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ENVIRONMENT-VEGETATION RELATIONSHIPS IN THE UNDERSTORY OF PYRENEAN *PINUS SYLVESTRIS* FORESTS II.: A CLASSIFICATION APPROACH

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Abstract. A correlation analysis between the vegetation of Pyrenean *Pinus sylvestris* forests (Spain) and some selected chemical-physical variables is presented based on an indirect classification approach. The results of a numerical classification of phytosociological relevés of the understory component are evaluated in terms of class separation based on chemical physical variables (external variables) and canonical analysis. The results suggest that the relevé groups obtained by clustering are environmentally well-differentiated, and that soil pH and humidity have the greatest discriminatory power between relevé groups.

Introduction

In a previous paper (Pausas and Feoli 1995), vegetation-environment relationships were evaluated on the basis of a direct measure of correlation between vegetation data and environmental variables using ordination methods and canonical correlation analysis (a direct approach). Here, an example of an indirect approach based on classification (Feoli 1983) is provided. This approach gives a measure of correlation between vegetation and environment by calculating the separation between the classes of vegetation data (species composition) using environmental (external) variables. Different methods of canonical analysis (Gittins 1985) can be applied to measure class separation. One group of methods is based on contingency table analysis and chi-square decomposition as proposed by Feoli (1983), using an example of correlation between grassland vegetation types and soil pH. Another group is based on the analysis of variance and covariance, as in discriminant analysis (DA). This was often used after classification for exploring relationships between species composition and environmental factors (Green and Vascotto 1978; Feoli 1983; Gerdol *et al.* 1985, Gittins 1985). Both methods, besides giving measures of predictivity of vegetation classification with respect to environmental variables, give also ordinations of the vegetation classes and environmental variables in the multidimensional space. This paper focuses on discriminant analysis and tests its performance as a linear technique in measuring the predictivity of a floristic classification with respect to chemical-physical variables, and, as an ordination method, in showing the mutual positions of community niches in the ecological space (Feoli, Ganis and Zerihun 1988).

Data

The original data used in this paper have been described in Pausas and Feoli (1995). In brief: the data comprise fifty-five relevés made in mature *Pinus sylvestris* forests from the eastern Pyrenees (NE of Iberian Peninsula). The data collected can be partitioned as follows:

1) Phytosociological data: species frequency in the understory was recorded as the number of small quadrats (25x25 cm) in which the species occur. In each relevé 100 systematically placed quadrats were sampled. In this paper, however, a matrix of presence/absence data is used only (Table 1).

2) Environmental data: a volumetric soil sample of the first 10 cm was collected in each plot. In each soil sample, pH in water (1:2.5), pH in potassium chloride (1:2.5), stoniness and soil density were measured. Carbonates were analyzed with a Bernard calcimeter, and C and N contents with a Carlo Erba elemental analyzer. Thickness of organic F and H layers was measured at 16 points on each relevé and the mean was used for numerical analysis. Altitude, slope, number of species and moisture index were also included in this data set. Moisture index (humidity) was calculated based on soil depth (estimated as the mean of 10 points), stoniness, soil texture, and aspect of the relevés, using the method described by Klinka *et al.* (1984). Pausas & Fons (1992) have given a more complete overview on the data, and the data have been also used by Pausas (1994).

Methods

Classification

The block clustering method proposed by Podani and Feoli (1991) was applied to the phytosociological data to find species and relevé groups. This method is based on an iterative relocation procedure that creates a block structured table by maximizing the sharpness of the blocks based on a chi-square criterion. Analysis of concentration (AOC, Feoli and Orlóci 1979) is applied to test whether the block structure obtained by the classification is significant and to generate an ordination of relevé and species groups (clusters). The relevé clusters defined by internal criteria, i.e. floristic similarity, should be interpreted as different plant communities (vegetation types) only if they are significantly different in terms of environmental variables as well (Feoli, Lagonegro and Biondani 1981). To justify the separation only in terms of floristic composition would be difficult since it is almost impossible to infer on the statistical distribution of the multiple variable called 'vegetation'. Notwithstanding that differential species groups may often be defined in AOC, we cannot decide whether these species combinations belong to the same or to different multivariate populations. Discriminant analysis (Gittins 1985) applied to external environmental data can help determine whether the clusters of relevés defined by floristic criteria belong to the same multivariate distribution, at least for the selected environmental variables.

