PLANT SPECIES DIVERSITY AND DISTRIBUTION ALONG ENVIRONMENTAL GRADIENTS IN A SUBMEDITERRANEAN FOREST LANDSCAPE (CENTRAL ITALY)

Andrea CATORCI*, Alessandra VITANZI**, Federico Maria TARDELLA*
**School of Environmental Sciences, University of Camerino, Via Pontoni, 5 - I-62032 Camerino, (Italy)*
E-mail: andrea.catorci@unicam.it, federico.tardella@unicam.it
***School of Advanced Studies, PhD Course in Environmental Sciences and Public Health, University of Camerino, Via Lili 55, I-62032 - Camerino, (Italy)*
E-mail: alessandra.vitanzi@unicam.it

ABSTRACT

A survey of a submediterranean forest landscape in central Italy was carried out to assess floristic diversity and species ecological behaviour in relation to some environmental gradients (altitude, aspect, light intensity on the undergrowth, soil pH, nitrogen content and texture). Diversity indices (species richness, Shannon-Wiener and Evenness) trends, calculated in relation to environmental parameters, showed to be mostly related to stress gradients. The highest diversity, in fact, is linked to the least stressful conditions. Redundancy analysis (RDA) allowed to identify six species sets, related to the environmental parameters, which were tested through bioindication values analysis. Intensity of stress factors and their combination select one or more groups of species with different ecological behaviour, leading to the local floristic differentiation of plant communities. This approach may be useful to predict floristic variation of forest ecosystems as a consequence of increasing stress levels, such as drought stress due to climatic changes, to the definition of plant diversity conservation guidelines and for biodiversity monitoring.

KEYWORDS: Diversity, environmental gradients, forest vegetation.

RIASSUNTO

È stata effettuata una campagna di rilievi in un paesaggio forestale submediterraneo nell'Italia centrale per valutare la diversità floristica ed il comportamento ecologico delle specie in relazione ad alcuni gradienti ambientali (altitudine, esposizione, intensità della luce nel sottobosco, pH, contenuto di azoto e tessitura del suolo. L'andamento degli indici di diversità (ricchezza di specie, Shannon-Wiener e Evenness), calcolati in relazione ai parametri ambientali, ha dimostrato di essere legato, per lo più, a gradienti di stress. La diversità più elevata è infatti associata alle condizioni meno stressanti. L'analisi della ridondanza (RDA) ha permesso di identificare sei gruppi di specie legati ai parametri ambientali, che sono stati testati con l'analisi dei valori di bioindicazione. L'intensità dei fattori di stress e la loro combinazione seleziona uno o più gruppi di specie con differente comportamento ecologico, portando alla differenziazione floristica locale delle comunità vegetali. Questo approccio può essere utile a predire le variazioni floristiche degli ecosistemi forestali come conseguenza dei crescenti livelli di stress come lo stress d'aridità dovuto ai cambiamenti climatici, alla definizione di linee guida per la conservazione della diversità vegetale e al monitoraggio della biodiversità.

INTRODUCTION

Since the classic studies of WHITTAKER (1956) and BRAY & CURTIS (1957), plant ecologists have sought to quantify the distribution of plant species along complex environmental gradients. Although over any large region the distribution of species richness is likely to be governed by two or more environmental gradients (MARGULES *et al.*, 1987; PAUSAS, 1994; PAUSAS & CARRERAS, 1995; AUSTIN *et al.*, 1996; PAUSAS & AUSTIN, 2001), species richness studies about this issue have been mainly single-factor studies (*e.g.* HUSTON, 1980; WILSON & KEDDY, 1988). Species diversity shifts in forest plant communities have been reported by several authors to be related to differences in environmental conditions, such as nutrients level, soil reaction, soil moisture and light intensity (*e.g.* FORMAN, 1995; ROSENZWEIG, 1995; BURNETT *et al.*, 1998; NICHOLS *et al.*, 1998; NASH SUDING, 2001; DECOCQ, 2002). These factors are, in turn, related to topography, bedrock geology, soil physic characteristics (soil depth, texture and drainage), overstory structure and land use history (HUTCHINSON *et al.*, 1999; DECOCQ, 2000). Moreover, floristic differentiation patterns in vegetation are usually too complex to be simplified in either strictly geographical differentiation or in a strictly edaphic or local topoclimatic differentiation (WHITTAKER, 1975; TZONEV *et al.*, 2006). Often these patterns are scale-dependent, showing stronger edaphic effects at finer scales and stronger geographic distinctions on broader scales (CHYTRÝ *et al.*, 2002; KUŽELOVÁ & CHYTRÝ, 2004).

The aim of this work was to assess the floristic diversity and ecological behaviour of species in relation to some environmental gradients (altitude, aspect, light intensity on the undergrowth, soil pH, nitrogen content and texture) in a submediterranean forest landscape, taking into account the hierarchical approach to the landscape characterization (BLASI *et al.*, 2000) and the phytosociological placement of plant communities, in order to reduce the scale-dependent effects on floristic differentiation pattern.

MATERIALS AND METHODS

STUDY AREA

The study area is a hilly and mountainous territory, placed in the central-southern part of Umbria-Marche Apennines (around Camerino, Foligno and Fabriano - central Italy), at altitudes ranging from 150 to 2,300 m a.s.l. (coordinates 43°20'-42°50' N; 12°26'-13°23' E).

From a geological viewpoint, this territory is characterized by calcareous, marly-calcareous, marly-arenaceous and arenaceous substrata. The most common morphologies are represented by reliefs with slightly steep tops and moderately to very steep slopes, which give rise to small flat bottomed valleys (BISCI & DRAMIS, 1991).

The study area is located within a submediterranean context, at the border between Temperate and Mediterranean macroclimatic regions (RIVAS-MARTÍNEZ, 2005).

The forest landscape is featured by mixed woods, in which *Quercus ilex* subsp. *ilex, Quercus pubescens* s.l., *Ostrya carpinifolia*, *Quercus cerris*, *Castanea sativa* and *Fagus sylvatica* subsp. *sylvatica* play a dominant or a

Tab. 1 - Main features of the Upper Mesotemperate bioclimatic belt. Termotype and Ombrotype classification follows RIVAS-MARTÍNEZ (2004); for the calculation of n. of months of drought stress and cold stress MITRAKOS' indices (1980, 1982) were applied (from: ORSOMANDO & CATORCI 2000, modified).

Bioclimatic belt	Altitudinal range (m a.s.l.)	Average annual temperature (°C)	Average annual precipitation (mm)	Average monthly temperature < 10 °C (n. of months)	Average monthly min. temperature < 0 °C (n. of months)	Thermotype	Ombrotype	Drought stress (n. of months)	Cold stress (n. of months)	Vegetative period (n. of days with average monthly min. temperature > 6 °C)
Upper Mesotemperate	500/600-1000/1100	11-13	850-1100	5-6	1-2	Upper Mesotemperate	Lower Humid	0	6-7	180-210

Tab. 2 - Scales for the environmental parameters used in RDA.

