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Phytogeography of parasteppic vegetation in the high Friulian Plain (NE Italy)

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Abstract

The vascular flora of pedologically conditioned, extensive dry grasslands occurring in a very rainy area of northeastern Italy, was submitted to phytogeographic analysis. The distributional ranges of 144 species were digitized into two presence-absence matrices of species and Operational Geographic Units (quadrants), one covering Europe, the other, limited to 56 species with extra-European distributions, extended to the Northern Hemisphere north of the Tropic of Cancer. These matrices were submitted to numerical classification, obtaining clusters of species with similar distributional patterns (chorotypes). For each cluster of species, the percent occurrencies in each quadrant were processed by a program of automatic mapping, producing a series of isoporic maps showing the joint distribution of the species of each cluster. The species can be subdivided into six main phytogeographical groups: (1) Narrow-ranging (34% of the total), including the endemic, subendemic, Illyrian-Balcanic and NW submediterranean elements, (2) Southern European-Submediterranean (18.8%), (3) Wide-ranging European (16.6%), (4) Eastern-Pontic (7.6%), (5) Southern Eurasiatic (10.5%), (6) Northern Eurasiatic (12.5%). The phytogeographic originality of the investigated grasslands is high, with more than one third of the species having narrow distributional ranges. Particularly relevant are the connections with the Balkanic-Illyrian and the eastern Alpine regions.

Abbreviations: OGU: Operational Geographic Unit.

Nomenclature:
Pignatti (1982).

Introduction

The region of Friuli, in northeastern Italy, hosts some of the rainiest areas in Europe. The sudden rise of the Carnic and Julian pre-Alps from the Friulian lowland, under the influence of humid air masses from the Adriatic Sea, produces precipitations which reach, in certain pre-Alpine localities, more than 4000 mm year^{-1}. Contrasting with this situation, vast parts of the northern Friulian plain are covered by steppe-like, dry grasslands, whose unusual appearance in such a rainy area already attracted the attention of early botanists and geographers (Gortani 1905; Lorenzi 1914; Zenari 1928). The main reason for this, is the widespread occurrence of imposing, extended, deep beds of calcareous gravel deposited by pre-alpine rivers, which constitute a veritable natural monument, being without any counterpart elsewhere in Europe. The gravel beds are occupied by a characteristic grassland formation, called '*magredi*' in the Friulian language, a term deriving from the Latin '*mager*', suggestive of an agriculturally miserable area, which was almost neglected by Roman colonization, and that, until recently, was only very sparsely inhabited. These grasslands were first studied in some detail by Pignatti (1953), who described the most widespread community under the name *Centaureo-Globularietum cordifoliae*. Poldini (1973a) was the first to stress the phytogeographical peculiarities of this vegetation, which is characterized by three main phytogeographic elements: the eastern

(Illyrian and Pontic), the Alpic and the endemic element. Two further papers dealing with '*magredi*' vegetation appeared in 1973. The first (Poldini 1973b) deals with the presence there of a Pontic-Pannonic plant, *Crambe tataria*, that in Friuli has a strong disjunction from its main distributional range; its occurrence is related to the repeated invasions of the Hungarians into Friuli from the end of the 9th to the half of the 10th centuries. The second article (Poldini 1973c) describes a new species of *Brassica*, endemic to the '*magredi*' grasslands (see also Martini 1987).

The most recent overview on xeric grasslands of northeastern Italy is that of Chiapella Feoli & Poldini (1993). There, the '*magredi*' vegetation is re-defined on the basis of a large number of relevés, with the distinction, besides pioneer stands on almost bare gravel, of three community-types: (a) *Centaureo-Globularietum cordifoliae*, the most typical '*magredi*' vegetation, (b) *Schoeno-Chrysopogonetum grylli*, an intermediate community, (c) *Chamaecytiso-Chrysopogonetum grylli*, the most mature stage of the succession. These authors, as well, pointed to the high phytogeographical interest of such grasslands, which are a real *unicum* in the European vegetational landscape, as they constitute an example of dry parasteppic vegetation occurring in a high-precipitation area because of local edaphic conditions. Furthermore, according to Poldini (1971) they have the highest biodiversity among all plant communities of northeastern Italy.

On the basis of these premises, we thought that the '*magredi*' grasslands were well worthy of a detailed phytogeographical analysis, whose results are presented in this paper. The analysis is based on the total distributional ranges of all plant species, and follows a methodology proposed by Nimis & Bolognini (1990), and developed further by Nimis et al. (1995). The main aim of the study is the description of the phytogeographic structure of '*magredi*' grasslands, as a first step toward a deeper understanding of their floristic genesis.

Survey area

The area covered by '*magredi*' grasslands extended, in the past, for c. 500 km^2 in the northern Friulian plain, between 50 and 300 m elevation, being delimited to the north by the Carnic Pre-Alps, and to the south by the low Friulian plain, where finer sediments favour the development of less xeric vegetation. Extensive, deep beds of alluvial, calcareous gravel deposited by the rivers Cellina and Meduna characterize the local landscape. The soils range from gravelly Regosols in habitats frequently subject to fluvial deposits, to Xerorendzinas which, in the less disturbed sites, are substituted by red 'Ferretto' soils. The latter derive from superficial alteration of the calcareous gravel, favoured by high precipitations and by the permeability of the substrata, and have a marked decalcification of the upper horizons, and accumulation of Iron and Aluminium Hydroxydes, which allows the settlement of some non strictly calciphilous species (Comel 1975). The gravel beds, which were deposited since pre-Pleistocene times, with a maximum during the Wurm glaciation, sometimes reach a depth of some hundred meters (Dal Prà & Antonelli 1979). The main rivers, accordingly, are mostly devoid of water for most of the year, water circulation being mainly subterranean. At the end of each Glacial period, the rivers started an intense erosional phase, which lead to the formation of broad terraces, and abandoned the old talus slopes on which the waters had formerly free way. Presently, deposition of new gravel is restricted to the immediate vicinity of the river beds during exceptionally rainy periods.

The climate of the '*magredi*' area (Gentilli 1964) is characterized by high yearly precipitations, ranging from 1800 mm in the northern part to 1100 mm in the south, with two maxima in early summer and late autumn, and no dry period during summer. Average yearly temperatures range from 10 to 12 °C, with a maximum of 36.2 °C in July. Winters are relatively mild, with only a few days of temperatures below zero. Such climatic conditions are certainly not ideal for the development of parasteppic, dry grasslands. The gravelly soils, however, are so permeable that most of the precipitation rapidly percolates without being available to the plants. Contrary to similar pedological situations of several localities in the northern Po-Plain, the frequency of fog is relatively low, which ensures long insolation periods, relatively high diurnal temperatures, and high thermic excursions between day and night, that are favourable for some steppic plants (Poldini 1971).

Until the second World War, the '*magredi*' landscape extended widely along the foot of the Carnic Pre-Alps. The recent introduction of new agricultural techniques, however, has resulted in a drastic reduction of the original grasslands, now largely substituted by extensive cultivations. In particular, the *Chamaecytiso-Chrysopogonetum* community, which settles on agri-

culturally better soils, has disappeared almost completely. The use of land for military purposes in a sparsely inhabited area has somehow helped in the preservation of '*magredi*' fragments, the survey area for this study actually corresponding with a military zone.

Data and methods

In order to illustrate the vegetation under study, 55 phytosociological relevés (following Braun-Blanquet, 1964) were taken along 11 transects from the gravelly bed to the right bank of the river Cellina, in the Province of Pordenone (Region Friuli), in a site locally called 'magredi di Cordenons e S. Foca', in June-August 1994. The transects were c. 200 m long, with 5 relevés per transect, at intervals of c. 40 m, on areas of c. 100 m^2. The matrix of relevés and species was submitted to numerical classification (Complete Linkage Clustering with Correlation Coefficient), using the package of Wildi & Orloci (1988).