Discriminant analysis

Stepwise discriminant analysis minimizing Wilks' lambda was used to introduce the environmental variables into the discriminatory process. Analysis of variance (ANOVA) and multivariate analysis of variance were also applied. The SPSS program package (Klecka 1975) was used to perform computations.

Results

Classification

Five relevé clusters and 6 species groups were obtained. The structured data matrix is presented in Table 1. The probability of each species group in each relevé cluster is given in Table 1. The X^2 value of the concentration table (blocks adjusted to equal size, see Feoli and Orlóci 1979) is 862.21, which is much higher than the critical value of $\chi^2_{0.05,20}$= 31.41. This result suggests that the block structure in Table 1 is significant, i.e. species groups can be found to characterize vegetation types corresponding to relevé clusters. However, if we consider the frequency distribution of relevés in the 5 clusters along the first canonical variate, a "normal distribution" may be fitted (group 4 with 9 relevés, group 5 with 13 relevés, group 1 with 15 relevés, group 2 with 12 relevés, group 3 with 6 relevés). This confirms what was previously stated concerning the definition of vegetation types based only on internal criteria.

The joint ordination of relevé clusters (1, 2, 3, 4 and 5) and species groups (a, b, c, d, e and f) according to the first two canonical variates is presented in Fig. 1. The correspondence between 1*d*, 2*c* and 3*e* is clearly evident. Relevé clusters 4 and 5 would be associated with species groups *a* and *b*, respectively, if we considered the third canonical variate (not shown) where 4 and *a* have negative values while 5 and *b* have positive values. Species group *f* is in the middle of the scattergram owing to its almost equal distribution in the relevé clusters (see Table 2).

By comparing the probability values of species groups in Table 2 with the mean values of environmental variables in Table 3, we can suggest that the species of groups *d*, *c* and *e* are acidophilous, while those in *a* and *b* are calcicolous. The results suggest that the first canonical variate of AOC is related with pH. In the acidophilous species groups, species such as *Luzula nivea*, *Oxalis acetosella* and *Vaccinium myrtillus* in *d* are mesophilous while species such as *Genista pilosa*, *Rhytidium rugosum* or *Cladonia sp. pl.* in *e* are xerophilous. In the calcicolous species groups more-xerophilous species are in *b* (*Abietinella abietina*, *Amelanchier ovalis*, *Rhamnus saxatilis*, *Teucrium pyrenaicum*, *T. chamaedrys*, *Viburnum lantana* and *Quercus rotundifolia*) and more-mesophilous species in *a* (*Pulsatilla alpina*, *Sorbus aria*, *Sesleria coerulea* and *Abies alba.*). Following the ordination pattern of Fig. 1 and the values in Tables 2 and 3, it appears that the environmental parameters most important in the separation of the relevé clusters are pH and humidity.

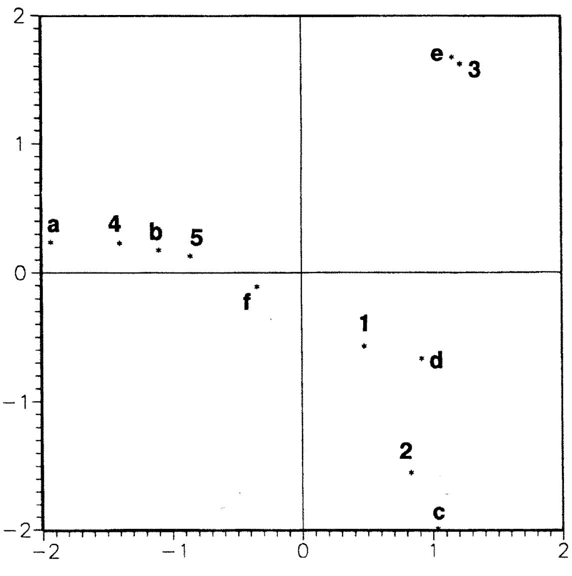

Figure 1. Joint plot of the relevé clusters (numbers) and species groups (letters) for canonical variates 1 and 2 in analysis of concentration.

