

# Species association

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## Introduction

- Classical problem in ecology (Whittaker 1962) –

« Interspecific associations arise when two or more species co-occur either more or less frequently than expected due to chance alone. **Positive associations** between two species can occur when both select the same habitat or have the same environmental requirements. Conversely, **negative associations** can occur if the species have differing ecological requirements (Dale 1977).

Association, in either the positive or negative direction, can also occur as a direct consequence of **biotic interactions** such as mutualism, competition and predation. Although it is not possible to unambiguously infer the action of specific processes from the examination of patterns alone (Schluter 1984, Rejmánek and Leps 1996), association analyses remain a valuable tool for ecologists. Such analyses can be used for generating hypotheses about the factors responsible for the patterns, and hence can be used for identifying particular patterns that may be worthy of further study.

A number of statistical tests have been utilized for detecting species associations. These include correlation analysis (Greig-Smith 1983, O'Connor and Aarssen 1987, Myster and Pickett 1992), analysis by contingency table (Greig-Smith 1983, Dale et al. 1991), variance tests (Schluter 1984, McCulloch 1985), and the use of cross-variograms (Rossi et al. 1992). [...] » (Roxburgh and Chesson 1998).

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Roxburgh, S. H., and P. Chesson. 1998. A new method for detecting species associations with spatially autocorrelated data. *Ecology* 79: 2180-2192.

Whittaker, R. R. 1962. Classification of natural communities. *The Botanical Review* 28: 1-239.

## Search for species association

An association, in the statistical sense, is a recurrent group of co-occurring (presence-absence data) or correlated (abundance data) species.

**Method (in steps):** search for concordance among species (Legendre 2005)

1. Look for correlations among species: find clusters of correlated species (several methods available)
2. Compute a global test of concordance among the species in each group. Are there concordant species in these groups?
3. Test the contribution of each species to the concordance of its group.

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Legendre, P. 2005. Species associations: the Kendall coefficient of concordance revisited. *Journal of Agricultural, Biological, and Environmental Statistics* 10: 226-245.

## Small R example using data from Legendre (2005, p. 230)

```
### Obtain mite data from vegan in R
### (70 soil cores x 35 species; Borcard & Legendre 1994)
library(vegan)
data(mite)

### Hellinger transformation of the species data
mite.hel <- decostand(mite, "hel")

### Extract a sub-matrix for test (10 sites, 4 species)
### (not all correlated)
mite.small <- mite.hel[c(4,9,14,22,31,34,45,53,61,69),
                       c(13,14,15,23)]
```

Table 1. Illustrative example. Upper panel: Hellinger-transformed abundances of four mite species at 10 sites selected along the long axis of Figure 5. The Hellinger transformation was computed for the full dataset (70 sites). Lower panel: the same data transformed into ranks (with ties); last column: sum of the ranks for each site.

	<i>Hellinger-transformed abundances</i>				
	<i>Species 13</i>	<i>Species 14</i>	<i>Species 15</i>	<i>Species 23</i>	
Site 4	.25087	.40538	.24380	.08362	
Site 9	.40324	.25503	.39303	.00000	
Site 14	.26577	.47620	.27267	.06097	
Site 22	.32350	.63337	.47003	.00000	
Site 31	.26312	.29089	.39223	.08771	
Site 34	.33675	.44836	.53727	.10153	
Site 45	.07956	.19487	.19487	.11251	
Site 53	.00000	.18570	.26261	.11744	
Site 61	.00000	.15430	.15430	.00000	
Site 69	.12769	.62987	.27584	.34578	
	<i>Ranks (species-wise)</i>				
	<i>Species 13</i>	<i>Species 14</i>	<i>Species 15</i>	<i>Species 23</i>	<i>Sum of ranks R<sub>i</sub></i>
Site 4	5	6	3	5	19.0
Site 9	10	4	8	2	24.0
Site 14	7	8	5	4	24.0
Site 22	8	10	9	2	29.0
Site 31	6	5	7	6	24.0
Site 34	9	7	10	7	33.0
Site 45	3	3	2	8	16.0
Site 53	1.5	2	4	9	16.5
Site 61	1.5	1	1	2	5.5
Site 69	4	9	6	10	29.0

```

### Load the library
library(kendall.W)

### Perform the global test of concordance
global.res <- kendall.global(mite.small, nperm=999)

$Concordance_analysis
      Group.1
W      0.44160305
F      2.37252221
Prob.F  0.04403791
Chi2    15.89770992
Prob.perm 0.04300000

### Perform a posteriori tests of concordance
post.res <- kendall.post(mite.small, mult="holm", nperm=999)

$A_posteriori_tests
      Spec13      Spec14      Spec15      Spec23
Spearman.mean 0.3265678 0.3965503 0.4570402 -0.1681251
W.per.species 0.4949258 0.5474127 0.5927802 0.1239061
Prob          0.0880000 0.0290000 0.0060000 0.7170000
Corrected prob 0.1760000 0.0870000 0.0240000 0.7170000

