have focused on this topic in the past three decades ((in particular in the Chinese literature, e.g., C. W. Sun and S. D. Zhao, 1996; C. H. Guo et al. 1997; Z. M. Shi et al. 2001; J. L. Li and J. T. Zhang, 2010; N. J. Wang et al. 2010), a computer programme for conducting the relevant analysis is lacking. Here we describe spaa, which stands for SPecies Association Analysis, an R package for conducting suche analysis.

1. The installation

spaa is an open source package written in R, available on CRAN.

To install, enter the command install.packages("spaa") in the R console, R will ask you to select a CRAN mirror, and the package will be automatically downloaded and installed.

The developing version is available at https://github.com/helixcn/spaa, to install it, type:

```
library(devtools)
install_github("helixcn/spaa")
```

2. Functions and datasets in spaa

2.1 Main Functions

- data2mat: convert field records into a species-site matrix
- freq.calc: calculate the relative abundance
- niche.overlap: calculate the niche overlap between all the species pairs
- niche.overlap.boot: bootstrap the confidence intervals for niche overlap
- niche.overlap.boot.pair: bootstrap the confidence intervals of niche overlap for each pair of species
- niche.overlap.pair: calculate the niche overlap for each pair of species
- niche.width: calculate niche width
- plotlowertri: visualize distance/similarity matrices
- plotnetwork: visualize network correlation
- sp.assoc: calculate the overall species association
- sp.pair: calculate the association between each pair of species
- sub.sp.matrix: subsetting the community matrix based on relative frequencies

2.2 Embedded datasets

- splist: An example dataframe of species, genus, family
- datasample: An example community matrix (wide format)
- testdata: An example community dataset (long format)

3. Calculating niche width

3.1 Converting community data into a matrix

Community data generally needs to be converted to a matrix (Table 1) when calculating diversity indices, species association, niche width, niche overlap, in which each row represents a plot (site, region or track), each column represents a species, and the number indicates the number of individuals.

Table 1 Community species matrix

	sp1	sp2	sp3	sp4	sp5	sp6	sp7
plot1	3	6	1	2	1	0	0
plot2	8	0	30	0	0	0	0
plot3	0	1	0	2	0	1	3

However, field data are generally recorded in two ways:

- 1. Individual-based Field Record Sheet
- 2. Plot-based Record Sheet

3.1.2 Individual-based Field Record Sheet

Individual-based Field Record Sheet is often used in forest plots census, in which every tree (usually when DBH >= 1cm) is tagged. Usually, for a woody species, both the main trunk and branches are recorded. The following columns are often included:

- 1. plot: indicates the name of the plot (20mX20m) the tree is located at. The first two digits "01" refers to the first 20mX20m from the origin (west to east), the second "01" refers to the first 20mX20m from the origin along the Y axist (south to north)
- 2. tag number: the number on the main trunk
- 3. species name: the species name of the individual

- 4. x-coordinate: the x coordinate of the individual (usually in a local Cartesian System, the unit is often meters easting from the origin)
- 5. y-coordinate: the y coordinate of the individual (usually in a local Cartesian System, the unit is often meters northing from the origin)
- 6. branch (0 refers to the main trunk, 1 is the second largest branch, 2 is the third largest branch and so on)
- 7. diameter at breast height (DBH, usually in cm)
- 8. height (usually in meters)
- 9. status (alive, dead but standing, collapsed, etc.)
- 10. remark, any thing to markdown

Table 1. Field record sheet

plot	tag	species	X	у	branch	dbh	height	status	remark
	btm0101001 btm0101002	1	_	5.8 12.1	-	15 12	12 10	alive alive	

.

Generating an example community matrix

```
plot <- c("0101", "0101", "0102")
tag <- c("btm0101001", "btm0101002", "btm0101003")
species <- c("sp1", "sp2", "sp1")
x <- c(1.5, 3.3, 4.1)
y <- c(5.8, 12.1, 8.9)
branch <- c(0, 0, 0)
dbh <- c(15, 12, 5)
height <- c(12, 10, 8)
status <- c("alive", "alive", "alive")
remark <- c("", "", "")
btmdata <- data.frame(plot, tag, species, x, y, branch, dbh, height, status, remark)
btmdata</pre>
```

```
##
    plot
                 tag species
                               Х
                                     y branch dbh height status remark
## 1 0101 btm0101001
                         sp1 1.5 5.8
                                            0
                                               15
                                                      12
                                                          alive
## 2 0101 btm0101002
                                            0
                                               12
                         sp2 3.3 12.1
                                                       10
                                                          alive
## 3 0102 btm0101003
                         sp1 4.1 8.9
                                            0
                                                5
                                                          alive
```

```
# generate a dataset
btm <- table(btmdata$plot, btmdata$species)
btm</pre>
```

3.1.2 Plot-based Record Sheet

Plot-based Record is much simpler, generally the first column is the name of plot, the second column is species, and the third column is the number of individuals of the species in the sample. Note the value is usually an integer, but could also be a decimal number when representing importance value (Kent M, 2011, page 175).