Environmental parameter		Class
Aspect	1	Southern (SE-WNW)
	2	Northern (NW-ESE)
Altitude (m a.s.l.)	1	500-800
	2	800-1100
Soil pH	1	< 6.0
	2	6.0-7.0
	3	> 7.0
Soil total nitrogen content (g/Kg)	1	< 2.0
	2	2.0-4.0
	3	> 4.0
Soil texture (sand %)	1	> 60.0
	2	40.0-60.0
	3	< 40.0
Light intensity (μmol m-2 s-1)	1	< 25.0
	2	25.0-50.0
	3	50.1-75.0
	4	> 75.0

codominant role. These woods are mainly managed as coppices with standards and cut down every 20-30 years.

EXPERIMENTAL DESIGN

To plan data collection, the study area was divided into homogeneous ecological units according to the BLASI *et al*. (2000) method, using the plant landscape geodatabase (G.I.S.) of Marches (CATORCI *et al*., 2007a; PESARESI *et al*., 2007) and Umbria (ORSOMANDO & CATORCI, 1999, 2000).

In order to reduce the number of environmental variables, woods belonging to the Upper Mesotemperate bioclimatic belt (BIONDI *et al*., 1995; CATORCI *et al*., 2007b) were selected; the main features of this belt are shown in Tab. 1.

The area was further divided into the main geologic systems (calcareous, marly-calcareous, marly-arenaceous and arenaceous), within each of them, two aspect classes regarding North-facing (from NW to ESE) and South-facing (from SE to WNW) slopes were distinguished. In fact, because of the transition between two macroclimatic contexts, on Southern aspects, characterized by higher temperature and insolation, summer drought stress increases and winter cold stress decreases (JACKSON, 1966; BONAN, 2008) compared to the mean conditions of the Upper Mesotemperate belt. Within each homogeneous ecological unit, five sampling plots (80 on the whole), covering 400 m^2 each (20x20 m), were randomly selected. In each of them floristic and field data were gathered.

DATA COLLECTION

Floristic and environmental data were collected in the period 2006-2007; species cover values were assessed using Braun-Blanquet classes (BRAUN-BLANQUET, 1964).

Each soil sample, collected in five locations in each plot within a depth ranging from 10 to 40 cm and thoroughly mixed, was analysed by a soils laboratory for pH, total nitrogen content (g/kg) and texture (sand, clay and silt %). Furthermore some field data (altitude and aspect) were also gathered. Measurements of light intensity on the undergrowth (¼mol m^{-2} s^{-1}) were performed in June/July, at 50 cm above soil level, using a ceptometer.

Information about species bioindication values were gathered from PIGNATTI (2005).

DATA ELABORATION

For statistical elaborations, species abundances were expressed in percent values using the average cover values of Braun-Blanquet classes; environmental parameters values (aspect, altitude, soil pH, soil total nitrogen content, soil sand %, light intensity on the undergrowth) were expressed in classes (Tab. 2).

Species richness, Shannon-Wiener and Evenness indices were calculated on two matrices: relevés x species (cover %) and relevés x environmental parameters (classes).

Cluster analysis of floristic data set was run on the matrix relevés x species, using the complete link method, based on Euclidean distance, after transformation of Braun-Blanquet classes according to VAN DER MAAREL'S (1979) scale. Groups of relevés were classified into *syntaxa* according to revision publications of Italian vegetation (BIONDI *et al*., 2002, 2003; BLASI *et al*., 2004), as well as local studies (CATORCI & ORSOMANDO, 2001; ALLEGREZZA *et al*., 2002; ALLEGREZZA, 2003; CATORCI *et al*., 2003, 2008, 2010).

A Redundancy analysis (RDA) on the matrix relevés x variables (floristic units and environmental parameters) was run to understand the amount of total variability related to ecological factors affecting species distribution and to define ecologically homogeneous species sets.

Ecological behaviour of the resulting species sets was tested using light, temperature, soil moisture, soil reaction and soil nutrients bioindication values.

Diversity indices were calculated using PCORD 5.0 software (MCCUNE & GRACE, 2002; MCCUNE & MEFFORD, 2006); cluster analysis and RDA were performed using SYN-TAX 2000 package (PODANI, 2001).

RESULTS

PHYTOSOCIOLOGICAL PLACEMENT

The multivariate analysis (Fig. 1) shows two main clusters: I) woodlands of South-facing slopes, with a dominance of *Quercus pubescens* s.l. (subclusters Ia_{1b}, Ia_2 and Ib) or *Quercus ilex* (subcluster Ia_{1a}), placed in *Quercetalia pubescenti-petraeae* and *Quercetalia ilicis* orders; II) woodlands of North-facing slopes with a dominance of *Ostrya carpinifolia* (subcluster IIa), *Quercus cerris* or *Castanea sativa* (subcluster IIb), placed in *Quercetalia pubescenti-petraeae* and *Fagetalia sylvaticae* orders. Subclusters are divided into groups which correspond to the syntaxonomical levels of association and subassociation. These *syntaxa* are shortly described in Tab. 3.

SPECIES DIVERSITY

A total of 214 species was collected. Species richness, Shannon-Wiener and Evenness diversity indices values, related to each environmental parameter class, are reported in Tab. 4. The highest richness and Shannon-Wiener index values were recorded for North-facing slopes, altitudes ranging

