Open Peer Review on Qeios

RESEARCH ARTICLE

A Quantitative Analysis of Co-occurrence Matrices in Ecological Systems: Measuring Connectance and Entropy

Enrico Feoli[1]

[1] Department of Life Sciences, University of Trieste, Italy

Funding: Logistic support from Department of Life Sciences, University of Trieste

Potential competing interests: No potential competing interests to declare.

Abstract

This study explores the use of co-occurrence matrices to quantify patterns of connectivity in ecological systems. By applying an entropy-based formula to both small-scale matrices and graphs, the analysis investigates how connections between species or system components can be modeled and understood through entropy and negentropy. The study also introduces a method for evaluating connectance using the ratio between observed and maximum negentropy values. Additionally, it compares this method to existing models, including Ricotta and Szeidl's entropy measure and various graph-theory metrics. The findings demonstrate how these measures reflect system complexity and the interactions between components, offering insights into community structure and species coexistence. Parameters such as Whittaker's Beta Diversity, evenness of eigenvalues, and nested similarity were examined to evaluate their correlations with connectance and entropy, in view to contribute to a deeper understanding the connections within ecological systems.

Corresponding author: Enrico Feoli, feoli@units.it

Introduction

As a consequence of the fact that in 1970-71 I was speaking everywhere almost fanatically about information theory, I was invited by some of my botanist friends to write a popular article in Italian for the journal *Informatore Botanico Italiano* on its possible applications to phytosociology[1]. Rather than taking care of mathematical formulas (in that paper, the minus sign in front of formula {7} was missing and I did not explain in detail the proposed formula {5} to be applied to pairwise co-occurrence matrices), I focused on transmitting the idea that vegetation should be interpreted as a system that is a potential source of redundant messages. These are redundant codes that we organize in matrices X(M, N), in which M is the number of components of the system, species (or other traits according to Barkman[2], Box[3], Feoli[4], Orlóci and Orlóci[5], Pillar and Orlóci[6], Kraft et al. (2015)[7], and references therein) and N is the number of sampled vegetation stands representing different vegetation states (see Orlóci[8] for an innovative view on the vegetation stand).

In my mind, formula {5} of that paper (here numbered (2)) should be useful to measure the entropy of the co-occurrence matrices C(M, M) obtained by the self-multiplication of the matrices X(M, N):

$$C(M, M) = X(M, N)\ X^T\ (M, N) \qquad (1)$$

or calculated by similarity functions between the M components (the scalar product is also a measure of similarity).

The formula of entropy I proposed for co-occurrence matrices[1] is the following (in the original paper, it was number {5})

$$H(C) = -(\Sigma_{(ii)} p_{ii} \ln p_{ii} - \Sigma_{(ih)} p_{ih} \ln p_{ih}) \qquad (2)$$

with (ii)=1,…, M, and (ih) = 1,…, M(M-1)/2. It is a combination of the Shannon's formula (see Gray[9]) where the pii and p_{ih} are calculated by the ratio between the cross product values (cii and cij) and their total of the upper or lower part, including the diagonal, of the co-occurrence matrix.

If $-\Sigma_{(ii)}\ p_{ii} \ln p_{ii}$ = H(D), i.e., the entropy of the diagonal of C(M, M), and $-\Sigma_{(ih)}\ p_{ih} \ln p_{ih}$ = H(T), i.e. the entropy of the upper or lower triangular part of C(M, M), we can write the formula (2) simply as H(D)-H(T). In terms of graph theory[10], H(D) is the entropy of the diagonal matrix of the nodes (D), and H(T) is the entropy of the upper (or lower) triangular part (T) of the adjacency matrix.

The outcome of formula (2) should be useful if correlated with the environmental factors in order to explore their effects on the uncertainty (or heterogeneity) of vegetation systems.

However, as influenced by Orlóci[11][12], I rather applied the formula of mutual information to C(M, M) to describe the spatial pattern in the grasslands of the Karst area[13] and to measure the similarity between vegetation types corresponding to dynamical states of the coastal vegetation described by Pignatti[14][15].

In the present paper, I apply formula (2) to some small ad hoc matrices X(M, N) and to some matrices obtained from simple graphs to test its capacity to quantify the pattern of graphs with respect to other used formulas.

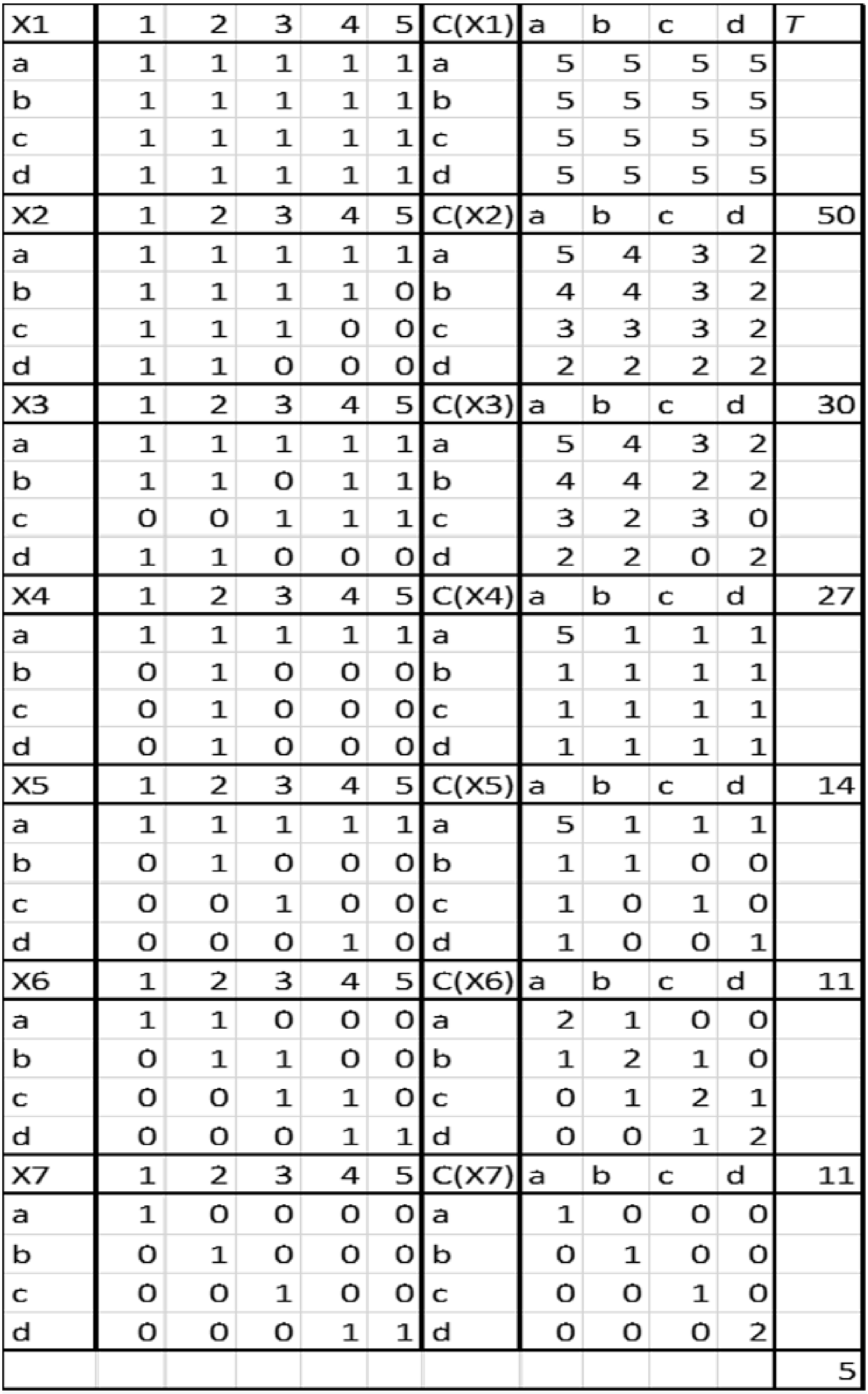
Data

To show the performance of formula (2), I used two sets of data. The first is presented in Table 1. It consists of 7 small matrices (X (M, N)), each with 4 rows (a, b, c, d), that are the components of the systems, and with 5 columns, representing the states of the systems. These matrices, X1,…, X7, give different tipologies of pairwise co-occurrence matrices, abbreviated by C(X1), …, C(X7) in Table 1. In this case, the nodes and edges of the corresponding graphs are weighted by the values obtained by the multiplication of each matrix by itself (formula 1)). For each matrix the Table indicates the column total that is entering in formula (2) to obtain the p_{ii} and p_{ih} for calculating the entropies H(D) and H(T).