Table 1. Presence/absence data matrix structured according to the simultaneous block clustering algorithm.

plot group	111111111111111	222222222222	333333	444444444	5555555555555
plot number	112222233445	112234455	1235	113334455	111223334444
	145393456809461	279142932324	380720	266787935	6578011450158
species group a					
Abies alba	....	....	......	1......1.	....
Anthyllis montana	....	....	......	.1......1	....
Campanula rapunculoides	....	....	......	.1..1....	....
Coronilla minima	....	....	......	......11.	....
Euphorbia cyparissias	1	...1........	......	..11..1.1	....
Goodyera repens	...1...........	....	......	....11...	....
Koeleria macrantha	....	....	......	11.......	.......1.....
Laserpitium nestleri	....	....	......	....1....	....
Leontodon hispidus	....	....	......	..1.1...1	....
Monotropa hypopitys	....	1	......	.1.1...11	....
Polygala calcarea	....	.1..........	......	11..111..	11.1.........
Potentilla neumaniana	..........1....	....	......	...1..1.1	.1...........
Pulsatilla alpina	....	....	......	111.1....	....
Pyrola uniflora	.1.............	....	......	......11.	....
Sesleria coerulea	.............1.	....	......	1....1.1.	...........1.
Sorbus arias	....	....	......	1.......1	..1..........
Taraxacum gr officinale	....	....	......	.1...11..	....
Trifolium pratense	..........1....	....	......	.....1..1	....
Vicia pyrenaica	....	....	......	.111.1.1.	1............
species group b					
Abietinella abietina	......1........	........1...	11	.1......1	111111....1.1
Amelanchier ovalis	1	.1..........	......	11.......	11..11.111111
Asplenium fontanum	....	....	......	....	.....1.1...1.
Bromus erectus	....	....	......	....	.1...........
Campanula percisifolia	....	...1....1...	......	....	1..1.....1...
Campanula trachelium	1	....	......	....	.......1....1
Carlina cynara	....	....	......	.1.......	.1...........
Daphne laureola	....	....	......	....	...........1.
Euphorbia amygdaloides	....	..........1.	......	1....1...	......11...1.
Helleborus foetidus	....	....	......	....	.......1.....
Homalothecium lutescens	.......1.......	...1...11...	....1.	11..1.1.1	11111111..111
Knautia catalaunica	....	....	......	1....11.1	.1.1.1.....1.
Lavandula angustifolia	....	....	......	.1.......	...1.........
Polypodium vulgare	11.........1...	....	......	....	..1......1.11
Quercus rotundifolia	....	....	......	....	.........1..1
Rhamnus saxatilis	....	....	......	....	.1.....1.....
Rodobryum roseum	....	....	......	.1.......	1.....1...1..
Rosa gr canina	....	....	......	..1......	11
Teucrium chamaedrys	....	....	......	....	.11.........1
Teucruim pyrenaicum	....	....	......	1	.1.1.......1.
Thuidium tamariscinum	....	....	......	1	..........1..
Tortella tortuosa	.............1.	....	......	....	..11..1......
Viburnum lantana	....	....	......	....	..1........1.
Viola wilkommii	....	....	......	1.1...1..	.1111..1....1
species group c					
Anthoxantum odoratum	....1.....1....	.1.1.....11.	......	....	....

Table 1 (continued).

Asplenium adiantum-nigrum	....	........1...	......	....	........1...
Asplenium trichomanes	....	........1...	......	....	....1.......
Bryum capillare	........1......	.11...1.....	......	....	....
Ceratodon purpurescens	..........1....	1	......	....	....
Dactylis glomerata	....	1...1.....1.	......	....	.1.1........
Digitalis lutea	...........1...	...1...1....	......	....	.........1..
Fagus sylvatica	.............1.	.1..........	......	....	....
Festuca gr ovina	....	111111....11	..1...	....	....1.......
Galium rotundifolium	....	.......1..1.	......	....	....
Genistella sagittalis	....	........1.1.	......	....	....
Helianthenum numularium	....	.1..........	......	....	....
Hieracium gr pilosella	..........1....	11........11	......	...1....1	.1..........
Mycelis muralis	1..............	........1...	......	....	....
Poa nemoralis	....	...1....1...	......	....	....
Potentilla micrantha	....	.........11.	......	....	....
Prunella pyrenaica	.1.1.......1...	.1.1....111.	......	....	..........1.
Rosa pimpinelifolia	....	.1.1........	......	....	....
Sedum reflexum	..........1....	1..1.1.11..1	..1...	....	....
Silene nutans	....	.1...1.111..	......	....	....
Solidago virgaurea	1	1...1.......	......	....	....1.......
Stellaria holostea	....	...11...111.	......	....	....
Tanacetum corymbosum	...........1...	....1....1..	......	....	..1.........
Tortura ruralis	....	.....11.1..1	..1...	....	....
Valeriana officinalis	....	...1........	......	....	..........1.
Veronica officinalis	.1.11...1.11...	1..111111111	......	.......1.	....