Table 2 Sample survey form

3

4

39.43

11.53

plot	species	abundance
plot1	sp1	3
plot1	sp2	6
plot1	sp3	1
plot1	sp4	2
plot1	sp5	1
plot2	sp1	8
plot2	sp3	30
plot3	sp4	2
plot3	sp2	1
plot3	sp6	1
plot3	sp7	3

The following code converts sample data to a community-species matrix.

```
library(reshape2)
library(spaa)
data(datasample)
datasample2 <- cbind(plot = row.names(datasample), datasample)</pre>
# Convert the modified matrix to the common format of data records
aaa <- melt(data = datasample2,</pre>
            id.vars = "plot",
            measure.vars = 2:ncol(datasample2),
            variable.name = "species",
            value.name = "abundance",
            factorsAsStrings = TRUE)
# is 0.00 because the species did not occur in some samples
aaa1 <- aaa[aaa$abundance > 0, ]
head(aaa1)
##
                    species abundance
    plot
## 1 1 Castanopsis.eyrei
                                25.58
## 2
       2 Castanopsis.eyrei
                                28.41
## 3
       3 Castanopsis.eyrei
                                39.43
## 4
       4 Castanopsis.eyrei
                               11.53
## 5
       5 Castanopsis.eyrei
                                35.01
## 6
       6 Castanopsis.eyrei
                                51.34
bbb <- acast(aaa1,
             formula = plot ~ species,
             value.var = "abundance",
             fill = 0)
bbb
     Castanopsis.eyrei Schima.superba Rhododendron.ovatum Cyclobalanopsis.glauca
##
## 1
                 25.58
                                 5.95
                                                      3.32
                                                                             12.10
## 2
                 28.41
                                 1.03
                                                     13.24
                                                                              1.85
```

14.37

6.45

5.06

3.01

0.00

9.04

```
35.01
                                                          0.00
## 5
                                    6.47
                                                                                  17.57
## 6
                  51.34
                                    8.65
                                                          9.96
                                                                                   0.00
## 7
                  26.83
                                   12.11
                                                          9.96
                                                                                   3.07
## 8
                  19.80
                                    7.61
                                                          2.64
                                                                                   0.00
##
     Daphniphyllum.oldhamii Loropetalum.chinensis Pinus.massoniana
## 1
                         7.53
                                                12.10
                                                                    0.00
## 2
                         4.71
                                                 0.00
                                                                    0.00
                        13.71
## 3
                                                 4.07
                                                                    5.14
## 4
                         0.00
                                                 4.12
                                                                    0.00
## 5
                         0.00
                                                 4.30
                                                                    2.17
## 6
                         0.95
                                                 0.00
                                                                    1.08
## 7
                                                 2.89
                         9.61
                                                                    4.41
## 8
                         3.85
                                                 3.86
                                                                    9.77
##
     Rhododendron.latoucheae Vaccinium.bracteatum Lithocarpus.glaber
## 1
                          1.07
                                                 6.99
                                                                      1.21
## 2
                          5.13
                                                 6.81
                                                                      7.18
## 3
                          1.16
                                                 0.00
                                                                      0.00
## 4
                          4.49
                                                 0.00
                                                                      3.71
## 5
                          0.00
                                                 0.00
                                                                      3.12
## 6
                          2.08
                                                 2.21
                                                                      0.00
## 7
                          0.00
                                                 0.00
                                                                      0.00
## 8
                          5.99
                                                 1.95
                                                                      0.00
##
     Syzygium.buxifolium Castanopsis.tibetana Castanopsis.fargesii
## 1
                     0.00
                                             0.00
                                                                    1.01
## 2
                     0.00
                                             0.96
                                                                    0.00
## 3
                     0.00
                                             0.00
                                                                    0.00
## 4
                     1.22
                                             2.15
                                                                    1.40
## 5
                     0.00
                                             0.00
                                                                    0.00
## 6
                     0.92
                                             0.00
                                                                    0.00
## 7
                     2.47
                                             0.00
                                                                    0.00
## 8
                     0.00
                                            0.00
                                                                    0.00
##
     Photinia.serrulata
## 1
                    0.00
## 2
                    1.21
## 3
                    0.00
## 4
                    0.00
## 5
                    0.00
## 6
                    0.00
## 7
                    0.00
                    0.88
## 8
```