If we consider the pairwise co-occurrence as an expression of the connection between the nodes representing the components in a graph, we can say that matrix C(X1) represents a complete graph with the nodes and edges of the same weight; C(X2), represents a graph where the connection is still complete, but the nodes and edges have different weights;

C(X3) represents a graph not completely connected, where the nodes of the graph have the same weight as those of C(X2), but the edges have different weights; C(X4) represents an extreme case of nestedness in which each component is linked to all others, but with connection between nodes weaker than those of the matrices C(X1) and CX(2); C(X5) represents a situation in which there is the minimal connection (M-1) between the nodes and where only node *a* is linked to all the others (strong centrality in the graph); C(X6) represents a situation in which there is the minimal connection between the nodes as in C(X5), but the nodes are connected only with 2 nodes at most. In this case, the graph is assuming the shape of a chain (these two last matrices represent two situations of the minimal connected graph as those of the graphs of Fig. 1 but with different centrality); C(X7) represents a completely disconnected situation, i.e., a graph with only nodes. In terms of beta diversity of Whittaker[16], i.e., the ratio between M and m, where m is the average number of components in the matrices X(M, N), it is the following: X1=1, X2=1,43, X3=1,54, X4=2,5, X5=2,5, X6=2,5 and X7=4. Three matrices have the same beta diversity (B=2.5), but they present quite different patterns.

The second data set is derived from the blackboard in Fig. 1, whose graphs were drawn by Will Hunting (a young mathematical genius interpreted by Matt Damon) in the movie “Good Will Hunting”. These graphs were chosen because I realized that they all have the same number of connections (M-1) (the edges of the graph), which represents the minimal connection, but they are all different as far as the degree of the nodes is concerned. They give rise easily (for this reason, I do not show them) to X(10,9) and C(10,10) matrices; those last ones are with the same trace (Dt=18) and the same total of the upper or lower triangular part of the co-occurrence matrix (Tt =9). Beside the co-occurrence matrices of these graphs (G), I considered also the co-occurrence matrix (the number 6 in Table 2) obtained by the graph corresponding to the one in which each node has at most only two edges, i.e., it is connected with only two nodes or only one (G6); topologically, it corresponds to the graph of matrix X6 in Table 1. Whittaker’s beta diversity of the X(10,9) matrices is equal to 5 for all of them, the average number of components all being equal to 2.



X1	1	2	3	4	5	C(X1)	a	b	c	d	*T*
a	1	1	1	1	1	a	5	5	5	5	
b	1	1	1	1	1	b	5	5	5	5	
c	1	1	1	1	1	c	5	5	5	5	
d	1	1	1	1	1	d	5	5	5	5	
X2	1	2	3	4	5	C(X2)	a	b	c	d	50
a	1	1	1	1	1	a	5	4	3	2	
b	1	1	1	1	0	b	4	4	3	2	
c	1	1	1	0	0	c	3	3	3	2	
d	1	1	0	0	0	d	2	2	2	2	
X3	1	2	3	4	5	C(X3)	a	b	c	d	30
a	1	1	1	1	1	a	5	4	3	2	
b	1	1	0	1	1	b	4	4	2	2	
c	0	0	1	1	1	c	3	2	3	0	
d	1	1	0	0	0	d	2	2	0	2	
X4	1	2	3	4	5	C(X4)	a	b	c	d	27
a	1	1	1	1	1	a	5	1	1	1	
b	0	1	0	0	0	b	1	1	1	1	
c	0	1	0	0	0	c	1	1	1	1	
d	0	1	0	0	0	d	1	1	1	1	
X5	1	2	3	4	5	C(X5)	a	b	c	d	14
a	1	1	1	1	1	a	5	1	1	1	
b	0	1	0	0	0	b	1	1	0	0	
c	0	0	1	0	0	c	1	0	1	0	
d	0	0	0	1	0	d	1	0	0	1	
X6	1	2	3	4	5	C(X6)	a	b	c	d	11
a	1	1	0	0	0	a	2	1	0	0	
b	0	1	1	0	0	b	1	2	1	0	
c	0	0	1	1	0	c	0	1	2	1	
d	0	0	0	1	1	d	0	0	1	2	
X7	1	2	3	4	5	C(X7)	a	b	c	d	11
a	1	0	0	0	0	a	1	0	0	0	
b	0	1	0	0	0	b	0	1	0	0	
c	0	0	1	0	0	c	0	0	1	0	
d	0	0	0	1	1	d	0	0	0	2	
											5

Table 1. Seven matrices X(M, N): X1,.., X7, giving rise to seven different co-occurrence matrices C (M, M): C(X1),…,

C(X7) of the components a, b, c, d (see text).