The phytogeographic analysis is based on the presence-absence of the species in Operational Geographic Units (OGUs, see Crovello 1981). Two sets of species and OGUs were used:
(1) The first set consists of all 144 species occurring in '*magredi*' grasslands (99 recorded by us, plus 45 species from Chiapella Feoli & Poldini 1993). The distributional range of each species was reported on a map, subdivided into 531 quadrants (OGUs), covering the whole of Europe, plus adjoining parts of Asia and North Africa, with marginal quadrants being multiples of the basic ones (see Nimis & Bolognini 1990).
(2) The second set consists of the 56 species whose distributional ranges widely extend outside Europe. The corresponding map covers the Northern Hemisphere north of the Tropic of Cancer, subdivided into 688 equal-sized quadrants (see Nimis et al. 1995).

On equal-area projections, such as those adopted in our maps, the areal scale is constant from point to point. The size of our Operational Geographic Units, is of c. 28.900 km^2 for the basic quadrants of the European map, of c. 90 000 km^2 for those of the extra-European one. These sizes were established on the basis of a compromise between degree of detail and computing load.

The data concerning the total distribution of the species derive from Hultén (1958, 1962, 1968ab, 1971), Hultén & Fries (1986), Meusel et al. (1965, 1978), Meusel & Jäger (1992), Jalas & Suominen (1972–1976), Daget (1980), Pignatti (1982), Poldini (1991), Flora Europaea (1964–1980), and from many other publications containing maps and/or other distributional data. The data are stored in a database at the Department of Biology of the University of Trieste, containing the distributional ranges of more than 2500 species of the Italian flora, and of c. 700 species of the circum-Arctic and -Boreal floras.

The further methodological step was to transform the distributional maps into presence-absence vectors of each species in the quadrants. The two matrices, deriving from the European and the Northern Hemisphere maps, were submitted to numerical classification, using Average Linkage Clustering (Anderberg 1973), and Similarity Ratio as a resemblance measure. The resulting dendrograms of species subdivide them into groups with similar distributions (chorotypes).

The last step of the analysis was to calculate, for every different species cluster, the percentage occurrencies of the species in each quadrant. These data produced a basic 'chorogram' in the sense of Nimis & Bolognini (1990). These were processed by a program of automatic mapping (program SURFER, Golden Inc., Golden, Colorado), obtaining a series of isopleth maps depicting the distributional patterns of all species clusters (chorotypes). The maps produced by SURFER are based on a grid, whose size is calculated on the basis of the extreme values of the data. The interpolation method is based on the percentage occurrencies of the species in the ten nearest points to the Z point of the grid: the influence of each point on the others is inversely proportional to their distances. The result is a matrix on which the program produces interpolations at each intersection between rows and columns, transforming the originally discrete data structure into a continuous distributional model.

Results

Analysis of vegetation

The numerical classification (not shown) of the matrix of relevés and species produced three main clusters of relevés (A, B, C see Table 1).

Cluster A has several species of open, gravelly soil, such as *Scabiosa graminifolia, Dryas octopetala, Petasites paradoxus, Matthiola carnica, Hieracium piloselloides* etc., and corresponds to the pioneer com-

Table 1.

Cluster nr.		A	B	C
Releve nr.		1 1 1 21 144 41241211224434224 42233233333433555555 09835622713140 48243961715645571827 9 68357943680029430215		
Scabiosa graminifolia	(c4)	+ ++ +1 +		
Dryas octopetala	(c4)	+ +++		
Salix elaeagnos	(c2)	1+r1+ r r		
Hypochoeris maculata	(b2)	++ + r		
Petasites paradoxus	(c2)	r ++		
Hieracium piloselloides	(b2)	+++r+ ++ rrr r		
Matthiola camica	(c1)	rr+++++r++++++ r+ rr++ r		
Reseda lutea	(a2, B1)	r rrrr r rrrr + + rr rr r r		
Linum catharticum	(a1, B1)	+ + + +		
Crambe tataria	(b2, C2)	+ rr + r +		
Leontodon hispidus	(a1, B1)	r r r r r +r r		
Scabiosa gramuntia	(b1)	r r rr r r r		
Allium montanum	(b1)	+ r+ r		
Plantago major	(a2, A2)	rr r r		
Silene vulgaris	(a2, A2)	+ r r +		
Potentilla australis	(c3)	++ + ++++ + + + + +		
Koeleria splendens	(c4)	r+ + + + + r r + +r++		
Schoenus nigricans	(b4)	r r+ r + 1+1 12r+3 + 2131+123333143134233		
Chrysopogon gryllus	(b3)	r r 1 +r + + r1+2 +1122++222+322		
Bothriochloa ischaemum	(b4, C1)	1r+ r + + ++ ++ +++2+ +11+1+1++++		
Chamaecytisus purpureus	(c1)	r ++ + 1+ +1 + +++1+11		
Genista sericea	(c3)	1 r 1 + 1 +1 + ++1++++ +		
Scorzonera purpurea	(b2, C2)	+ rr + r r++ r r + +		
Agropyrum pungens	(c4)	r + r2 r 2 r1 +		
Satureja variegata	(c3)	rr + r + + +		
Lotus corniculatus	(a2, A1)	+ + + + +++++++++ +		
Dactylis glomerata	(a2, A1)	r1 r +r ++r+++++		
Centaurea scabiosa	(a1, B2)	+ ++ + r + r		
Ranunculus acris	(a1, A2)	r r r r		
Genista tinctoria	(a1, B2)	++ + ++ 1 +		
Allium carinatum	(b3)	+ + +		
Poa pratensis	(a2, A2)	+ + r+		
Filipendula vulgaris	(a1, B2)	+ +		
Prunella vulgaris	(a2, A2)	+ +		
Blackstonia perfoliata	(b4)	r r		
Fumana procumbens	(b3)	++11+ 1+11++++ ++++++r++++ +r +r +r r+ ++r+r+ rr+		
Plantago holosteum	(b3)	+r++ 1r11 r+r ++++ ++++++++++++ ++ +++ + ++++		
Inula ensifolia	(c2)	+++ + + ++r + ++r ++r +++++r+rrr + r+r rr		
Stipa eriocaulis	(b3)	r r rr r+r +1433rr41r++1r23+4 r4 2r++ ++++rr++		
Artemisia alba	(b3, A1)	+ +r r + 1 + r +1r r		
Globularia cordifolia	(c4)	1 1 +1+1 1 + 11++++++++++1++1r++ + ++rrrr +r1 +r		
Trinia glauca	(b3)	+ + + +rr + + + + r ++ + r r		
Gypsophila repens	(c2)	++ ++ ++ r ++ ++ +++ + ++ + +r++r+		
Euphorbia triflora	(c1)	+ + ++ + ++ + ++++++1++++++1 ++++++ ++++++r r++ +r+		
Centaurea dichroantha	(c1)	rr+++r++++++++ ++++++r+++1++++++++r+ +r++++++++++++r+rrr+		
Teucrium montanum	(b3, B2)	+++11+ +1+111 ++11++r2++++1+1+21++1 111++r+++11+2++++++		
Thymus serpyllum	(a2, A2)	+++1++1+11++++ ++++++r++++++r+++++r+ ++++++++++++++++++r+		
Koeleria pyramidata	(b2)	++1+1+1111111+ ++ ++1++++++1++++1++ +1+ +1+++1++++++ +++		
Teucrium chamaedrys	(b4)	+111+ +++++ +r+ r+1r1rr++r r r 22 2r 3r1 rr +		
Diplotaxis tenuifolia	(b1)	++rr +r + r+ r+ r+r r+++r + rr r r r r+		
Bromus condensatus	(c3)	+++++++11111 2 + +22+12++2 +11+221 122123111+111++ + +1		
Helianthemum ovatum	(a1, B1)	+++++ +++r++++ ++++1+3++1++++ +++1++ ++ +++ + ++++++++++		
Peucedanum oreoselinum	(b1)	+ + ++++++r+ ++++++++++r+1+++ +++ +++++ ++++++++++r+		
Carex mucronata	(c1)	+ 1+1 +1++221 221112212112212212 21 1121322122+22 r ++		
Galium verum	(a2, A2)	+rr ++r++ ++r+ ++++++++++++1+++++++ ++++++++++++++++ ++		
Sanguisorba minor	(a2, C1)	r ++ +++r ++ +1 + + + + +1 + ++++ +++ + + r +		
Thesium divaricatum	(b3)	r++r+ +++++++ +r ++ +++ ++ + ++ r+++ + ++++++ + +++		
Sesleria albicans	(c2)	rr++21 ++ 121++1r 212+3+ 2 +1 11231132322 1 ++		
Erica herbacea	(c2, C2)	rr + r 11+1 12++ +1+++111+1r ++ +++++ + ++ +++ +		
Euphorbia cyparissias	(a1, B1)	+ r + ++ + + + + +r		
Anthericum ramosum	(b1)	r r r + +++		
Scorzonera austriaca	(c2)	+ + +		
Gymnadenia conopsea	(a1, A2)	+ r		
Daphne cneorum	(c1)	++		
Hippocrepis comosa	(b3)	+ r		
Populus nigra	(a2, B2)	r r r		
Centaurea jacea	(a1, B1)	r r +		
Globularia punctata	(b3)	+ r r		
Arrhenatherum elatius	(a2, B1)	rr		
Seseli gouani	(c3)	r r+		
Asperula cynanchica	(b2)	r r		
Allium sphaerocephalum	(b2)	r +		
Petrorhagia saxifraga	(b3)	+ +		
Plantago argentea	(c4)	+ r		

