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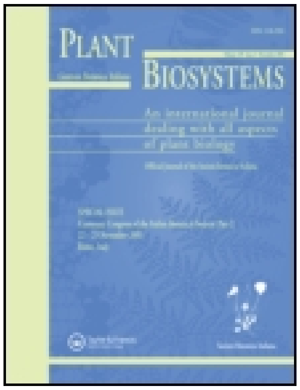

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Correlations among biodiversity, biomass and other plant community parameters using the phytosociological approach: A case study from the south-eastern Alps

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Abstract

The present study deals with the grassland complex of communities which may be found on the limestones in the south-eastern Alps; these communities show in fact a particular interest for their high biodiversity degree and for their importance for the traditional land-use economy of the south-European mountain regions. Phytosociological relevés corresponding to well-defined plant associations have been used in order to get information on the relationships among plant species diversity, biomass, chorotypes, pollination types, functional strategies and soil characteristics. The analysis was carried out both along an altitudinal and a soil evolution gradient. The analysis of the correlations among the variables and the application of the principal component analysis shows a positive correlation between soil parameters and biomass, eurichory, anemogamy and C- and R-strategies; on the contrary, a negative correlation among stenochory, entomogamy and S-strategy with the soil evolution seems to be present. This article shows how the phytosociological approach can be used to get information and knowledge on the correlations between several variables useful to understand the complex nature of the plant communities in order to support management plans.

Keywords: *SE Alps, grassland ecology, functional traits, edaphic properties, phytosociological data*

Abbreviations: D = dispersion; H = soil moisture; Hm = humus; N = nutrients

Introduction

The availability of phytosociological data is increasing all around the European continent (see Feoli & Orloci 1991; Feoli et al. 2006; Schaminé et al. 2009) and the possibility to use such data to study the relationships between biodiversity and other relevant parameters of plant communities with the aim to assess management conservation plans becomes more feasible. The advantage to use phytosociological data for discovering relationships among environmental parameters, functional and structural features (plant traits) of plant communities (Redžić 2007; Diekmann et al. 2008; Ewald 2008; Zelnik & Čarni 2008) was already clearly shown by Feoli (1984) with a simple approach based on matrix multiplication. This approach generates different vegetation spaces according to the description of plant species by different biological and environmental characters obtained from different sources (e.g. literature, herbaria, etc.) constituting the database of the phytosociologist's knowledge. We use such an approach to assess the correlation among plant diversity, some functional and chorological characters and some soil chemico-physical variables of a vegetation system that is rich of biodiversity and still of economic importance, namely the natural and semi-natural grasslands on limestone of south-eastern (SE) Alpine chain.

The study is addressed to assess a scientific background on which to base managing plans for biodiversity conservation of the area.

Materials and methods

The analysis is based on phytosociological data, both published and unpublished, related to nine

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vegetation types (see Table I) of natural and semi-natural grasslands of the SE Alps and their forelands (NE Italy, S. Austria and Slovenia) (Poldini & Feoli 1976; Pignatti & Pignatti 1984; Poldini 1985; Isda 1986; Lasen 1989; Feoli Chiapella & Poldini 1994; Buffa et al. 1995; Poldini & Oriolo 1995; Sburlino et al. 1999; Tasinazzo 2001; Surina 2005). All the relevés were made according to the standard Central-European phytosociological method (Braun-Blanquet 1964; Westhoff & van der Maarel 1978). We selected 15–20 relevés for each type corresponding to different locations in order to cover in a satisfactory way the geographic area under interest. In total, we obtained 175 relevés including 685 species. With these species and relevés we have obtained matrix **X** with 685 rows (species) and 175 columns (relevés). The cover values were transformed according to the van der Maarel's Scale (1979).

Each species was described by:

1. a vector showing the Landolt's (1977) indices of nutrients, soil texture, soil moisture and humus giving rise to a matrix **S** of 4 rows and 685 columns,
2. a vector of chorotypes according to Poldini (1991) and Aeschimann et al. (2004), giving rise to a matrix **C** of 18 rows and 685 columns,
3. a vector of types of pollination according to Faegri and van der Pijl (1971), Riciardelli D'Albore and Persano Oddo (1981), Lindacher (ed., 1995) and Oberdorfer (2001) giving rise to a matrix **P** of 8 rows and 685 columns,
4. a vector of the functional strategies according to Grime (1979). With regard to the functional strategies (C-S-R) we referred to Grime (1974, 1977, 1979, 2001), Grime et al. (1988), Hodgson et al. (1999), Flora Web (1999–2001), Cornellissen et al. (2003) giving rise to a matrix **F** of 8 rows and 685 columns. Owing to the lack of data for almost all the species found outside the lowland–hilly belt, this matrix was used only to test the relationships among biomass, plant diversity and functional strategies within this belt.

The list of indices and characters for matrices **S**, **C** and **P** are given in Table II, while the list for matrix **F** is given in Table IV. Matrices **S**, **C**, **P** and **F** have been multiplied by the matrix **X** considering its cover scores. The scores of the resulting four matrices have been averaged according to the corresponding column totals of **X**. The matrices obtained by the matrix multiplication have been used to calculate the centroids of the relevés belonging to each type. With the centroids we have built a new matrix (Table II) showing the description of the vegetation types according to the parameters among which we wanted to test the correlation. For chorological elements, pollination type and Grime's strategies we have calculated the percentage.