```

Table 2. Results of (a) the overall and (b) the *a posteriori* tests of concordance among the mite species. *P* = permutational probability, based upon 9,999 random permutations. (c) Complementary Spearman correlation coefficients (*r*) with results of one-tailed tests of significance, and partial concordance statistics  $\bar{r}_j$  and  $W_j$  for each species *j* described in Section 5. \* Reject  $H_0$  at  $\alpha = .05$ .

(a) Overall test of the <i>W</i> statistic. $H_0$ : The four species are not concordant with one another							
Kendall's <i>W</i> =		.44160					
Friedman's chi-square =		15.89771		<i>P</i> = .0448*			Reject $H_0$
(b) A posteriori tests		$H_0$ : This species is not concordant with the other three					
Species 13		<i>P</i> = .0766		Do not reject $H_0$			
Species 14		<i>P</i> = .0240*		Reject $H_0$			
Species 15		<i>P</i> = .0051*		Reject $H_0$			
Species 23		<i>P</i> = .7070		Do not reject $H_0$			
(c) Spearman correlation table		$H_0: r = 0; H_1: r > 0$ (one-tailed test)					
		Species 13	Species 14	Species 15	Species 23	$\bar{r}_j$	$W_j$
Species 13	<i>r</i>	1.0000	.5593	.8389	-.4185	.32657	.49493
	<i>P</i>	—	.0464	.0012	.8856		
Species 14	<i>r</i>	.5593	1.0000	.6242	.0061	.39655	.54741
	<i>P</i>	.0464	—	.0269	.4933		
Species 15	<i>r</i>	.8389	.6242	1.0000	-.0920	.45704	.59278
	<i>P</i>	.0012	.0269	—	.5998		
Species 23	<i>r</i>	-.4185	.0061	-.0920	1.0000	-.16813	.12391
	<i>P</i>	.8856	.4933	.5998	—		

## Details of the method

1. Look for correlations among species: find clusters of correlated species (several method available)

- Principal component analysis (PCA): can distinguish two groups.
- Agglomerative clustering on correlation matrix (Pearson, Spearman) among species: the most common method (e.g. Ward agglomerative clustering).
- *K*-mean partitioning of the standardized species.

2. Compute a global test of concordance among the species in each group. Are there concordant species in the groups?

Compute the Kendall (*W*) coefficient of concordance:

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	Species 1	Species 2	Species 3	Sum of ranks
	(ranks of abundances)			in each row
Site 1	1	1	6	8
Site 2	6	5	3	14
Site 3	3	6	2	11
Site 4	2	4	5	11
Site 5	5	2	4	11
Site 6	4	3	1	8

---

*W* is the variance of the sums of ranks divided by the maximum value that sum can take. That maximum value is obtained when there is total agreement among the judges (species) with regard to the order of the objects (sites).

$$W = \frac{12 \sum_{i=1}^n (R_i - \bar{R})^2}{p^2(n^3 - n) - pT}$$

Tied ranks should be dealt with in a special manner.

$$T = \sum_{k=1}^m (t_k^3 - t_k)$$

$t_k$  is the number of tied ranks in each of  $m$  groups of ties. Ex. from Table 1:

Site	Rank of species 13	$t_k$
4	5	1
9	10	1
14	7	1
22	8	1
31	6	1
34	9	1
45	3	1
53	1.5	} 2
61	1.5	
69	4	1

$W$  can also be computed from the mean  $\bar{r}$  of the Spearman correlations between all species in a group:

$$W = \frac{(p-1)\bar{r} + 1}{p}$$

$W$  can be transformed to a Friedman chi-square statistic before testing:

$$\chi^2 = p(n-1)W$$

$W$  can also be transformed to an  $F$ -statistic before testing:

$$F = \frac{(p-1)W}{1-W}$$

The results can be tested parametrically (not recommended) or by permutation. The groups that are not significantly concordant are dropped.

3. Test the contribution of each species to the concordance of its group.

- Compute  $\bar{r}_j$ , the mean of the Spearman correlations between species  $j$  and all the other species in the same group.
- A partial  $W_j$  statistic measuring the contribution of species  $j$  to the concordance of its group can be computed as follows:

$$W_j = \frac{(p_{gr} - 1)\bar{r}_j + 1}{p_{gr}}$$

- Permutation test: only the ranks of species  $j$  are permuted in the table before recomputing the statistic under permutations. Statistics  $\bar{r}_j$  and  $W_j$  are equivalent for this permutation test. Either one can thus be used.

⇒ If some species have negative values of  $\bar{r}_j$ , that means these species are negatively correlated to several species of the group. The group is thus too inclusive. The analysis needs to be redone with the group subdivided.

### Corrections for multiple testing

When more than one test is carried out on the same data, a correction needs to be applied to the  $P$ -values resulting from these multiple tests.

Holm correction:  $P_{Holm} = (m - k + 1) \times P$

Bonferonni correction:  $P_{Bonferonni} = m \times P$

Sidak correction:  $P_{Sidak} = 1 - (1 - P)^m$

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### Numerical simulations (Legendre 2005)

- Correct type I error: when the species are not correlated, the test rejects  $H_0$  in a proportion of the cases equal to the significance level (e.g. 5%). This is true for both the  $F$  and  $\chi^2$  statistics.

- When species are correlated, the power of the test increases with the number of intercorrelated species included in the analysis.