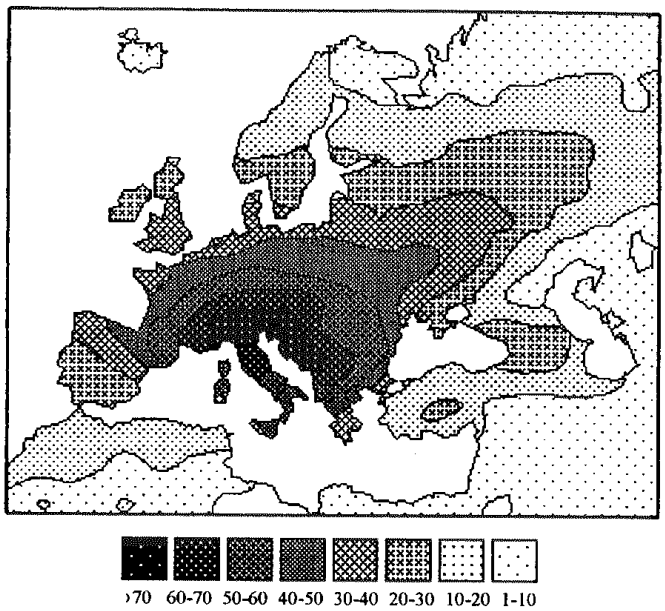

Figure 1. Joint European distribution of the 144 vascular plants occurring in the '*magredi*' grasslands. Different shadings indicate percentage representations of species, as in the legend.

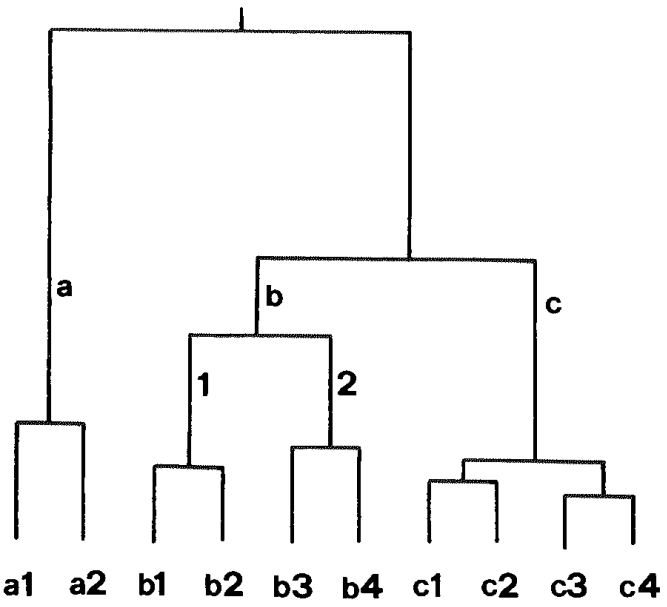

Figure 2. Dendrogram of the 144 species of '*magredi*' grasslands, based on their occurrence in the 531 Operational Geographic Units covering the European territory. Only the main clusters and subclusters are shown (see text).

munity called *Centaureo-Globularietum cordifoliae* (Chiapella Feoli & Poldini 1993).

Cluster C has a large set of species typical of closer, older grasslands, such as *Schoenus nigricans*, *Chrysopogon gryllus*, *Chamaecytisus purpureus*, *Botriochloa ischaemum*, *Genista sericea*, etc., plus some species of mesic meadows such as *Lotus corniculatus*, *Dactylis glomerata*, *Ranunculus acris*. It corresponds to the *Schoeno-Chrysopogonetum grylli* (Chiapella Feoli & Poldini 1993). The last six relevés, without several xerophytic species, are a humid variant in small depressions with silty soil.

Cluster B represents the ecotonal transition from pioneer, open stands to older grasslands. It does not have any differential species but, interestingly, it is here that *Stipa eriocaulis*, a characteristic steppe-plant, attains its maximum cover.

Classification of species (Europe)

The joint distribution of the 144 species in Europe is shown in Figure 1. The general pattern is of a northern submediterranean type, with most of the species being distributed in an area including northern Italy and the northwestern portion of the Balkan Peninsula, corresponding to the Illyrian-Dinaric phytogeographic region. Less than 40% of the species penetrate into the Ukrainian and Russian Plain, and only a few broad-ranging taxa do occur in northern Europe.

The dendrogram of species, based on their distribution in Europe, is shown in Figure 2. Four main clusters are formed (a, b1, b2, c), which can be further subdivided into 10 subclusters (chorotypes). The chorograms of the four main clusters are shown in Figure 3:

– cluster a) mainly includes broad-ranging species, most of which widely extend through Europe and into Asia. They make up almost one third (29%) of the flora of the '*magredi*', and belong to several different phytogeographic elements, which will be discussed in the next chapter (Northern Hemisphere maps).

– cluster b1) has a clearly continental, eastern distributional pattern, the main area extending from the southern part of eastern Europe into the Pontic phytogeographic region. The species of this cluster make up 14% of the total flora.

– cluster b2) includes many relatively broad-ranging, submediterranean species, which are 21% of the total flora.

– cluster c) mainly includes narrow-ranging species, belonging to the endemic, east-alpine and Illyrian elements. They are the most consistent phytogeographic group (36% of the total).

In the following, the chorograms of the ten subclusters (Figure 3) will be briefly commented on.

