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Do co-occurrence matrices suggest more than usual when comparing vegetation types? A test based on data from *Picea abies* and *Abies alba* forests in the Friulian Alps.

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Abstract

In this study, we introduce a framework for comparing vegetation types based on species co-occurrence matrices. The comparison relies on two complementary approaches: (1) quantifying the negentropy of the co-occurrence matrix for each vegetation type, and (2) evaluating the evenness of eigenvalues derived from pairwise co-occurrence matrices extracted from the overall species co-occurrence matrix of the vegetation system. The method is illustrated using phytosociological relevés from *Picea abies* and *Abies alba* forests of the Friulian Alps (NE Italy).

Our results show that vegetation types associated with more mesophilic environmental conditions—according to Landolt's ecological indicators—exhibit co-occurrence matrices with higher species connectance, as captured by information-based metrics. Furthermore, for the dataset considered, similarity matrices derived from species co-occurrence patterns outperform traditional approaches (frequency vectors, mean cover, presence/absence data, and standard similarity indices) in predicting ecological indicator patterns.

Keywords Classification, Ecological indicator values, Homogeneity, Interactions, Information theory, Neg-entropy, Operational Sampling Units, Vegetation descriptors

Introduction

.Every community data matrix X(M,N), such as a phytosociological table, can be considered mathematically as a primary co-occurrence matrix, since it records how M species or other "Vegetation Descriptors" (VDs) appear together ("co-occur") in N units that we refer to as

Operational Sampling Units (OSUs). These OSUs may take different forms—individual stands, combinations of stands, or sets of stands (Westhoff and van der Maarel 1973; Mucina and van der Maarel 1989; see Orlóci 2019 for a recent reinterpretation of the vegetation stand).

From any data matrix **X**(M,N), regardless of the nature of the OSUs, it is possible to derive several secondary matrices (McIntosh 1973) of the form **S**(N,N) and/or **C**(M,M). These are obtained by performing pairwise comparisons among the N OSUs (Q-approach) and among the M "characters" (species or traits) describing the OSUs (R-approach), using any of the many available similarity indices (Anderberg 1973; Orlóci 1978; Podani 2000; Wildi 2017). The choice of a specific index is left to the researcher (Dale 1988; Wildi 2017; Feoli 2018).

In this paper, where OSUs correspond to vegetation stands, our aim is to compare vegetation types through their species co-occurrence matrices and to evaluate the predictive value of the similarity matrix derived from these co-occurrence patterns with respect to the ecological indicator values of Landolt (1977).

The use of co-occurrence matrices to analyse vegetation patterns has a long history (e.g. Williams and Lambert 1959; Feoli and Feoli Chiapella 1980; Feoli and Scoppola 1980; Blanchet et al. 2020; Feoli 2024 and references therein). However, as noted by Blanchet et al. (2020), the raw co-occurrence value between species (or other descriptors) reflects only the net outcome of the various possible interactions among them, and therefore requires careful interpretation. It is therefore evident that targeted experiments and careful ecological observations are indispensable for understanding the real relationships among species within the communities (cf. Bever 2003; Adler et al. 2018). As ecologists with a biological background, we fully recognize this requirement, and we hope that research grounded in these approaches will continue to progress in the direction that ecological understanding demands.

Data

For testing the performance of co-occurrence matrices we have chosen to use the data of Poldini and Bressan (2007) that have beeen collectect following the Braun-Blanquet approach (Weshoff and van der Maarel 1973; Mueller-Dombois and Ellenberg 1974; Wildi 2017). The data set is given by a matrix **X**(368,141) corresponding to a phytosociological table with 368 species (rows) and 141 relevés (columns). In this matrix, each entry is the cover value of the m-th species in n-th relevé, expressed by the van der Maarel scale (van der Maarel 1979).

The relevés have been made across an altitudinal gradient spanning from 700 to 2000 meters a.s.l., encompassing diverse slope aspects and inclinations. They represents a vegetation system that is well recognizable in the SE-Alps sector of Friuli (N-East Italy) dominated by *Picea abies* and/or *Abies alba* (see Poldini and Bressan 2007). The average species number per relevé is 39.8 so the Whittaker's beta diversity (Whittaker 1972) is 9.246 (368/39.8= 9.246). this would suggest that we could expect to define about 9 vegetation types in the table (Feoli 2018).

Owing to the difficulty to measure directly the chemical-physical factors influencing the vegetation states represented by the relevés, we assume that the chemical, physical and biological situation of each relevé could be described in relative terms (i.e. with respect to the other relevés), by the vector of the average ecological indicator values of its species, as defined by Ellenberg (1974) or Landolt (1977). In the present paper we use those of Landolt (1977). For a recent review on the application of these indicator values see Ivanova and Zolotova (2023). In this way, the relevés find their position in a multidimensional space defined by the following 8 indicator values: H = humidity, pH = pH, N

= nutrients, Hm = humus, D = dimensions of soil particles, L = light, T = temperature, K = continentality.

Methods

Our data analysis is organized in the following 4 steps.