When the abundance column only contains integers, it can be converted using data2mat(). Note that the names of the columns should be named "plotname", "species", "abundance" (note R is case sensitive).

```
library(spaa)
data(testdata)
testdata
```

```
##
      plotname species abundance
## 1
         plot1
                     sp1
                                  3
## 2
         plot1
                     sp2
                                  6
## 3
                                  1
         plot1
                     sp3
                                  2
## 4
         plot1
                     sp4
## 5
         plot1
                                  1
                     sp5
## 6
         plot2
                     sp1
                                  8
```

```
## 7
          plot2
                     sp3
                                 30
## 8
                     sp4
                                  2
          plot3
## 9
          plot3
                     sp2
                                  1
## 10
                                  1
          plot3
                     sp6
## 11
          plot3
                     sp7
                                  3
data2mat(testdata)
##
            sp1 sp2 sp3 sp4 sp5 sp6 sp7
## plots
##
              3
                   6
                            2
                                1
     plot1
                       1
##
     plot2
              8
                   0
                      30
                            0
                                0
                                     0
                                         0
     plot3
##
                       0
                                0
                                     1
                                         3
```

3.2 Calculating species associations

Interspecific associations, including association among all the species and specific association between each pair of species could be computed using spaa (Zhou Xianye et al. 2000; Shi Zuomin et al. 2001; Zhang Siyu and Zheng Shiqun 2002; Zhang Zhiyong et al. 2003; Kang Bing et al. 2005; Wang Wenjin et al. 2007; Wang Naijiang et al. 2010).

3.2.1 Species association of the community as a whole

The function sp.assoc() computes the following indices and the output is a list with the following elements.

- pi: Species frequency
- N: Number of plots
- S: Number of species
- Tj: Total number of species for each plot
- Numspmean: Mean number of species
- sigmaTsq: Variance of species relative frequency
- STsq: Variance of species number
- var.ratio: Variance ratio
- W: W statiscit: used in comparison with the Chi Square.

An example:

```
data(testdata)
spmatrix <- data2mat(testdata)</pre>
sp.assoc(spmatrix)
## $pi
##
                                                     sp5
                    sp2
                               sp3
         sp1
                                          sp4
                                                               sp6
                                                                          sp7
## 0.6666667 0.6666667 0.6666667 0.6666667 0.3333333 0.3333333 0.3333333
##
## $N
## [1] 3
##
## $S
## [1] 7
##
## $Ti
## plot1 plot2 plot3
##
       5
              2
##
## $Numspmean
## [1] 3.666667
```

```
##
## $sigmaTsq
## [1] 1.55556
##
## $STsq
## [1] 1.55556
##
## $var.ratio
## [1] 1
##
## $W
## [1] 3
```

$$\delta_T^2 = \sum_{i=1}^s P_i (1 - P_i)$$

Figure 1: Equation 1

1. Variance of species relative frequency (Equation 1) sigmaTsq:

$$S_T^2 = 1/N \sum_{j=1}^N (T_j - t)^2$$

Figure 2: Equation 2

2. Variance of the number of species (Equation 2) STsq

$$P_i = n_i/N$$

Figure 3: Equation 3

- 3. Species' relative frequency (Equation 3) pi
- 4. Variance ratio (Equation 4) var.ratio
 - If VR > 1, positive correlation
 - if VR < 1, negative correlation

5. The W statistic (Equation 5) The W statistic is used to test the significance of the variance ratio (Qianmei Zhang et al., 2006) with 95% confidence intervals of Chi 0.95,N2 < W < Chi 0.05, N2

In Equations 1-5, N is the number of plots, S is the total number of species, n is the number of plots occupied by a species, T_{j} is the number of species in each plot, and t is the average of the number of species in all plots.

$$VR = S_T^2/\delta_T^2$$

Figure 4: Equation 4

$$W = VR \times N$$

Figure 5: Equation 5

3.2.2 Significance test of inters-pecific associations

The association between each pair of species could be calculated using the following code:

```
data(testdata)
spmatrix <- data2mat(testdata)
result <- sp.pair(spmatrix)</pre>
```

In this test, a 2X2 contingent table is usually used. If there are species X and species Y occurring in the plots, a, b, c, d denote co-occurrence and non-occurrence between them, respectively (Kent M., 2012, page 114):

- a: Number of plots where both species X and Y are present;
- b: Number of plots where X is present but not Y;
- c: Number of plots where Y is present but not X;
- d: Number of plots where neither X nor Y is present.
- n: Total number of plot n = a+b+c+d

The Yates-corrected Chi-square is used when determining whether there is a significant association for small samples (Kent M., 2012, page 114).