Subcluster a1. It includes 20 species (13% of the total): *Betonica officinalis*, *Briza media*, *Carex cary-*

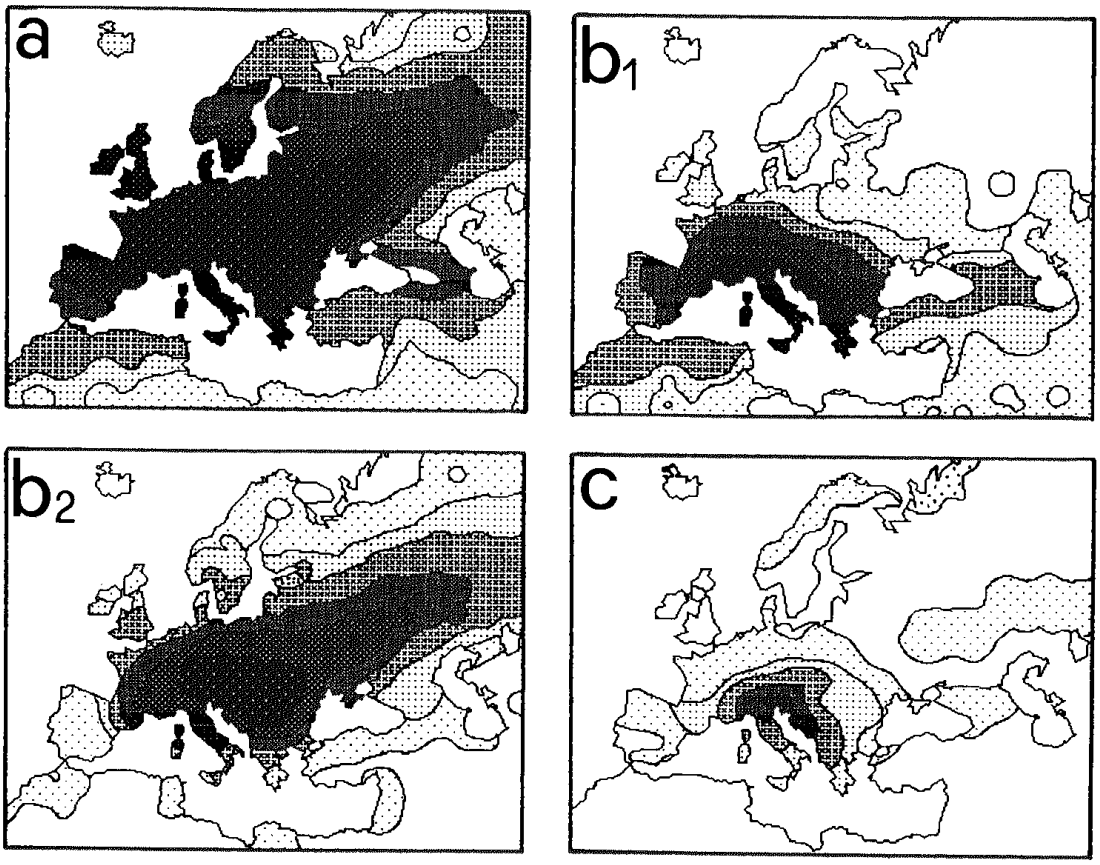

Figure 3. Joint distribution of all species included into the four main clusters obtained by numerical classification of the species based on their European distributions. Cluster numbers are as in Figure 2. Different shadings indicate percentage representations of species, as in the legend to Figure 1.

ophyllea, *Carum carvi*, *Centaurea jacea* s.lat., *Centaurea scabiosa*, *Euphorbia cyparissias*, *Festuca rubra*, *Filipendula vulgaris*, *Genista tinctoria*, *Gymnadenia conopsea*, *Helianthemum ovatum*, *Leontodon hispidus*, *Linum catharticum*, *Orchis morio*, *Pimpinella saxifraga*, *Potentilla erecta*, *Ranunculus acris*, *Serratula tinctoria*, *Tragopogon orientalis*. These species have broad distributional ranges, encompassing the whole of Temperate Europe and often extending eastwards into Asia. Only a few, however, are present in the Mediterranean Region. 18 species also occur outside Europe.

Subcluster a2. This subcluster includes 24 species (16%): *Anthyllis vulneraria*, *Arrenatherum elatius*, *Centaurium erythraea*, *Cuscuta epithymum*, *Dactylis glomerata*, *Eupatorium cannabinum*, *Galium verum*, *Hypericum perforatum*, *Leucanthemum heterophyllum*, *Lotus corniculatus*, *Melilotus alba*, *Plantago lanceolata*, *P. major*, *P. media*, *Poa pratensis*, *Populus nigra*, *Prunella vulgaris*, *Reseda lutea*, *Sanguisorba minor*, *Senecio jacobaea*, *Silene vulgaris*, *Thalictrum minus*, *Thymus serpyllum* s.lat., *Trifolium pratense*. The joint distribution very much resembles that of the previous group, the main difference being a generally broader distributional area, both to the south (many species occur in the Mediterranean Region), and to the north. 22 species also occur outside Europe.

Subcluster b1. It includes 9 species (6%): *Allium montanum*, *Anthericum ramosum*, *Carex humilis*, *Diplotaxis tenuifolia*, *Erigeron annuus*, *Ononis spinosa*, *Peucedanum oreoselinum*, *Prunella grandiflora*, *Scabiosa gramuntia*. They mainly have a Central-European-submediterranean distribution, with the northernmost limit in southern Scandinavia. They tend to avoid the Mediterranean Region, and only a few extend eastwards to the Russian plains.

Subcluster b2. This group includes 11 species (8% of the total): *Allium sphaerocephalon*, *Asperula chynanchica*, *Campanula sibirica*, *Crambe tatarica*, *Epipactis atrorubens*, *Hieracium piloselloides*, *Hypochoeris maculata*, *Inula hirta*, *Koeleria pyr-*

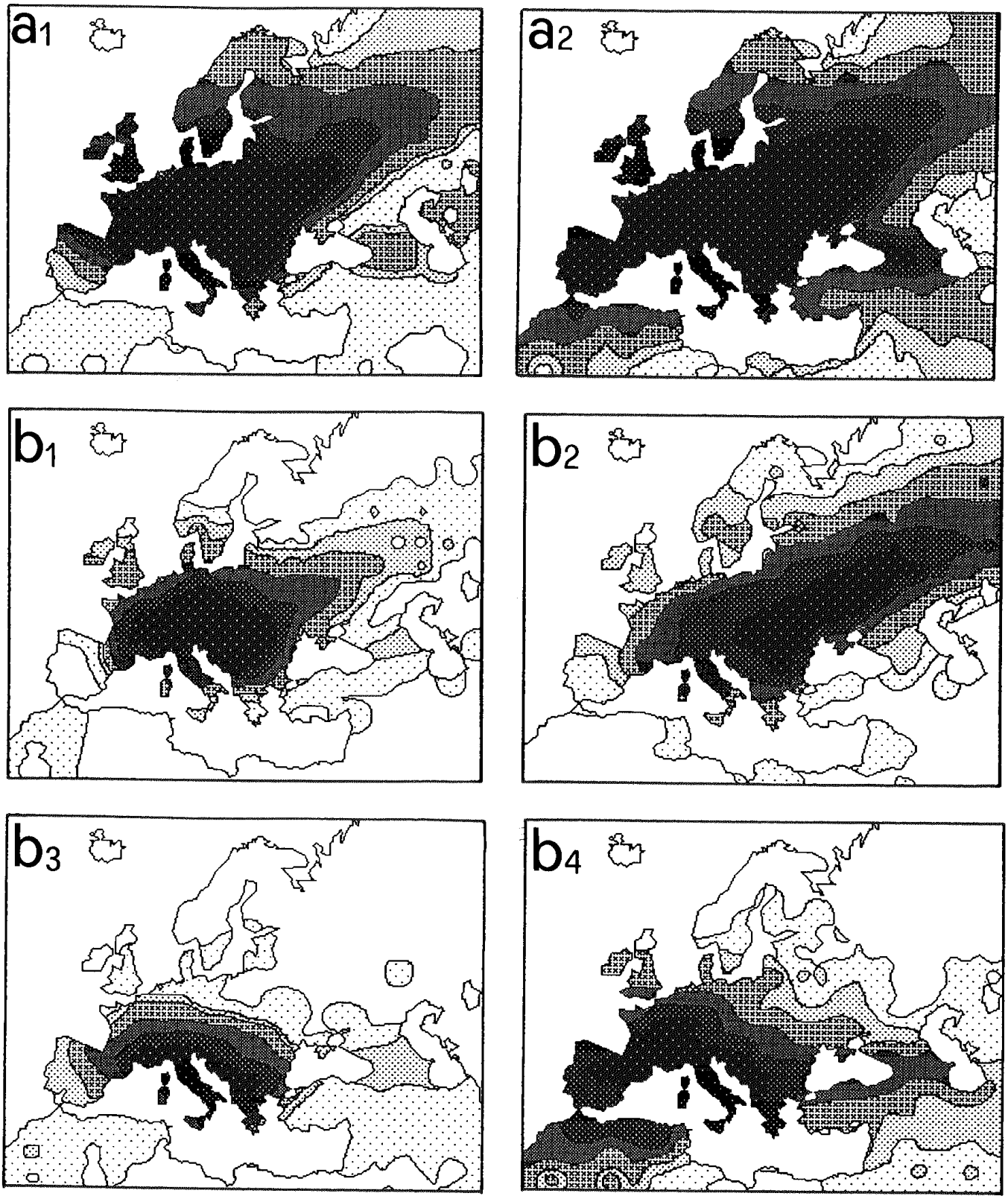

Figure 4. Joint distribution of all species included into the ten subclusters obtained on the basis of their distribution in the 531 Operational Geographic Units covering the European territory. The subclusters are abbreviated as in Figure 2. Different shadings indicate percentage representations of species, as in the legend to Figure 1.