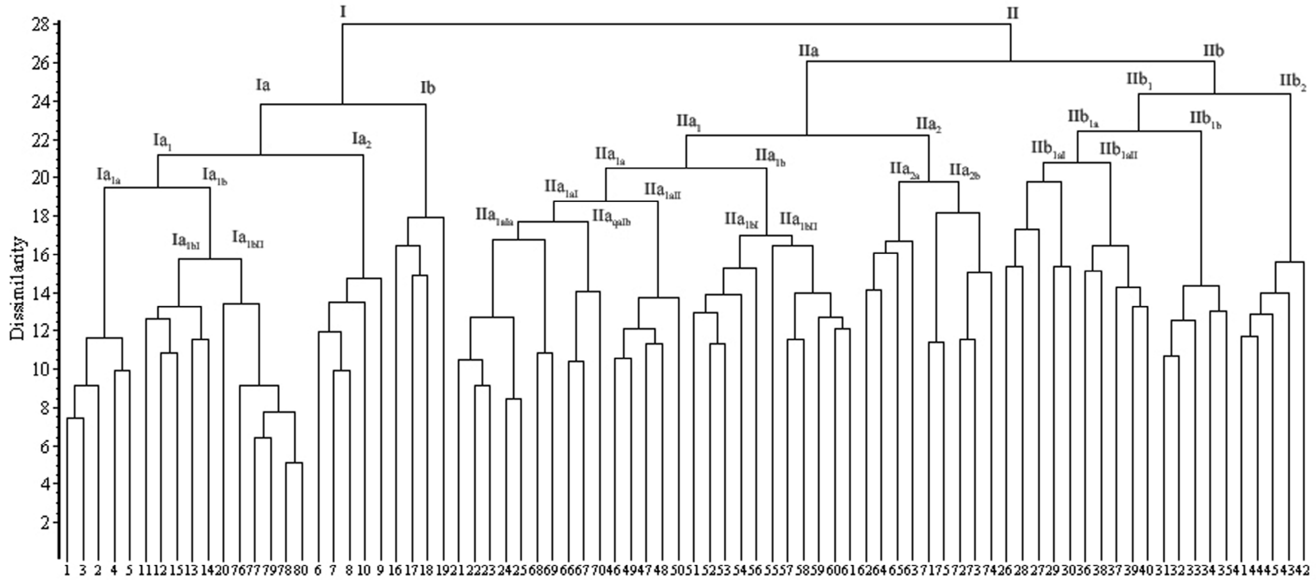

Fig. 1 - Dendrogram of phytosociological relevés (Ia_{1a} - *Cyclamino hederifolii-Quercetum ilicis cyclaminetosum hederifolii*; Ia_{1bI} - *Cytiso sessilifolii-Quercetum pubescentis*; Ia_{1bII} - *Quercus cerris* and *Quercus pubescens* s.l. community; Ia_2 - *Erico arboreae-Quercetum pubescentis ericetosum arboreae*; Ib - *Peucedano cervariae-Quercetum pubescentis peucedanetosum cervariae*; IIa_{1aIa} - *Aceri obtusati-Quercetum cerridis*; IIa_{1aIb} - *Scutellario columnae-Ostryetum carpinifoliae prunetosum avium*; IIa_{1aII} - *Hieracio murorum-Ostryetum carpinifoliae hieracietosum murorum*; IIa_{1bI} - *Scutellario columnae-Ostryetum carpinifoliae cytisetosum sessilifolii*; IIa_{1bII} - *Scutellario columnae-Ostryetum carpinifoliae violetosum reichenbachianae*; IIa_{2a} - *Scutellario columnae-Ostryetum carpinifoliae fagetosum sylvaticae*; IIa_{2b} - *Carici digitatae-Ostryetum carpinifoliae*; IIb_{1aI} - *Aceri obtusati-Quercetum cerridis fagetosum sylvaticae*; IIb_{1a2} - *Carici sylvaticae-Quercetum cerridis*; IIb_{1b} - *Cephalanthero longifoliae-Quercetum cerridis*; IIb_2 - *Cyclamino hederifolii-Castaneetum sativae*).

Tab. 3 - Description of the forest *syntaxa* of the study area.

Ia_{1a} - *Cyclamino hederifolii-Quercetum ilicis* Biondi, Casavecchia et Gigante 2003 *cyclaminetosum hederifolii* Biondi, Casavecchia et Gigante 2003: woodlands with a dominance of *Quercus ilex* subsp. *ilex*, growing on calcareous South-facing very steep slopes.

Ia_{1bI} - *Cytiso sessilifolii-Quercetum pubescentis* Blasi, Feoli et Avena 1982: woodlands with a dominance of *Quercus pubescens* s.l., growing on calcareous detritic South-facing, moderately to very steep slopes.

Ia_{1bII} - *Quercus pubescens* s.l. and *Quercus cerris* community (*Carpinion orientalis*): woodlands with a dominance of *Quercus pubescens* s.l. and *Q. cerris*, growing on marly-arenaceous South-facing, moderately to very steep slopes.

Ia_2 - *Erico arboreae-Quercetum pubescentis ericetosum arboreae* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008: woodlands with a dominance of *Quercus pubescens* s.l., growing on sandstone South-facing, moderately to very steep slopes.

Ib - *Peucedano cervariae-Quercetum pubescentis* (Ubaldi *et al.*, 1984) Ubaldi 1988 *peucedanetosum cervariae* Allegrezza, Baldoni, Biondi, Taffetani et Zuccarello 2002: woodlands with a dominance of *Quercus pubescens* s.l., growing on marly-calcareous South-facing, slightly to moderately steep slopes.

IIa_{1aIa} - *Aceri obtusati-Quercetum cerridis* Ubaldi et Speranza 1982: woodlands with a dominance of *Ostrya carpinifolia* and *Quercus cerris*, growing on marly-arenaceous North-facing, slightly to moderately steep slopes.

IIa_{1aIb} - *Scutellario columnae-Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *prunetosum avium* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia*, growing on marly-calcareous North-facing, moderately to very steep slopes.

IIa_{1aII} - *Hieracio murorum-Ostryetum carpinifoliae* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008 *hieracietosum murorum* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008: woodlands with a dominance of *Ostrya carpinifolia*, growing on arenaceous North-facing, moderately to very steep slopes.

IIa_{1bI} - *Scutellario columnae-Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *cytisetosum sessilifolii* Biondi, Allegrezza et Taffetani 1990: woodlands with a dominance of *Ostrya carpinifolia*, growing on calcareous South-facing, moderately to very steep slopes.

IIa_{1bII} - *Scutellario columnae-Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *violetosum reichenbachianae* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia*, growing on calcareous North-facing, moderately to very steep slopes.

IIa_{2a} - *Scutellario columnae-Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *fagetosum sylvaticae* Pedrotti, Ballelli et Biondi 1982: woodlands with a dominance of *Ostrya carpinifolia* and *Fagus sylvatica*, growing on calcareous North-facing, moderately to very steep slopes.

IIa_{2b} - *Carici digitatae-Ostryetum carpinifoliae* Catorci, Gatti et Sparvoli 2003: woodlands with a dominance *Ostrya carpinifolia*, growing on calcareous North-facing slopes, with medium-high angle.

IIb_{1aI} - *Aceri obtusati-Quercetum cerridis* Ubaldi et Speranza 1982 *fagetosum sylvaticae* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia* and *Quercus cerris*, growing on calcareous North-facing, moderately to very steep slopes.

IIb_{1a2} - *Carici sylvaticae-Quercetum cerridis* Catorci et Orsomando 2001: woodlands with a dominance of *Quercus cerris*, growing on calcareous North-facing, slightly steep slopes.

IIb_{1b} - *Cephalanthero longifoliae-Quercetum cerridis* Scoppola et Filesi 1997: woodlands with a dominance of *Quercus cerris*, growing on sandstone North-facing, slightly steep slopes.

IIb_2 - *Cyclamino hederifolii-Castaneetum sativae* Allegrezza 2003: woodlands with a dominance of *Castanea sativa*, growing on sandstone North-facing, slightly to moderately steep slopes.

Tab. 4 - Richness, Shannon-Wiener and Evenness indices calculated for the environmental parameter classes.