species group d

Agrostis capillaris	1.1...1.1..1...	...1...11...	......	.......1.	....
Calluna vulgaris	...11.....11...	1...........	1.1...	....	....
Crataegus monogynea	.11....1.......	....	......	1........	....
Ctenidium molluscum	......1......1.	......1.....	......	....	.....1......
Deschampsia flexuosa	11.11111111111.	..11111111.1	111111	....	....
Doronicum pardalianche	.1.....1.......	....	......	....	....
Fregaria vesca	111...11.11.11	.1.1......1.	......	..1....1.	..1...1.....
Lathyrus montana	...1.11111.1...	..........1.	......	....	....
Luzula nivea	....1..11.11...	...1........	......	....	....
Melampyrum pratense	...11.....1..1.	..........1.	...1..	1........	....
Oxalis acetosella	11..1..........	....	......	.......1.	....
Pyrola secunda	.........11...1	....	......	....	....
Quercus petraea	...1.......1...	..1.........	......	....	....
Rubus idaeus	........1..1...	....	......	....	..1.........
Vaccinium myrtillus	1..11..11111.1.	...1......1.	1..11.	....	....
Vicia sepium	1......1...1...	...1........	......	....	....
Vincetoxicum hirundinaria	.......11......	....1.......	......	....	....
Viola sylvestris	.11111.11.1111.	...1.....111	......	.......1.	..........1.

species group e

Arctostaphylos uva-ursi	.....1.....1...	.......1....	...11.	....1....	....
Cetraria islandica	....	.....1......	.1....	....	.........1..
Cladonia gr furcata	....	....	11.11.	....	........1...
Cladonia gr pyxidata	....1..........	.....1...1..	11....	.1.......	...1........
Genista pilosa	..........1.1..	.....1......	11111.	....	....
Medicago suffruticosa	..........1....	....	1	1	....
Pyrola chlorantha	......1...1...1	....	.1111.	1.1......	1
Quercus pubencens	..1............	....	1.....	....	....
Rhytidium rugosum	.....1.........	.1......11..	111111	11	.1.1.1...11.

Table 1 (continued).

Sarothamnus scoparius	....	1...........	..1...	....	....
species group f					
Avena pratense	..1....11..11..	....1...11..	......	.11111...	11.1...1...11
Brachitecium velutinum	..1........1.1.	...1.11..1.1	1	11......1	.111.111...1.
Buxus sempervirens	111........111.	11.1....1...	1...1.	1111.1.11	1111111111.11
Campanula gr rotundifolia	......11...11..	..1......1.1	..1...	111.1.11.	.....1....1..
Corylus avellana	1.1............	...1........	......	1.......1	..1..........
Cruciata glabra	111111111.11111	..11......1.	..1...	111111.11	11...1..1..11
Dianthus hyssopipholius	..........11...	.........1..	......	.1.....11	.....1....1..
Dicranum scoparium	.1...1111111.11	11.111111111	111111	11.111111	111111.111111
Festuca gautieri	1111111..111111	111.11..1..1	.11.1.	111111111	1111.1.11..11
Galium gr pilosella	......1..11111.	11.111..1..1	..1...	1111.1...	1.1..1...11.1
Galium vernum	........1.1....	....	......	....1.1..	....
Hepatica nobilis	111.11111111111	...1.....1..	......	111111111	11.1.1.11..1.
Hieracium gr murorum	11..1.11.1111.1	1.11.1.11111	......	11..11.11	11..1....11..
Hylocomium splendens	11111.11111111.	.1.1....1...	11.111	111111111	1111111..1111
Hypnum cupressiforme	1..1.1111111..1	11.1111.11.1	111111	1..111.11	.1111111.1111
Juniperus communis	1111111.1.1.11.	.1.........1.	1.1.1.	11111.11.	.1.1.1.1..111
Lathyrus pratense	11.....1....1.1	....	......	1..1.1.1.	11...........
Lilium martagon	...........1...	....	......	....	.....1.......
Lonicera xylosteum	111...........1	...1........	......	1.11.....	..11.........
Lotus corniculatus	.........1.1..	.......1..1.	......	....1.1..	....
Pimpinella saxifraga	.......11.11...	..........1.	......	1....1...	1...........1
Plagiomnium undulatum	..1.......1....	...1........	......	.1.....1.	......1...1..
Pleurozium schreberi	11.11111111111.	.1......1...	111111	1111111.1	1...11...111.
Primula veris	.......1.......	...1........	......	..1.1....	1....1.......
Pseudoscleropodium purum	1.11.......1.1.	.1..........	......	..11.11.1	11..11..11.11
Quercus pubescens	1......11......	.1......1...	..1...	....	1...1....11..
Rhytidiadelphus tricheter	11111.1.1111.1.	...1........	1.....	1..1.1.11	....11...1.1.
Rosa pendulina	....11.......1.	....	......	....1...1	....
Thymus polegioides	..........1....	....	......	.1.......	.1...........
Tortella sp	....	.......1....	...1..	.1......1	.......1.....
Valeriana montana	.1...........1.	....	......	..1..1...	.....1.......
Vicia incana	......1.1..11..	...1........	......	1.1111...	........1....