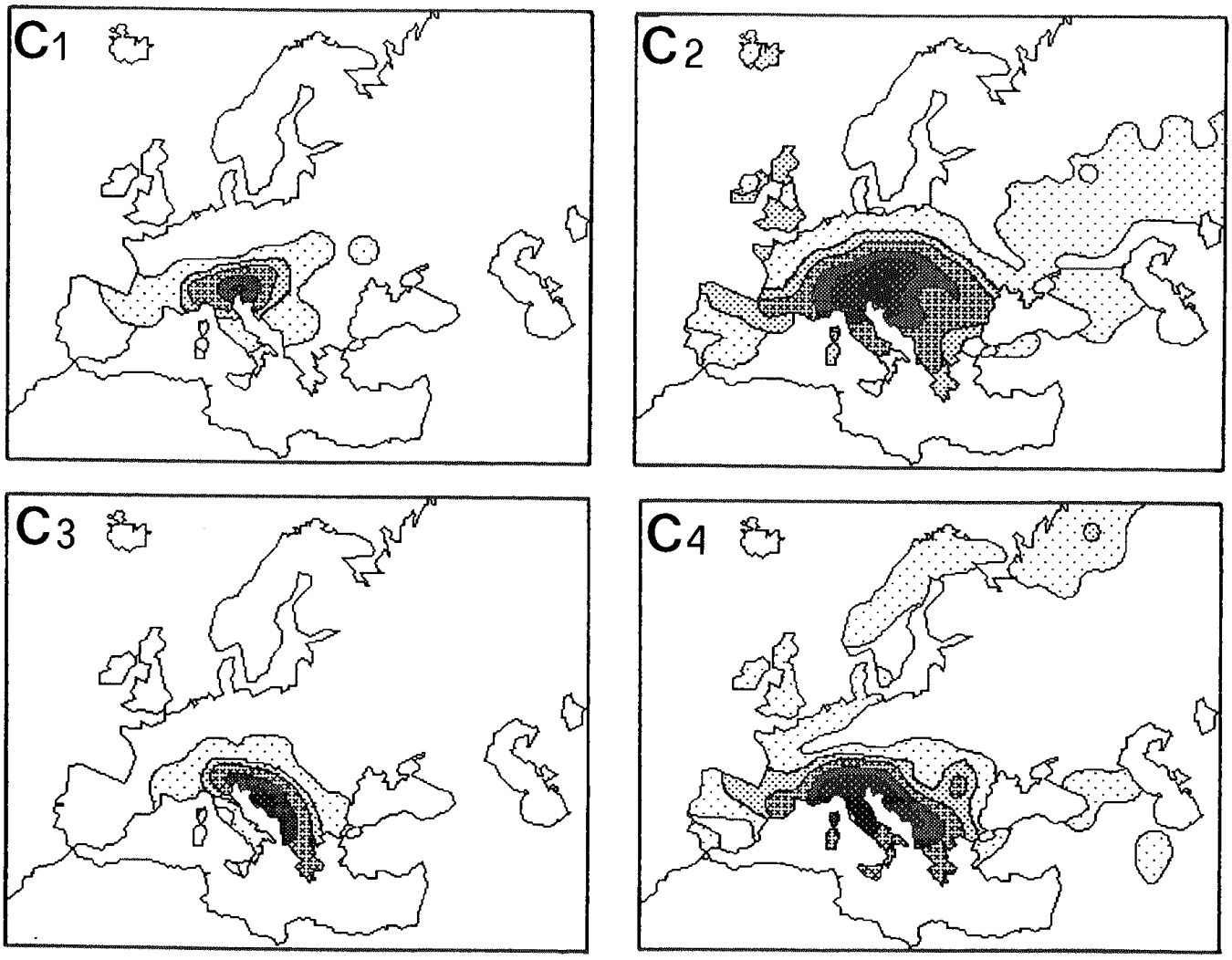

Figure 4. Continued.

amidata, *Scorzonera purpurea*, *Trifolium montanum*. These are mainly eastern species, whose distributional ranges widely extend into Eurasia, with the principal distributional area corresponding to the Pontic phytogeographical region. Their continental character is also reflected in the sharp decline along the Atlantic coasts of western Europe. Seven species have an extra-European distribution.

Subcluster b3. It includes 18 species (13%): *Aethionema saxatile*, *Allium carinatum*, *Artemisia alba*, *Centaurea triumfettii*, *Crysopogon gryllus*, *Dorycnium herbaceum*, *Fumana procumbens*, *Galium lucidum*, *Globularia punctata*, *Hippocrepis comosa*, *Melica ciliata*, *Petrorhagia saxifraga*, *Plantago holosteum*, *Rumex scutatus*, *Stipa eriocaulis*, *Teucrium montanum*, *Thesium divaricatum*, *Trinia glauca*. The joint distribution of these species clearly has a northern submediterranean pattern, from the northern Iberian Peninsula to the Balkans. Southern Central Europe constitutes a sharp distributional limit for most of the species.

Subcluster b4. This subcluster includes 11 species (8%): *Anacamptis pyramidalis*, *Blackstonia perfoliata*, *Botriochloa ischaemon*, *Carex flacca*, *Linum tenuifolium*, *Medicago lupulina*, *Ophrys apifera*, *Ranunculus bulbosus*, *Scrophularia canina*, *Schoenus nigricans*, *Teucrium chamaedrys*. Several widespread Mediterranean and southern submediterranean plants belong to this group. The joint distribution includes all European Mediterranean countries, plus the Mediterranean part of northwestern Africa, with several species extending to Central Europe northwards, and to the Caucasus eastwards.

Subcluster c1. It includes 14 species (10%): *Brassica glabrescens*, *Buphthalmum salicifolium*, *Campanula*

caespitosa, *Carex mucronata*, *Centaurea nigrescens* ssp. *vochinensis*, *C. dichroantha*, *Chamaecytisus purpureus*, *Daphne cneorum*, *Euphorbia triflora* ssp. *kerneri*, *Euphrasia cuspidata*, *Hieracium porrifolium*, *Knautia ressmannii*, *Matthiola carnica*, *Rhinanthus freynii*. This subcluster includes all endemic species, plus a subendemic element with narrow-ranging distributions, sometimes extending to the Dinaric Alps.

Subcluster c2. This group includes 17 species (12%): *Allium ochroleucum*, *Carlina acaulis* ssp.*simplex*, *Cirsium pannonicum*, *Epilobium dodonaei*, *Erica herbacea*, *Euphorbia verrucosa*, *Gentiana clusii*, *Gypsophila repens*, *Inula ensifolia*, *Leontodon incanus*, *Medicago prostrata*, *Petasites paradoxus*, *Polygala chamaebuxus*, *Rhinanthus glacialis*, *Salix elaeagnos*, *Scorzonera austriaca*, *Sesleria albicans*. The distributional ranges are centered on the eastern Alps, extending to the northern Apennines and into the northern part of the Balkan Peninsula.