1) *Definition of significant clusters of relevés and the corresponding vegetation types at the level of association on the basis of species composition.*

To the matrix **X**(368,141), we applied the Sørensen index (*Sørensen* 1948) obtaining the matrix **S**(141,141). Since we are interested in evaluating the co-occurrence matrices we have considred only the binary data. In this case the Sørensen index is just twice the intersection of two sets over their sum. To the matrix, **S**(141,141) we have applied cluster analysis by single, group average and complete linkage sorting algorithms (Sneath and Sokal 1973; Anderberg 1973; Podani 2000). To define a number of clusters significantly separated we have used the method suggested by Feoli et al. (2009) and Feoli and Ganis (2019, 2021). This is based on the evenness of the eigenvalues of the within/between average cluster similarity matrices and on a permutation technique (Orlóci and Pillar 1991). To characterize the vegetation types by the species, we have applied the Pearson's product moment correlation coefficient between the cover values of the species and the fuzzy sets corresponding to the types, as suggested by Feoli and Ganis (2019, 2021). The fuzzy sets have been defined according to the method proposed by Feoli and Zuccarello (1986), where the degrees of belonging are given by the the average similarity that each relevé has with each vegetation type. We want to stress that the correlation coefficient does not give information on the quantity of a species in the corresponding vegetation type, but it gives a value of the tendency of the species to be present there. Thus it may be interpreted as a degree of belonging of the species to a given vegetation type. A significant positive correlation (that can be established by consulting the probability table of the Pearson correlation coefficient), would indicate that the degree of belonging of a certain species to a given vegetation type could be considered significant irrespective its relative frequency or cover values.

2) *Connectance between species of vegetation types by co-occurrence matrices and diversity of the vegetation system*.

We consider the co-occurrence between the species a variable that can be used to evaluate the connectance between the species in a given vegetation system. The connectance can be "measured" by the application of information theoretical formulas, as suggested by Feoli (1972, 2024), to the matrix of co-occurrence of the species. Also in this case we have applied the Sørensen index to obtain the matrix **C**(386,386). To the different matrices of co-occurrence corresponding to the vegetation types defined in step 1, we have applied the formula of neg-entropy as by suggestd by Feoli (1972, 2024)*:*

$$\mathrm{NegH}(\mathbf{C}) = -(\Sigma_{(ii)}\, p_{ii}\ln p_{ii} - \Sigma_{(ih)}\, p_{ih}\ln p_{ih}) \qquad (1)$$

where H means entropy and **C** the matrix of co-occurrence, (ii) = 1,…, M, and (ih) = 1,…, M(M-1)/2, p_{ii} = the ratios between the diagonal values (c_{ii}) of the co-occurrence matrix and the total (T) of the triangular co-occurrence matrix including the diagonal values, while p_{ih} = the ratios between the values (c_{ih}) ouside the diagonal and T.

If we call for convenience $-\Sigma_{(ii)} p_{ii} \ln p_{ii} = H(D)$, i.e. the entropy of the diagonal of **C** and $-\Sigma_{(ih)} p_{ih} \ln p_{ih} = H(U)$, the entropy of the upper or lower triangular part of **C**, we can write the formula (1) as NegH(C) = H(D)-H(U). If H(U) is equal to zero, it means that there is no co-occurrence between species, i.e. all the species are isolated. We can assume that the more the species co-occur, the more they are connected, consequently, the more the vegetation system under study should be predictable (i.e. the presence of a species would mean the presence of other connected species).

In terms of graph theory (Diestel 2017), H(D) and H(U) are respectively the entropy of the diagonal matrix of the nodes (D) and the entropy of the upper (or lower) triangular part (U) that is called the adjacency matrix of a graph. Formula (1) has its maximum value when all the species are connected and the co-occurrence between the species is the same. This happens when all the M species are present in all the N relevés, so the maximal neg-entropy of formula (1) would be expressed by the following formula :

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

The ratio between (1) and (2) gives a relative measure of "connectance" or association (based on co-occurrence):

$$R_1\text{NegH(C)} = \text{NegH(C)}/\text{NegH(C)max} \quad (3)$$

This formula is positive when NegH(C) is negative since formula (2) will always be negative. It will be indeterminate when M=3 since formula 2) equals to 0 when M=3. A detailed explanation of formula (1) as applied to co-occurrence matrices is given in Feoli (2024). However in that paper it was not mentioned the obvious drawback of M=3 because it is very rare that a community has less than 4 species. A simple solution that would avoid the indeterminacy in the case of M=3 could be to divide the result of formula (1) by the maximal entropy of the co-occurrence matrix that is realized when all the species co-occurr with all the others:

$$\text{NegH(C) max(b)} = \ln (M(M+1)/2) \quad (4)$$

Formula (3) will become:

$$R_2\text{NegH(C)} = \text{NegH(C)}/ \ln (M(M+1)/2) \quad (5)$$

An alternative formula to formula (3), could be also the following one:

$$R_3\text{NegH(C)} = -\Sigma_{(ih)} p_{ih} \ln p_{ih} / \ln (M(M+1)/2) \quad (6)$$

where h can be =i in case of the diagonal elements, (ih)= 1,,..,(M(M+1)/2).

We have used all the three formulas for calculating R. It is clear that we can expect that the values calculated with formulas (3), (5) and (6) would be significantly linearly correlated.

3) Definition of position of vegetation types in the ecological space defined by the ecological indicator values.