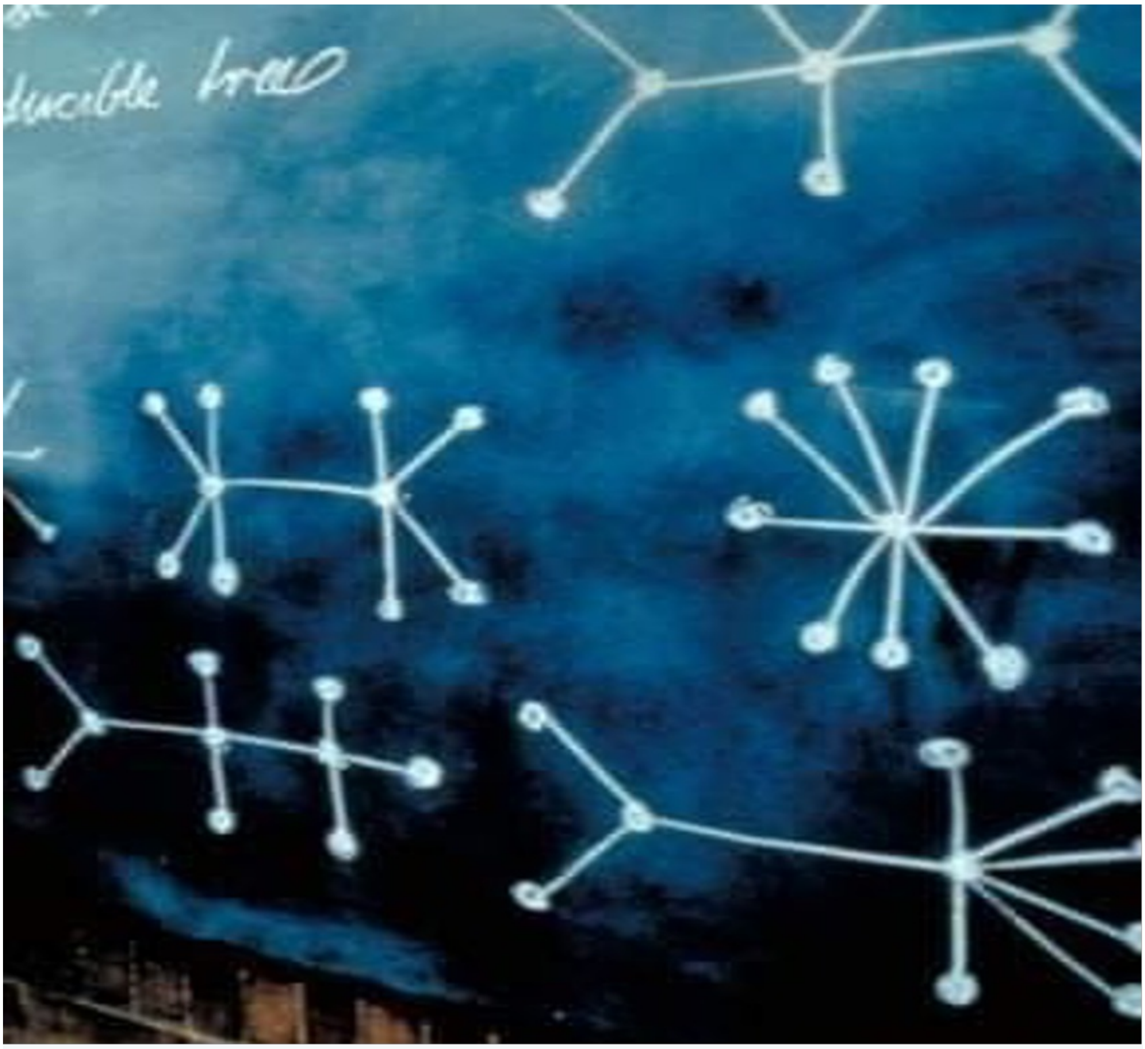


Figure 1. The 5 graphs (G) drawn by Will Hunting (a young mathematical genius interpreted by Matt Damon) in the movie Good Will Hunting, from which I obtained 5 co-occurrence matrices. They can be expressed as 10 by 9 data matrices and as 10 by 10 co-occurrence matrices that can be easily written. All of them have 10 nodes and 9 edges. In the Table 2 they are indicated with the letter G: G1, with 3 centres, is on the top right, although partially visible; G2 with 2 centres is the first one of line 2; G 3 with only one centre is the last in line 2. G4 with 3 centres and G5 with 2 centres are on line 3.

Methods

All the matrices of co-occurrence obtained from the X matrices in Table 1 and from the graphs of Fig. 1 represent different patterns of connection between the nodes of the corresponding graphs (as said before, only the patterns of the graph of matrix X6 and that of G6 of Table 2 are topologically similar, with each node in connection with at maximum 2 nodes). What we could expect from a good formula of connectance is that it would give different values for each different graph. Formula (2) quantifies in a weighted way the connections within a system: the lower the entropy, the higher the negentropy, the higher the connectance. This can be obtained by dividing the observed negentropy by the value of negentropy corresponding to the situation in which there is the highest number of connections. This corresponds to the graph with all connected nodes and with the same weight (or equivalence) of nodes and edges (Table 1, matrix X1). It is easy to show that the maximum value of negentropy is given by the following formula:

$$H(C)\text{ ref max } = -((2/(M+1))\ln(2/M(M+1)) - ((M-1)/(M+1))\ln(2/(M(M+1))) = -((3-M)/(M+1))\ln(2/(M(M+1)) \qquad (3)$$

The ratio between (2) and (3) could be considered a relative weighted measure of connectance (based on co-occurrence):

$$K(C) = H(C)/H(C)\text{ ref max} \qquad (4)$$

K(C) can be positive or negative; it is negative when H(C) is positive, i.e., when the entropy of the diagonal of the co-occurrence matrix is higher than the entropy of the upper or lower triangular part of the matrix (i.e., H(D)>H(T)).

In the paper of 1972, I proposed to calculate the maximum entropy of a community data matrix**X**(M, N) by the formula:

$$Hmax = -m\ln m/M \qquad (5)$$

where m is the average number of components for the N communities in**X**(M, N). I suggested this formula (number {7} in that paper) because it is unrealistic to think that a community would have only one component. In other words, each vegetation system or/and subsystem would have an entropy that depends on its average number of components in the stands by which it is described. The closer the average number of components is to the total number, the more homogeneous the vegetation system described by X(M, N), and the lower the entropy, or uncertainty, relative to the system's definition (the higher the negentropy). The uncertainty of a system of completely connected components would be zero. This formula is in fact equal to 0 when m=M, and it is ln M when m=1. If it is used to calculate the redundancy of a matrix (R(**X**(M, N)) as I suggested in 1972:

$$R(X(M,N) = 1 - H(C)/(Hmax) \qquad (6)$$

the values of redundancy R(**X**(M, N)) would become higher than 1 for H(C) negative (this happens when H(T) is higher than H(D)), and it will approach 2 as the absolute value of H(C) approaches Hmax. If Hmax is 0, i.e., when m=M, then H(C) is equal to H(C) ref max (formula 3), and R(X(M, N)) has an indeterminate value. In this case, the redundancy would be maximum. This can be viewed as a drawback of the formula; however, I think it useful to be compared with values obtained by K(C). It should be clear that when we are dealing with the triangular part of matrices of co-occurrence given by D+T (D=diagonal, T= triangular part withot diagonal), their maximum entropy values are equal to:

$$Hmax(D+T) = \ln M(M+1)/2 \qquad (7)$$

So I compared K(C) also with the ratio:

$$H(D+T)\text{ rel } = H(D+T)/Hmax(D+T) \qquad (8)$$

H(C) was compared also with the formula of Ricotta and Szeidl[17] that introduces in Shannon's formula the matrix of co-occurrence ρ between the components where the values of co-occurrence are transformed to the range [0,1]:

$$D(O) = -\Sigma_i p_i \ln(\Sigma j \neq i \rho_{ij} p_j) \qquad (9)$$

In this equation, p_i is one element of the vector P (1, M) that shows the proportions between the weights of the nodes, ρ_{ij} is the ij-th element in the co-occurrence matrix C(M, M), which is obtained by the Jaccard coefficient[18] applied between the

M components of the matrix X(M, N), p_j is the component j-th of the vector of the proportions of the weight of the M nodes P (1, M)^T transposed, i.e., P(M,1).

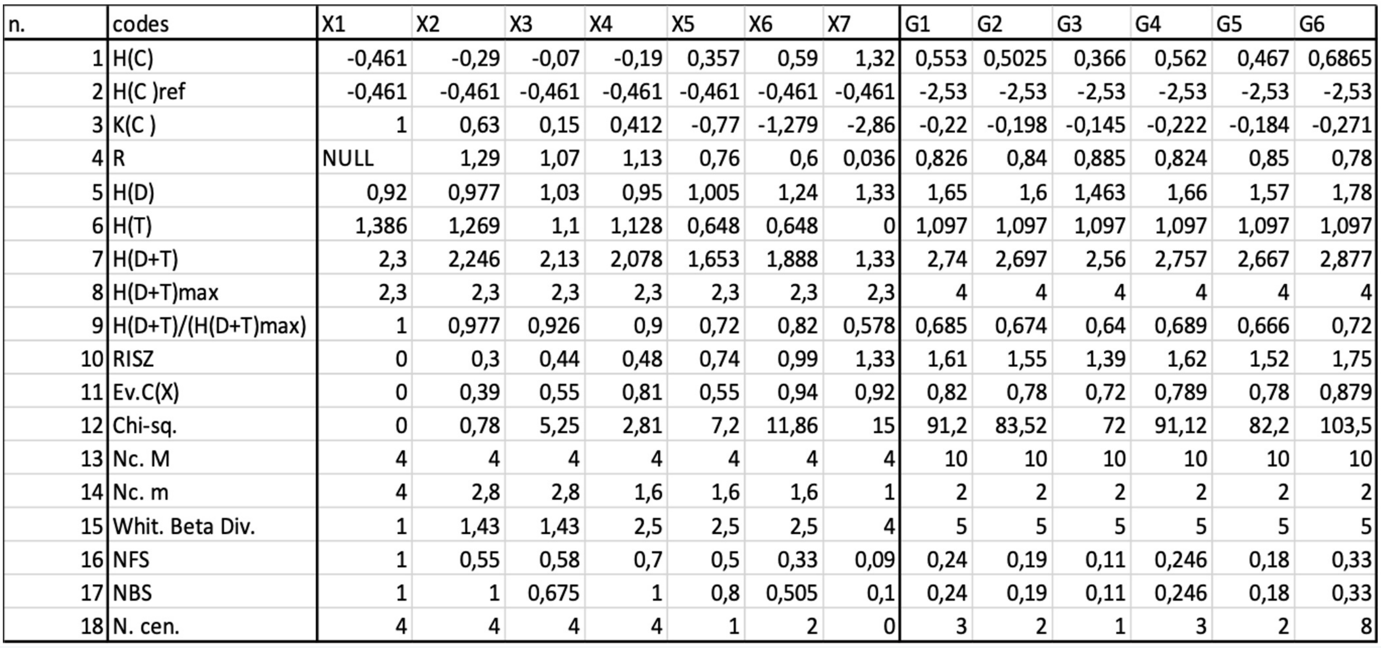
In summary, I have considered for each of the co-occurrence matrices, those obtained by the matrices X (Table 1) and those obtained by graphs (Fig. 1), the following parameters as listed in Table 2 of the results:

1. the H(C) obtained by formula (2). It indicates in absolute terms how much the entropy of the edges H(T) is higher with respect to the entropy H(D) of the nodes: the higher the negative values in absolute terms, the higher the connection of the M components;
2. the H(C) ref max given by formula (3);
3. the K(C) obtained as the ratio between H (C) and H(C) ref max according to formula (4). It indicates a relative measure of connection (connectance weighted by nodes and edges) between the M components; the higher its value, the higher the connectance;
4. the redundancy (R) according to formula (6);
5. the H(D), i.e., the entropy of the diagonal D of the co-occurrence matrices;
6. the H(T), i.e., entropy of the upper or lower triangular part T of the co-occurrence matrices of Table 1 and those obtained by graphs of Fig. 1;
7. the H(D+T), i.e., the entropy of the triangular matrix obtained by D+T;
8. H(D+T) max, i.e., the maximal entropy of the triangular matrices obtained by (D + T), obtained by formula (7);
9. the ratio H(D+T)/(H(D+T) max) (formula (8)), i.e., the relative entropy of matrix (D+T);
10. the entropy of Ricotta and Szeidel's (RISZ) by formula (9);
11. the evenness of the eigenvalues (Eλ) of the co-occurrence matrices[19], it indicates how much the values of the matrix are concentrated on the diagonal. It is maximum when there are no connections (no edges) and the nodes have the same weight. In this case, the diagonal values are directly the eigenvalues of the matrices, and the neg-entropy of the eigenvalues is obviously equal to the entropy of the nodes based on their weight. The evenness becomes lower as the nodes are connected;
12. the chi-square of the co-occurrence matrices which, as shown by Kullback[20], approximates twice the mutual information (cf. Orlóci[12], Feoli et al.[21] for applications in phytosociology). As in the case of Eλ, it is maximum when there are only values in the diagonal of the matrix and they are all equal; the chi-square is zero when the co-occurrence matrix has all equal values;
13. the number of components (M);
14. the average number of components (m);
15. Whittaker's Beta Diversity[16], i.e., the ratio between M and m;
16. the nested free average similarity (NFS) and
17. the nested based similarity (NBS)[22][23]. In both cases 16) and 17), the similarity has been calculated by considering the Jaccard similarity function[18]. It is to stress that for vectors given by only two components, such as those obtained by the graphs in Fig. 1, the two values (NBS and NFS) are identical;
18. and finally, the number of centres of each graph obtained by all the co-occurrence matrices.

Between these parameters, I have calculated the Pearson correlation coefficient, and to the correlation matrix, I have applied the ranking procedure suggested by Orloci[12] for weighting variables. I did this procedure following the thought that a good parameter, among those chosen to describe the connection pattern of graphs corresponding to co-occurrence matrices, should be the one that would explain most of the variability of the other parameters. Finally, I calculated the similarity between the graphs of the matrices and between the graphs of Fig. 1, both on the basis of all the parameters, excluding those that are constant, and considering only the single parameter which explains the maximum cumulative variance with respect to all the others, by the index of Gower (see Podani[24]), and I classified separately the graphs of the 7 matrices and those of Fig. 1. All the computations were done by the program MATEDIT[25].

Results

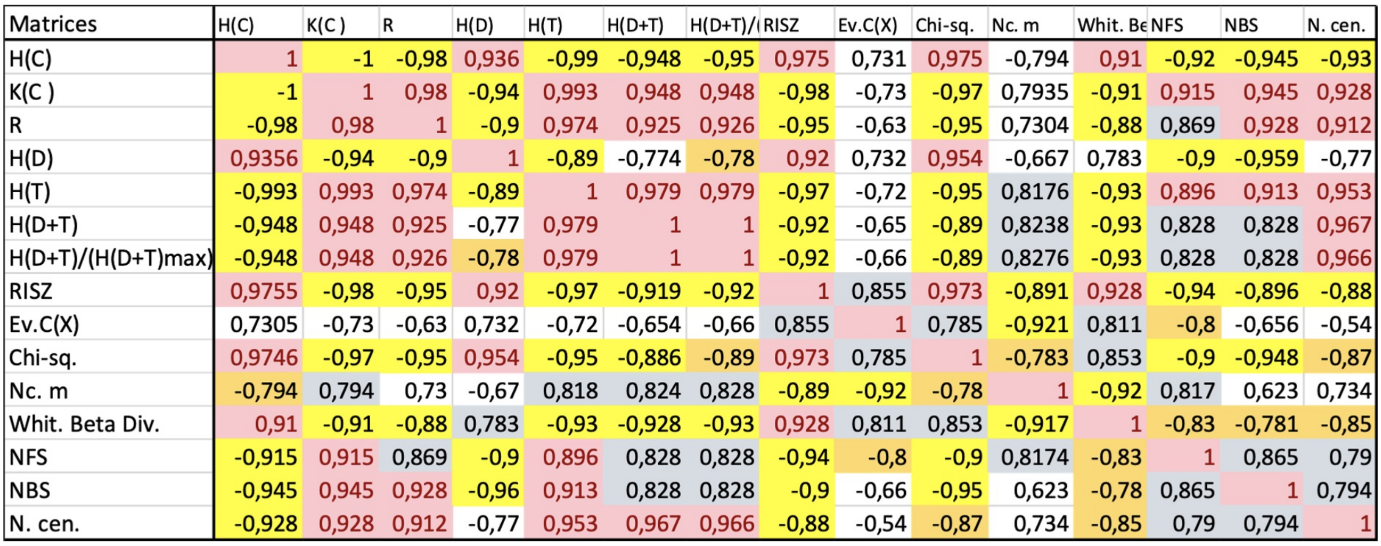
Table 2 shows the values of the 18 parameters calculated for each of the 7 matrices (X) in Table 1 and for the co-occurrence matrices obtained for the graphs (G). Table 3 and Table 4 show the Pearson correlation coefficients between the considered parameters (the constants are excluded). Table 5 shows the results of the ranking procedure applied to the matrices in Tables 3 and 4. It is clear from these tables that the correlation between H(C) and K(C) with all the other parameters is significant at a very high level of probability, i.e., 0.01 (pink colour for positive correlation, yellow colour for negative ones). In proportion, the significative correlations are more frequent for the co-occurrence matrices obtained by graphs; this can be explained by the fact that graphs give a more homogeneous set concerning the connections, which are in all cases 9.



n.	codes	X1	X2	X3	X4	X5	X6	X7	G1	G2	G3	G4	G5	G6
1	H(C)	-0,461	-0,29	-0,07	-0,19	0,357	0,59	1,32	0,553	0,5025	0,366	0,562	0,467	0,6865
2	H(C)ref	-0,461	-0,461	-0,461	-0,461	-0,461	-0,461	-0,461	-2,53	-2,53	-2,53	-2,53	-2,53	-2,53
3	K(C)	1	0,63	0,15	0,412	-0,77	-1,279	-2,86	-0,22	-0,198	-0,145	-0,222	-0,184	-0,271
4	R	NULL	1,29	1,07	1,13	0,76	0,6	0,036	0,826	0,84	0,885	0,824	0,85	0,78
5	H(D)	0,92	0,977	1,03	0,95	1,005	1,24	1,33	1,65	1,6	1,463	1,66	1,57	1,78
6	H(T)	1,386	1,269	1,1	1,128	0,648	0,648	0	1,097	1,097	1,097	1,097	1,097	1,097
7	H(D+T)	2,3	2,246	2,13	2,078	1,653	1,888	1,33	2,74	2,697	2,56	2,757	2,667	2,877
8	H(D+T)max	2,3	2,3	2,3	2,3	2,3	2,3	2,3	4	4	4	4	4	4
9	H(D+T)/(H(D+T)max)	1	0,977	0,926	0,9	0,72	0,82	0,578	0,685	0,674	0,64	0,689	0,666	0,72
10	RISZ	0	0,3	0,44	0,48	0,74	0,99	1,33	1,61	1,55	1,39	1,62	1,52	1,75
11	Ev.C(X)	0	0,39	0,55	0,81	0,55	0,94	0,92	0,82	0,78	0,72	0,789	0,78	0,879
12	Chi-sq.	0	0,78	5,25	2,81	7,2	11,86	15	91,2	83,52	72	91,12	82,2	103,5
13	Nc. M	4	4	4	4	4	4	4	10	10	10	10	10	10
14	Nc. m	4	2,8	2,8	1,6	1,6	1,6	1	2	2	2	2	2	2
15	Whit. Beta Div.	1	1,43	1,43	2,5	2,5	2,5	4	5	5	5	5	5	5
16	NFS	1	0,55	0,58	0,7	0,5	0,33	0,09	0,24	0,19	0,11	0,246	0,18	0,33
17	NBS	1	1	0,675	1	0,8	0,505	0,1	0,24	0,19	0,11	0,246	0,18	0,33
18	N. cen.	4	4	4	4	1	2	0	3	2	1	3	2	8

