

Exploring the influence of shrubs on herbaceous communities in a Mediterranean climatic context of two spatial scales

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Abstract Communities of plants determine non-random spatial patterns defined by the intervention of abiotic and biotic factors acting at different spatial scales. We consider the influence of shrubs as one of the most important factors (biotic) affecting these spatial patterns at microscale. The macroclimate could be considered one of the most important factors (abiotic) at regional scale. To study the role and the floristic implications of each factor on the global patterns of herbaceous communities, we have developed a stratified sampling design that integrates both micro and macroscale on a 100 Km-long transect (east–west) in western central Spain. The results suggest that macroclimate could be one of the most important factors in determining herbaceous spatial patterns. Moreover, shrubs create a microspatial environmental heterogeneity that could alter such global climate patterns, modifying the spatial affinities established among species. This implies that environmental heterogeneity related to microhabitat could play a key role in spatial patterns at broad spatial scales, and consequently in the dynamics of the distribution and establishment of herbaceous species.

Keywords Herbaceous species · Macroclimate · Microhabitat · Shrub influence · Spatial patterns · CCA

Introduction

Over the last decades, interactions among plants have acquired great importance in community ecology (Shmida and Whittaker 1981; Puerto and Rico 1994; Tielbörger and Kadmon 1995, 1997; Wilson 1998; Holzapfel and Mahall 1999; Köchy and Wilson 2000). The functional and structural features of the communities that emerge from these interactions could have profound implications in plant distribution at broad spatial scales (Hooper and Dukes 2004). Plant ecologists have tested the importance of these processes from the point of view of the positive or negative nature of the balance established among coexisting species (Greenlee 1977; Franco and Nobel 1989; Callaway 1995; Callaway and Walker 1997; Callaway 1998; Brooker and Callaghan 1998; Callaway and Puignaire 1999; Holmgreen et al. 1997; Tielborger and Kadmon 2000; Puignaire et al. 2001). Thus, several authors have focused on the study of the interactions between shrubs and herbaceous communities (Moro et al. 1997; Casado et al. 2004). The influence of shrubs on herbaceous species usually seems positive when the latter undergo harsh environmental conditions, taking into account that

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the canopy of shrubs could reduce this harshness (Callaway and Puignaire 1999; Puignaire et al. 2001). Nevertheless, this generalized trend has been questioned several times by some authors (Olofsson et al. 1999; Forseth et al. 2001).

Regarding structural community features, other studies have shown the importance of nurse plants (shrubs) when environmental gradients of stress or harsh conditions determine an important reduction in herbaceous diversity and richness outside the protection of the shrub canopy (Puignaire and Luque 2001).

In many cases, the implications of climate on plant spatial patterns have also been described (Woodward 1987). These broad patterns have been studied previously in our latitudes (Gavilán and Fernández González 1997; Gavilán et al. 1998; Retuerto and Carballeira 2004; Pausas et al. 2003) and they highlight the importance not only of water availability in Mediterranean ecosystems but also of the effects of low temperatures.

The present study attempts to evaluate the effects of shrubs on the spatial patterns of the herbaceous composition and their implications on a relatively broad scale represented by a 100-Km transect (from east to west) in the western central Spain, where there is an important environmental heterogeneity related to macroclimate. Thus, we focused our objectives on linking microhabitat and macroclimate effects. Shrubs (microspatial scale) are responsible for the generation of an important degree of local heterogeneity (Guo 1998; Hotchtrasser and Peters 2004) and must therefore be considered decisive elements for the understanding of the patterns of herbaceous communities in our Mediterranean region. The issues are thus what floristic implications does the presence of shrubs has for broad patterns of herbaceous communities, and what relationship is there between these results and those obtained under other environmental conditions (where shrublands represent mature natural communities). In our case, shrublands are merely transitional stages maintained by human disturbance (Pausas J. 1999) which is why we suspect that their role in our herbaceous communities could be different not only because of their different morphology, but also due to their implications in successional processes.

Methods

Study area

The area selected for the study was the northern orientation of the western sector of the *Sistema Central* Mountains (Spain). This area has a broad variety of climate types within generalized Mediterranean conditions and hence different types of shrubland communities (Anta-Ferrero et al. 1988; Madrigal et al. 2007). Seven localities were chosen along an east–west transect 100 Km long (west geographical coordinates: 6°51'17" W–40°16'16" N; east geographical coordinate: 5°43'48" W–41°21'55" N). Representative patches of shrubland within this spatial range were selected and the abundance of herbaceous species was sampled by counting aboveground individuals.