The vegetation types were described by ecological indicator values in the following 5 ways:

1) the matrix describing the species by indicator values, **E**(8,368), was multiplied by the binary data matrix **X**(368,141), the elements e_{ij} of the resulting matrix **E**(8,141) have been divided by the number of species of the jth relevé, then we have obtained a matrix $\mathbf{E_1}$(8,K) (with K = number of vegetation types obtained in step1)) by averaging the ecological indicator values of the relevés of each vegetation type (we call this resulting matrix as ECOLB);
2) the matrix **E**(8,368) was multiplied by the cover data matrix **X**(368,141), each element e_{ij} of the resulting matrix **E**(8,141) was divided by the total cover of the species in the jth relevé, then we have obtained another matrix $\mathbf{E_2}$(8,K) by averaging the ecological indicator values for each of the K types (we call this resulting matrix as ECOLC);
3) the matrix **E**(8,368) was multiplied by the matrix $\mathbf{V}_b$(368,K), where the K types were described by the presence/absence of the species (1,0). Each element e_{ij} of the resulting matrix $\mathbf{E_3}$(8,K) was divided by the total number of species of the jth type (we call the resulting matrix SYNTEB);
4) the matrix **E**(8,368) was multiplied by the matrix $\mathbf{V}_f$(368,K), where the K types were described by the relative frequency of the species in each type ($f_{ij} = n_{ij}/n_{j,}$ where n_{ij} is the number of relevés with species i and $n_{j.}$ is the number of relevés of type j), then each element e_{ij} of the resulting matrix $\mathbf{E_4}$(8,K) was divided by the sum of the relative frequencies of species in the jth type (we call the resulting matrix SYNTEF);
5) the matrix **E**(8,368) was multiplied by the matrix $\mathbf{V}_c$(368,K), where the K types were described by the cover of the species. Each element e_{ij} of the resulting matrix $\mathbf{E_5}$(8,K) was divided by the total cover of the species in the jth type (we call the resulting matrix SYNTEC).

For each of the 5 $\mathbf{E}_i$(8,K) matrices (ECOLB, ECOLC, SYNTEB, SYNTEF and SYNTEC) we have calculated the similarity matrix between the vegetation types using the Gower index, the Bray-Curtis formula and the Similarity Ratio (Podani 2000). For the resulting matrics we have calculated the evenness of the eigenvalues and we have chosen to use the matrix with the highest evenness to order and classify the vegetation types on the basis of ecological indicators. The same matrix has been used in step 4).

We expect the types which are relatively more mesophilic to have higher average similarity with all the other types, because of their intermediate indicator values. So we can say that: the higher the average similarity, the higher the degree of relative mesophily of the types. For the ordination we have use the Minimum Spanning Tree (MST) according to the criterion of maximal intersection (Feoli 1977, Feoli & Lagonegro 1979) applied to the chosen similarity matrix.

4) Correlation between the vegetation types and the indicator values on the basis of the description of the types based on co-occurrence matrices.

Among the 5 similarity matrices between the types based on ECOLB, ECOLC, SYNTEB, SYNTEF

and SYNTEC, we have chosen the one that has shown the highest separation between the types in terms of the evenness of its eigenvalues. With this matrix we calculated in an indirect way the correlation between the species composition of the types and the environmental factors by he Mantel test (Mantel 1967) using the following matrices of similarity between the types based on the species:

1) three similarity matrices have been obtained by the complement of the Bray-Curtis index (Podani 2000) considering the K vegetation types described by: a) the average cover values of the species (resemblance matrix **BCav.cov**(K,K)); b) the frequency of the species (matrix **BCF**(K,K); and c) the presence/absence of the species (**BCB**(K,K)) the resulting similarity matrix (in this last case the Bray-Curtis index reduces to the Sørensen index, Podani 2000).
2) A similarity matrix (EVAR) was obtained based on the evenness of eigenvalues derived from the K(K−1)/2 pairwise comparisons matrices between the K types, using the matrix of similarity calculated in step 1 by Sørensen index.
3) Finally a similarity matrix is obtained by evaluating the evenness of the eigenvalues of the 2×2 matrices resulting from the pairwise association of co-occurrence matrices between species (EVAOVL) based on the Sørensen index matrix **C**(368×368) that is the total co-occurrence matrix.

Before presenting the results, it is worth recalling that Mantel's test (Mantel 1967) measures the correlation between two symmetric matrices of the same size that compare *N* objects (variables or cases) using two different sets of descriptors. In our case, higher absolute values of the Mantel statistic indicate a stronger correspondence between species composition and the ecological characterization of vegetation types. In other words, the similarity matrix between vegetation types based on species data that shows the highest correlation with the similarity matrix based on ecological indicator values is the one that best reflects the relationships between vegetation types and their environmental conditions.

All calculations were performed using the program MATEDIT (Burba et al. 2008). The software and its manual are available upon request at feoli@units.it (the manual is currently available only in Italian).

Results and discussion

The results of step 1 are summarized in Table 1. Among the several classifications that proved significant at different hierarchical levels of the dendrograms, we selected the solution with nine clusters because this number is very close to Whittaker's beta diversity (cf. Feoli 2018) and because eight of these clusters correspond closely to the eight associations described by Poldini and Bressan (2007) (Table 2). The remaining cluster (VT8), which does not appear in Table 2, includes relevés with high cover of *Fagus sylvatica* and *Pinus sylvestris*. These relevés are distributed across different tables in Poldini and Bressan (2007), who used various numerical clustering methods and a neural network to assign relevés to classes of a predefined (supervised) classification. This cluster may represent an association within the vegetation system dominated by *Picea abies* and/or *Abies alba*, occurring at lower average elevations and on more rocky soils. However, its syntaxonomic interpretation will be addressed in detail in a separate paper.In Table 1 the 9 vegetation types (VT) are described by the correlation coefficients between the cover of the trees and shrubs and the fuzzy sets. From Table 1 it is clear what are the species that are characterizing the types in positive and/or

negative way.