Table II has been integrated with mean values of altitude, biomass and three diversity indices for each *syntaxa*. To get an estimation of the mean above ground biomass, we have used an index that corrects the sum of cover of the species by using the leaf surface of the most frequent species according the following formula:

$$\mathrm{Bm}c = \frac{\sum_{i=1}^{n} [(\mathrm{Sl}i \times \mathrm{hm}i) \times Ci]}{\mathrm{NR}}$$

where Bm = mean biomass, Sl = leaf surface, hm = mean height of species according to literature (Pignatti 1982; Conert 1998; Rothmaler et al. 2000), n = number of species with a frequency > 20%, c = community type ($c = 1, \ldots\ldots, 9$), C = cover, NR = number of relevés.

The Sl of each species was obtained by multiplying the average of width and length of 3–10 leaves of herbarium specimens from various stations in the area.

Table I. Grasslands coenosis considered of the south-eastern Alps.

Community name	Acronym	Altitudinal belt	Ecology
Saturejo variegatae-Brometum condensati Poldini et Feoli Chiapella in Feoli Chiapella et Poldini 1994	S-B	Lowland and hilly	Hyper-xerophilous
Onobrychido arenariae-Brometum erecti Poldini et Feoli Chiapella in Feoli Chiapella et Poldini 1994	O-B	Lowland and hilly	Xerophilous
Anthoxantho-Brometum erecti Poldini 1980	A-B	Flat and hilly	Meso-xerophilous
Centaureo carniolicae-Arrhenatheretum Oberdorfer 1964 corr. Poldini et Oriolo 1995	C-A	Lowland and hilly	Meso-eutrophic
Carici ornithopodae-Seslerietum albicantis Poldini et Feoli Chiapella in Feoli Chiapella et Poldini 1994	Ca-S	Montane	Xerophilous
Crepido aureae-Poetum alpinae Poldini et Oriolo 1995	C-P	High montane – subalpine	Meso-eutrophic
Campanulo-Festucetum noricae Isda 1986	C-F	Subalpine–alpine	Meso-xerophilous
Ranunculo hybridi-Caricetum sempervirentis Poldini et Feoli Chiapella in Feoli Chiapella et Poldini 1994	Ra-C	Subalpine–alpine	Xerophilous
Gentiano terglouensis-Caricetum firmae T. Wraber 1970	G-C	Subalpine–alpine	Hyper-xerophilous

Table II. Values of biological variables and edaphic parameters in the nine grasslands coenosis of the south-eastern Alps.

	S-B	O-B	A-B	C-A	Ca-S	C-P	C-F	Ra-C	G-C
Altitude (m a.s.l.)	317	404	285.5	456	1420.7	1731.5	1914	1958	2124.5
Mean number of species	36.5	44.3	42.3	39.7	37.3	44.7	51.7	42.9	22.2
Diversity (Shannon)	2.00	2.32	2.09	2.24	1.94	2.23	2.65	2.07	1.34
Eveness	0.57	0.62	0.57	0.61	0.54	0.60	0.68	0.55	0.44
Biomass	43410.67	135299.32	58906.11982	252195.20	18979.26	65492.73	87506.66	16132.16	1076.13
Alpine s.l.	0.28	0.23		0.76	12.34	10.51	17.18	26.46	34.68
Alien	0.14		0.71	0.88					
Circumboreal	2.78	3.28	8.75	10.96	5.37	10.51	6.66	3.86	2.70
Cosmopolitan	1.11	0.34	3.43	5.16	0.72	3.91	2.90	0.47	0.23
Endemic	4.31	2.82	0.95	1.89	4.11	1.34	1.74	3.98	13.96
Eurasiatic	9.72	17.85	25.53	23.68	19.50	13.53	9.75	6.44	6.98
Eurio-Mediterranean	22.08	10.40	10.17	6.42	1.79	3.13	4.05	0.94	0.23
European	18.75	23.28	14.78	15.49	14.67	12.42	14.29	10.19	6.98
Eurosiberian	5.14	10.40	4.37	6.55	3.58	5.93	4.05	0.70	
Atlantic s.l.	1.53	2.71	2.48	1.13	0.89	0.34	0.77	0.12	
Mediterranean-montane	15.00	9.27	1.54	1.64	32.38	29.75	32.92	40.40	31.53
Mediterranean-Pontic	3.19	0.45	2.13	1.01					
N-Illyric	0.56	0.11			1.61	0.45	1.16	4.22	2.70
Palaeotemperate	4.31	6.44	16.43	20.15	1.97	7.05	3.38	2.22	
Pontic	5.42	6.55	0.71	0.25	0.18	0.34	1.16		
SE European	5.42	4.63	7.33	3.78	0.54	0.78			
S Illyric	0.14	1.02	0.35	0.25	0.36				
Stenomediterranean	0.14	0.23	0.35						
Anemogamy	20.28	23.28	25.77	29.47	23.26	25.06	19.88	15.11	16.22
Anemogamy/autogamy		0.11		0.13					
Anemogamy/entomogamy	3.19	1.69	1.77	2.39	1.07	0.56	0.68		
Autogamy	2.36	0.23	0.12	0.50	1.25	2.01	0.77	0.70	0.68
Entomogamy	59.17	56.95	49.76	51.01	62.61	56.82	64.96	71.90	76.80
Entomogamy/autogamy	14.86	16.95	20.33	15.62	9.66	13.42	11.58	10.77	4.73
Entomogamy/autogamy/anemogamy		0.68	2.25	0.76	1.43	0.89	0.97		
Hydrogamy	0.14	0.11		0.13	0.72	1.23	1.16	1.52	1.58
Soil texture (D)	3.099	3.248	3.808	4.039	2.853	4.050	3.558	2.765	2.704
Soil moisture (H)	1.223	1.660	2.330	2.850	2.093	3.001	2.296	2.073	2.086
Humus (Hm)	2.524	2.407	2.947	3.070	2.948	3.158	3.087	3.039	2.915
Nutrient (N)	2.051	1.807	2.621	3.390	2.199	3.094	2.344	2.050	1.385