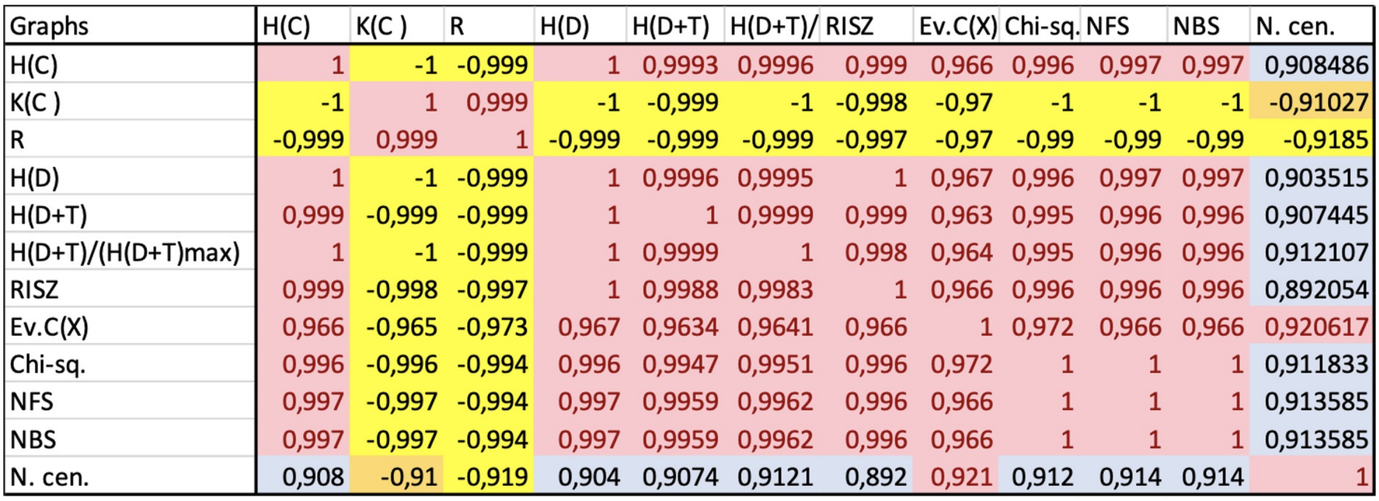
Table 2. Values of the 18 parameters for each of the matrices Xi in Table 1 (matrices) and for the matrices obtained from the graphs of Fig. 1 (graphs G). Symbols or abbreviations: 1) H (C)= entropy of the co-occurrence matrices given by formula 2); 2) H(C) ref max given by formula 3); 3) K(C)= ratio between H (C) and H(C) ref max according to formula 5); 4) R= redundancy according to formula 7); 5) H(D) = entropy of the diagonal D of the co-occurrence matrices; 6) H(T) = entropy of the upper or lower triangular part T of the co-occurrence matrices; 7) H(D+T)= entropy of the triangular matrix obtained by D+T; 8) H(D+T) max= the maximal entropy of the triangular matrices obtained by (D + T); 9) H(D+T)/(H(D+T) max)=

relative entropy of matrix (D+T); 10) RISZ= Ricotta and Szeidel's entropy formula[17]; 11) Ev.C(X)=evenness of the eigenvalues of the co-occurrence matrices[19]; 12) Chi-sq.= Chi-square of the co-occurrence matrices; 13) Nc.M= number of components M; 14) Nc. m= average number of components; 15) Whit.Beta Div = Whittaker's Beta Diversity =.; 16) NFS= nested free average similarity; 17) NBS= nested based similarity; 18) N. cen.= number of centres.



Matrices	H(C)	K(C)	R	H(D)	H(T)	H(D+T)	H(D+T)/(	RISZ	Ev.C(X)	Chi-sq.	Nc. m	Whit. Be	NFS	NBS	N. cen.
H(C)	1	-1	-0,98	0,936	-0,99	-0,948	-0,95	0,975	0,731	0,975	-0,794	0,91	-0,92	-0,945	-0,93
K(C)	-1	1	0,98	-0,94	0,993	0,948	0,948	-0,98	-0,73	-0,97	0,7935	-0,91	0,915	0,945	0,928
R	-0,98	0,98	1	-0,9	0,974	0,925	0,926	-0,95	-0,63	-0,95	0,7304	-0,88	0,869	0,928	0,912
H(D)	0,9356	-0,94	-0,9	1	-0,89	-0,774	-0,78	0,92	0,732	0,954	-0,667	0,783	-0,9	-0,959	-0,77
H(T)	-0,993	0,993	0,974	-0,89	1	0,979	0,979	-0,97	-0,72	-0,95	0,8176	-0,93	0,896	0,913	0,953
H(D+T)	-0,948	0,948	0,925	-0,77	0,979	1	1	-0,92	-0,65	-0,89	0,8238	-0,93	0,828	0,828	0,967
H(D+T)/(H(D+T)max)	-0,948	0,948	0,926	-0,78	0,979	1	1	-0,92	-0,66	-0,89	0,8276	-0,93	0,828	0,828	0,966
RISZ	0,9755	-0,98	-0,95	0,92	-0,97	-0,919	-0,92	1	0,855	0,973	-0,891	0,928	-0,94	-0,896	-0,88
Ev.C(X)	0,7305	-0,73	-0,63	0,732	-0,72	-0,654	-0,66	0,855	1	0,785	-0,921	0,811	-0,8	-0,656	-0,54
Chi-sq.	0,9746	-0,97	-0,95	0,954	-0,95	-0,886	-0,89	0,973	0,785	1	-0,783	0,853	-0,9	-0,948	-0,87
Nc. m	-0,794	0,794	0,73	-0,67	0,818	0,824	0,828	-0,89	-0,92	-0,78	1	-0,92	0,817	0,623	0,734
Whit. Beta Div.	0,91	-0,91	-0,88	0,783	-0,93	-0,928	-0,93	0,928	0,811	0,853	-0,917	1	-0,83	-0,781	-0,85
NFS	-0,915	0,915	0,869	-0,9	0,896	0,828	0,828	-0,94	-0,8	-0,9	0,8174	-0,83	1	0,865	0,79
NBS	-0,945	0,945	0,928	-0,96	0,913	0,828	0,828	-0,9	-0,66	-0,95	0,623	-0,78	0,865	1	0,794
N. cen.	-0,928	0,928	0,912	-0,77	0,953	0,967	0,966	-0,88	-0,54	-0,87	0,734	-0,85	0,79	0,794	1

Table 3. Correlations between the parameters of the matrices (X1,…X7) in Table 2 (p=0.01, r= 0.875; p=0.05, r=0.775). The 3 constants, H(C) ref, H(D+T) max, and Nc.M, are excluded from the table. Negative and positive correlations for probability lower or equal to 0.01 are respectively in yellow and pink; correlations for p lower or equal 0.05 and greater than 0.01 are in light blue.