The output is a list containing the following elements:

- chisq: chi square matrix
- chisqass: chi square matrix information
- V: Value indicating species association is positive or negative
- Ochiai: Ochiai's index
- Dice: Dice's index
- Jaccard: Jaccard's index
- Pearson: Pearson's correlation
- Spearman's rank correlation
- PCC: Point correlation coefficient
- AC: Association coefficient

The equations are shown below:

1. Yates-corrected chi-square test for significance (Equation 6), see chisq and chisqass Note: - chisqass is the Chi-square - chisq is the Chi-square with Yates' correction for small samples (Kent M., 2012, page 114)

$$\chi^2_{Yates'} = \frac{(|ad - bc| - 0.5n)^2 n}{(a+b)(a+c)(b+d)(c+d)}$$

Figure 6: Equation 6

$$V = \frac{(a+d) - (b+c)}{a+b+c+d}$$

Figure 7: Equation 7

2. V ratio (Equation 7) V Indicating whether the species association is positive (>0) or negative (<0)

$$JD = a/(a+b+c)$$

Figure 8: Equation 8

3. Jaccard's index (Equation 8) Jaccard:

$$OI = \frac{a}{\sqrt{(a+b)(a+c)}}$$

Figure 9: Equation 9

- 4. Ochiai index (Equation 9) Ochiai:
- 5. Dice Index (Equation 10) Dice:
- 6. PCC: Point Correlation Coefficient PCC (Equation 11)
- 7. AC Association coefficient (Equation 12) AC
 - If a*d >= b*c:
 - If b*c > a*d, and d >= a, then (Equation 13):
 - If b*c > a*d and d < a, then (Equation 14):
- 8. Spearman's rank correlation coefficient Spearman (Equation 15)
- 9. Pearson's correlation coefficient Pearson (Equation 16)
- 3.3 Calculating niche width

Niche width is commonly measured by the Levins or Shannon indices.

- 1. Levins niche width index (Equation 17)
- 2. Shannon's niche width index (Equation 18)

where B_{-i} is the niche width of the *i*th species, *j* denotes jth plot, and *r* denotes the number of plots.

The function niche.width() can calculate the niche width of each species. The arguments are: niche.width(mat, method = c("shannon", "levins")), where mat is the sample-species matrix and method is eighther "shannon" or "levins".

$$DI = \frac{2a}{2a+b+c}$$

Figure 10: Equation 10

$$PCC = \frac{ad - bc}{\sqrt{(a+b)(a+c)(c+d)(b+d)}}$$

Figure 11: Equation 11

$$AC = \frac{ad - bc}{(a+b)(b+d)}$$

Figure 12: Equation 12

$$AC = \frac{ad - bc}{(a+b)(a+c)}$$

Figure 13: Equation 13

$$AC = \frac{ad - bc}{(b+d)(d+c)}$$

Figure 14: Equation 14

$$r_{ik} = 1 - \frac{6\sum_{j=1}^{N} (x_{ij} - x_{kj})_{j}^{2}}{N^{3} - N}$$

Figure 15: Equation 15

$$r_{ik} = \frac{\sum_{j=1}^{N} (x_{ij} - \bar{x}_i)(x_{kj} - \bar{x}_k)}{\sqrt{\sum_{j=1}^{N} (x_{ij} - \bar{x}_i)^2 \sum_{j=1}^{N} (x_{kj} - \bar{x}_k)^2}}$$

Figure 16: Equation 16

$$B_i = \frac{1}{\sum_{j=1}^{r} (P_{ij})^2}$$

Figure 17: Equation 17

3.4 Niche overlap

niche.overlap() calculates the niche overlap coefficients between all species pairs, including: "levins" (Note this is different from niche width), "schoener", "petraitis", "pianka", "morisita", etc. The output is a distance matrix. These indices are defined as below:

- 1. Levin's niche overlap index (Equation 19)
- 2. Schoener's niche overlap index (Equation 20)
- 3. Petraitis's niche overlap index (Equation 21)
- 4. Pianka's niche overlap index (Equation 22)
- 5. Czechanowski's niche overlap index (Equation 23)
- 6. the simplified Morisita index (Equation 24)

where O_ik is the niche overlap of species i and species k, P_ij and P_kj are the number of individuals of species i and species k in the jth sample, respectively, r is the total number of plots (sites), and e is the base of the natural logarithm.