Alpine s.l., E Alpine + Arctic-Alpine + Alpine-Carpathic; Atlantic s.l., Atlantic + Mediterranean-Atlantic; A-B, *Anthoxantho-Brometum erecti*; C-A, *Centaureo carniolicae-Arrhenatheretum*; C-F, *Campanulo-Festucetum noricae*; C-P, *Crepido aureae-Poetum alpinae*; Ca-S, *Carici ornithopodae-Seslerietum albicantis*; G-C, *Gentiano terglouensis-Caricetum firmae*; O-B, *Onobrychido arenariae-Brometum erecti*; Ra-C, *Ranunculo hybridi-Caricetum sempervirentis*; S-B, *Saturejo variegatae-Brometum condensati*.

For each community, the diversity was calculated using the STADIV programme (Ganis 1991) which besides giving the number of species provides several indices, among those we use the richness index, Shannon index and Pielou's Index *J*.

The analysis of correlation between the variables was carried out considering the effect of the altitudinal gradient and by trying to remove such effect. For this aim the following sequences were identified:

1. altitudinal gradient
2. soil evolution gradient within lowland–hilly belt and subalpine–alpine belt.

The matrices thus obtained were subjected to a numerical processing package using Syntax 5.0 (Podani 1993). The principal components analysis (PCA) was used, giving the order both of the variables and the objects (the communities) on the same graph. A method of correlation that allows a comparison between the heterogenous variables was chosen.

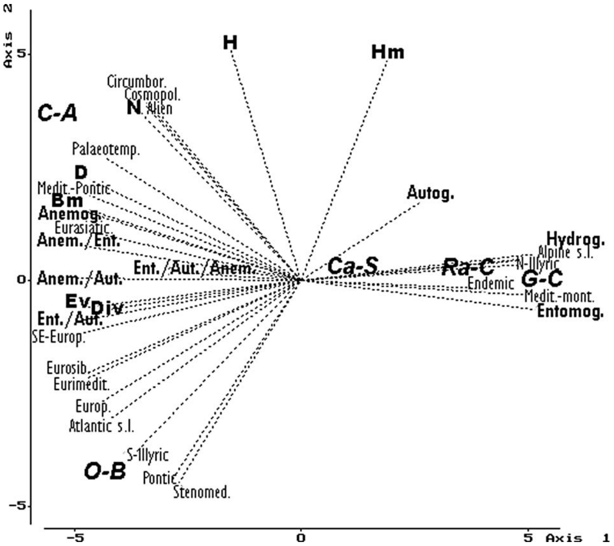

Figure 1. PCA of the altitudinal gradient. Bm, mean biomass; D, dispersion; Div, diversity; Ev, eveness; H, soil moisture; Hm, humus; N, nutrients; C-A, *Centaureo carniolicae-Arrhenatheretum*; Ca-S, *Carici ornithopodae-Seslerietum albicantis*; G-C, *Gentiano terglouensis-Caricetum firmae*; O-B, *Onobrychido arenariae-Brometum erecti*; Ra-C, *Ranunculo hybridi-Caricetum sempervirentis*.

The altitudinal gradient, besides representing a gradient of temperature corresponds to the crest–slope–piedmont–valley model (Rivas-Martínez 2005) that supposes a soil evolution with increasing from high up down towards the valley bottom owing to an increasing process of accumulation (deposition) *versus* a decreasing process of soil erosion.

In order to calculate the correlation between plant diversity, biomass and soil parameters, the communities *Centaureo carniolicae-Arrhenatheretum, Carici ornithopodae-Seslerietum albicantis, Gentiano terglouensis-Caricetum firmae, Onobrychido arenariae-Brometum erecti* and *Ranunculo hybridi-Caricetum sempervirentis* are considered on the altitudinal gradient; on the soil evolution gradient the communities *Anthoxantho-Brometum erecti, Centaureo carniolicae-Arrhenatheretum, Onobrychido arenariae-Brometum erecti* and *Saturejo variegatae-Brometum condensati* are considered within lowland–hilly belt and *Campanulo-Festucetum noricae, Crepido aureae-Poetum alpinae* and *Ranunculo hybridi-Caricetum sempervirentis* within subalpine–alpine belt (Table II). Only in the second case we have considered the Grime's strategies; these were used only for the communities in the lowland–hilly belt for which sufficiently detailed data were available.