Graphs	H(C)	K(C)	R	H(D)	H(D+T)	H(D+T)/	RISZ	Ev.C(X)	Chi-sq.	NFS	NBS	N. cen.
H(C)	1	-1	-0,999	1	0,9993	0,9996	0,999	0,966	0,996	0,997	0,997	0,908486
K(C)	-1	1	0,999	-1	-0,999	-1	-0,998	-0,97	-1	-1	-1	-0,91027
R	-0,999	0,999	1	-0,999	-0,999	-0,999	-0,997	-0,97	-0,99	-0,99	-0,99	-0,9185
H(D)	1	-1	-0,999	1	0,9996	0,9995	1	0,967	0,996	0,997	0,997	0,903515
H(D+T)	0,999	-0,999	-0,999	1	1	0,9999	0,999	0,963	0,995	0,996	0,996	0,907445
H(D+T)/(H(D+T)max)	1	-1	-0,999	1	0,9999	1	0,998	0,964	0,995	0,996	0,996	0,912107
RISZ	0,999	-0,998	-0,997	1	0,9988	0,9983	1	0,966	0,996	0,996	0,996	0,892054
Ev.C(X)	0,966	-0,965	-0,973	0,967	0,9634	0,9641	0,966	1	0,972	0,966	0,966	0,920617
Chi-sq.	0,996	-0,996	-0,994	0,996	0,9947	0,9951	0,996	0,972	1	1	1	0,911833
NFS	0,997	-0,997	-0,994	0,997	0,9959	0,9962	0,996	0,966	1	1	1	0,913585
NBS	0,997	-0,997	-0,994	0,997	0,9959	0,9962	0,996	0,966	1	1	1	0,913585
N. cen.	0,908	-0,91	-0,919	0,904	0,9074	0,9121	0,892	0,921	0,912	0,914	0,914	1

Table 4. Correlations between the parameters of the graphs in Table 2 (p=0.01, r=0.917; p=0.05, r=0.811). The constants, H(C) ref, H(T), H(D+T) max, Nc.M, Nc.m, Whit. Beta Div., are excluded from the table. Negative and positive correlations for probability lower or equal to 0.01 are in yellow and pink, respectively; correlations for probability lower or equal 0.05 and greater than 0.01 are in light blue.

By comparing the two correlation matrices, we can see that the graphs of Fig. 1 show that the correlations between the parameters are all significant, at least at the level of probability of 0.05, while the correlations between the parameters calculated for Table 1 are not all significant. In both cases, 5 parameters are enough to explain 100% of the total variance.

Rank Matrices	Sum of sq.	% spec.	% cum.	Rank Graphs	Sum of sq.	% spec.	% cum.
H(C)	13,1051	87,3674	87,3674	R	11,7386	97,822	97,8219
Nc. m	0,9429	6,2865	93,654	N. cen.	0,1675	1,3962	99,2181
K(C)	0,7886	4,2573	97,911	Ev.C(X)	0,05221	0,4351	99,65
Ev.C(X)	0,0622	1,1526	99,06	H(D+T)/(H(D+T)max)	0,0402	0,3353	99,9886
RISZ	0,0231	0,9395	100	NFS	0,0014	0,0114	100

Table 5. Results of the ranking procedure suggested by Orlóci [12], applied respectively to the matrix of Table 3 (Rank Matrices) and to the matrix of Table 4 (Rank Graphs). Sum of sq. = Sum of squares; %spec. = sum of squares specific to the single parameter with respect to the others; % cum. = cumulative sum of squares.

From Table 5, it is clear that for the matrices of Table 1, H(C) is the most redundant parameter, i.e., the one that explains better than others the pattern of the graphs, while for the graphs of Fig. 1 and Table 2, the most redundant parameter is the redundancy R (X(M, N)) of formula 6), which explains better the variability of the others in terms of sum of squares.

The classification of the 7 matrices X1,..., X7 on the basis of all the parameters and on the basis of H(C), that is, the parameter with the highest specific sum of squares, is presented by the dendrograms of Fig. 2 a) and b). These are obtained by complete linkage clustering and show almost equal topology both for a) and b); only the position of matrices X3 and X4 is changed within the same main cluster (X2, X3, X4). This proves that H(C) is a good parameter that can explain all the variability of the other parameters. The classification of the graphs of Fig. 1 based on all the parameters and only on the redundancy (R) of formula 6) shows dendrograms c) and d) that are topologically identical. In any case, thanks to the very high correlation between R(X(M, N)) and H(C) (see Tables 3 and 4), the dendrogram e), obtained by using H(C), is topologically identical to dendrograms c) and d).

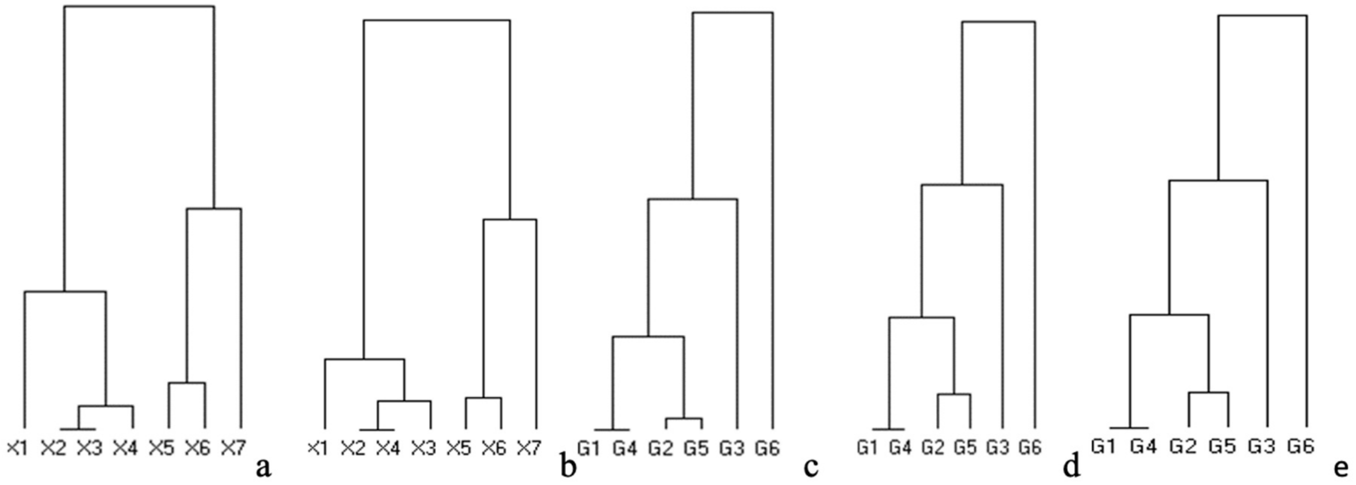


Figure 2. Classification of the seven graphs originated by the matrices X of Table 1 by using all the parameters in Table 2 (a) and by using only H(C) (b), and classification of the graphs of Fig. 1 and Table 2 by using all the parameters (c) and by using only the redundancy of formula 6) (d). The dendrogram (e) shows the classification of the six graphs (G) using only H(C).

Discussion and Conclusion

- *Co-occurrence matrices, graphs, connections, connectivity, connectance, and negentropy as a conceptual tool to define community patterns*

I think that, today, and among ecologists, it is trivial to recall from Encyclopedia Britannica[26] that: “What makes a system a system, and not simply a collection of elements, is the connections and interactions between its components, as well as the effect that these linkages have on its behaviour”, but I consider it useful to mention the concept anyway.

In general terms, every entity can be considered a system when it is seen as a set of connected components by one or all of the following relationships: contact, exchange of materials and energy, and exchange of information. See Allen and Starr[27] for a discussion of connectedness, connectivity, and connectance in the context of complex systems. I want to stress here that systems may be open or closed, static or dynamic, and the connections between their components may be direct or indirect, i.e., via interposed components.

When we analyse ecological communities, we have to take into consideration that the concept of coexistence is strictly related to the spatial and temporal scales. It is obvious that if I considered sampling units of a few cm^2, the co-occurrence would be realized only for the microbes or small species that are found in these sampling units; if I considered sampling units of 1 km^2, I would find in them several species of microbes, plants, and animals of different sizes. It is instructive to visit the web with the keywords: scale, species-area curves, biodiversity, to have a lot of information on the area–species richness relationship. The time interval is also very important, especially in the study of animal communities. If I stay in a site just for a few hours, I can see very few animals, but if I observe the area for days, then I can record several animals that are visiting the area for grazing or hunting. Even for plants, time could be important; annual species are visible in some periods of the year and not in others.