Example:

```
data(datasample)
niche.overlap(mat, method = c("levins", "schoener", "petraitis", "pianka", "czech", "morisita"))
```

where mat is the community matrix and method is either: "levins", "schoener", "petraitis", "pianka", "czech" or "morisita".

niche.overlap.pair() computes the niche overlap between a specific pair. For example:

$$B_i = -\sum_{j=1}^r (P_{ij} \ln P_{ij})$$

Figure 18: Equation 18

$$O_{ik} = \frac{\sum_{j=1}^{r} P_{ij} P_{kj}}{\sum_{j=1}^{r} (P_{ij})^2}$$

Figure 19: Equation 19

$$O_{ik} = 1 - \frac{1}{2} \sum_{i=1}^{r} |P_{ij} - P_{kj}|$$

Figure 20: Equation 20

$$O_{ik} = e^{\sum_{j=1}^{r} (P_{ij} \ln P_{kj}) - \sum_{j=1}^{r} (P_{ij} \ln P_{ij})}$$

Figure 21: Equation 21

$$O_{ik} = \frac{\sum_{j=1}^{r} P_{ij} P_{kj}}{\sqrt{(\sum_{j=1}^{r} P_{ij})^{2} (\sum_{j=1}^{r} P_{kj})^{2}}}$$

Figure 22: Equation 22

$$O_{12} = O_{21} = 1 - 0.5 \sum_{i=1}^{n} |p_{1i} - p_{2i}|$$

Figure 23: Equation 23

$$O_{ik} = \frac{2\sum_{j=1}^{r} P_{ij} P_{kj}}{\sum_{j=1}^{r} P_{ij}^2 + \sum_{j=1}^{r} P_{kj}^2}$$

Figure 24: Equation 24

```
"petraitis", "czech",
"morisita", "levins"))
```

Where VectA and vectB are two vectors indicating the number of individuals of species A and species B in the plots, respectively, and method is either "pianka", "schoener", "petraitis", "czech", "morisita", "levins".

3.5 Bootstrap of the confidence intervals for niche width

The confidence interval of niche overlap between each pair of species could be estimated using bootstrap by niche.overlap.boot(), which is show below:

where mat is the input species distribution matrix. method is the niche overlap index, times is the times of bootstrap to be performed, and quant is the quantile of the niche overlap index. By defaults, the 95% confidence interval (0.025 and 0.975) is used.

niche.overlap.boot() is a wrapper of niche.overlap.boot.pair(). In most cases, users do not need to call niche.overlap.boot.pair().

```
> niche.overlap.boot(datasample[,1:4], method = "pianka")
                                            Observed Boot mean Boot std Boot CI1
Castanopsis.eyrei-Schima.superba
                                               0.887
                                                          0.893
                                                                   0.048
                                                                            0.788
Castanopsis.eyrei-Rhododendron.ovatum
                                               0.820
                                                          0.831
                                                                   0.084
                                                                            0.625
Castanopsis.eyrei-Cyclobalanopsis.glauca
                                                                            0.272
                                               0.551
                                                          0.570
                                                                   0.148
Schima.superba-Rhododendron.ovatum
                                               0.693
                                                          0.714
                                                                   0.147
                                                                            0.407
Schima.superba-Cyclobalanopsis.glauca
                                               0.491
                                                           NaN
                                                                      NA
                                                                            0.273
Rhododendron.ovatum-Cyclobalanopsis.glauca
                                               0.253
                                                          0.308
                                                                   0.140
                                                                            0.090
                                            Boot CI2 times
                                               0.977
Castanopsis.eyrei-Schima.superba
                                                      1000
Castanopsis.eyrei-Rhododendron.ovatum
                                               0.959
                                                      1000
Castanopsis.eyrei-Cyclobalanopsis.glauca
                                               0.847
                                                      1000
Schima.superba-Rhododendron.ovatum
                                               0.944
                                                      1000
Schima.superba-Cyclobalanopsis.glauca
                                               0.787
                                                      1000
Rhododendron.ovatum-Cyclobalanopsis.glauca
                                               0.616
                                                      1000
```

Figure 25: Confidence intervals of species niche overlap analysis

The columns are as follows.