This region represents a mountainous area with an important altitudinal range, where different bioclimatic belts, within the generalized Mediterranean climate could be recognised (Rivas Martinez 1985). The lowest altitudes include the presence of holm oak (*Quercus suber* L.) potential vegetation series, whereas the highest ones include the presence of sessile oak series (*Quercus pyrenaica* Willd.). Differences in temperature, precipitation, oceanic or continental influences, and the Mediterranean character of the area (based on the Mediterranean index; Rivas Martinez 1987) determine the existence of an important degree of biological heterogeneity. Among the localities selected, the most Mediterranean ones (*Puentes del Alagón* (Pa) and *Sotoserrano* (St)) are dominated by sclerophyllous broad-leaved shrubs. Most degraded sites are dominated by *Cistus ladanifer* L., whereas the most mature ones are dominated by *Arbutus unedo* L. in highly diversified communities. The localities with the most significant oceanic influence (*Navasfrias* (Na) and *La Alberca* (Al)) contain communities dominated by narrow-leaved shrub species such as *Erica umbellata* Loeffl. ex L. and *Calluna vulgaris* (L.) Hull. These areas are characterised by abundant annual precipitation and warmer temperatures.

Finally, it is possible recognize a variety of shrublands in the area that are subject to more continental conditions. Typically subhumid continental environments are represented by “*escobonar*”

communities, dominated by the leguminous *Cytisus multiflorus* (L'Hér.) Sweet. The locality chosen with this kind of climatic influence was Serradilla del Llano (Sr), with the lowest amount of annual and spring precipitation and an important temperature contrast. Other types of communities under continental influence are those dominated by the leguminous *Genista cinerascens* Lange. These species dominate at higher altitudes with higher amounts of rainfall than shrublands featuring *Cytisus multiflorus*. The locality selected was Navacarros-Candelario (Ca). The most elevated locality is the Alto Valle del Agadón (Monsagro (Mo); 1300–1400 m), with shrublands dominated by *Erica australis* ssp. *aragonensis* L. and the leguminous *Pterospartum tridentatum* L.

All the selected shrubland communities represent degraded stages of the mature forest of sessile-oak and holm-oak tree species. These areas were cultivated until the 70s and were then abandoned. Since then, livestock grazing together with furtive incendiary practices have been the most important human activities affecting the landscape, allowing the maintenance of shrublands, but preventing the establishment of trees. On several occasions (Alto Valle del Agadón and Serradilla del Llano), reforestation with productive pine or eucalyptus species has been implemented, which has further increased the disturbance of soil properties.

Sampling design and data analyses

Data on the abundance of herbaceous species were collected using a stratified sampling design and recording square samples of 25 cm/side at three different positions with respect to the shrub canopy: under the canopy (UC); at the canopy edge (defined by the orthogonal projection of the canopy on the ground) (EC); and outside the influence of the shrub canopy (OC). Four samples were taken at each position for each shrubland patch, which were identified with a homogeneous shrubland community of 1 ha area (10000 m²), where covered and bare spaces could be recognized. One shrubland patch each was considered for Navasfrias, Candelario and Puentes del Alagón and three shrubland patches for Serradilla del Llano, Alto Valle del Agadón, Sotoserrano and La Alberca. A total of 15 shrubland

patches within seven localities were sampled, with the observation of 140 herbaceous species. Initially, a matrix of 140 species × 180 sample quadrants was elaborated. In order to reduce this, we first calculated the average abundance per locality and position with respect to the shrub canopy. In a second step we transformed the dataset by taking logarithms of the abundance (McCune and Grace 2002). The result was a matrix of 21 rows × 140 columns, representing seven localities and 140 species. One of the rows, corresponding to the community outside the shrub the canopy at *Puentes del Alagón*, was eliminated from the analysis, because of the low influence of shrubs due to the small size of bare gaps.

Finally, rare species were removed from the analysis. We decided to include a species in the analysis, whenever it was possible to recognise its presence in more than two out of the seven localities selected. To conduct the analysis, 39 species from the whole regional pool were considered. The patterns described upon including rare species also showed the same tendencies but reduced the variance explained by the principle axes.