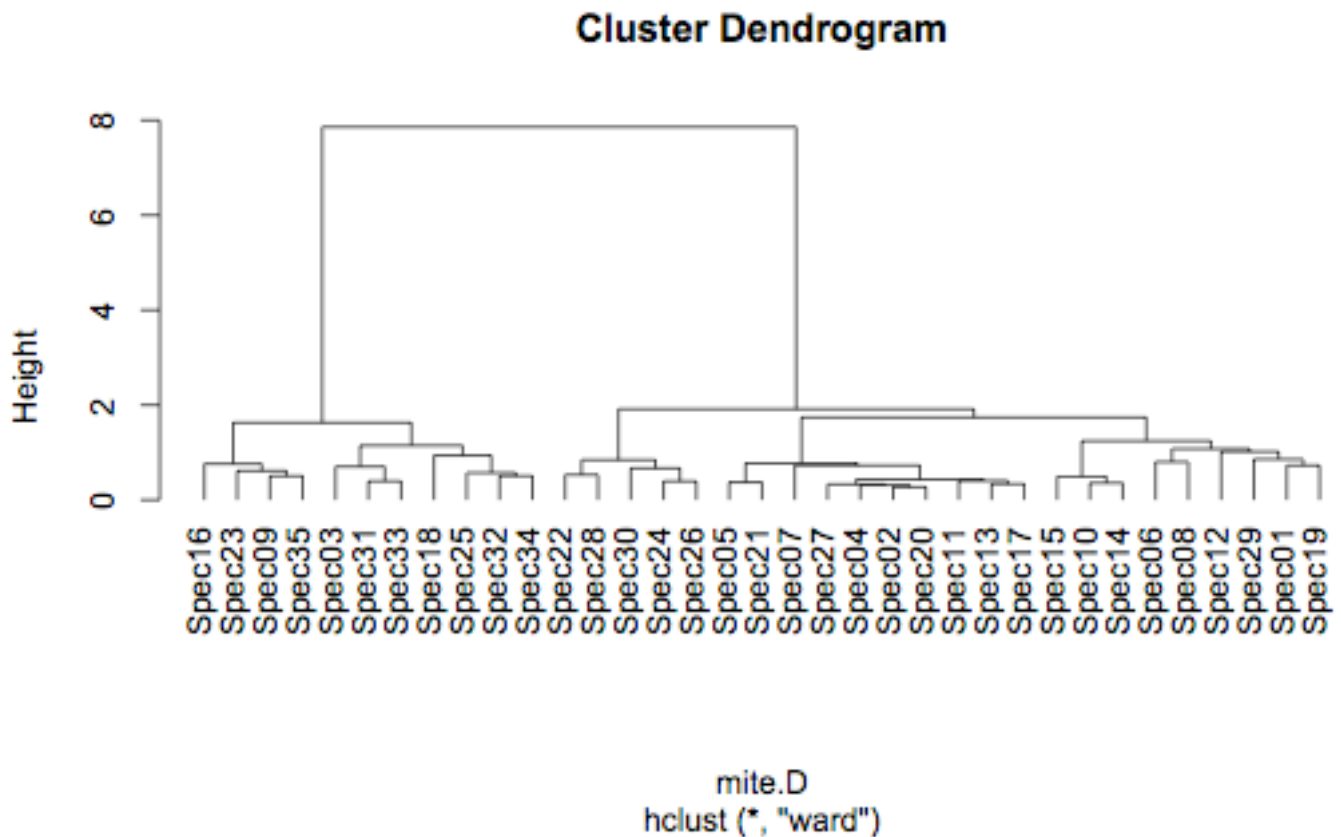
## Full example in R: soil oribatid mites

```
### Extract mite data from vegan in R
### (70 soil cores x 35 species ; Borcard & Legendre 1994)
library(vegan)
data(mite)

### Hellinger transformation on the data
mite.hel <- decostand(mite, "hel")

### Spearman correlation matrix between species
mite.cor <- cor(mite.hel, method="spearman")

### Ward agglomerative clustering (ascending classification)
mite.D <- as.dist(1 - mite.cor)
mite.clust <- hclust(mite.D, "ward")
plot(mite.clust, hang=-1)
```





```
# Cut the dendrogram; divide the species in 2 groups
mite.2gr <- cutree(mite.clust, k=2)
```

```
Spec01 Spec02 Spec03 Spec04 Spec05 Spec06 Spec07 Spec08 Spec09 Spec10
      1      1      2      1      1      1      1      1      2      1
Spec11 Spec12 Spec13 Spec14 Spec15 Spec16 Spec17 Spec18 Spec19 Spec20
      1      1      1      1      1      2      1      2      1      1
Spec21 Spec22 Spec23 Spec24 Spec25 Spec26 Spec27 Spec28 Spec29 Spec30
      1      1      2      1      2      1      1      1      1      1
Spec31 Spec32 Spec33 Spec34 Spec35
      2      2      2      2      2
```

```
### Open library
library(kendall.W)
```

```
### Global test of each group
global.res <- kendall.global(mite.hel, group= mite.2gr)
```

```
$Concordance_analysis
```

	Group.1	Group.2
W	3.097870e-01	2.911888e-01
F	1.032305e+01	4.108130e+00
Prob.F	1.177138e-85	4.676566e-22
Corrected prob.F	2.354275e-85	4.676566e-22
Chi2	5.130073e+02	2.210123e+02
Prob.perm	1.000000e-03	1.000000e-03
Corrected prob.perm	2.000000e-03	2.000000e-03

```
### A posteriori test of the contribution of each species
### to the concordance of its group
post.res <- kendall.post(mite.hel, group=mite.2gr,
                        mult="holm", nperm=999)
```

```
$A_posteriori_tests_Group[[1]]
```