Having said this, I want to stress also that when we complete a list of species or traits of a given area (a sampling unit, stands, traps, etc.), we have originated a vector of co-occurrence. This is the basic unit in the study of variation of ecological communities with respect to environmental heterogeneity and/or gradients. It may be considered alone or together with other N-1 vectors that we could call diversity vectors of a matrix X(M, N). This matrix, with vectors j from 1 to N, can be considered the primary co-occurrence matrix that can be used to obtain a pairwise co-occurrence matrix by formula 1). The co-occurrence matrices C(M, M) may be considered as one of the quantitative expressions of the pattern of coexistence of the components of a system. It is obvious that just the co-occurrence of given M components of any type of system, as obtained from formula 1), would not explain the interactions between them; experiments and/or careful observations are necessary to understand the nature of co-occurrence (e.g., Bever[28], Adler et al.[29], and references therein). It is clear that a matrix of co-occurrence may have different meanings, but from a mathematical point of view, it is always a symmetric matrix that can be used to construct a graph according to graph theory[10]. In this paper, I consider the pairwise co-occurrence matrix just as a mathematical expression, and I do not want to revise the vast literature on coexistence of species or other community components where the concept of co-occurrence is implicit. This literature spans from the biogeography of birds to different ecological aspects of food webs, soil microbiology, and landscape ecology (e.g., Diamond[30], Pimm[31]; Jordan[32], Jordan[33]; Jordan et al.[34], Scotti and Jordan[35]; Heleno et al.[36], Veech[37], Poisot et al.[38], van Altena et al.[39], Turnbull et al.[40], Liccari et al.[41], and references therein). I do not want to review all the formulas and models related to co-occurrence, but I want just to say that the study of the connection between the system components led to the concept of connectivity (see Turnbull et al.[40] for a deep discussion about its meanings in different disciplines), and to that of connectance (cf. Allen and Starr[27]). The first is an absolute measure of the consistency of a graph, the second is a relative measure of connections with respect to what I call the maximum diversity of connections. With diversity of connections, I mean the combination between the richness of the nodes and the edges and the proportion of their importance. The maximum diversity of connections is realized when all the nodes of a graph are connected with all the others and nodes and edges have the same weight. The diagonal component (D) and the triangular upper or lower part of a C(M, M) matrix (T) are representing the triangular matrix of the diversity of connections with M(M+1)/2 maximum number of cells to be occupied by non-zero values. When we use a co-occurrence matrix to obtain a graph of the connections between the M components of a system, the nodes and edges are always weighted as a consequence of C(M, M) being the self-product of the matrix X(M, N). It is obvious that if X(M, N) is a binary matrix[42], Wilson[43]), C(M, M) is a symmetric matrix in which the diagonal is showing the frequency of each of the M components and the elements outside the diagonal are the frequency with which each component occurs with each other component (pairwise co-occurrence); in this context, I do not find the room to discuss about null models on which there is a plethora of papers (e.g., Gotelli[44], Gotelli[45]).

The novelty of my proposal in 1972, with respect to the applications of information theory in ecology, by the seminal works of Margalef[46][47], Orlóci[11], and Lausi[48], is the fact that I suggested the formula of neg-entropy specifically for the upper or lower triangular part—diagonal included—of the pairwise co-occurrence matrices C(M, M), rather than for the usual single vectors X(M,1), as is done by the application of several indices of diversity. In this way, the formula 2) can be interpreted as a diversity measure based on Shannon’s index that includes a quantification of the connection between the components of the communities and, if we consider the co-occurrence a way to express connections, the formula 4), which is a relativization of formula 2), is a measure of weighted connectance. It is true that Margalef and Gutierrez[49] suggested a method to incorporate connectance in the diversity measures; however, they do not consider X(M, N) matrices, but they applied a formula similar to that proposed by Rao[50] to the matrix of the cross product of the M elements of a single diversity vector. In this way, the graph is supposed to be completely connected, and different weights are given to the nodes as a consequence of the scalar product between the values of the vector X(M,1). However, I do not think that we should accept the idea of complete connections between all the species of a community on the basis of a single diversity vector, being the ecological communities subjected to great variability along ecoclines and ecotones[51][52].

The formula (2) is an expression of negentropy because it depends on H(T), which is a measure of the links or connections between the M components in an X(M, N) matrix, a direct measure of their interdependence and/or cohesion: the higher H(T) is, the higher the homogeneity of the system represented by X(M, N), and the lower its entropy, i.e., its uncertainty. It is important to stress that the interpretation of the entropy of a co-occurrence matrix is different from the interpretation of the entropy of a diversity vector X(M,1). The formula has positive values only when H(D)>H(T), it is equal to zero if H(D)=H(T), and it has a negative value when H(T)> H(D). It is clear that if we consider the negative values of entropy, they are expressing a neg-entropy, i.e., the contrary of entropy and thus the contrary of uncertainty. The smaller H(D) is and the higher H(T) is, the higher the neg-entropy of H(C)) and the smaller the entropy. In summary, if we consider the co-occurrence values between the M components of a system as measures of their connection, the entropy gives a value of such a connection in positive or negative terms: the lower the entropy, the higher the neg-entropy of the system, i.e., its cohesion and predictability. In this paper, I considered two other relevant parameters to measure the uncertainty of a co-occurrence matrix, such as H(D)+H(T)/ H(D+T) max and the Ricotta and Szeidl[17] entropy (formula 9)), and two parameters of the primary matrices of co-occurrence X(M, N) that are the average nested similarity and the average free nested similarity. The Pearson correlation between them has shown that all these 4 parameters are highly correlated (positively or negatively), so the following question arises automatically: Why choose the H(C)-based ones, e.g., K(C) or R?. The answer is simple: they put in evidence directly the difference between the entropy of the nodes and the entropy of the edges of the graphs corresponding to the co-occurrence matrices, and because they are showing the highest capacity for explaining the variability of the other parameters.

I think and I suggest that the co-occurrence between the living components of ecosystems could be calculated at different hierarchical levels and could be interpreted always as an expression of connections between the components. In community ecology (the study of ecological communities), the idea to characterize an ecological system by parametrizing the links between the species (or other characters: traits) within the combinations that could characterize community types at different hierarchical levels is not yet very well explored; for this reason, I would like to send the interested reader to the views of Aleksandrova[53] and Dale[54] and references therein, since they explicitly address the idea of hierarchical combinations. With this, I want to conclude that a matrix of co-occurrence can be obtained from community tables irrespective of the hierarchical level of the N vectors of the matrices X(M, N) and that formula 2) can help in quantifying the pattern of the coexistence of species or traits at different hierarchical levels of ecological communities. In this respect, I would like to remember the paper of Wilson[55], in which he summarizes twelve theories of co-existence for plant communities. I think that it would be interesting to challenge these theories in other types of ecological communities where the hierarchical pattern is not yet explored in a syntaxonomical sense, such as in phytosociology[56][57], notwithstanding the stimulating book of Allen and Starr[27] on hierarchy as a context for mathematical modelling.

Acknowledgements

Many thanks are due to Cornelia Breitkopf, Zafer Aslan, Janos Podani, and the Queios Editorial Board for their comments, suggestions and corrections.