We used multivariate statistics to order and classify the samples and species (Teer Braak and Prentice 1988). We first ran a Principal Components Analysis (PCA) to organize the sites, considering only climate variables. Then, a Correspondence Analysis (CA) was used to organize communities and herbaceous species not under the influence of environmental variables (Jongman et al. 1995; Leps and Smilauer 2003). Canonical Correspondence Analysis (CCA) was conducted to obtain a constrained ordination of communities and species, with environmental variables performing as in a multiple regression (Teer Braak and Prentice 1988; Jongman et al. 1995; Leps and Smilauer 2003), but with several advantages (Graham 2003). These environmental variables were climatic variables and variables (dummy) related to position with respect to the shrub canopy (UC, BC and OC). Finally, cluster analysis was conducted using the species scores on the three-principle axes of the CCA. This technique led us to use the ecological optimum values of species extracted from the main gradients in our study area and hence to classify communities using a more ecological than strictly taxonomic criterion (Leps and Smilauer 2003).

Results

Macroclimate patterns

We first ran an ordination analysis (Principal Component Analysis–PCA) using climatic variables (Table 1) to obtain the principal gradients related to macroclimatic variability (Fig. 1). These gradients are exclusively climatic and represent a purely climatic ordering of localities that should subsequently be taken as a reference. This ordering afforded three clearly separated zones in the multivariate space. The most Mediterranean-influenced sites were separated from the others through the first gradient, which was related to temperature variables and the Mediterranean index (Im) (Rivas Martinez 1987). The second axis was related to precipitation variables such the spring rainfall (SRF) or annual rainfall (ARF). This gradient separates oceanic-influenced sites from the others due to greater precipitation at those sites and to warmer prevailing temperatures. The third axis was related to the influence of the continental conditions (Ck: Kerner continental influence index).

On comparing the results obtained in the analysis using only climatic information versus the results

obtained in the analysis using only the abundance of herbaceous species, it was seen that—despite the small difference—the patterns described by site positions were very similar in both. Macroclimate variability seemed to be a decisive element governing the regional patterns of the herbaceous community.

Influence of shrubs on species composition patterns

Correspondence Analysis (CA) (Table 2) revealed the species composition patterns obtained with the herbaceous abundance data of the sample average per site and position with respect to shrub coverage (Fig. 2). The first axis pointed to a distribution of sites in the ordination space similar to that obtained with the previous analysis, in which only macroclimate information was considered. We found two ways to describe the effects of shrubs on species composition patterns: (1) the greatest contrast was observed only between “under the shrub canopy” and other positions. (2) The effect of shrubs may vary with macroclimate influence. Thus, the most Mediterranean sites showed a lower influence of shrubs on species composition within the broad spatial pattern

Table 1 Average values of climatic variables

Climate data	PA	St	Sr	Na	Ca	Al	Mo
ATS (°C)	15.1	15	10.8	10.4	10.3	10.6	10.3
MXATS (°C)	22.1	23.1	18.4	16.4	16.2	15.2	16.4
MATS (°C)	8.2	6.8	3.2	4.5	4.4	6	4.3
MXAATS (°C)	30.3	31.6	27.4	22.8	23.5	22.3	25.8
MAATS (°C)	2.8	1.9	−0.2	0.2	−1.5	1.4	−1.6
SRF (mm)	333	318	238	375	328	419	349
MATMC (°C)	3.9	2.9	0	1.1	1.1	2.6	0.8
MAT (°C)	14.6	14.8	11	10.6	10	10.7	10.7
ARF (mm)	1124.9	1127.7	698	1382.9	1079	1419.3	1035.1
Im (index)	8.17	8.14	7.27	6.96	5.62	7.93	6.24
Ck (index)	13.37	14.44	15.47	12.42	19.52	18.02	21.11
Qe (index)	3.19	2.45	2.62	5.4	5	4.28	3
Rmf (index)	10.8	12.5	8.9	7	8.7	7	8.9
SumRF (mm)	33	29.9	24.4	37.9	35.5	30.8	24.9