Subcluster c3. It includes 8 species (6%): *Bromus condensatus*, *Crepis froelichiana*, *Dorycnium pentaphyllunm*, *Genista sericea*, *Knautia illyrica*, *Potentilla australis*, *Satureja variegata*, *Seseli gouanii*. These are clearly Illyrian species which, in the survey area, are close to their northern and western distributional limit.

Subcluster c4. It includes 12 species (8%): *Achnatherum calamagrostis*, *Agropyrum pungens*, *Asperula purpurea*, *Biscutella laevigata*, *Dianthus monspessulanus*, *Dryas octopetala*, *Eryngium amethystinum*, *Globularia cordifolia*, *Helianthemum alpestre*, *Plantago argentea*, *Polygala nicaeensis*, *Scabiosa graminifolia*. These species mostly have a narrow, northern and eastern submediterranean range. The main distributional area extends from northern and central Italy to the Illyrian region. One species, *Dryas octopetala*, with an Arctic-Alpine distribution, is clearly an outlier in this group.

Classification of species (Northern Hemisphere)

The joint distribution of the 56 species with extra-European distribution is depicted in Figure 5. The general pattern is mainly Temperate, extending from Europe to Central Siberia, with an important distributional limit in the Lake Baikal area.

The dendrogram of the species, based on their distribution in the Northern Hemisphere, is shown in Figure 6. Three main clusters (A, B, C) are formed, each with two subclusters, for a total of six chorotypes. Two species, *Festuca rubra* and *Dryas octopetala*, behave like outliers. In the following, the chorograms of the subclusters (Figure 7) will be briefly commented on.

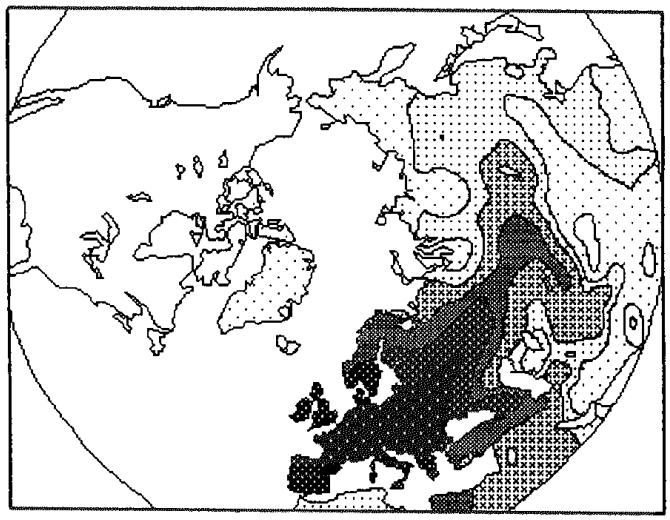

Figure 5. Joint distribution of the 56 vascular plant species with extra-European ranges. Different shadings indicate percentage representations of species, as in the legend to Figure 1.

Subcluster A1. It includes six species (Figure 6), whose joint distribution widely extends into Eurasia, encompassing several bioclimatic zones. Most of the species are common weeds, bound to anthropogenous habitats.

Subcluster A2. It includes 12 species (Figure 6), whose joint distribution extends throughout Temperate and Boreal Eurasia, extending up to the Arctic zone in Europe, but avoiding the most continental parts of northeastern Siberia. Most of them are typical of mesic to dry grasslands.

Subcluster B1. It includes 14 species (Figure 6), whose joint distribution does not extend so much into eastern Eurasia as that of the previous group. Most of the species have their eastern distributional limit just behind the Ural mountains. They also tend to avoid Arctic and Boreal latitudes in Europe.

Subcluster B2. It includes 11 species (Figure 6), whose joint distribution has a clearly Temperate, rather southern pattern, extending from Central and southern Europe to southern Siberia.

Subcluster C1. This small group includes only four species (Figure 6), whose joint distribution extends from Europe, including its Mediterranean part, to the mountains of the Irano-Turanian region.

Subcluster C2. It includes seven species (Figure 6), whose joint distribution is centered in the southern part of eastern Europe, extending widely into the steppe regions of Eurasia. The general pattern resembles that of subcluster B2, with a more southern tendency.

Phytogeographic synthesis

On the basis of the previous results, the species of '*magredi*' grasslands can be subdivided into six main groups:
(1) Narrow-ranging (34% of the total), including all species of clusters c1–c4, i.e. the endemic, subendemic, Illyrian-Balcanic and NW submediterranean elements. They are important also vegetationally, with many species differentiating the two main community-types, and several locally common and often dominant plants (see Table 1).
(2) Southern European (18.8%), including the species of clusters b3 and b4, with distributions centered in southern Europe, mainly in the submediterranean region. Many are common and widespread in both community-types (see Table 1).
(3) European wide-ranging (16.6%), including the species of clusters b1 and B1, distributed across Europe. With a few exceptions, they are scarcely represented in our set of relevés (see Table 1).
(4) Eastern-Pontic (7.6%), including the species of clusters b2 and C2, which widely extend into the steppe regions of Eurasia. Among them there are some of the most typical elements of the '*magredi*' grasslands, such as *Crambe tataria* and *Scorzonera purpurea*.
(5) Southern Eurasiatic (10.5%), including the species of clusters B2 and C1, with broad Eurasiatic distributional ranges, not reaching the Arctic zone. Most of them are not important in characterizing the '*magredi*' vegetation (see Table 1).
(6) Northern Eurasiatic (12.5%) including the species of clusters A1 and A2, with a broad Eurasiatic distribution reaching the Boreal, and often the Arctic zones. This group includes several common weeds, and plants of mesic mowed meadows, which are not important in our grasslands; some of them (Table 1) sporadically occur in mature stages, but rarely attain high cover.

Discussion and conclusions

The phytogeographic originality of '*magredi*' grasslands is evident: more than one third of the species have narrow distributional ranges, with six endemic plants: *Brassica glabrescens*, *Centaurea dichroantha*, *Knautia ressmannii*, *Euphorbia triflora* ssp. *kerneri*, *Leontodon berinii* and *Matthiola carnica*, most of which can be interpreted as neoendemic taxa (see Martini 1987; Poldini et al. 1991). Particularly relevant are the connections with the Balkanic-Illyrian and the eastern Alpine regions. Some plants with optimum at higher altitudes are able to thrive also in the '*magredi*' grasslands, favoured by periodical transport of propagules by pre-Alpine rivers, and by low concurrence in the most primitive successional stages. Among them we can cite *Biscutella laevigata*, *Daphne cneorum*, *Dryas octopetala*, *Helianthemum alpestre*, *Matthiola carnica*, etc. The presence of a small set of Pontic-eastern species which, in the survey area, are close to their western distributional limits, enhances the phytogeographic interest of this vegetation. Altogether, narrow-ranging and eastern-Pontic taxa make up more than 40% of the total flora, and include several characteristic, and often dominant elements. According to Poldini (1973a) the older Wurmian deposits have a higher share of eastern species, while neoendemic and especially Alpic species are more frequent on recent deposits. The relatively high incidence of submediterranean species (18.8%) reflects the prevalent phytogeographic conditions of the high Friulian plain and of the adjoining pre-Alpine slopes, which are mostly covered by submediterranean woodlands. The remaining taxa have much broader distributions, some limited to Europe, others extending widely through Eurasia. For most of them, however, the broad distribution is reflected in a wide ecological amplitude: many of these wide-ranging species occur, often with higher cover and frequency, in other types of grasslands, and some are common and widespread weeds. The initial stages of colonization (*Centaureo-Globularietum cordifoliae*), have the smallest share of wide-ranging species.