- Row names, Species pair Castanopsis.eirei-Schima.superba for both columns, indicating the corresponding species pair
- Observed: the valued niche overlap index used
- Boot mean: the mean of bootstrap niche overlap index
- Boot std: the standard deviation (sd()) of the niche overlap index
- Boot CI1: the lower quantile of the niche overlap index, the default is the 0.025 quantile
- Boot CI2: the upper quantile of the niche overlap index, the default is the 0.975 quantile

Note: If a species is missing, NaN will appear during in the bootstrap results, which indicates that the denominators is 0.

3.6 Visualisation

3.6.1 Semi-matrix plots

The spaa package also provides some functions for visualising the results of species association.

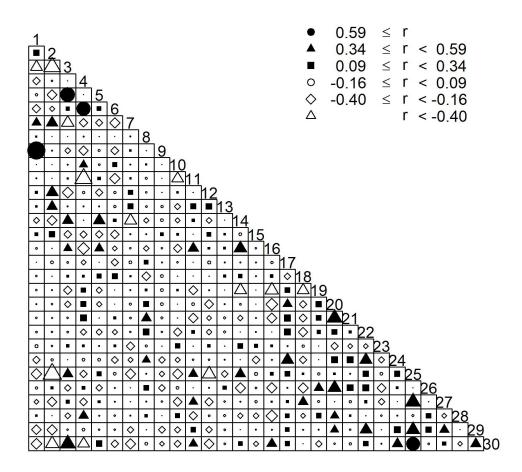


Figure 26: semi-matrix visualized by the plotlowertri() function

The arguments are:

```
plotlowertri(input, valuename = "r",
    pchlist = c(19, 17, 15, 1, 5, 2, 7),
    interval = 6,    cex = 1,    ncex = 1,
    int =1.2,    add.number = TRUE,
    size = FALSE,    add.text = FALSE,
```

```
show.legend = TRUE, digits = 2)
```

A correlation coefficient matrix or a distance matrix could easily be visuallized using this function (Figure 1).

3.6.2 Species association network

Networks can be used to show the interconnectedness of species, i.e., in different colors, line widths, or line styles connecting the species to another other, or the similarity of species composition between sites. spaa's plotnetwork() can visualize the relationship (Figure 3). However, network plot should not be used to represent the relationship between a large number of species, for example, more than 10, it could be too crowded.

Pearson Correlation Network

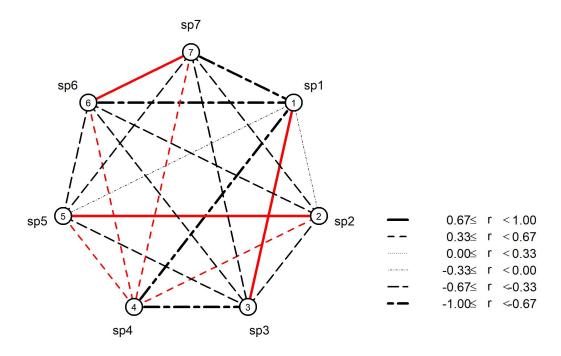


Figure 27: A network plot generated using plotnetwork()

3.7 Other functions

3.7.1 Obtain the most frequently occurred species in the community matrix

the sub.sp.matrix(spmatrix, freq = 0.5, common = NULL) can select the species based on relative frequency, for example, freq = 0.5 will only keep the species whose relative frequency greater than 0.5, or common = 10 will select the top 10 species with highest relative frequency.

3.7.2 Other useful functions

- lgeodist(), geodist() calculates the great circle distance between two locations given their latitude and longitude;
- deg2dec() converts degrees, minutes and seconds to decimal degrees;
- dist2list() converts distance matrix to a data.frame, similar to simba::liste()
- turnover() calculates species turnover, and could be used in computing beta diversity for forest dynamic plot
- lab.mat() and XYname() can generate the names of quadrats of a forest dynamic plot.
- add.col() will add a column to the target dataframe, if give there is one column in common among the two data.frames. Note this is experimental and users are encouraged to call merge().
- data2mat() converts dataframe to community matrix, similar to the function picante::sample2matrix(), see Section 3.1.2 of this tutorial for the conversion if there is a decimal number in the sample.
- list2dist() Convert pairwise list to distance matrix, a inversion to dist2list().

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