Environmental parameter	Class	Species nr.	Shannon-Wiener index	Evenness index
Aspect	1	27,8	1,898	0,583
	2	36,6	2,157	0,603
Altitude	1	32,9	2,000	0,582
	2	34,9	2,327	0,658
Soil pH	1	30,5	1,972	0,582
	2	27,9	2,070	0,626
	3	38,4	2,133	0,593
Soil total nitrogen content	1	28,9	1,884	0,566
	2	32,2	2,111	0,616
	3	45,0	2,255	0,596
Soil texture (sand %)	1	27,1	1,879	0,577
	2	32,4	1,983	0,580
	3	38,8	2,304	0,635
Light intensity	1	19,0	1,267	0,431
	2	37,3	2,268	0,633
	3	38,6	1,928	0,530
	4	24,6	2,025	0,638

Tab. 5 - RDA axes summary statistics and intraset correlations for environmental parameters.

				Intraset correlations					
Axis	**Eigenvalue**	**Eigenvalue as percentage of total**	**% variance of interset relation**	**Aspect**	**Altitude**	**Soil pH**	**Soil total nitrogen content**	**Soil texture (sand %)**	**Light intensity**
1	16,82	8,58	32,52	0,78	0,71	-0,03	0,43	0,31	0,53
2	11,35	5,79	21,95	-0,30	-0,30	0,90	0,72	0,46	0,14
3	8,14	4,16	15,75	0,16	-0,48	0,04	-0,15	-0,75	0,43
4	7,11	3,63	13,75	-0,42	0,43	0,28	0,40	-0,12	0,17
5	4,44	2,27	8,59	0,29	-0,02	0,02	-0,33	0,33	0,69
6	3,85	1,96	7,44	0,12	-0,05	0,33	-0,12	-0,09	-0,12

from 800 to 1,100 m a.s.l., neutral-basic and nitrogen-rich soils with a low sand content, intermediate light intensities on the undergrowth; the lowest values were recorded for South-facing slopes, altitudes ranging from 500 to 800 m a.s.l., neutral/neutral-acid, nitrogen-poor soils, with a high sand percentage, low light intensities on the undergrowth. Evenness index shows the same trends, except for acid soils (minimum index value), high light intensities, intermediate soil nitrogen content and neutral/neutral-acid soils (maximum index values). More in particular, the highest species richness (45.0) is linked to the highest soil nitrogen content (> 4 g/kg), the lowest (19.0) to the lowest light intensity on the undergrowth (< 25 ¼mol m^{-2} s^{-1}). The highest Shannon-Wiener and Evenness indices are related to the highest altitudes (800-1,000 m a.s.l.) and to the least soil sand percentage (2.30-2.33 and 0.64-0.66, respectively), the lowest to low light intensity (1.27 and 0.43, respectively).

SPECIES ECOLOGICAL BEHAVIOUR

RDA canonical axes explain 26.39% of total variance of species data set. The first axis, explaining 32.52% of variance of interset relation (8.58% of total variance) is particularly related to light intensity on the undergrowth, aspect and altitude; the second axis, explaining 21.95% (5.79% of total variance) is primarily linked to soil pH and secondarily to soil total nitrogen content; the third axis, explaining 15.75% of variance of interset relation (4.16% of total variance) is related to soil sand percentage (Tab. 5).

In the RDA triplot (Fig. 2) two groups of species can be distinguished: one group, near axes origin, not particularly linked to the analyzed combination of environmental features (about 53% of total species number) and another one directly linked to one or more of them (about 47%), which may be divided into six sub-groups (Tab. 6). The mean and median bioindication values, calculated for each of these groups (Tab. 7), are compared according to the main gradients highlighted by RDA. In comparison with the other species sets, groups A and F show the highest light and temperature bioindication values and the lowest soil moisture and nutrients ones, while they differ for soil reaction values. Groups B and E present the same light, temperature, soil moisture and nutrients bioindication values, but quite different soil reaction values. Groups C and D show similar light and soil reaction values; in fact they are nearer to axis 1 than the other groups, while they have quite different temperature mean values.

The ecological behaviour characterization of each group and the relations among species sets, environmental stresses and ecological factors are summarized in Tab. 8. Species belonging to group A are linked to high level of dryness (high solar radiation due to Southern exposure or draining substrata) and low or medium-low nitrogen content; those included in group F are also linked to acid, sandy soils. Both species of A and F groups are light-demanding.

Species of groups B and E mainly differ for soil pH and are both related to medium-low light intensity on the undergrowth. From an ecological viewpoint, species belonging to group B are linked to neutral, clayey, nitrogen-rich soils, while those included in group E are related to acid, sandy-clayey soils with intermediate nitrogen content. Both groups characterize plant communities of North-facing slopes.

Species belonging to groups C and D are both typically linked to low light intensity on the undergrowth. From an ecological viewpoint, species included in group C are related to neutral and clayey soils with high nitrogen content, while group D includes floristic units of subacid and sandy-clayey soils with intermediate nitrogen content. Species of the two groups are water-demanding and low light intensity-tolerators. Both groups characterize phytocoenoses of North-facing slopes.