The peculiar geographical location of the high Friulian Plain is responsible for the remarkable phytogeographical diversity of the local dry grasslands: this region is open to migratory currents of steppic plants from the east and, at the same time, has had intense floristic exchange with the eastern pre-Alps, one of the main cradles of endemism in the Alpine system. Furthermore, this region is transitional between

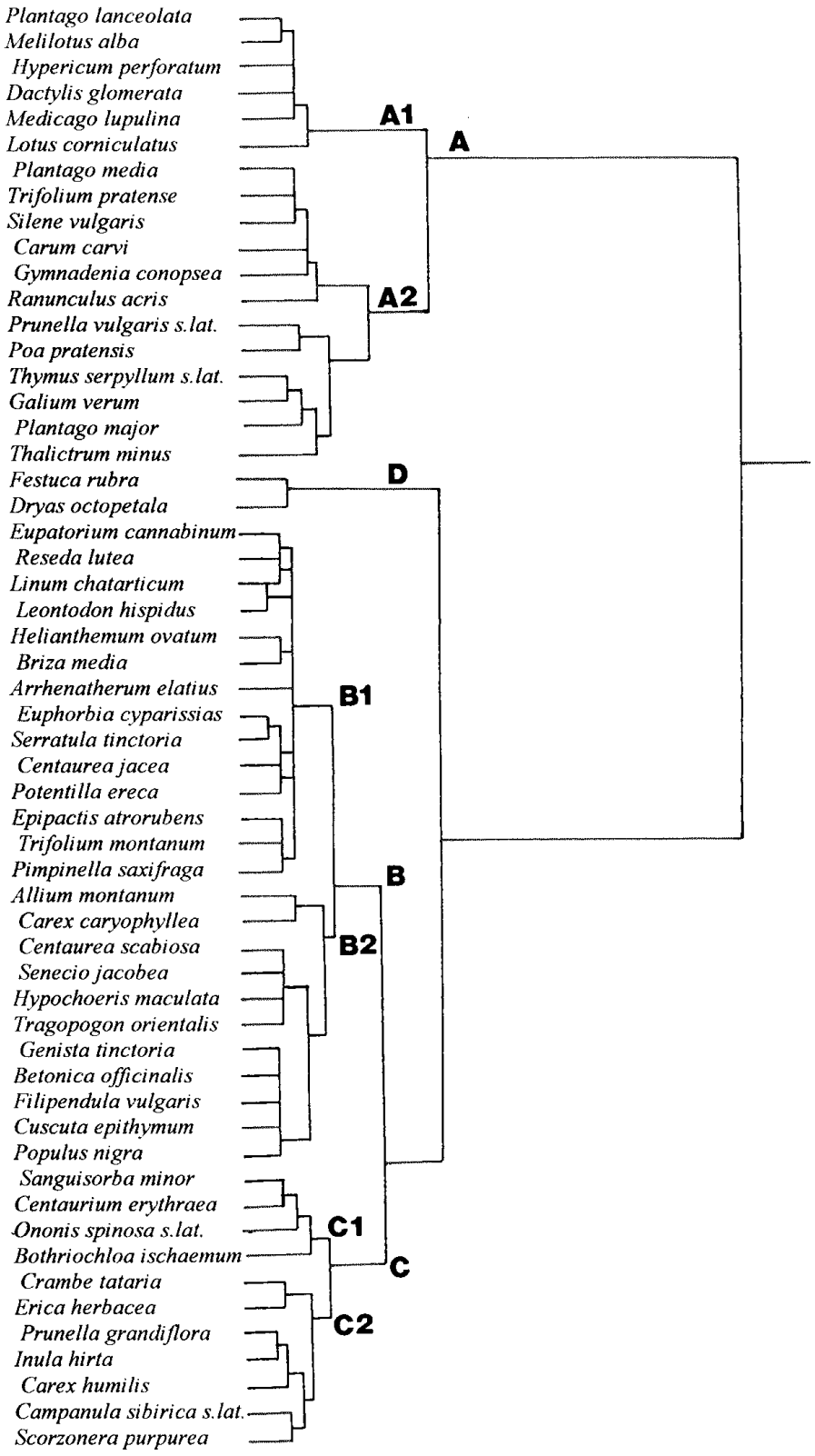

Figure 6. Dendrogram of the 56 extra-European species, based on their occurrence in the 688 Operational Geographic Units covering the Northern Hemisphere north of the Tropic of Cancer.

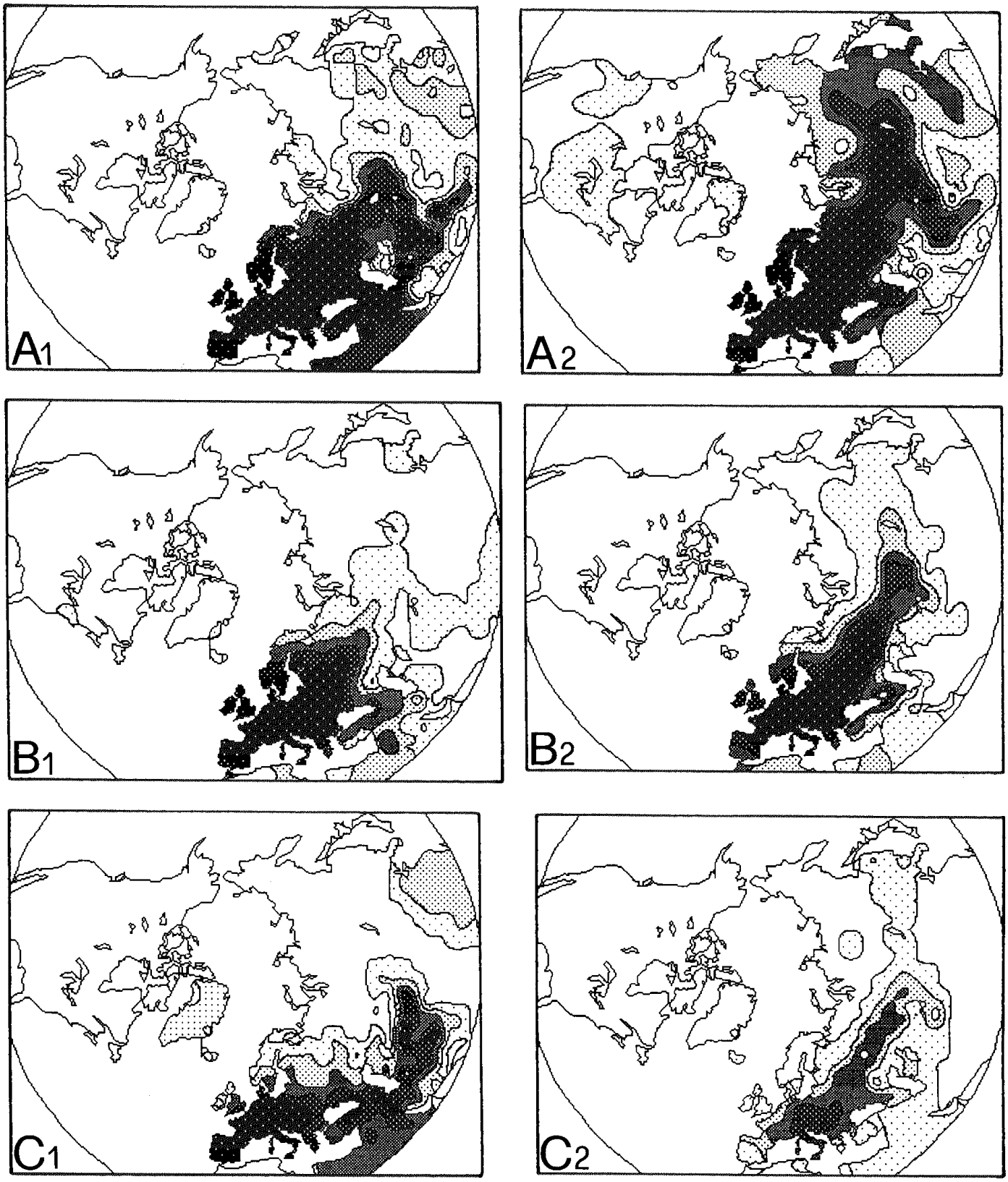

Figure 7. Joint distribution of all species included into the six subclusters obtained on the basis of their distribution in the 688 Operational Geographic Units covering the Northern Hemisphere north of the Tropic of Cancer. The subclusters are abbreviated as in Figure 6. Different shadings indicate percentage representations of species, as in the legend to figure 1.

the Central-European and the Mediterranean biomes, with a clear prevalence of submediterranean species (Poldini 1971). The strong originality of its flora finds a marked counterpart in the peculiar cultural and linguistic traits of its population, who still speaks an ancient Rheto-Romanic language (Friulian), that has maintained itself in spite of the repeated invasions of foreign populations from the east. The '*magredi*' grasslands somehow mirror these cultural-historical peculiarities. They constitute a unique type of vegetation with outstanding phytogeographical interest, and their last remnants, presently menaced of total disappearance, should be preserved as an important part of the European natural heritage.