Table 1. Description of the nine vegetation types based on the correlation coefficients between tree and shrub species and the fuzzy sets defined by cluster analysis (Feoli and Zuccarello 1986), which yield a classification that is significantly sharp according to the evenness of eigenvalues (Feoli and Ganis 2019, 2021). Species showing significant positive correlations at $p < 0.01$ (i.e., Pearson's $r \geq 0.22$; a value of 0 indicates absence of the species) are indicated in **bold**, whereas species with significant negative correlations are shown in small boxes. Species nomenclature follows Poldini et al. (2001). Abbreviations: VT = vegetation type; F+ = frequency of significant positive correlations between tree and shrub species and the fuzzy sets of the vegetation types; F– = frequency of significant negative correlations. The sequence of VTs in the table follows the ordination obtained in step 3 and shown in Fig. 1

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Species	VT1	VT2	VT3	VT8	VT7	VT9	VT6	VT4	VT5	F+	F-
Sorbus aucuparia subsp. glabrata	**0,64**	0	0	0	0	0	0	0	0	1	0
Salix appendiculata	0	**0,34**	0,19	0	0,04	0	-0,1	0	0,01	1	0
Ribes alpinum	0	**0,37**	0	0	0,05	0	-0,1	0	0	1	0
Sorbus chamaemespilus	0,2	0,1	**0,43**	0	0	0	0	0	0	1	0
Pinus sylvestris	0	0	0	**0,61**	0	0	0	0	0	1	0
Cornus mas	-0,17	-0,04	-0,08	0,02	0,12	**0,29**	0,08	-0,05	-0,12	1	0
Viburnum lantana	0	0	0	0	0,08	**0,31**	0	0	0	1	0
Larix decidua	**0,36**	0,01	**0,38**	-0	-0,3	0	-0,4	-0,24	-0,06	2	3
Vaccinium vitis-idaea	**0,52**	0,18	**0,53**	0,04	-0,3	-0,5	-0,6	-0,43	0,17	2	4
Lonicera caerulea	0,09	**0,42**	**0,34**	0	0	0	-0,3	0	-0,08	2	0
Sorbus aria	0	0,02	-0	0	**0,44**	**0,41**	0,19	-0,06	0	2	0
Lonicera alpigena	-0,27	**0,39**	**0,26**	0	**0,44**	**0,27**	0,2	0	0	2	1
Fraxinus excelsior	0	0	0	0	0,2	**0,5**	**0,24**	0	0	2	0
Sambucus racemosa	-0,11	0,07	-0,12	0	0	0,13	**0,32**	**0,26**	0	2	0
Rubus saxatilis	0	**0,54**	**0,61**	0,02	**0,23**	0,07	-0,2	0	-0,19	3	0
Acer pseudoplatanus	0	0,14	0	-0	**0,45**	**0,51**	**0,3**	0	0	3	0
Corylus avellana	-0,43	0	0	0	**0,38**	**0,6**	**0,49**	0,14	-0,09	3	1
Rubus hirtus	0	0	0	0	**0,41**	**0,54**	**0,57**	0,19	-0,12	3	0
Lonicera xylosteum	-0,37	-0,07	-0,18	0,01	**0,41**	**0,52**	**0,28**	-0,1	-0,2	3	1
Rubus idaeus	-0,09	0,19	-0,16	0	**0,22**	0,14	**0,49**	**0,41**	0,1	3	0
Vaccinium myrtillus	**0,51**	0,05	**0,4**	**0,37**	-0,1	-0,3	-0,5	-0,13	**0,37**	4	2
Fagus sylvatica	-0,34	-0,04	-0,14	**0,35**	**0,32**	**0,42**	**0,34**	0,18	-0,05	4	1
Abies alba	-0,26	0,12	-0,16	0,17	**0,58**	**0,48**	**0,63**	**0,52**	**0,31**	5	1
Lonicera nigra	-0,21	**0,62**	**0,22**	0	**0,55**	**0,3**	**0,41**	**0,32**	0,19	6	0
Sorbus aucuparia subsp. aucuparia	-0,24	**0,36**	0,15	0,06	**0,45**	**0,37**	**0,37**	**0,32**	**0,26**	6	1

Table 2 Correspondence between the 8 associations of Poldini and Bressan (2007) and 8 of the 9 clusters in Table 1. Letter A indicates the order of the types in the paper of Poldini and Bressan (2007), letter B the name of the vegetation types (at association syntaxonomical level) and C our clusters in the order of Table 1.

A	B	C
1	*Homogyno alpinae-Piceetum*	cluster 1
2	*Luzulo nemorosae-Piceetum*	cluster 5
3	*Cardamino pentaphylli-Abietetum*	cluster 7
4	*Anemono-Abietetum*	cluster 9
5	*Laburno-Piceetum*	cluster 6
6	*Rhodothamno-Piceetum*	cluster 2
7	*Homogyno sylvestris Piceetum*	cluster 3
8	*Senecioni cacaliastri-Piceetum*	cluster 4

The results of step 2 are shown in Table 3. From this table, it is evident that vegetation types 3 and 7 exhibit the highest connectance (RNegH) values according to formulas (3), (5), and (6). These two types also have a total number of species that is closest to the overall average. When calculating the correlation coefficients among the eight variables reported in Table 3 (Table 4), it becomes clear that the three RNegH(C) values are significantly correlated with one another. However, it is important to note that none of them shows a significant correlation with the total number of species. This indicates that co-occurrence does not follow a simple statistical expectation—where having more or fewer species would automatically imply higher or lower connectance. Instead, the observed co-occurrence patterns appear to reflect underlying biological processes, likely driven by environmental filtering and mutual adaptations (Baecher 2024; De Wit 2025; Goulpeau et al. 2025; Long et al. 2025, and references therein).