Table III. The most significant correlation coefficients and their level of significance in the grasslands communities in an altimetric sequence.

		r	Sign.			*R*	Sign.
Div	Ev	0.988	0.001**	Eurasiatic	Hydrog.	−0.924	0.025*
Div	Ent./Aut.	0.953	0.012*	Eurimedit.	Anem./Aut.	0.913	0.031*
Div	Endemic	−0.965	0.008**	Eurimedit.	Ent./Aut.	0.900	0.037*
Ev	Ent./Aut.	0.982	0.003**	Eurimedit.	Hydrog.	−0.882	0.048*
Ev	Alpine s.l.	−0.902	0.036*	Europ.	Hydrog.	−0.883	0.047*
Ev	Endemic	−0.943	0.016*	Eurosib.	Ent./Aut.	0.894	0.041*
Bm	Medit.-Pontic	0.996	0.000***	Eurosib.	Hydrog.	−0.937	0.019*
Bm	Paleotemp.	0.969	0.007**	Medit.-mont.	Hydrog.	0.884	0.046*
Bm	Anem./Aut.	0.946	0.015*	Medit.-mont.	Anem./Aut.	−0.974	0.005**
Bm	Anem./Ent.	0.916	0.029*	Medit.-mont.	Anem./Ent.	−0.922	0.026*
Bm	D	0.989	0.001**	Medit.-mont.	D	−0.910	0.032*
Bm	Medit.-mont.	−0.945	0.015*	Medit.-Pontic	Anem./Aut.	0.926	0.024*
Bm	Entomog.	−0.888	0.044*	Medit.-Pontic	Anem./Ent.	0.892	0.042*
Alpine s.l.	Entomog.	0.977	0.004**	Medit.-Pontic	D	0.993	0.001***
Alpine s.l.	Hydrog.	0.986	0.002**	N-Illyric	Hydrog.	0.945	0.015*
Alpine s.l.	Anemog.	−0.888	0.044*	N-Illyric	Anemog.	−0.902	0.036*
Alpine s.l.	Anem./Ent.	−0.949	0.014*	N-Illyric	Anem./Ent.	−0.932	0.021*
Alpine s.l.	Ent./Aut.	−0.913	0.030*	Paleotemp.	D	0.992	0.001***
Alien	D	0.924	0.025*	Paleotemp.	N	0.904	0.035*
Alien	H	0.905	0.035*	Pontic	Hm	−0.967	0.007**
Alien	N	0.912	0.031*	SE-Europ.	Anem./Aut.	0.974	0.005**
Circumbor.	H	0.904	0.035*	SE-Europ.	Ent./Aut.	0.897	0.039*
Circumbor.	N	0.980	0.003**	SE-Europ.	Hydrog.	−0.915	0.029*
Cosmopol.	D	0.919	0.028*	S-Illyric	Hm	−0.893	0.041*
Cosmopol.	H	0.913	0.030*	Stenomed.	Hm	−0.972	0.006**
Cosmopol.	N	0.941	0.017*	Anemog.	D	0.884	0.046*
Eurasiatic	Anemog.	0.980	0.003**	Anem./Aut.	D	0.891	0.042*
Eurasiatic	Anem./Ent.	0.949	0.014*	Anem./Ent.	D	0.908	0.033*
Eurasiatic	Entomog.	−0.943	0.016*	Entomog.	D	−0.878	0.050*

r, Pearson's correlation coefficient; sign., level of significance (* ≤ 0.05→0.01; ** ≤ 0.01–0.001; *** < 0.001); Bm, mean biomass; D, dispersion; Div, diversity; Ev, eveness; H, soil moisture; Hm, humus; N, nutrients.

To complement and confirm the results of the PCA, multiple linear and polynomial regressions, applied to all vegetation types, were conducted to explain the relationships between biomass, chorological types, diversity parameters, anemogamy and entomogamy taken individually as response variables, and altitude and nutrients chosen as explanatory variables. The parameter of nutrients was selected as representative of all edaphic parameters being more correlated to all others and being the best indicator of the eutrophication of the soil.

Polynomial regression was chosen only for diversity parameters because of their quadratics relationships with the independent variables.

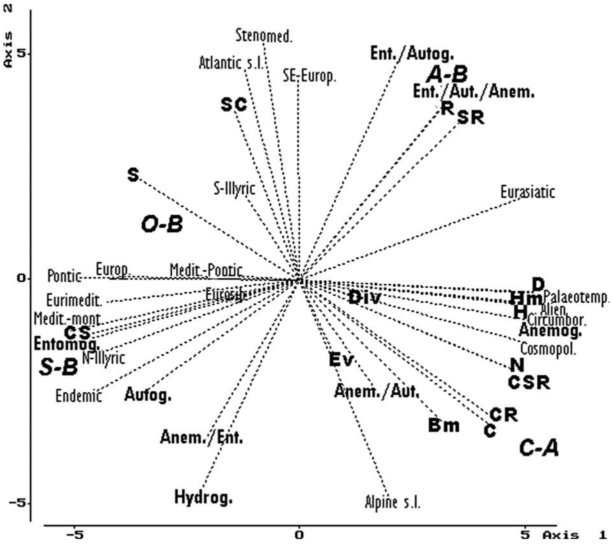

Figure 2. PCA of the lowland–hilly belt. Bm, mean biomass; D, dispersion; Div, diversity; Ev, eveness; H, soil moisture; Hm, humus; N, nutrients, C, competitive species; R, ruderal species; S, stress-tolerant species; A-B, *Anthoxantho-Brometum erecti*; C-A, *Centaureo carniolicae-Arrhenatheretum*; O-B, *Onobrychido arenariae-Brometum erecti*; S-B, *Saturejo variegatae-Brometum condensati*.

Table IV. Values of functional strategies in the lowland–hilly communities.

	S-B	O-B	A-B	C-A
Competitors (C)	8.29	4.16	12.70	38.91
Competitors/Ruderals (CR)	1.05	1.54	1.86	5.16
Competitors/Stress-tolerators (CS)	8.03	3.51	1.78	1.37
Competitors/Stress-tolerators/Ruderals (CSR)	9.97	8.93	21.99	38.71
Ruderals (R)	0.03	0.02	6.69	1.35
Stress-tolerators (S)	15.90	26.26	14.25	8.41
Stress-tolerators/Competitors (SC)	5.85	43.05	24.66	0.83
Stress-tolerators/Ruderals (SR)	0.10	1.08	10.45	3.51

A-B, *Anthoxantho-Brometum erecti*; C-A, *Centaureo carniolicae-Arrhenatheretum*; O-B, *Onobrychido arenariae-Brometum erecti*; S-B, *Saturejo variegatae-Brometum condensati*.