Variable names: ATS—Monthly Average Temperature of Spring; MXATS—Maximum Average Temperature of Spring; MATS—Minimum Average Temperature of Spring; MXAATS—Maximum Absolute Average Temperature of Spring; MAATS—Minimum Absolute Average Temperature of Spring; SRF—Spring Rainfall; MATMC—Minimum Average Temperature of Coldest Month; MAT—Monthly Average Temperature; ARF—Annual Average Rainfall; Im—Mediterranean Index (Rivas Martinez 1987); Ck—Kerner Index; Qe—Baudiere Index of humidity; Rmf—Temperature Contrast Index; SumRF—Summer Rainfall

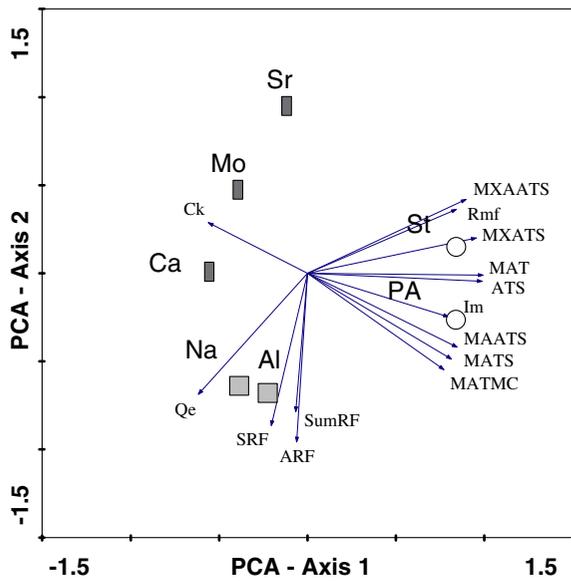


Fig. 1 Ordination diagram (PCA) with climate variables as dependent variables. Most oceanic-influenced sites—grey squares; most Mediterranean-influenced sites—white circles; most continental influenced sites—grey boxes. The first gradient separates the more Mediterranean-influenced sites from the others due to higher temperatures regimes and the Mediterranean index (Im). The second gradient separates the less Mediterranean-influenced sites due to the quantity of rainfall and continental influence (Kerner index). Sites names: Al—Alberca; Ca—Candelario; Mo—Monsagro; Na—Navasfrías; Pa—Puentes del Alagón; Sr—Serradilla del Llano; St—Sotoserrano

than the oceanic- or most of the humid continentally-influenced ones.

Due to their similarity, Canonical Correspondence Analysis (CCA) supported the results obtained in CA (Table 3). The most statistically significant variables were the Minimum Absolute Average Spring

Table 2 Joint information of CA and CCA analyses

Axes	CA			CCA		
	1	2	3	1	2	3
Multivariate analyses results						
Eigenvalues	0.458	0.341	0.281	0.395	0.248	0.119
% VSD	20.6	36	48.6	15.9	25.8	30.6
% SER	–	–	–	49.1	80.0	94.8
Total inertia	2.222			2.494		

% VSD—Cumulative percentage variance of species data; % SER—Cumulative percentage variance of species-environment relationship

Eigenvalues—variance explained by axis

Temperatures (MAAST), the effect of the shrub canopy (UC) and the spring rainfall amount (SRF) ($P < 0.01$; Monte Carlo test, 999 permutations) (Table 4). In this case, the constrained ordination (CCA) revealed a generalized effect of the shrub canopy at all sites, despite the fact that we found less influence of shrubs at the most Mediterranean sites in the Indirect Gradient Analysis (CA). MAATS was mainly related to the first axis; UC to the second axis, and SRF to the third axis. Microhabitat acquired great importance in the regional spatial pattern due to a characteristic pool of species typically from these covered sites.