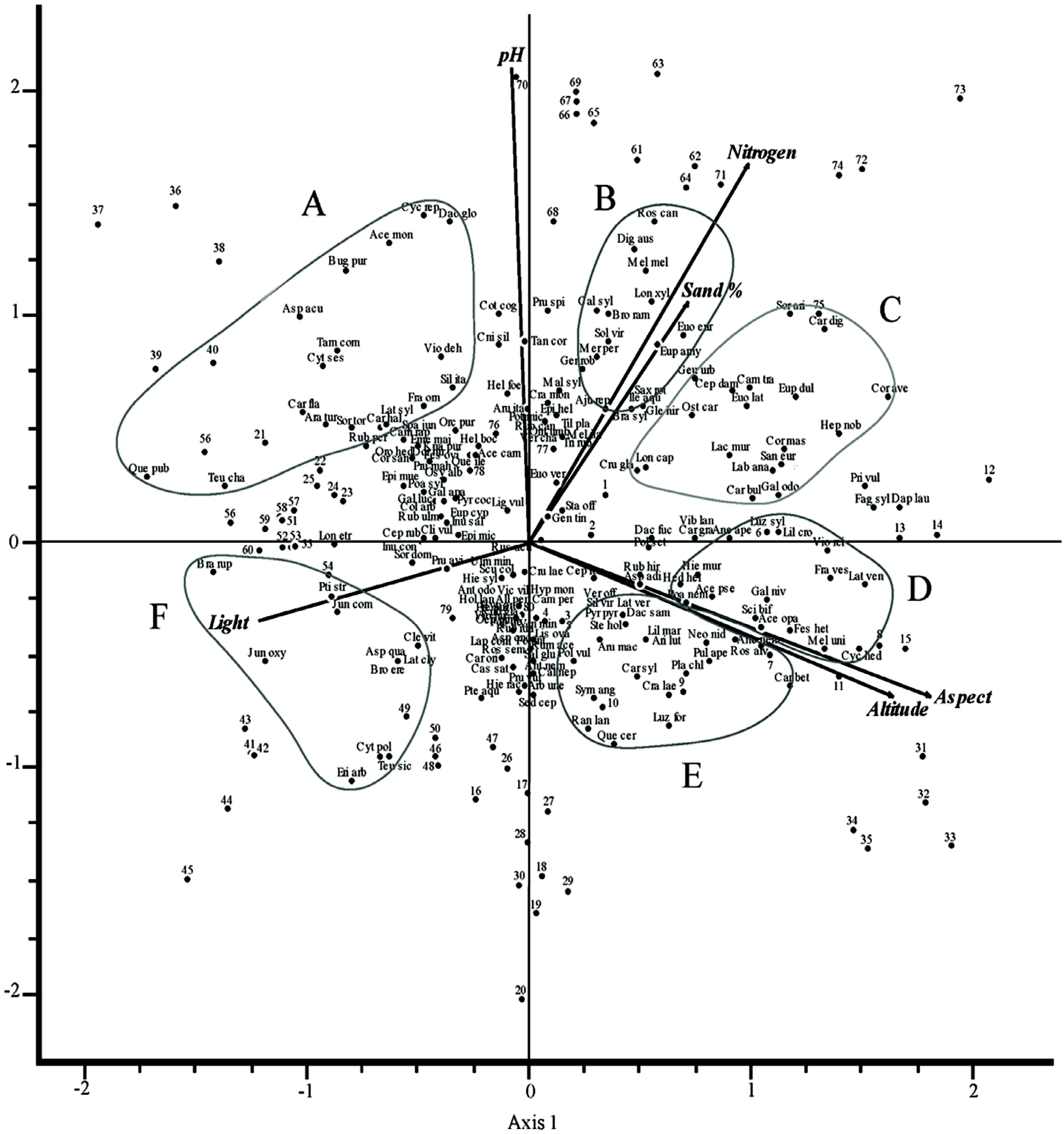

Fig. 2 - Ordination scatterogram from a Redundancy analysis on 80 objects (relevés) and 220 variables (214 species and 6 ecological parameters). Relevés are numbered, species are labelled. Letters A-F indicate species groups reported in Tab. 6.

DISCUSSION

Research findings highlight that in the study area the most important stress factors are soil dryness (related to aspect and soil texture), low nitrogen availability and acid pH. These results are in accordance with the ones of many authors (*e.g.* Burnett *et al.*, 1998; Nichols *et al.*, 1998; Schaffers, 2002; Härdtle *et al.*, 2003). Also light intensity is important to determine the floristic composition of the undergrowth, as demonstrated also by Moore & Vankat (1986), Collins & Pickett (1988) and Schmidt (2005).

From a floristic point of view, the studied forest landscape is composed of two main species groups. The first one is made up of species whose distribution seems not to be linked to the local scale environmental features (species near axes origin), but, instead, to broader scale factors, such as macroclimatic conditions and biogeographic features; the second species group distribution, instead, is linked to local scale environmental features and to one or more of the considered environmental constraints. Furthermore, it is possible to state that intense stress (drought stress on South-facing slopes, nitrogen-poor soils with a high sand percentage or low light intensity) lowers richness and induces the dominance of one or few species (low Shannon and Evenness indices values). The opposite trend is related to low stress level; as a matter of fact, the highest richness and Shannon-Wiener index values were recorded for the least stressful conditions. These results are in accordance with those emphasized by Pausas & Carreras (1995), Burnett *et al.* (1998) and Decocq (2000).

The lowest richness was not found in relation to acid soils, but to neutral/neutral-acid ones, probably because of the overlapping of other environmental stresses (Pausas & Austin, 2001) such as soil dryness and low nitrogen con-

Tab. 6 - Groups of species highlighted by Redundancy analysis (in brackets labels used in Fig. 2 are reported).

Group A. *Acer monspessulanum* subsp. *monspessulanum (Ace mon)*, *Arabis turrita (Ara tur)*, *Asparagus acutifolius (Asp acu)*, *Buglossoides purpurocaerulea (Bug pur)*, *Carex flacca* s.l. *(Car fla)*, *Carex halleriana (Car hal)*, *Cyclamen repandum* subsp. *repandum (Cyc rep)*, *Cytisophyllum sessilifolium (Cyt ses)*, *Dactylis glomerata* subsp. *glomerata (Dac glo)*, *Fraxinus ornus* subsp. *ornus (Fra orn)*, *Lathyrus sylvestris (Lat syl)*, *Quercus pubescens* s.l. *(Que pub)*, *Silene italica (Sil ita)*, *Sorbus torminalis (Sor tor)*, *Tamus communis (Tam com)*, *Teucrium chamaedrys* subsp. *chamaedrys (Teu cha)*, *Viola alba* subsp. *dehnhardtii (Vio deh)*.

Group B. *Ajuga reptans (Aju rep)*, *Brachypodium sylvaticum (Bra syl)*, *Bromus ramosus (Bro ram)*, *Calamintha nepeta* subsp. *sylvatica (Cal syl)*, *Digitalis lutea* subsp. *australis (Dig aus)*, *Euonymus europaeus (Euo eur)*, *Euphorbia amygdaloides* subsp. *amygdaloides (Eup amy)*, *Geranium robertianum (Ger rob)*, *Glechoma hirsuta (Gle hir)*, *Ilex aquifolium (Ile aqu)*, *Lonicera xylosteum (Lon xyl)*, *Melittis melissophyllum* subsp. *melissophyllum (Mel mel)*, *Mercurialis perennis (Mer per)*, *Rosa canina* s.l. *(Ros can)*, *Saxifraga rotundifolia (Sax rot)*, *Solidago virgaurea* subsp. *virgaurea (Sol vir)*.

Group C. *Campanula trachelium* subsp. *trachelium (Cam tra)*, *Cardamine bulbifera (Car bul)*, *Carex digitata (Car dig)*, *Cephalanthera damasonium (Cep dam)*, *Cornus mas (Cor mas)*, *Corylus avellana (Cor ave)*, *Cruciata glabra* subsp. *glabra (Cru gla)*, *Euonymus latifolius (Euo lat)*, *Euphorbia dulcis (Eup dul)*, *Galium odoratum (Gal odo)*, *Geum urbanum (Geu urb)*, *Hepatica nobilis (Hep nob)*, *Laburnum anagyroides* subsp. *anagyroides (Lab ana)*, *Lactuca muralis (Lac mur)*, *Lonicera caprifolium (Lon cap)*, *Ostrya carpinifolia (Ost car)*, *Sanicula europaea (San eur)*, *Sorbus aria* subsp. *aria (Sor ari)*.

Group D. *Acer opalus* subsp. *obtusatum (Ace obt)*, *Acer pseudoplatanus (Ace pse)*, *Anemone apennina* subsp. *apennina (Ane ape)*, *Cyclamen hederifolium* subsp. *hederifolium (Cyc hed)*, *Festuca heterophylla (Fes het)*, *Fragaria vesca* subsp. *vesca (Fra ves)*, *Galanthus nivalis* subsp. *nivalis (Gal niv)*, *Hedera helix* subsp. *helix (Hed hel)*, *Hieracium murorum (Hie mur)*, *Lathyrus venetus (Lat ven)*, *Lilium bulbiferum* subsp. *croceum (Lil cro)*, *Luzula sylvatica* subsp. *sylvatica (Luz syl)*, *Melica uniflora (Mel uni)*, *Poa nemoralis (Poa nem)*, *Scilla bifolia (Sci bif)*, *Viola reichenbachiana (Vio rei)*.