Results

Altitudinal gradient (Figure 1)

The communities used are: *Centaureo carniolicae-Arrhenatheretum, Onobrychido arenariae-Brometum erecti, Carici ornithopodae-Seslerietum albicantis, Ranunculo hybridi-Caricetum sempervirentis* and *Gentiano terglouensis-Caricetum firmae*.

In Figure 1, the associations are arranged in an altimetric sequence. On the left occurs the lowland–hilly communities, in an intermediate position the montane *Carici ornithopodae-Seslerietum* and on the right the subalpine–alpine *Ranunculo-Caricetum sempervirentis* and *Gentiano terglouensis-Caricetum firmae*.

Table V. The most significant correlation coefficients and their level of significance in the lowland–hilly communities.

		r	Sign.
Div	Ev	0.966	0.034*
Div	Medit.-Pontic	−0.994	0.006**
Ev	Anem./Aut.	0.985	0.015*
Ev	Medit.-Pontic	−0.951	0.049*
Alien	D	0.963	0.037*
Alien	Hm	1.000	0.000***
Alien	N	0.956	0.044*
Circumbor.	D	0.996	0.004**
Circumbor.	H	0.977	0.023*
Circumbor.	Hm	0.978	0.022*
Circumbor.	N	0.953	0.047*
Circumbor.	CSR	0.955	0.045*
Cosmopol.	D	0.954	0.046*
Cosmopol.	Hm	0.985	0.015*
Cosmopol.	N	0.991	0.009**
Cosmopol.	CSR	0.977	0.023*
Endemic	Entomog.	0.957	0.043*
Eurasiatic	Entomog.	−0.960	0.040*
Eurasiatic	CS	−0.974	0.026*
Eurimedit.	CS	0.974	0.026*
Atlantic s.l.	SC	0.958	0.042*
Medit.-mont.	Entomog.	0.981	0.019*
Medit.-mont.	CS	0.958	0.042*
Medit.-mont.	D	−0.951	0.049*
N-Illyric	Autog.	0.960	0.040*
N-Illyric	CS	0.993	0.007**
Paleotemp.	Anemog.	0.956	0.044*
Paleotemp.	D	1.000	0.000***
Paleotemp.	H	0.985	0.015*
Paleotemp.	Hm	0.965	0.035*
Pontic	Hm	−0.995	0.005**
Anemog.	D	0.963	0.037*
Ent./Aut./Anem.	R	0.956	0.044*
Ent./Aut./Anem.	SR	0.975	0.025*
Hydrog.	R	−0.967	0.033*
Hydrog.	SR	−0.953	0.047*
N	C	0.958	0.042*

r, Pearson's correlation coefficient; Sign., level of significance; (* ≤ 0.05→0.01; ** ≤ 0.01–0.001; *** < 0.001); C, competitors; CSR, competitors/stress-tolerators/ruderals; CS, competitors/stress-tolerators; D, dispersion; Div, diversity; Ev, eveness; H, soil moisture; Hm, humus; N, nutrients; R, ruderals; SC, stress-tolerators/competitors; SR, stress-tolerators/ruderals.

The highest value of biomass lies in proximity to *Centaureo-Arrhenatheretum*, corresponding to more favourable soil parameters (Hm, H, N, D). The highest degree of diversity is in the intermediate situation between the *Centaureo-Arrhenatheretum* and *Onobrychido-Brometum*, in parallel to a decrease in the trophic level.

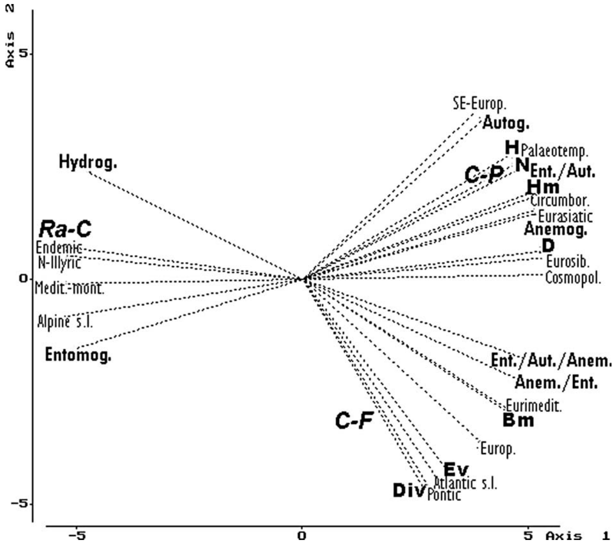

Figure 3. PCA of the subalpine–alpine belt. Bm, mean biomass; D, dispersion; Div, diversity; Ev, eveness; H: soil moisture; Hm, humus; N, nutrients; C-F, *Campanulo-Festucetum noricae*; C-P, *Crepido aureae-Poetum alpinae*; Ra-C, *Ranunculo hybridi-Caricetum sempervirentis*.