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References

Anderberg, M. R. 1973. Cluster Analysis for Applications. Academic Press, New York.

Braun-Blanquet, J. 1964. Pflanzensoziologie, Grundzüge der Vegetationskunde. 3rd ed. Springer, Wien.

Chiapella Feoli, L. & Poldini, L. 1995. Prati e pascoli del Friuli (NE Italia) su substrati basici. Studia Geobot. 13: 3–140.

Comel, A. 1975. Le basi pedologiche per la valutazione dei terreni. Edagricole, Bologna.

Crovello, T. J. 1981. Quantitative biogegraphy. Taxon 30: 563–575.

Dal Prà, A. & Antonelli, R. 1979. Indagini geologico-tecniche sul sottosuolo della pianura alluvionale dei torrenti Cellina e Meduna (Pordenone). Studi Trentini Sc. Nat. 56: 101–112.

Daget, P. 1980. Atlas d' Areologie Periméditerranéenne. Fasc. I. Naturalia Monspeliensia nr. h. sér., 731 pp.

Flora Europaea, 1964-1980. vol. 1 (1964); vol. 2 (1968); vol. 3 (1972); vol. 4 (1976); vol. 5 (1980). Cambridge University Press, Cambridge, UK.

Gentilli, J. 1964. Il Friuli. I Climi. Cam. Commercio, Udine.

Gortani, L. & M. 1905. Flora Friulana. Udine.

Hultén, E. 1937. Outline of the History of Arctic and Boreal Biota during the Quaternary Period. Aktiebolaget Thule, Stockholm.

Hultén, E. 1962. The Circumpolar Plants, Kungl. Svenska Vet. Akad. Handl. 8/5.

Hultén, E. 1968a. Flora of Alaska and Neighbouring Territories. Stanford University Press, Stanford, Calif.

Hultén, E. 1968b. The Circumpolar Plants. Vascular Cryptograms, Conifers, Monocotyledons. Almquist & Wiksell, Stockholm, Goteborg and Uppsala.

Hultén, E. 1971. The Circumpolar Plants. Dicotyledons. Almquist & Wiksell, Stockholm, Goteborg and Uppsala.

Hultén, E. & Fries, M. 1986. Atlas of North European Vascular Plants north of the Tropic of Cancer. 3 voll. Koeltz, Königsberg.

Jalas, J. & Suominen, J. (eds.) 1972-1986. Atlas Florae Europaeae. Distribution of Vascular Plants in Europe. vol. 1 (1972), vol. 2 (1973), vol. 3 (1976), vol. 4 (1979), vol. 5 (1980), vol. 6 (1983), vol. 7 (1986), vol. 8 (1989), vol. 9 (1991). Soc. Biol. Fennica Vanamo, Helsinki.

Lorenzi, A. 1914. Studi sui tipi antropogeografici della pianura padana: tipo dei magredi del Friuli occidentale. Riv. Geogr. Ital. 21.

Martini, F. 1987. L' endemismo vegetale nel Friuli-Venezia Giulia. Biogeographia 13: 339-399.

Meusel, H., Jäger, E. J. & Weinert, E. 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 1. Fischer, Jena.

Meusel, H., Jäger, E. J., Rauschert, S. & Weinert, E. 1978. Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 2. Fischer, Jena.

Meusel, H. & Jäger, E. J. 1992. Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 3. Fischer, Jena, Stuttgart & New York.

Nimis, P. L. & Bolognini, G. 1990. The use of chorograms in quantitative phytogeography and in phytosociological syntaxonomy. Fitosociologia 25: 67–88.

Nimis, P. L. & Bolognini, G. 1993. Quantitative phytogeography of the Italian beech forests. Vegetatio 109: 125–143.

Nimis, P. L., Malyshev, L. I. & Bolognini, G. 1994. A phytogeographic analysis of birch woodlands in the southern part of West Siberia. Vegetatio 113: 25–39.

Nimis, P. L., Malyshev, L. I, Bolognini, G. & Friesen, N. 1995. Phytogeographic diversity of the Putorana flora (N-Siberia). Ann. Bot. Fennici 32: 1–17.

Pignatti, S. 1953. Introduzione allo studio fitosociologico della pianura veneta orientale, con particolare riguardo alla vegetazione litoranea. Arch. Bot. Fitogeogr. Ital. 29, 1: 1–25.

Pignatti, S. 1982. Flora d' Italia. 3 voll. Edagricole, Bologna.

Poldini, L. 1971. La vegetazione della regione. In: AA.VV:: Enciclopedia Monografica del Friuli-Venezia Giulia Vol. 1. Udine. Pp. 507–604.

Poldini, L. 1973a. I magredi. Inf. Bot. Ital. 5, 2: 146–148.

Poldini, L.1973b. *Brassica glabrescens*, eine neue Art aus Nordost-Italien. Giorn. Bot. Ital. 107, 4: 181–189.

Poldini, L. 1973c. Ad floram italicam notulae taxonomicae et geobotanicae. *Crambe tataria* Seb. Webbia 28: 31–36.

Poldini, L. 1991. Atlante corologico delle piante vascolari nel Friuli-Venezia Giulia. Dir. For. Parchi, Reg. Friuli-V. Giulia, Trieste.

Poldini, L., Martini, F. & Pertot, M. 1990. Structural and ecological variation of the Pontic phytogeographical element from the coastal Karst to the southwestern Alps. Studia Geobot. 10: 133–145.

Poldini, L., Martini, F., Ganis, P. & Vidali, M. 1991. Floristic databanks and the phytogeographic analysis of a territory. An example concerning northeastern Italy, pp. 159–181. In: Nimis, P. L. & Crovello, T. J. (eds.): Quantitative approaches to Phytogeography. Kluwer Academic Publishers, Dordrecht-Boston-New York.

Wildi, O. & Orloci, L. 1988. MULVA-4, a package for multivariate analysis of vegetation data. Swiss Fed. Inst. For. Res. Rep. Birmensdorf, pp. 1–122.

Zenari, S. 1928. La vegetazione dei 'magredi' nell'alta pianura del Friuli occidentale. Atti Acc. Sc. Ven. Trent.-Istriana 19: 51–56.

Appendix – Sporadic species in Table 1 (chorotype; relevé nr.: cover value)

Biscutella laevigata (c4; 6: +), *Carex liparocarpos* (a1; 50: +), *Centaurea triumfettii* (b3; 37: r), *Centaurium erythraea* (a2, C5; 55: +), *Dianthus monspessulanus* (c4; 12: +), *Dorycnium pentaphyllum* (c3; 37: r), *Erigeron annuus* (b1; 19: +), *Eupatorium cannabinum* (a2, B1; 6: +), *Festuca rubra* (a1; 19: r), *Hieracium porrifolium* (c1; 31: +), *Hypericum perforatum* (a2, A1; 53: +), *Inula hirta* (b2, C2; 31: +), *Melica ciliata* (b3; 54: +), *Melilotus alba* (a2; 19: r), *Plantago argentea* (c4; 48: r), *Polygala nicaeensis* (c4; 50: +), *Scrophularia canina* (b4; 41: +).