Table 3 Results of the application of formulas (1) to (6) to the co-occurrence matrices of the 9 vegetation types and Total Number of Species. Av. = average; SD = standard deviation

cluster number	1	2	3	4	5	6	7	8	9	Av.	SD
NegH (C) (formula1)	6,71	7,44	7,43	6,7	6,07	7,11	7,92	6,21	7,6	7,02	0,64
NegH(C) max (formula 2)	8,75	9,65	9,04	8,61	7,96	9,79	8,97	8,23	9,4	8,93	0,62
R1NegH (C) (formula 3)	0,77	0,77	**0,82**	0,78	0,76	0,73	**0,88**	0,76	0,8	0,79	0,04
NegH(C) max (formula 4)	9,03	9,65	9,32	8,9	8,29	9,99	9,22	8,56	9,61	9,17	0,54
R2NegH(C) (formula 5)	0,74	0,77	**0,8**	0,75	0,73	0,71	**0,86**	0,73	0,79	0,76	0,05
$-\Sigma_{(ih)}\, p_{ih} \ln p_{ih}$	7,35	7,93	7,83	7,36	6,64	7,87	7,74	6,71	8	7,49	0,52
R3NegH (C) (formula 6)	0,81	0,82	**0,84**	0,83	0,8	0,79	**0,84**	0,78	0,83	0,82	0,02
Total Number Species	129	176	**149**	121	89	209	**142**	102	173	**143,3**	38,17

Table 4. Matrix of Pearson's correlation coefficient between the variables in Table 3. In bold are the values with the values of $p < 0,05$ ($r=0,666$). In Italics are the correlations of the relative neg-entropy (RNegH(C)).

		1	2	3	4	5	6	7	8
1	NegH (C) (formula1)	1	**0,754**	*0,663*	**0,756**	***0,784***	**0,91**	***0,772***	**0,691**
2	NegH(C) max (formula 2)	**0,754**	1	*0,012*	**0,993**	*0,189*	**0,925**	*0,297*	**0,984**
3	R1NegH (C) (formula 3)	*0,663*	*0,012*	*1*	*0,026*	***0,974***	*0,328*	***0,818***	*-0,065*
4	NegH(C) max (formula 4)	**0,756**	**0,993**	*0,026*	1	*0,189*	**0,929**	*0,297*	**0,991**
5	R2NegH(C) (formula 5)	***0,784***	*0,189*	***0,974***	*0,189*	*1*	*0,48*	***0,864***	*0,099*
6	$-\Sigma(ih)\ p_{ih}\ln p_{ih}$	**0,91**	**0,925**	*0,328*	**0,929**	*0,48*	1	*0,627*	**0,882**
7	R3NegH (C) (formula 6)	***0,772***	*0,297*	***0,818***	*0,297*	***0,864***	*0,627*	*1*	*0,2*
8	Total Number Species	**0,691**	**0,984**	*-0,07*	**0,991**	*0,099*	**0,882**	*0,2*	1

The results of step 3 are presented in Table 5. Table 5A provides the description of the vegetation types based on ecological indicator values. This representation produced the sharpest distinction among vegetation types, as measured by the evenness of the eigenvalues of the five matrices computed using the five approaches described in the text (ECOLB, ECOLC, SYNTEB, SYNTEF, and SYNTEC) (Table 6).

Table 5B shows the similarity between vegetation types based on ecological indicator values calculated using Gower's index (Podani 2000), which yielded the clearest separation among types in terms of their ecological indicator profiles. Together with the matrices obtained using the Bray–Curtis index and the similarity ratio, this matrix indicates that vegetation types VT3 and VT7 have the highest average similarity to the other vegetation types (Table 7) with respect to ecological indicator values. Notably, these two types do not display any minimum or maximum values in the average ecological indicators reported in Table 5A. This pattern suggests that VT3 and VT7 represent the most mesophilic vegetation types within their respective groups: VT1, VT2, VT3, VT8 on one side, and VT4, VT5, VT6, VT7, VT9 on the other.

Table 5. A) Description of the nine vegetation types (VT) based on average ecological indicator values. These values were obtained by multiplying the species × ecological indicator matrix (H = humidity; pH = soil reaction; N = nutrients; Hm = humus; D = soil particle size; L = light; T = temperature; K = continentality) by the presence–absence matrix of species in vegetation types (1 = present, 0 = absent), and then averaging the resulting values by the total number of species in each type. Maximum values are highlighted in yellow and minimum values in blue. This matrix corresponds to SYNTEB in Table 6. **B)** Similarity matrix between vegetation types based on Gower's index applied to matrix A (GWECOL).