Table VI. The most significant correlation coefficients and their level of significance in the subalpine–alpine communities.

		r	Sign.
Div	Atlantic s.l.	0.998	0.042*
Div	Pontic	1.000	0.011*
Ev	Atlantic s.l.	1.000	0.009**
Ev	Pontic	0.998	0.040*
Bm	Eurimedit.	1.000	0.009**
Alpine s.l.	D	−0.999	0.025*
Circumbor.	Anemog.	0.998	0.044*
Circumbor.	Hm	1.000	0.013*
Circumbor.	Entomog.	−0.999	0.029*
Eurasiatic	Anemog.	1.000	0.010*
Eurasiatic	Hm	0.997	0.047*
Eurasiatic	Entomog.	−1.000	0.005**
Eurosib.	D	1.000	0.018*
Paleotemp.	Ent./Aut.	0.997	0.046*
Paleotemp.	H	1.000	0.001***
Paleotemp.	N	0.999	0.029*
SE-Europ.	Autog.	0.999	0.030*
Anem./Ent.	Hydrog.	−1.000	0.017*
Entomog.	Hm	−0.998	0.042*
Ent./Aut.	H	0.997	0.045*
Ent./Aut.	N	1.000	0.016*

r, Pearson's correlation coefficient; Sign., level of significance (*≤ 0.05→0.01; **≤ 0.01–0.001; *** < 0.001); Bm, mean biomass; D, dispersion; Div, diversity; Ev, eveness; H, soil moisture; Hm, humus; N, nutrients.

As far as pollination is concerned, these communities show greater affinity for anemophilous strategies, the communities of higher altitude demonstrate a greater degree of entomogamy, and a higher percentage of stenochorous species, particularly endemic ones, the latter pass from about 2% in *Centaureo-Arrhenatheretum* community to 14% in *Gentiano terglouensis-Caricetum firmae* (Table II). Table III shows the most significant correlation coefficients between the variables considered and their level of significance.

Lowland–hilly belt (Figure 2)

The communities used are: *Anthoxantho-Brometum erecti, Onobrychido arenariae-Brometum erecti, Saturejo variegatae-Brometum condensati* and *Centaureo carniolicae-Arrhenatheretum*.

Figure 2 shows, from left to right, the passage from the most xerophilous associations (*Saturejo variegatae-Brometum condensati*) to the more mesophilous ones (*Centaureo carniolicae-Arrhenatheretum*), with gradual increase in nutrient availability and a general improvement in the soil parameters.

The communities with greater biomass are those which have higher percentages of nutrients and anemophilous species (*Anthoxantho-Brometum* and *Centaureo carniolicae-Arrhenatheretum*). The highest degree of diversity is in the intermediate position between the edaphoxerophilous communities (*Saturejo-Brometum* and *Onobrychido-Brometum*) and the edaphomesophilous ones (*Anthoxantho-Brometum* and *Centaureo carniolicae-Arrhenatheretum*) although closer to the latter. In *Saturejo-Brometum*, the highest degree of endemism and entomogamy is reached (Table II). Figure 2 also shows how the most stenochorous elements are concentrated at the higher oligotrophic values while eurichory finds its greatest expression in meso-eutrophic situations. With regard to the functional strategies it can be seen that the stress-tolerant entities are concentrated in *Saturejo-Brometum* and *Onobrychido-Brometum* while the competitive and ruderal ones gravitate in *Anthoxantho-Brometum* and *Centaureo-Arrhenatheretum* (Table IV). Table V shows the most significant correlation coefficients between the variables considered and their level of significance.

Subalpine–alpine belt (Figure 3)

The communities are: *Ranunculo hybridi-Caricetum sempervirentis, Campanulo-Festucetum noricae* and *Crepido aureae-Poetum alpinae*.

From left to right the associations arrange themselves along a trophic gradient: to the left the xero-oligotrophic *Ranunculo-Caricetum* and to the right the meso-eutrophic *Crepido-Poetum*.

The highest values of biomass and diversity are achieved in the intermediate section (*Campanulo-Festucetum noricae*). The coexistence of a more marked anemogamy and eurichory is confirmed for the community with the greatest nutrient availability (*Crepido-Poetum*), the highest values of entomogamy and stenochory being found in the more oligotrophic association (*Ranunculo-Caricetum sempervirentis*) (Table II). Table VI shows the most significant correlation coefficients between

Table VII. Results of quadratic (A) and linear (B) multiple regressions analysis for the vegetation type.

	r^2 adj	*F*(4,5)	*p*		*b*	*t*	*p*	Sign.
A								
Mean no. of species	0.967	67.98	0.000	Altitude	4.29 E−03	0.155	0.883	
				Altitude^2	−2.00 E−06	−0.167	0.874	
				Nutrient	2.99 E+01	3.543	0.017	⋆
				Nutrient^2	−5.24 E+00	−2.429	0.059	†
Shannon	0.9774	98.18	0.000	Altitude	8.71 E−05	0.073	0.945	
				Altitude^2	−5.29 E−08	−0.101	0.924	
				Nutrient	1.59 E+00	4.355	0.007	⋆⋆
				Nutrient^2	−2.77 E+00	−2.965	0.031	⋆
Eveness	0.9892	206.7	0.000	Altitude	8.71 E−05	0.073	0.945	
				Altitude^2	−5.29 E−08	−0.101	0.924	
				Nutrient	1.59 E+00	4.355	0.007	⋆⋆
				Nutrient^2	−2.77 E−01	−2.965	0.031	⋆