Group E. *Anemone nemorosa (Ane nem)*, *Aristolochia lutea (Ari lut)*, *Arum maculatum (Aru mac)*, *Carex sylvatica (Car syl)*, *Carpinus betulus (Car bet)*, *Crataegus laevigata (Cra lae)*, *Dactylorhiza sambucina (Dac sam)*, *Lathyrus vernus (Lat ver)*, *Lilium martagon (Lil mar)*, *Luzula forsteri (Luz for)*, *Neottia nidus-avis (Neo nid)*, *Platanthera chlorantha (Pla chl)*, *Polypodium vulgare (Pol vul)*, *Pulmonaria apennina (Pul ape)*, *Pyrus pyraster (Pyr pyr)*, *Quercus cerris (Que cer)*, *Ranunculus lanuginosus (Ran lan)*, *Rosa arvensis (Ros arv)*, *Silene viridiflora (Sil vir)*, *Stellaria holostea (Ste hol)*, *Symphytum tuberosum* subsp. *angustifolium (Sym ang)*, *Veronica officinalis (Ver off)*.

Group F. *Asplenium trichomanes* subsp. *quadrivalens (Asp qua)*, *Brachypodium rupestre (Bra rup)*, *Bromus erectus* subsp. *erectus (Bro ere)*, *Clematis vitalba (Cle vit)*, *Cytisus hirsutus* subsp. *polytrichus (Cyt pol)*, *Erica arborea (Eri arb)*, *Juniperus communis (Jun com)*, *Juniperus oxycedrus* subsp. *oxycedrus (Jun oxy)*, *Lathyrus clymenum (Lat cly)*, *Ptilostemon strictum (Pti str)*, *Teucrium siculum* subsp. *siculum (Teu sic)*.

tent. Richness decrease in the most light condition corresponds to South-facing slopes (*Cytiso sessilifolii-Quercetum pubescentis*, *Quercus cerris* and *Quercus pubescens* community and *Erico arboreae-Quercetum pubescentis*), characterized in turn by the most intense drought stress. Shannon-Wiener and Evenness indices decrease in the range 50-75 ¼mol m^{-2} s^{-1}, is probably related to the management kind (high forest) of *Quercus cerris* and *Carpinus betulus* woods (*Carici sylvaticae-Quercetum cerridis*) which tends to make tree canopy more homogeneous from a floristic viewpoint. Furthermore, evenness shows an increasing trend from high to low stressful conditions, in accordance with Shannon diversity and species number, except for soil pH and total nitrogen concentration. In fact, at the highest nitrogen content and on neutral-basic soils, evenness decreases, unlike richness and Shannon index. It means that the higher value of nutrient availability in the study area probably is not enough to determine a richness decrease through competitive exclusion and the spread of dominant species (GRIME, 2001) but lead to a change in species abundances distribution pattern, making forest community species set less evenly distributed.

Stress gradients act not only on species diversity, but also on plant communities species composition. Species strongly related to the most stressful environmental conditions are those of A and F groups (Fig. 2, Tab. 6). From an ecological viewpoint species of group A would be considered nemoral, light-

Tab. 7 - Mean and median of bioindication values calculated for species groups highlighted by RDA.

	Light		Temperature		Soil moisture		Soil reaction		Soil nutrients	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Group A	5,7	6,0	6,9	7,0	3,9	4,0	6,4	7,0	4,2	4,0
Group B	4,9	5,0	5,2	5,0	4,7	5,0	6,6	7,0	5,1	5,0
Group C	4,2	4,0	5,7	5,0	4,7	5,0	6,5	7,0	5,4	5,0
Group D	4,5	4,0	5,2	5,0	4,9	5,0	6,5	7,0	5,5	5,0
Group E	4,7	5,0	5,5	5,0	4,9	5,0	5,8	6,0	5,2	5,0
Group F	6,7	7,0	7,0	7,0	3,8	4,0	5,7	6,5	3,4	3,0

Tab. 8 - Matrix summarizing the ecological characterization of each group highlighted by RDA (A-F) and the related environmental stresses and ecological factors.

Groups of species	**A**	**B**	**C**	**D**	**E**	**F**
Ecological behaviour	Dryness-tolerators, light-demanding species	Nitrogen-demanding midshadow species	Water and Nitrogen-demanding species, low light intensity-tolerators	Water and nitrogen-demanding species, low light intensity and slight acidity-tolerators	Low nitrogen-demanding, acidity-tolerator species	Dryness and acidity-tolerators, light-demanding species
Environmental stresses	Draining soils, strong insolation, low soil depth	Intermediate-low light intensity	Low light intensity	Low light intensity, slightly acid pH	Intermediate-low light intensity, acid pH	Low soil nitrogen content, acid pH, sandy soil texture
Light intensity	High	Intermediate-low	Low	Low	Intermediate-low	High
pH	Neutral	Neutral	Neutral	Subacid	Acid	Acid
Texture	Sandy-clayey	Clayey	Clayey	Sandy-clayey	Sandy-clayey	Sandy
Nitrogen	Intermediate	High	High	Intermediate	Intermediate	Low
Aspect	South	North	North	North	North	South

demanding species or living in forest edges and clearings, while those of group F are pioneer species of open habitats, ingressive in woods probably because of soil deterioration or for the excessive forest canopy openings due to forestry activity. In fact, light-demanding oaks, as *Quercus pubescens* s.l., and the related undergrowth species, have been often favoured by past forest management and by direct facilitation (MANTEL, 1990; WALLNÖFER & HOTTER, 2008).

Species belonging to group B can be considered edge or semipioneer floristic units. They live under the canopy of the forest edge and are probably favoured by the periodic wood cutting linked to the forest management (BARTHA *et al*., 2008). Group E includes specialist sciaphilous nemoral, acidophilous and relatively soil moisture-demanding species. This ecological behaviour type is very different from that of B group. The only joining point is the same light demand, but this similarity is probably due to different causes: forestry management history and structure (group B) and light permeability of woods canopy (group E).

Groups C and D may be considered to be composed by "ancient forest species" (HERMY *et al*., 1999), which prefer cool and moist soils with intermediate pH.

CONCLUSIONS

The research results allowed to ascertain that, as stated by GRIME (1973), also in the submediterranean forest landscape, stress level acts to define species diversity. Moreover, results permit to hypothesize that, in homogeneous bioclimatic conditions, Shannon-Wiener, Simpson and Evenness indices could be used as stress indicators within a forest landscape.