A	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
H	2.62	2.66	2.71	2.88	2.82	**2.91**	2.73	*2.59*	2.8
pH	***2.29***	2.69	2.76	2.58	2.43	2.87	2.9	2.64	**3.02**
N	2.44	2.44	2.5	2.75	2.53	**2.79**	2.56	***2.43***	2.75
Hm	3.26	***3.17***	3.29	3.46	**3.51**	3.44	3.39	3.25	3.38

D	3.34	***3.18***	3.3	3.6	**3.64**	3.59	3.39	3.45	3.5
L	2.33	2.43	2.44	***2.24***	2.33	2.38	2.32	**2.59**	2.45
T	***2.34***	2.38	2.45	2.62	2.66	2.93	2.85	2.7	**3.06**
K	***2.47***	2.53	2.59	2.48	2.66	2.57	2.64	**2.71**	2.66

B	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VT1	1	0.77	0.72	0.51	0.54	0.36	0.57	0.62	0.34
VT2	0.77	1	0.82	0.43	0.45	0.4	0.57	0.65	0.42
VT3	0.72	0.82	1	0.51	0.6	0.55	0.74	0.7	0.60
VT4	0.51	0.43	0.51	1	0.71	0.76	0.59	0.39	0.59
VT5	0.54	0.45	0.6	0.71	1	0.64	0.72	0.57	0.61
VT6	0.36	0.4	0.55	0.76	0.64	1	0.7	0.42	0.77
VT7	0.57	0.57	0.74	0.59	0.72	0.7	1	0.63	0.76
VT8	0.62	0.65	0.7	0.39	0.57	0.42	0.63	1	0.55
VT9	0.34	0.42	0.60	0.59	0.61	0.77	0.76	0.55	1

Table 6. Comparison of 5 matrices (ECOLB, ECOLC, SYNTEB, SYNTEF and SYNTEC) of description of the 9 vegetation types by average indicator values in terms of the evenness of the eigenvalues (EVA) of the Gower similarity index (see method in the text).

Type of matrix on which Gower's index was calculated	EVA
ECOLB (species binary)	0.54
ECOLC (species cover weighted)	0.55
SYNTEB (species binary)	**0.59**
SYNTEF (species frequency)	0.54
SYNTEC (species cover weighted)	0.58

From the matrix in Table 5A, the vegetation types can be briefly characterized according to their average ecological indicator values as follows:

- **VT1**, corresponding to *Homogyno alpinae–Piceetum* (see Table 2), shows the minimum values of pH, humidity (H), temperature (T), and continentality (K). It is clearly the coolest vegetation type, consistent with the high elevation of its relevés (1500–1800 m a.s.l.), the highest among all types.
- **VT2**, corresponding to *Rhodothamno–Piceetum*, exhibits the minimum value of soil particle dispersion (D). The relevés occur between 1250 and 1480 m a.s.l.
- **VT3**, corresponding to *Homogyno sylvestris–Piceetum*, shows no minimum or maximum values for any ecological indicator. This pattern suggests relatively mesophilic conditions, a conclusion supported by Table 7, where VT3 displays the first or second highest average similarity (based on ecological indicator values) to the other vegetation types. Its relevés range from 1400 to 1600 m a.s.l.
- **VT4**, corresponding to *Senecioni cacaliastri–Piceetum*, has the lowest value of light (L). The relevés occur between 1360 and 1520 m a.s.l.

- **VT5**, corresponding to *Luzulo nemorosae–Piceetum*, shows the highest values of humus (Hm) and soil dispersion (D). Its elevation range is broad, from 740 to 1600 m a.s.l.
- **VT6**, corresponding to *Laburno–Piceetum*, displays the highest values of humidity (H) and nutrients (N). The relevés range between 800 and 1400 m a.s.l.
- **VT7**, corresponding to *Cardamino pentaphylli–Abietetum*, does not show any minimum or maximum values of the ecological indicators. As suggested by the similarity values in Table 6, it represents another mesophilous vegetation type. Its relevés occur between 850 and 1450 m a.s.l.
- **VT8**, which does not correspond to any association described by Poldini and Bressan (2007), shows the maximum values of light (L) and continentality (K), and the minimum values of nutrients (N) and humus (Hm). It is characterized by high cover of *Pinus sylvestris* and *Vaccinium myrtillus*. The relevés range from 700 to 1400 m a.s.l. Its syntaxonomic interpretation will be addressed in a separate paper currently in preparation.
- **VT9**, corresponding to *Anemono–Abietetum*, shows the maximum values of temperature (T) and pH. The relevés occur between 800 and 1400 m a.s.l.

The relationships among vegetation types, represented by the graph of maximal similarity (Feoli & Lagonegro 1979), are shown in Fig. 1. This graph corresponds to a Minimum Spanning Tree constructed from the complement of the similarity values reported in Table 5B. The central position of vegetation types 3 and 7 in the graph clearly reflects their mesophilic character.