	r^2 adj	*F*(2,7)	*p*		*b*	*t*	*p*	Sign.
B								
Biomass	0.70	11.54	0.006	Altitude	−4.23 E+01	−1.920	0.096	
				Nutrient	5.45 E+04	4.248	0.004	⋆⋆
Anemogamy	0.972	155.42	0.000	Altitude	0.00 E+00	−0.324	0.756	
				Nutrient	9.47 E+00	11.250	0.000	⋆⋆⋆
Entomogamy	0.929	59.72	0.000	Altitude	1.90 E–02	2.957	0.021	⋆
				Nutrient	1.56 E+01	4.252	0.004	⋆⋆
Endemic	0.484	5.22	0.041	Altitude	3.00 E–03	2.148	0.069	†
				Nutrient	−1.49 E–01	−0.172	0.868	
Alpine s.l.	0.92	52.40	0.000	Altitude	1.50 E–02	8.230	0.000	⋆⋆⋆
				Nutrient	−2.75 E+00	−2.634	0.034	⋆
Circumboreal	0.93	60.37	0.000	Altitude	−1.00 E–03	−0.764	0.470	
				Nutrient	3.01 E+00	7.435	0.000	⋆⋆⋆
Cosmopolitan	0.788	17.70	0.002	Altitude	−1.00 E–03	−1.463	0.187	
				Nutrient	1.30 E+00	4.741	0.002	⋆⋆
Eurasiatic	0.90	40.60	0.000	Altitude	−4.00 E–03	−1.805	0.114	
				Nutrient	7.99 E+00	6.918	0.000	⋆⋆⋆
Euro-Mediterranean	0.512	5.73	0.034	Altitude	−4.00 E–03	−1.637	0.146	
				Nutrient	4.50 E+00	3.127	0.017	⋆
European	0.842	24.90	0.001	Altitude	−1.00 E–03	−0.529	0.613	
				Nutrient	6.47 E+00	4.803	0.002	⋆⋆
Eurosiberian	0.753	14.721	0.003	Altitude	−2.00 E–03	−1.574	0.160	
				Nutrient	2.67 E+00	4.470	0.003	⋆⋆
Atlantic s.l.	0.631	8.686	0.013	Altitude	−1.00 E–03	−1.880	0.102	
				Nutrient	7.38 E–01	3.790	0.007	⋆⋆
Mediterranean-Montane	0.942	74.108	0.000	Altitude	1.80E-02	7.611	0.000	⋆⋆⋆
				Nutrient	−2.90 E–02	−0.021	0.984	
Mediterranean-Pontic	0.447	4.636	0.052	Altitude	−1.00 E–03	−2.002	0.085	
				Nutrient	6.60 E−01	2.996	0.020	⋆
N-Illyric	0.705	11.778	0.006	Altitude	1.00 E−03	3.801	0.007	⋆⋆
				Nutrient	−2.38 E–01	−1.088	0.313	
Paleotemperate	0.876	32.812	0.000	Altitude	−5.00 E−03	−3.891	0.006	⋆⋆
				Nutrient	5.54 E+00	7.473	0.000	⋆⋆⋆
SE-European	0.723	12.748	0.005	Altitude	−2.00 E−03	−3.098	0.017	⋆
				Nutrient	2.10 E+00	4.909	0.002	⋆⋆
Stenomediterranean	0.289	2.826	0.126	Altitude	−7.34 E−02	−1.541	0.167	
				Nutrient	6.50 E−02	2.334	0.052	†

r^2 agj, adjusted r^2; *F*, *F* test with degrees of freedom in brackets; *p*, level of significance; *b*, regression coefficient; *t*, *t* test; level of significance (sign.), ⋆$p \le 0.05$; ⋆⋆$p \le 0.01$; ⋆⋆⋆$p \le 0.001$; $^{\dagger}p \le 0.1$.

the variables considered and their level of significance.

Discussion

The altimetric gradient reflects the shortening of the growing season, which can be inferred indirectly through the crowding of the microthermic chorotypes (Alpine *sensu latu*, Mediterranean-montane, N-Illyric). The trophic level also decreases from the bottom of the valley towards the mountain ridges depending on the ratio between the erosive and accumulative processes. In principle, the biomass is positively correlated with nutrient availability and, more generally, with more favourable soil conditions. This relationship is evident in the altimetric gradient (see Figure 1) and in the lowland–hilly belt (see Figure 2). In the subalpine–alpine belt (see Figure 3) the highest biomass value does not correspond to the highest trophic levels, this being reached in *Campanulo-Festucetum*; this anomaly can be simply explained in that this association is subject to greater grazing by ungulates, and only sporadically by cattle, which allows for the development of tall herbs that cannot withstand the stress caused by intensive grazing to which the *Crepido-Poetum* is still subject to. Anemogamy is also connected with a high availability of nutrients and, in general, with greater eurichory. At higher altitudes, the lack of nutrients seems to correlate with high percentages of entomogamy and stenochory, mostly represented by endemic entities. This trend is also confirmed by analysing the horizontal sequences.

As far as the functional strategies are concerned, albeit within the limits of available data, one can observe that the stress-tolerant entities dominate the more natural and xero-oligotrophic communities while the competitive and ruderal ones gravitate within the semi-natural, human-managed associations which develop under conditions of better trophism.

These results fit also with Grime's succession theory. According to this model, the major factor determining the role of strategies in vegetation succession is the potential productivity of the habitat, so that in a primary succession stress-tolerators prevail in the early successional phase, the colonisation of a new and skeletal habitat, and in the final phase, the natural potential vegetation, in correspondence with a depletion of nutrients.

On the contrary, in the middle phases or in a secondary succession, ruderals and competitors become dominant depending on the level of disturbance and/or nutrient availability. Analogous correlation among morpho-functional traits and biomass production was investigated by Ceriani et al. (2008).