From a floristic point of view, intensity and combination of stress factors select one or more groups of species with different ecological behaviour, leading to the local floristic differentiation of plant communities. Within the pool of species adapted to the different sets of environmental factors, forest management and land use history act, determining the temporal pattern of the different ecological behaviour type species groups (BARTHA *et al*., 2008). In fact, the ingression of edge and clearing nitrophilous (group B) or open habitat species (group F) in forest communities, could be interpreted as a result of frequent coppicing and/or past soil erosion. On the other hand, the prevalence of nemoral species (groups D and E) indicates a higher forest soil cover because of longer turnover or higher forest topsoil cover after cutting down (HÄRDTLE *et al*., 2004; REIF & GÄRTNER, 2007). Moreover, it can be hypothesized that the presence of such species also depends on land use history and in particular on the continuity of forest cover over the time (DECOCQ, 2003).

The results of this study represent a useful tool for future research, aimed to define plant diversity conservation guidelines and biodiversity monitoring. This approach will be useful in the future, because climatic change will certainly increase drought stress and the possibility to predict species shifting and floristic variation of forest ecosystems would be a very important goal for their future management. Moreover, it could be important also for plant communities phytosociological characterization, in order to better select the diagnostic group of species of each *syntaxon* taking into account their local meaning from an ecological point of view.

REFERENCES

ALLEGREZZA M., 2003 - *Vegetazione e paesaggio vegetale della dorsale del Monte San Vicino (Appennino centrale).* Fitosociologia, 40(1): 3-118.

ALLEGREZZA M., BALDONI M., BIONDI E., TAFFETANI F., ZUCCARELLO V., 2002 - *Studio fitosociologico dei boschi a Quercus pubescens s.l. delle Marche e di alcune zone contigue dell'Appennino centro-settentrionale (Italia centrale).* Fitosociologia, 39(1): 161-171.

AUSTIN M.P., PAUSAS J.G., NICHOLLS A.O., 1996 - *Patterns of tree species richness in relation to environment in south-eastern New South Wales.* Aust. J. Ecol., 21: 154-164.

BARTHA S., MEROLLI A., CAMPETELLA G., CANULLO R., 2008 - *Changes of vascular plant diversity along a chronosequence of beech coppice stands, central Apennines, Italy.* Plant Biosyst., 142(3): 572-583.

BIONDI E., BALDONI M.A., TALAMONTI M.C., 1995 - *Il fitoclima delle Marche.* In: Atti del Convegno "Salvaguardia e gestione dei beni ambientali nelle Marche" (Ancona, 8-9 aprile 1991): 21-70. Tipolit. Trifogli, Ancona.

BIONDI E., CASAVECCHIA S., GIGANTE D., 2003 - *Contribution to the syntaxonomic knowledge of the Quercus ilex L. woods of the central European Mediterranean basin.* Fitosociologia, 40(1): 129-156.

BIONDI E., CASAVECCHIA S., PINZI M., ALLEGREZZA M., BALDONI M.A., 2002 - *The syntaxonomy of the mesophilous woods of the Central and Northern Apennines (Italy).* Fitosociologia, 39(2): 71-93.

BISCI C., DRAMIS F., 1991 - *La geomorfologia delle Marche.* In: Regione Marche - Giunta Regionale - Assessorato Urbanistica e Ambiente (ed.), L'ambiente fisico delle Marche. Geologia Geomorfologia Idrogeologia: 81-113. S.EL.CA., Firenze.

BLASI C., CARRANZA M., FRONDONI R., ROSATI L., 2000 - *Ecosystem classification and mapping: a proposal for italian landscape.* Appl. Veg. Sci., 3: 233-242.

BLASI C., DI PIETRO R., FILESI L., 2004 - *Syntaxonomical revision of Quercetalia pubescenti-petraeae in the Italian Peninsula.* Fitosociologia, 41(1): 87-164.

BONAN G., 2008 - *Ecological Climatology. Concepts and Applications.* Cambridge University Press, New York.

BRAUN-BLANQUET J., 1964 - *Pflanzensoziologie.* 3rd ed. Springer, Wien - New York.

BRAY J.R., CURTIS J.T., 1957 - *An ordination of the upland forest communities of southern Wisconsin.* Ecol. Monogr., 27(4): 325-349.

BURNETT M.R., AUGUST P.V., BROWN J.H., KILLINGBECK K.T., 1998 - *The influence of geomorphological heterogeneity on biodiversity. I-A patch-scale perspective*. Conserv. Biol., 12: 363-370.

CATORCI A., BIONDI E., CASAVECCHIA S., PESARESI S., VITANZI A., FOGLIA M., GALASSI S., PINZI M., ANGELINI E., BIANCHELLI M., VENTRONE F., CESARETTI S., GATTI R., 2007a - *La Carta della vegetazione e degli elementi di paesaggio vegetale delle Marche (scala 1:50.000) per la progettazione e la gestione della rete ecologica regionale.* In: BIONDI E. (ed.), Atti del 43° Congresso della Società Italiana Scienza della Vegetazione; "L'applicazione della Direttiva Habitat in Italia e in Europa". Fitosociologia, 44(2) Suppl. 1: 115-118.

CATORCI A., CESARETTI S., MARCHETTI P. (eds.), 2007b - *Vocazionalità del territorio della Comunità Montana di Camerino per la produzione di biomasse solide agro-forestali* *ad uso energetico.* L'Uomo e l'Ambiente (Camerino), 47: 1-75.

CATORCI A., GATTI R., SPARVOLI D., 2003 - *Contributo alla conoscenza dei boschi basso montani dell'Appennino maceratese (Marche - Italia centrale).* Fitosociologia, 40(2): 43-53.

CATORCI A., ORSOMANDO E., 2001 - *Note illustrative della Carta della Vegetazione del Foglio Nocera Umbra (N. 312 - Carta d'Italia I.G.M. - 1: 50.000).* Braun-Blanquetia, 23: 1-129.

CATORCI A., VITANZI A., PAURA B., IOCCHI M., BALLELLI S., 2008 - *La vegetazione forestale dei substrati arenacei della Val d'Aso (Marche, Italia centrale)*. Fitosociologia, 45(2): 41-76.

CATORCI A., VITANZI A., BALLELLI S., 2010 - *Phytosociological study of beech and beech-mixed woods in Monti Sibillini National Park (Central Apennines, Italy).* Hacquetia, 9(1): 23-75.

CHYTRÝ M., EXNER A., HRIVNÁK R., UJHÁZY K., VALACHOVIČ M., WILLNER W., 2002 - *Context dependence of diagnostic species: A case study of the Central European spruce forests.* Folia Geobot., 37: 403-417.

COLLINS B.S., PICKETT S.T.A., 1988 - *Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest.* J. Ecol., 76(2): 437-450.

DECOCQ G., 2000 - *The "masking effect" of silviculture on substrate-induced plant diversity in oak-hornbeam forests from northern France.* Biodiv. and Conserv., 9: 1467-1491.

DECOCQ G., 2002 - *Patterns of plant species and community diversity at different organization levels in a forested riparian landscape.* J. Veg. Sci., 13: 91-106.

DECOCQ G., 2003 - *Phytosociologie, sindinamique et archeologie du paysage*. Contribuții Botanice, 38: 13-23.