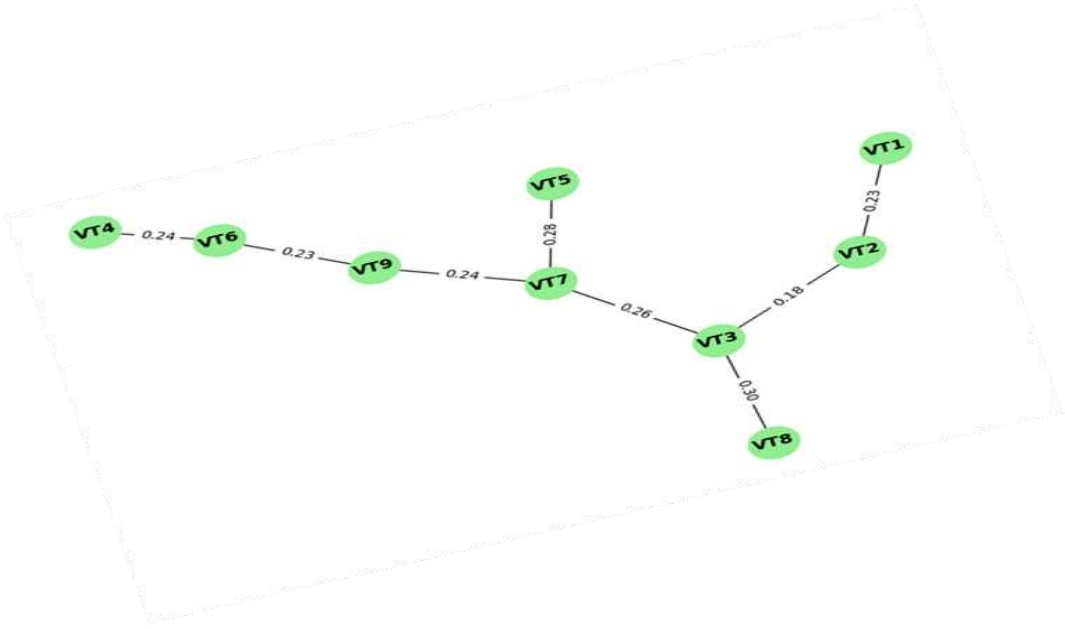

Fig. 1. Minimum Spanning Tree among the vegetation types, constructed from the complement (1 – Sij) of the similarity values reported in matrix B of Table 5.

Table 7. Average similarity that each vegetation type (VT) has with the other vegetation types on the basis of Gower index, Bray-Curtis index (BC), and Similarity ratio applied to matrix in Table 5 A), i.e. on the basis of ecological indicators. The averages, the standard deviations (SD) and the evenness

of the eigenvalues (EVA) of the similarity matrices are also given.

	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9	Average	SD	EVA
Gower	0.603	0.612	**0.693**	0.61	0.649	0.622	**0.698**	0.614	0.626	0,6363	0,036	0,59
BC	0.967	0.97	**0.976**	0.972	0.973	0.971	**0.976**	0.972	0.969	0,9718	0,003	0,08
Sim. Ratio	0.992	0.994	**0.996**	0.995	0.995	0.994	**0.996**	0.995	0.992	0,9943	0,002	0,02

The results of step 4) are presented in Table 8 and Table 9. Table 8 presents the similarity-dissimilarity matrices between the 9 vegetation types according to the selected methods, while Table 9 presents the results of the Mantel's test between the resemblance matrices in Table 8 and the matrix in Table5 **B**).

From Table 9 we can see that the highest correlation between the matrices of similarity based on species and that based on ecological indicator values is reached by the matrix that measures the resemblance between types on the basis of the evenness of their co-occurrence matrices between species.

Table 8 Resemblance (similarity or dis-similarity) matrices between the 9 vegetation types of the forests of *Picea abies* and *Abies alba* of the Friulian Alps based on step 4 (see methods for the sequence of the matrices). Matrices A), B), C) show the Bray-Curtis's similarity values between the types (VT) described respectively by the average cover values of the species (BC av.cov.); by the average frequency of the species (BCF) and by the presence absence of the species (BCB). Matrices D) and E) show respectively the dis-similarity between the vegetation types based on the evenness of the eigenvalues of the pairwise comparison matrices of their set of relevés (EVAR) and the similarity based on the evenness of the eigenvalues of the pairwise comparison matrices of their species co-occurrence (EVAOL).

A) BC av.cov.	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VTI	1	0.47	0.51	0.49	0.59	0.32	0.39	0.37	0.28
VT2	0.47	1	0.62	0.55	0.52	0.49	0.56	0.33	0.41
VT3	0.51	0.62	1	0.45	0.5	0.39	0.51	0.41	0.41
VT4	0.49	0.55	0.45	1	0.62	0.62	0.57	0.4	0.47
VT5	0.59	0.52	0.5	0.62	1	0.47	0.54	0.43	0.41
VT6	0.32	0.49	0.39	0.62	0.47	1	0.61	0.33	0.57
VT7	0.39	0.56	0.51	0.57	0.54	0.61	1	0.46	0.62
VT8	0.37	0.33	0.41	0.4	0.43	0.33	0.46	1	0.43
VT9	0.28	0.41	0.41	0.47	0.41	0.57	0.62	0.43	1

B) BCF	VT1	V2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VTI	1	0.45	0.5	0.5	0.56	0.33	0.39	0.38	0.27
VT2	0.45	1	0.63	0.56	0.5	0.5	0.56	0.33	0.42
VT3	0.5	0.63	1	0.46	0.47	0.41	0.52	0.41	0.42
VT4	0.5	0.56	0.46	1	0.6	0.62	0.54	0.38	0.45

VT5	0.56	0.5	0.47	0.6	1	0.48	0.53	0.42	0.41
VT6	0.33	0.5	0.41	0.62	0.48	1	0.6	0.35	0.58
VT7	0.39	0.56	0.52	0.54	0.53	0.6	1	0.46	0.62
VT8	0.38	0.33	0.41	0.38	0.42	0.35	0.46	1	0.42
VT9	0.27	0.42	0.42	0.45	0.41	0.58	0.62	0.42	1