Table 2. Probability matrix of species groups in relevé clusters according to the adjusted concentration values of Table 1.

Species groups	Relevé groups 1	2	3	4	5	Total
a	0.03	0.02	0.00	0.30	0.04	0.09
b	0.03	0.04	0.03	0.11	0.34	0.10
c	0.06	0.35	0.03	0.01	0.05	0.09
d	0.37	0.18	0.14	0.04	0.03	0.15
e	0.08	0.10	0.56	0.07	0.09	0.18
f	0.44	0.30	0.25	0.47	0.45	0.39

Discriminant analysis with environmental variables

The 13 'environmental' variables, including the number of species, and their corresponding *F*-ratios resulting from the univariate analysis of variance are shown in Table 3. Eleven variables, were selected from the 13 to be included in the discriminant analysis by the stepwise method. These environmental variables and the corresponding order are shown in Table 4. pH and humidity are the first two variables (with the highest Wilks' lambda). This confirms the results of concentration analysis.

Two significant ($p<0.05$) canonical correlations are found (Table 5) between relevé clusters (binary-valued dummy variables, Gittins 1985) and environmental variables. The cumulative percentage of variance accounted for the first two discriminant functions is very high (Table 5).

The joint plot of centroids of the relevé groups and environmental variables is shown in Fig. 2 according to the first two discriminant functions. The first discriminant function is mainly correlated with soil pH (pH, carbonates and dif-

Table 3. Means (m), standard deviations (sd) and univariate F ratios of the environmental variables for the five relevé clusters.

		Gr1	Gr2	Gr3	Gr4	Gr5	F	p	
n		15	12	6	9	13			
Altitude (m)	m	1409.67	1569.58	1351.67	1531.11	1359.23	5.39	0.0011	**
	sd	101.66	160.83	183.46	84.92	162.51			
F Thickness (cm)	m	2.06	1.33	1.16	1.97	1.71	2.92	0.0302	*
	sd	0.85	0.57	0.64	0.50	0.82			
H Thickness (cm)	m	2.99	2.48	1.79	3.67	3.10	1.48	0.2234	ns
	sd	1.86	1.50	1.65	1.12	1.71			
pH	m	5.89	5.23	5.48	7.37	7.22	13.76	0.00001	***
	sd	1.06	0.47	0.49	0.94	0.97			
pH(H20)-pH(CIK)	m	1.03	1.19	1.25	0.79	0.75	5.02	0.0018	**
	sd	0.41	0.21	0.17	0.30	0.33			
Soil density (gr/cm2)	m	1.58	1.75	1.78	1.41	1.59	1.71	0.1627	ns
	sd	0.30	0.46	0.36	0.24	0.30			
CaCO3 (%)	m	1.35	0.00	0.00	12.89	9.08	5.94	0.0005	***
	sd	4.14	0.00	0.00	14.19	9.72			
Stoniness (%)	m	48.68	56.13	58.38	53.16	54.10	0.51	0.7313	ns
	sd	19.24	13.27	11.67	14.71	19.96			
C (%)	m	4.05	4.64	3.16	5.30	5.13	0.88	0.4848	ns
	sd	2.15	2.97	1.47	2.23	3.44			
N (%)	m	0.26	0.28	0.18	0.40	0.29	1.90	0.1253	ns
	sd	0.12	0.17	0.09	0.21	0.18			
C/N	m	16.20	18.28	18.26	14.88	17.70	0.74	0.5717	ns
	sd	5.60	6.40	6.04	4.64	4.21			
Num. ssp	m	23.87	19.92	14.17	28.89	22.15	3.79	0.0091	**
	sd	9.02	9.08	2.99	5.64	7.06			
Humidity	m	3.75	2.25	3.00	3.44	3.30	10.52	0.00001	***
	sd	0.47	0.72	0.55	0.68	0.67			