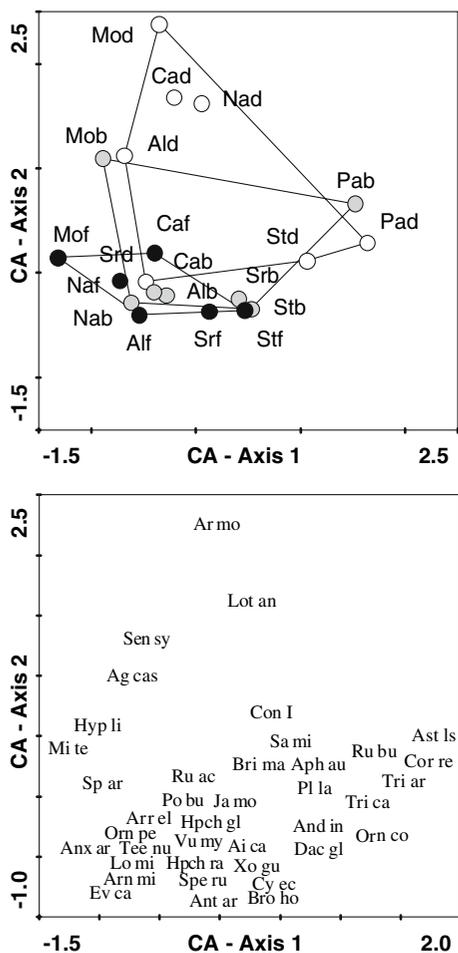
Species responses

Figure 3a shows the species distribution in the multivariate space defined by the first and second axes of the Canonical Correspondence Analysis. The species scores on the first three axes of this constrained ordination were taken to elaborate a species classification using the Pearson coefficient (Fig. 3b). The results revealed two main groups: (1) the first one contained species related to the edge of canopy or outside its influence of the less Mediterranean-influenced environments. (2) the other group may be divided into two different groups of plants each time: (2i) those related to the “under the shrub canopy” position of the less-Mediterranean-influenced sites, and (2ii) those related to typically Mediterranean sites. Higher affinities joined species from the shrub understory of the less-Mediterranean sites and species from typically Mediterranean sites. These results allowed us to consider shrub species as generators of microhabitat conditions that reduce the effects of minimum temperatures on herbaceous communities and that furthermore contain under the canopy an interesting pool of species related to forest environmental conditions. Most Mediterranean sites pointed to a lesser influence of shrubs on the compositional patterns of herbaceous species.

Discussion

Macroclimate patterns and herbaceous distribution

The results obtained when we used only climate information revealed a clear segregation of localities in the multivariate space that was simply due to the



◀ **Fig. 2** (a) Ordination diagram (CA; axis1–axis2) representing samples grouped by their position with respect to shrubs: Samples under the shrub canopy; Samples at the edge of the shrub canopy; Samples outside the shrub canopy. (b) Ordination Diagram (CA) showing species distributions in multivariate space (Axis1–Axis2). Shrub influence seems to be higher at less Mediterranean-influenced sites in relation to distances between samples under and outside the shrub canopy on the second axis. Species names: Ag cas—*Agrostis castellana* Boiss. et Reut., Ai ca—*Aira caryophylla* L., And in—*Andryala integrifolia* L., Ant ar—*Anthemis arvensis* L., Anx ar—*Anthoxanthum aristatum* Boiss., Aph au—*Aphanes australis* Rydb., Ar mo—*Arenaria montana* L., Arn mi—*Arnoseria minima* Schbei. et Koe., Arr el—*Arrhenantherum elatius* (L.) Beauv. ex J. et C. Presl., Ast ls—*Asterolinon linum-stellatum* (L.) Duby, Bri ma—*Briza máxima* L., Bro ho—*Bromus hordeaceus* L., Con I—*Conopodium* sp., Cor re—*Coronilla remanda* (Poir.) Guss., Cy ec—*Cynosorus echinatus* L., Dac gl—*Dactylis glomerata* L., Ev ca—*Evax carpetana* Lange, Hpch gl—*Hypochoeris glabra* L., Hpch ra—*Hypochoeris radicata* L., Hyp li—*Hypericum linariifolium* Vahl, Ja mo—*Jasione montana* L., Lo mi—*Logfia minima* (SM.) Dumort, Lot an—*Lotus angustissimus* L., Mi te—*Micropyrum tenellum* (L.) Link, Orn co—*Ornithopus compressus* L., Orn pe—*Ornithopus perpusillus* L., Pl la—*Plantago lanceolata* L., Po bu—*Poa bulbos* L., Ru ac—*Rumex acetosella* L., Ru bu—*Rumex bucephalophorus* L., Sa mi—*Sanguisorba minor* gr. Scop., Sen sy—*Senecio sylvaticus* L., Sp ar—*Spergula arvensis* L., Spe ru—*Spergularia rubra* (L.) J. et K. Presl., Tee nu—*Teesdalia nudicaulis* (L.) R. Br., Tri ar—*Trifolium arvense* L., Tri ca—*Trifolium campestre* Schreber, Vu my—*Vulpia myuros* gr. (L.) C. C. Gmelin, Xo gu—*Xolantha gutata* (L.) Raf. (*Tuberaria gutata* L. Fourr)