C) BC B	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VT1	1	0.58	0.6	0.58	0.59	0.47	0.51	0.52	0.44
VT2	0.58	1	0.66	0.59	0.48	0.58	0.6	0.42	0.5
VT3	0.6	0.66	1	0.55	0.51	0.56	0.59	0.5	0.52
VT4	0.58	0.59	0.55	1	0.56	0.64	0.59	0.47	0.53
VT5	0.59	0.48	0.51	0.56	1	0.48	0.57	0.47	0.49
VT6	0.47	0.58	0.56	0.64	0.48	1	0.64	0.42	0.69
VT7	0.51	0.6	0.59	0.59	0.57	0.64	1	0.54	0.68
VT8	0.52	0.42	0.5	0.47	0.47	0.42	0.54	1	0.47
VT9	0.44	0.5	0.52	0.53	0.49	0.69	0.68	0.47	1

D) EVAR	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VT1	0	0.71	0.6	0.65	0.53	0.84	0.78	0.79	0.9
VT2	0.71	0	0.38	0.54	0.61	0.62	0.52	0.83	0.73
VT3	0.6	0.38	0	0.68	0.64	0.77	0.57	0.73	0.75
VT4	0.65	0.54	0.68	0	0.41	0.4	0.56	0.75	0.68
VT5	0.53	0.61	0.64	0.41	0	0.64	0.56	0.68	0.75
VT6	0.84	0.62	0.77	0.4	0.64	0	0.44	0.82	0.5
VT7	0.78	0.52	0.57	0.56	0.56	0.44	0	0.66	0.38
VT8	0.79	0.83	0.73	0.75	0.68	0.82	0.66	0	0.69
VT9	0.9	0.73	0.75	0.68	0.75	0.5	0.38	0.69	0

E) EVAOVL	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9
VT1	0	0.23	0.22	0.24	0.17	0.4	0.3	0.31	0.46
VT2	0.23	0	0.15	0.23	0.23	0.32	0.22	0.4	0.39
VT3	0.22	0.15	0	0.3	0.26	0.34	0.25	0.34	0.4
VT4	0.24	0.23	0.3	0	0.14	0.19	0.19	0.37	0.3
VT5	0.17	0.23	0.26	0.14	0	0.25	0.16	0.29	0.3
VT6	0.4	0.32	0.34	0.19	0.25	0	0.18	0.4	0.14
VT7	0.3	0.22	0.25	0.19	0.16	0.18	0	0.27	0.17
VT8	0.31	0.4	0.34	0.37	0.29	0.4	0.27	0	0.36
VT9	0.46	0.39	0.4	0.3	0.3	0.14	0.17	0.36	0

Table 9 Mantel's test applied to the comparison of the matrix GWECOL in Table 5 B), with all the matrices in Table 8. All the comparisons are highly significant $p<0.001$. The sequence of the matrices in the table follows the decreasing values of Mantel's test.

	GWECOL
EVAOVL	**-0.656**

BC BIN	0.60
EVAR	-0.59
BCF	0.57
BC av.cov	0.56

Conclusion

The results of this study can be summarized as follows:

1. **Within the vegetation system considered, the highest levels of species connectance—expressed through co-occurrence—were found in the two most mesophilic vegetation types.** Mesophily was quantified as the average similarity of each vegetation type to all others in terms of ecological indicator values. This finding supports the hypothesis that connectance may serve as an indirect proxy for stability: vegetation types occurring under mesophilic conditions appear to exhibit higher stability than those occupying more extreme environments, at least within the system examined (see Pimm 1984; Ives and Carpenter 2007; Landi et al. 2018). This interpretation aligns with broader ecological theory: in a given ecosystem, stability tends to peak under mesophilic conditions—moderate temperature, pH, and environmental stress—where metabolic and ecological processes operate most efficiently. As environmental parameters deviate from these mesophilic optima, ecosystem stability typically declines due to reduced biodiversity, narrower functional niches, and increased physiological stress (Feller and Gerday 2003; Mythrayee and Gayathri 2024; Zhang et al. 2023).
2. **The classification of vegetation types based on species co-occurrence proved more predictive of ecological indicator patterns than classifications derived from species frequency, mean cover, or presence/absence data.** This result emerged consistently across the multiple analytical steps performed, including the evaluation of negentropy, the evenness of eigenvalues, and the comparison of similarity matrices. Together, these analyses demonstrate that co-occurrence patterns capture ecological information that is not fully represented by traditional phytosociological descriptors.

Taken together, these findings may have broad implications for ecology, particularly when species co-occurrence in ecological communities is interpreted through the lens of graph connectivity. The index RNegH(C) (formula 3) appears to be a promising measure of connectance—bearing in mind that, in graph theory, *connectivity* refers to whether nodes are connected at all, whereas *connectance* quantifies the proportion of all possible links that are realized. Our results suggest that co-occurrence matrices, and the parameters derived from them, can provide valuable complementary information in both phytosociology and community ecology (e.g., Jordán et al. 2007; Jordán 2009; Scotti and Jordán 2010).

In the broader framework of general systems theory (von Bertalanffy 1968; Kish et al. 2021), the hypothesis that a system's graph becomes increasingly connected as the system approaches the average values of the factors governing its existence is particularly intriguing. This idea—echoing the classical principle *in medio stat virtus*—deserves systematic testing across diverse ecological datasets to evaluate its generality and potential theoretical significance.

In conclusion, and returning to the question posed in the title of this paper, our analyses show that species co-occurrence matrices offer a powerful and informative set of tools for improving our understanding of vegetation systems. They provide supplementary insights into species assemblage patterns and into the relationships between vegetation types and environmental factors—insights that may remain hidden when relying solely on traditional phytosociological descriptors.

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Statements and Declarations

Competing interests

The authors did not receive support from any organization for the submitted work. The authors have no competing interests to declare that are relevant to the content of this article.

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