	<b>Spec01</b>	<b>Spec02</b>	<b>Spec04</b>	<b>Spec05</b>	<b>Spec06</b>	<b>Spec07</b>
Spearman.mean	<b>0.1851177</b>	<b>0.4258111</b>	<b>0.3590580</b>	<b>0.2505486</b>	<b>0.1802160</b>	<b>0.2833298</b>
W.per.species	<b>0.2190711</b>	<b>0.4497357</b>	<b>0.3857640</b>	<b>0.2817757</b>	<b>0.2143736</b>	<b>0.3131911</b>
Prob	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0040000</b>	<b>0.0010000</b>
Corrected prob	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0360000</b>	<b>0.0350000</b>
	<b>Spec08</b>	<b>Spec10</b>	<b>Spec11</b>	<b>Spec12</b>	<b>Spec13</b>	<b>Spec14</b>
Spearman.mean	0.09248024	<b>0.2444656</b>	<b>0.4138494</b>	0.1263751	<b>0.4177343</b>	<b>0.3301159</b>
W.per.species	0.13029357	<b>0.2759462</b>	<b>0.4382723</b>	0.1627761	<b>0.4419954</b>	<b>0.3580278</b>
Prob	0.08900000	<b>0.0010000</b>	<b>0.0010000</b>	0.0330000	<b>0.0010000</b>	<b>0.0010000</b>
Corrected prob	0.17400000	<b>0.0350000</b>	<b>0.0350000</b>	0.1740000	<b>0.0350000</b>	<b>0.0350000</b>
	<b>Spec15</b>	<b>Spec17</b>	<b>Spec19</b>	<b>Spec20</b>	<b>Spec21</b>	<b>Spec22</b>
Spearman.mean	<b>0.2185421</b>	<b>0.4212160</b>	<b>0.2574779</b>	<b>0.4180699</b>	<b>0.3623428</b>	0.1250230
W.per.species	<b>0.2511028</b>	<b>0.4453320</b>	<b>0.2884163</b>	<b>0.4423170</b>	<b>0.3889118</b>	0.1614804
Prob	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	0.0300000
Corrected prob	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	0.1740000
	<b>Spec24</b>	<b>Spec26</b>	<b>Spec27</b>	<b>Spec28</b>	<b>Spec29</b>	<b>Spec30</b>
Spearman.mean	<b>0.2188216</b>	<b>0.3016159</b>	<b>0.4217606</b>	<b>0.2577037</b>	0.1108022	<b>0.2301430</b>
W.per.species	<b>0.2513707</b>	<b>0.3307153</b>	<b>0.4458539</b>	<b>0.2886327</b>	0.1478521	<b>0.2622203</b>
Prob	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	<b>0.0010000</b>	0.0560000	<b>0.0010000</b>
Corrected prob	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	0.1740000	<b>0.0350000</b>

```
$A_posteriori_tests_Group[[2]]
```

	<b>Spec03</b>	<b>Spec09</b>	<b>Spec16</b>	<b>Spec18</b>	<b>Spec23</b>	<b>Spec25</b>
Spearman.mean	0.1222579	<b>0.2712078</b>	<b>0.1906408</b>	0.1375601	0.1342409	<b>0.3342345</b>
W.per.species	0.2020527	<b>0.3374616</b>	<b>0.2642189</b>	0.2159637	0.2129463	<b>0.3947586</b>
Prob	0.0460000	<b>0.0010000</b>	<b>0.0010000</b>	0.0220000	0.0290000	<b>0.0010000</b>
Corrected prob	0.1740000	<b>0.0350000</b>	<b>0.0350000</b>	0.1540000	0.1740000	<b>0.0350000</b>
	<b>Spec31</b>	<b>Spec32</b>	<b>Spec33</b>	<b>Spec34</b>	<b>Spec35</b>	
Spearman.mean	<b>0.3446561</b>	<b>0.1833099</b>	<b>0.3188922</b>	<b>0.1764232</b>	<b>0.2498877</b>	
W.per.species	<b>0.4042328</b>	<b>0.2575544</b>	<b>0.3808111</b>	<b>0.2512938</b>	<b>0.3180797</b>	
Prob	<b>0.0010000</b>	<b>0.0030000</b>	<b>0.0010000</b>	<b>0.0030000</b>	<b>0.0010000</b>	
Corrected prob	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0350000</b>	<b>0.0390000</b>	<b>0.0350000</b>	

### PCA of centered and scaled species