***, $p<0.001$, **, $p<0.01$, *, $p<0.05$

Table 4. Environmental variables entered in each step and the corresponding Wilk's lambda (Λ) in stepwise discriminant analysis.

Step	Variable entered	Λ
1	pH	0.47607
2	humidity	0.26140
3	altitude	0.19433
4	number of sp.	0.16910
5	pH_{H2O}-pH_{ClK}	0.15332
6	F thickness	0.14243
7	H thickness	0.12533
8	$CaCO_3$	0.11479
9	soil density	0.10706
10	C	0.10029
11	N	0.09533

Table 5. Eigenvalues, cumulative percentages of variance, canonical correlations (R), Wilk's lambda and χ^2 tests for each discriminant function (DF).

DF	λ	%	R	Λ	X^2	df.	p
1	2.47	63	0.84	.09	108.1	44	.0000
2	0.83	85	0.67	.33	50.8	30	.0101
3	0.49	97	0.57	.61	23.0	18	.1889
4	0.10	100	0.31	.90	4.6	8	.9775

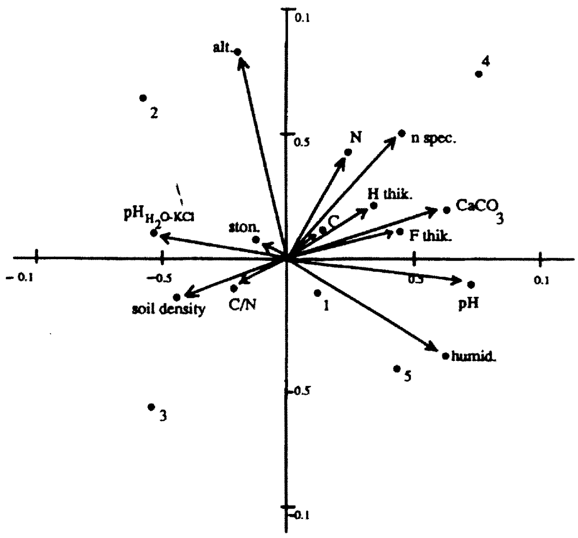

Figure 2. Joint plot of the centroids of the relevé clusters (numbers) and environmental variables for the discriminant functions.

ference in pH) and with humidity. Thus the first discriminant function separates forests with basic and humid soil in the positive part and forests with acidic and drier soil in the negative part. The second discriminant function is higly correlated with altitude, and it separates forests at high altitude in the positive part, and forests at low altitude in the negative part (Fig 2). The pattern of variation of the understory vegetation of the considered forests can be described on the basis of the ordination scattergram of Fig. 2. The mutual position of the centroids of the sets of relevés may be considered as the centroids of the community niches corresponding to the relevé clusters. This is justified by the fact that the five relevé groups is significantly different from all the others at least for one environmental variable. It can be concluded that the relevé groups 3 and 4 are the most distant, while 4 and 5 are the closest. Fig. 2 suggests that relevé group 1 has a central position in the ecological space and that from it there are two main trends of variation: one related to soil pH and humidity and the other related to altidute.

Conclusions

The pattern of variation of the understory vegetation of Pyrenean *Pinus sylvestris* forests may be explained in terms of environmental variables. Discriminant analysis provides a clear description of the relationships between vegetation classes (relevé clusters) and environmental variables. This demonstrates the utility of vegetation classification in simplifying the vegetation system. The vegetation relevé may be seen as a state of a composite variable (vegetation) whose variability and frequency distribution are quite difficult to detect. Cluster analysis may help in showing groups of relevés useful to define a vegetation classification, however, the differences in terms of species may only generate hypotheses concerning differences in terms of environmental variables. This paper demonstrates that DA can be applied to test such differences by contributing with a clear underlying linear model to determine the causes of patterns in the distribution, abundance, and dynamics of the vegetation.

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