From the above, some exciting types of correlation emerge between apparently unrelated phenomena: trophic levels, biomass, diversity, chorotypes, floral attractiveness, pollination and functional strategies. A general theory able to link these issues could be found in a principle of energetic parsimony interconnected with the Grime strategies and co-evolution. It seems that the greater availability of nutrients provides a notable dissipation of germ cells with a high protein content by air currents. This consideration applies to eurychorous competitive species which are present in large numbers and capable of producing large amounts of biomass. Conversely, a lack of nutrients leads the species to invest in floral attractiveness (Poldini & Vidali 1987) and consequently in the less dissipative entomogamic strategy; this explanation applies to fewer stenochorous species, mostly present with lower levels of biomass.

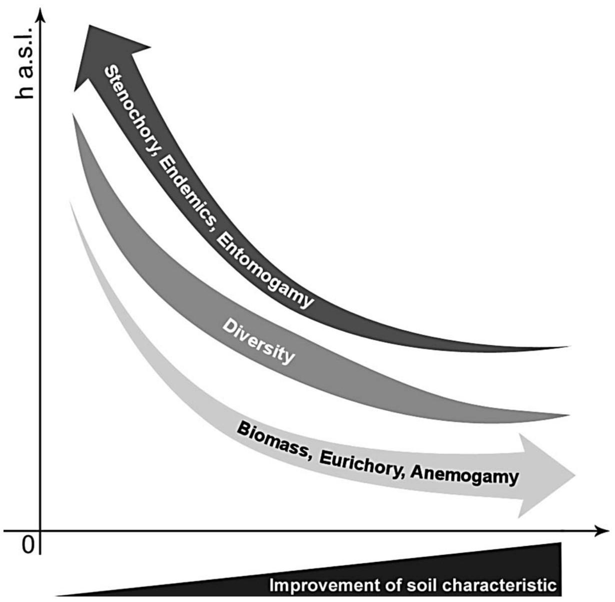

Figure 4. Relationships between the improvement of soil characteristics and the analysed biological properties.

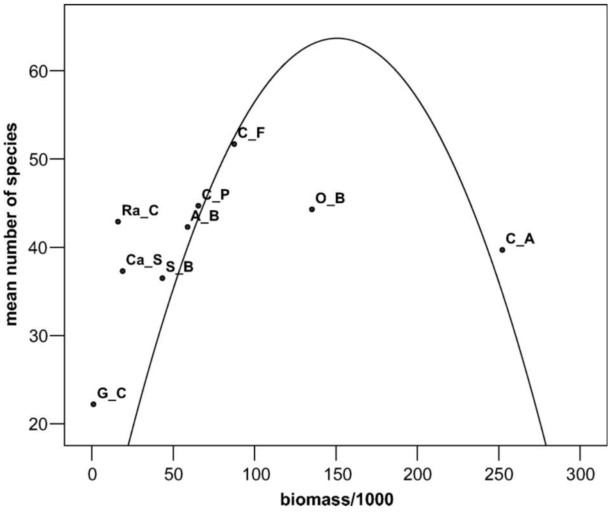

Figure 5. Graph of the quadratic regression model between the mean number of species and the biomass/1000.

In summary, the following assertions may be made:

(a) oligotrophic habitats seem to promote both entomogamy (therefore the plant/animal relationships or co-evolution) and stenochory, in particular endemism;
(b) mesic habitats seem to allow, on average, higher values of biomass and diversity;
(c) eutrophic habitats show high biomass, low diversity levels, high eurichory and anemogamy.

The results of the multiple regressions applied to all vegetation types to model the relationships between many of the variables in Table II and the two principal gradients of altitude and nutrients, showed in Table VII, confirm these assertions.

All polynomial regression models of the diversity parameters are significant even if their contribution to their response is due principally to nutrients.

Figure 4 summarises the relationship between some biological characteristics and the improvement of soil characteristics.

The diagram represents a confirmation and completion of the second biocenotic principle of Thienemann (1920, 1956), which states that when environmental conditions deviate from the normal, there is a decreases in the number of species and an increase in the number of individuals. In other words, diversity and biomass vary in an inverse manner. Evidently, this is a principle of general value, the study case being a particular aspect, referred to soil characteristics. The scheme can also constitute a theoretical basis for the management criteria of protected areas and of the territory in general. Mesotrophic environments are best suited to the preservation of the highest levels of diversity at a territorial scale, while more oligotrophic settings should be identified for the conservation of the highest levels of stenochorous entities, especially endemic ones, but without forgetting the importance of the production of biomass in the more eutrophic situations.

The selected variables can explain the effects of soil nutrients, texture, moisture and humus content on the species diversity of plant communities and biomass and the relationship between the biomass and species diversity, as already analysed by other authors (Al-Mufti et al. 1977; Tilman et al. 1997, 2001; Verginella et al. 2010).

The parameters of the quadratic regression model (Figure 5) for these two variables are shown below:

	r^2 adj	F(2,7)	*p*		*B*	*t*	*p*	Significance
Mean no. of species	80726	19.85	0.001	Biomass/1000	0.845	5.261	0.001	***
				$(\text{Biomass}/1000)^2$	−0.003	−3.694	0.008	**

The study of pollination strategies allows highlighting the correlations to the floral structure evolution, the pollinators and the behaviour conditions.

Moreover, correlation patterns have been detected between plant diversity and some functional variables along both an altitudinal and a soil evolution gradient within two altitudinal belts, homogenous with respect to the parent material.

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