effects of temperatures. The Mediterranean-influenced sites have higher-temperature regimes than other sites in our study area. Continental-influenced zones are separated by the effects of different precipitation regimes and temperature contrasts. Species abundance followed a similar pattern on the first gradient of the CA and CCA. It seems clear that macroclimate has important effects on species community composition (Woodward 1987). The role of different climatic variables has been studied in other works, in which it was assumed that low temperature must be an important climatic factor influencing the spatial patterns of plants in Mediterranean environments (Cabezas and Escudero 1992; Gavilan and Fernández-González 1997; Gavilan et al. 1998; Retuerto and Carballeira 2004; Pausas 1999; Barboni et al. 2004). Taking into account the effects of frost and cold temperatures on plant physiology

(Woodward 1987; Jones 1992), the minimum absolute temperature of spring could be an important factor in explaining herbaceous species distribution, playing a key role in the communities at these sites despite traditional considerations that have given more relevance to water availability in Mediterranean-type ecosystems (Nahal 1981; Specht et al. 1983), and furthermore when these temperatures lie between positive and negative values and hence are in the adaptive threshold of plants to damage by cold and freezing (Woodward 1987). Frost and chilling damage requires different physiological strategies for the plants to survive because it has different effects on plants. This would be a reason to consider that minimum temperature would be correlated with the principal axis of the CCA, and therefore implies the highest segregation of species in the broad spatial context.

Table 3 Correlation matrix between sample scores on the CA and CCA axes

Paired correlation between CA and CCA axes	CCA—Axis 1	CCA—Axis 2	CCA—Axis 3
CA—Axis 1	0.770 ^a	−0.351	0.069
CA—Axis 2	0.367	0.886 ^a	0.065
CA—Axis 3	−0.10	0.098	0.365

^a $P < 0.01$

A statistically significant correlation is seen between the first–first axes and second–second axes (CA–CCA)

Table 4 Matrix of correlations between statistically significant variables and canonical axes in the CCA analysis, and matrix of correlations among environmental variables

Axes	CCA			MAATS	UC	SRF
	1	2	3			
Relationship between environmental variables and CCA axes						
MAATS	−0.736	0.042	0.521	1.000	–	–
UC	−0.064	0.830	0.042	0.060	1.000	–
SRF	0.524	−0.116	0.688	0.085	−0.005	1.000

MAATS correlates more with the first gradient; UC correlates more with the second gradient; SRF correlates more with the third gradient

No significant correlation is seen between the environmental variables included

Influence of shrubs on herbaceous spatial patterns

The problem of scale and its implications for plant spatial patterns have been studied by several authors (Levin 1992; Huston 1994; Bengtsson et al. 2002; Ferrer-Castán and Vetaas 2003). Local and microspatial environmental factors could be involved in the determination of regional spatial patterns owing to their effects on biological heterogeneity (Guo 1998; Hotchtrasser and Peters 2004). In this sense, the effects of shrubs on the herbaceous community, as an important microspatial factor generating microclimate and soil heterogeneity (Haase et al. 1996), should be evaluated within a hierarchical spatial view. Our results suggest that this microspatial heterogeneity introduced by shrubs determines an important compositional contrast among herbaceous species both under and distant from the shrub canopy. Nevertheless, this influence does not seem to be as important as that predicted in most works appearing in the literature, especially taking into account other studies conducted in arid and semiarid regions of the Iberian Peninsula (Tielborger and Kadmon 2000; Puignaire and Luque 2001). We found that the

Mediterranean environments of this supra-Mediterranean bioclimatic belt showed lower-compositional contrasts with respect to the influence of shrubs than meso-Mediterranean belt did. In contrast, colder sites showed the greatest compositional contrasts between the flora under and outside the shrub canopy. Despite this, our main regional gradient was basically related to minimum temperatures and less so to water availability, which is why we suspect that our results do not contradict the established theory concerning facilitative processes and water availability gradients.