FORMAN R.T.T., 1995 - *Some general principles of landscape and regional ecology.* Landscape Ecology, 10(3): 133-142.

GRIME J.P., 1973 - *Competitive exclusion in herbaceous vegetation*. Nature, 242: 344-347.

GRIME J.P., 2001 - *Plant strategies, vegetation processes and ecosystem properties.* John Wiley & Sons, Chichester (UK).

HÄRDTLE W., EWALD J., HÖLZEN N., 2004 - *Walder des Tieflandes und der Mittelgebirge.* Ulmer, Stuttgart.

HÄRDTLE W., VON OHEIMB G., WESTPHAL C., 2003 - *The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein).* Forest Ecol. and Manag., 182: 327-338.

HERMY M., HONNAY O., FIRBANK L., GRASHOF-BOKDAM C., LAWESSON J.E., 1999 - *An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation.* Biol. Conserv., 91: 9-22.

HUSTON M., 1980 - *Soil nutrients and tree species richness in Costa Rican forests.* J. Biogeogr., 7: 147-157.

HUTCHINSON T.F., BOERNER R.E.J., IVERSON L.R., SUTHERLAND S., KENNEDY SUTHERLAND E., 1999 - *Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) Quercus forests.* Plant Ecology, 144: 177-189.

JACKSON M.T., 1966 - *Effects of microclimate on spring flowering phenology.* Ecology, 47: 407-415.

KUŽELOVÁ I., CHYTRÝ M., 2004 - *Interspecific associations in phytosociological data sets: how do they change between local and regional scale?* Plant Ecol., 173: 247-257.

MAAREL (VAN DER) E., 1979 - *Trasformation of cover-abundance values in phytosociology and its effects on community similarity.* Vegetatio, 39: 97-144.

MANTEL K., 1990 - *Wald und Forst in der Geschichte: ein Lehr- und Handbuch.* Schaper Verlag, Alfeld, Hannover.

MARGULES C.R., NICHOLLS A.O., AUSTIN M.P., 1987 - *Diversity of Eucalyptus species predicted by multi-variable environmental gradient*. Oecologia (Berl.), 71: 229-232.

MCCUNE B., GRACE J.B., 2002 - *Analysis of Ecological Communities.* MjM Software Design. Gleneden Beach, Oregon.

MCCUNE B., MEFFORD M.J., 2006 - *PC-ORD. Multivariate Analysis of Ecological Data. Version 5.* MjM Software Design. Gleneden Beach, Oregon.

MITRAKOS K., 1980 - *A theory for Mediterranean plant life.* Acta Oecol. / Oecol. Plant., 1(15), 3: 245-252.

MITRAKOS K., 1982 - *Winter low temperatures in mediterranean-type ecosystems.* Ecol. Medit., 8(1-2): 95-102.

MOORE M.R., VANKAT J.L., 1986 - *Responses of the herb layer to the gap dynamics of a mature beech-maple forest.* Am. Mid. Nat., 115(2): 336-347.

NASH SUDING K., 2001 - *The effects of gap creation on competitive interactions: separating changes in overall intensity from relative rankings.* Oikos, 94: 219-227.

NICHOLS W.F., KILLINGBECK K.T., AUGUST P.V., 1998 - *The influence of geomorphological heterogeneity on biodiversity. II-A landscape perspective.* Conserv. Biol., 12: 371-379.

ORSOMANDO E., CATORCI A., 1999 - *Carta della vegetazione naturale potenziale dell'Umbria. Scala 1: 200.000.* Regione dell'Umbria. Università di Camerino.

ORSOMANDO E., CATORCI A., 2000 - *The phytoclimate of Umbria.* Parlatorea, 6: 5-24.

PAUSAS J.G., 1994 - *Species richness patterns in the understorey of Pyrenean Pinus sylvestris forest.* J. Veg. Sci., 5: 517-524.

PAUSAS J.G., AUSTIN M.P., 2001 - *Patterns of plant species richness in relation to different environments: an appraisal.* J. Veg. Sci., 12: 153-166.

PAUSAS J.G., CARRERAS J., 1995 - *The effect of bedrock type, temperature and moisture on species richness in Pyrenean Scots pine (Pinus sylvestris L.) forests.* Vegetatio, 116: 85-92.

PESARESI S., BIONDI E., CATORCI A., CASAVECCHIA S., FOGLIA M., 2007 - *Il Geodatabase del Sistema Informativo Vegetazionale delle Marche.* In: BIONDI E. (ed.), Atti del 43° congresso della Società Italiana Scienza della Vegetazione; "L'applicazione della Direttiva Habitat in Italia e in Europa". Fitosociologia, 44(2) Suppl. 1: 95-101.

PIGNATTI S., 2005 - *Valori di bioindicazione delle piante vascolari della Flora d'Italia.* Braun-Blanquetia, 39: 1-97.

PODANI J., 2001 - *SYN-TAX 2000 computer program for data analysis in ecology and systematics.* Budapest.

REIF A., GÄRTNER S., 2007 - *Die natürliche Verjüngung der laubabwerfenden Eichenarten Stieleiche (Quercus robur L.) und Traubeneiche (Quercus petraea Liebl.) - eine Literaturstudie mit besonderer Berücksichtigung der Waldweide.* Waldökologie online, 5: 79-116.

RIVAS-MARTÍNEZ S., 2004 - *Global bio-*

climatics. http://www.globalbioclimatics.org (versione 23/04/04; 27/08/04).
Rivas-Martínez S., 2005 - *Notions on dynamic-catenal phytosociology as a basis of landscape science.* Plant Biosyst., 139(2): 135-144.
Rosenzweig M.L., 1995 - *Species diversity in space and time.* Cambridge University Press, Cambridge.
Schaffers A., 2002 - *Soil, biomass and management of semi-natural vegetation. Part II. Factors controlling species diversity.* Plant Ecol., 158: 247-268.
Schmidt W., 2005 - *Herb layer species as indicators of biodiversity of managed and unmanaged beech forests.* For. Snow Landsc. Res., 79(1-2): 111-125.
Tzonev R., Dimitrov M., Chytrý M., Roussakova V., Dimova D., Gussev C., Pavlov D., Vulchev V., Vitkova A., Gogoushev G., Nikolov I., Borisova D., Ganeva A., 2006 - *Beech forest communities in Bulgaria.* Phytocoenol., 36(2): 247-279.
Wallnöfer S., Hotter M., 2008 - *Syntaxonomy and site ecology of mixed oak forest communities in the Inner and Intermedial Alps of Tyrol (Austria).* Bot. Helv., 118: 21-43.
Whittaker R.H., 1956 - *Vegetation of the Great Smoky Mountains.* Ecol. Monogr., 26: 1-80.
Whittaker R.H., 1975 - *Evolution and measurements of species diversity.* Taxon, 21: 213-251.
Wilson S.D., Keddy P.A., 1988 - *Species richness, survivorship and biomass accumulation along environmental gradient*. Oikos, 53: 375-380.