References

1. a, b *Feoli E (1972) Rudimenti della teoria dell'informazione in fitosociologia. Inform Bot Ital 4:202-208.*
2. ^ *Barkman JJ (1979) The investigation of vegetation texture and structure. In: MJA. Werger (ed.) The study of Vegetation. Junk, The Hague, Boston.*

3. ^Box EO (1981) Macroclimate and plant forms: an introduction to predictive modelling in phytogeography. Task for Vegetation Science. 1. Dr. W. Junk Publisher, The Hague.
4. ^Feoli E (1984) Some aspects of classification and ordination of vegetation data in perspective. Studia Geobot 4:7–21.
5. ^Orlóci L, Orlóci M (1985). "Comparison of communities without the use of species: model and examples". Ann. Bot.. 43:275–285.
6. ^Pillar V, Orlóci L (1993). Character-Based Community Analysis: The Theory and an Application Program. SPB Academic Publishing bv, The Hague, The Netherlands.
7. ^Kraft NJ, Godoy O, Levine JM. Plant functional traits and the multidimensional nature of species coexistence. Proc Natl Acad Sci U S A. 2015;112(3):797-802. doi: 10.1073/pnas.1413650112.
8. ^Orlóci L (2020). "Statistical quantum ecology. Essay on the resonator complex model of the vegetation stand". SCADA Publishing, Canada.
9. ^Gray R M (2023) Entropy and Information Theory, Stanford University.
10. a, bDiestel R (2017) Graph Theory. 5th ed. Springer Verlag, Heidelberg.
11. a, bOrlóci L (1968). "Information analysis in phytosociology: partition, classification and prediction". J. Theor. Biol.. 20:271-284.
12. a, b, c, dOrlóci L (1978). Multivariate Analysis in Vegetation Research. 2nd ed. Dr. Junk, The Hague.
13. ^Feoli E, Feoli-Chiapella L, Ganis P, Sorge A (1980) Spatial pattern analysis of abandoned grasslands of the Karst region by Trieste and Gorizia. Studia Geobot 1 (1), 213-221.
14. ^Pignatti S (1960). "Ricerche sull'ecologia e sul popolamento delle dune del litorale di Venezia. Il popolamento vegetale". Bull Mus Civ St Nat Venezia. 12:61–142.
15. ^Feoli E, Scoppola A (1980) Analisi informazionale degli schemi di dinamica della vegetazione. Un esempio sul popolamento vegetale delle dune di Venezia. Giorn Bot Ital 114:227-236.
16. a, bWhittaker RH (1972). "Evolution and measurement of species diversity". Taxon. 21: 213–251.
17. a, b, cRicotta C, Szeidl L (2006). "Towards a unifying approach to diversity measures: bridging the gap between Shannon entropy and Rao's quadratic index". Theor. Popul. Biol.. 70:237–243.
18. a, bPodani J (2022). "The wonder of the Jaccard coefficient: from alpine floras to bipartite networks". Fl. Medit.. 31 (Special Issue):105-123. doi:10.7320/FlMedit31SI.105.
19. a, bFeoli E, Ganis P (2021) Similarity, classification and diversity an Eternal Golden Braid in quantitative vegetation studies. Fl Medit 31 (Special Issue):23-41. doi:10.7320/FlMedit31SI.023.
20. ^Kullback S (1959). Information Theory and Statistics. Wiley, New York.
21. ^Feoli E, Lagonegro M, Orlóci L (1984) Information Analysis of Vegetation Data. Dr. W. Junk Publishers, The Hague.
22. ^Ulrich W, Almeida-Neto M, Gotelli NJ (2009). "A consumer's guide to nestedness analysis". Oikos. 118:3-17.
23. ^Feoli E, Ganis P, Ibáñez JJ, R Pérez-Gómez (2019) On the use of nestedness-based similarity functions (NBSF) to classify and/or order operational geographic units (OGUs). Community Ecology 20 (3): 223-229.
24. ^Podani J (2000). Introduction to the Exploration of Multivariate Biological Data. Backhuys Publishers, Leiden.

25. ^Burba N, Feoli E, Malaroda M (2008) MATEDIT: A software tool to integrate information in decision making processes. In: Neves R, Baretta JW, Mateus M (eds) Perspectives on Integrated Coastal Management in South America. IST Press, Lisbon, Portugal.
26. ^Encyclopedia Britannica (https://www.britannica.com/science/complexity-scientific-theory/Connectivity)
27. a, b, c Allen TFH, Starr TB (1982) Hierarchy. Perspectives for Ecological Complexity. The University of Chicago Press. Chicago and London.
28. ^Bever JD (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. New Phytol 157:465–473.
29. ^Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, Meiners JM, Tredennick AT, Veblen KE (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. Ecol Lett 21:1319–1329.
30. ^Diamond J (1975) Assembly of species communities. In: Ecology and evolution of communities, M. Cody and J. Diamond (eds.). Belknap Cambridge, Massachusetts. p. 342-444.
31. ^Pimm SL (1984). "The Complexity and Stability of Ecosystems". Nature. 307(5949):321-326.
32. ^Jordán F (2001) Seasonal changes in the positional importance of components in the trophic flow network of the Chesapeake Bay. J. Marine Syst. 27: 289-300.
33. ^Jordán, F. (2009) Keystone species and food webs. Phil. Trans. R. Soc. B 364: 1733-1741.
34. ^Jordán F, Benedek Z, Podani J (2007). "Quantifying positional importance in food webs: a comparison of centrality indices". Ecological Modelling. 205(1):270-275.
35. ^Scotti M, Jordán F (2010). "Relationships between centrality indices and trophic levels in food webs". Community Ecology. 11:59-67.
36. ^Heleno R, Devoto M , Pocock M (2012) Connectance of species interaction networks and conservation value: Is it any good to be well connected? Ecological Indicators 14 (1): 7-10.
37. ^Veech JA (2013). "A probabilistic model for analysing species co-occurrence". Global Ecology and Biogeography. 22: 252–260.
38. ^Poisot T, Stouffer DB, Gravel D. Beyond species: why ecological interaction networks vary in space and time. Oikos. 2015;124:243-51.
39. ^van Altena C, Hemerik L, de Ruiter PC (2016). "Food web stability and weighted connectance: the complexity-stability debate revisited". Theoretical Ecology. 9:49-58. doi:10.1007/s12080-015-0291-7.
40. a, b Turnbull L, Hütt MT, Ioannides AA, Kininmonth S, Poeppl R, Tockner K, Bracken LJ, Keesstra S, Liu L, Rens Masselink R, Parsons AJ (2018). "Connectivity and complex systems: learning from a multi-disciplinary perspective". Applied Network Science. 3:11. doi:10.1007/s41109-018-0067-2.
41. ^Liccari F, Boscutti F, Bacaro G, Sigura M (2022). "Connectivity, landscape structure, and plant diversity across agricultural landscapes: novel insight into effective ecological network planning". Journal of Environmental Management. 317:115358. doi:10.1016/j.jenvman.2022.115358. PMID 35636109.

42. ^*Avena G, Blasi C, Feoli E, Scoppola A (1981) Measurement of the predictive value of species lists for species cover in phytosociological samples. Vegetatio 45:77–84.*

43. ^*Wilson JB (2012). "Species presence/absence sometimes represents a plant community as well as species abundances do, or better". Journal of Vegetation Science. 23: 1013–1023.*

44. ^*Gotelli N J (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621.*

45. ^*Gotelli N J (2001) Research frontiers in null model analysis. Global Ecology and Biogeography Letters 10:337–343.*

46. ^*Margalef R (1958). "Information Theory in ecology". In: L. van Bertalanffy and Rapoport (eds), General Systems, Yearbook of the Society for General System Research. 3:36-71.*

47. ^*Margalef R (1968). Perspectives in Ecological Theory. Univ, Chicago Press, Chicago.*

48. ^*Lausi D (1970). "Die Logik der Pflanzensoziologischen Vegetaionanalyse- Ein Deutungsversuch". Berict uber das Internat. Symposium in Rinteln, Den Haag.*

49. ^*Margalef R, Gutierrez E (1983). "How to Introduce Connectance in the Frame of an Expression for Diversity". The American Naturalist. 121(5):601-607.*

50. ^*Rao CR (1982). "Diversity and dissimilarity measurements: a unified approach". Theor. Popul. Biol.. 21:24–43.*

51. ^*Whittaker RH (1975). Community and Ecosystems. MacMillan Publishers, New York.*

52. ^*Odum EP, Barrett GW (2005). Fundamental of Ecology. Fifth Edition, Cengage Learning India Private Limited, 2005.*

53. ^*Aleksandrova VD (1973) Russian approaches to classification of vegetation. In: R.H Whittaker ed. Ordination and classification of communities. Dr. W.Junk Publishers, The Hague.*

54. ^*Dale, M. B. (2001) Functional synonyms and environmental homologues: an empirical approach to guild delimitation. Community Ecology 2:67-79.*

55. ^*Wilson JB (2011). "The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored". Journal of Vegetation Science. 22: 184–195.*

56. ^*Pignatti S (1980). "Reflections on the phytosociological approach and the epistemological basis of vegetation science". Vegetatio. 42:181-185.*

57. ^*Pignatti S (1990). "Towards a prodrome of plant communities". J. Veg. Sci.. 1:425-426.*