Macroclimate and microhabitat seem to be two decisive elements that govern the herbaceous spatial pattern, considering that both act at two extremely different spatial scales. Local and regional spatial scales would determine global compositional patterns acting at the same time (Ferrer-Castán and Veetas 2003), each effect being integrated in the features of the physiology of herbaceous species. Thus, community composition and diversity assemblage depend not only on broad or local process independently, but also on both interacting at the same time. Thus, shrub influence as a microhabitat factor should be considered a decisive element influencing ecological

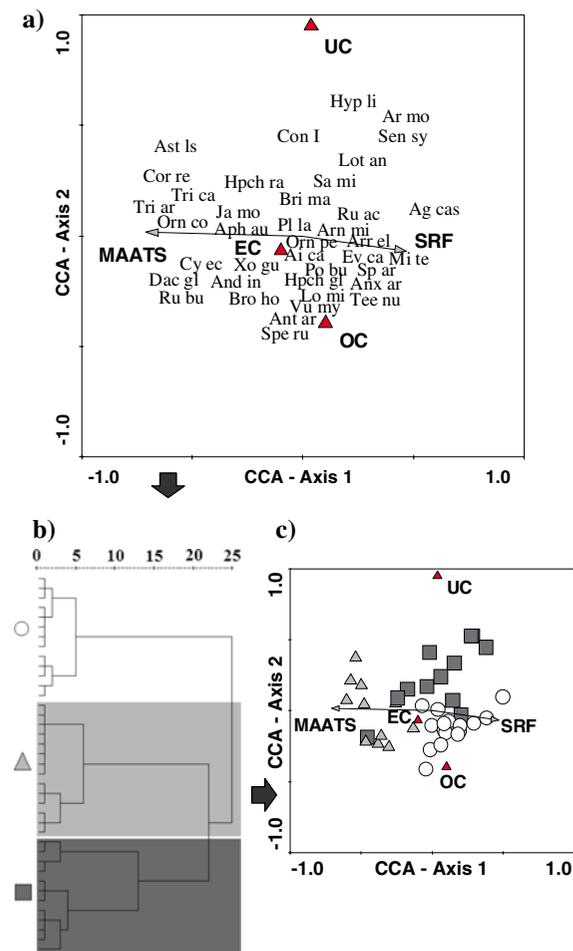


Fig. 3 (a) Ordination diagram (CCA) with species and statistically significant environmental variables. Triangles represent nominal variables (dummy). (b) Cluster analysis elaborated using species scores on the three principle axes of the CCA. (c) CCA ordination diagram showing the species symbols extracted from the cluster analysis. Squares represent species typically occurring under the shrub canopy at less Mediterranean-influenced sites. Triangles represent species typically occurring at more Mediterranean-influenced sites (without considering position with respect to shrubs). Circles contain species typically occurring at the edge or outside the shrub canopy at less Mediterranean-influenced sites

processes and landscape structure across scales (Chen et al. 1999).

Species spatial affinities

From a purely botanical perspective of species relationships, cluster analysis revealed an interesting link between species from colder zones under the

shrub canopy and those outside or under the shrub canopy of the less cold sites (Fig. 3b). The shrub canopy seems to act as a protective cover for herbaceous species that generate a microclimate, whose conditions resemble those of the most Mediterranean-influenced environments in the colder spring months. These conditions would be related to temperature in the sense of reducing the coldest temperatures under the canopy, thus preventing frost damage to herbaceous species. Therefore, evidence of the effects of microspatial conditions on global patterns should help to understand regional and local community dynamics. As mentioned above, these shrubland communities are the result of human disturbance to natural oak forests. In this sense, the herbaceous communities established after forest destruction undergo an important compositional change in which generalist species expand their presence (Bazzaz 1996). Herbaceous communities undergo harder-macroclimate conditions on bare sites than on covered ones, and hence these generalists tend to find a place to colonize and grow. When colonizing these bare sites, shrubs introduce a first sub-forest stage where successional processes begin to act again and the forest herbaceous layer starts to assemble again. This assembly occurs in a similar functional context, although not necessarily in the same way and towards the same community (Margalef 1991; Mitchel et al. 1997). This argument does not imply that herbaceous under shrub canopies would not be affected by climate, but does recognise that the role of climate in ecological succession would change according to the changes that community development produces in microspatial heterogeneity. Thus, a successional process, as a local event, affects the regional spatial patterns of herbaceous communities through changes in microhabitat related to shrub colonization during the transition to forest regeneration (Bazzaz 1996).

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