

Original article

Remnant shrubs in Mediterranean semi-arid steppes: effects of shrub size, abiotic factors and species identity on understorey richness and occurrence

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Received 23 October 2004; accepted 25 November 2004

Available online 20 January 2005

Abstract

Isolated shrub patches are a key element for community structure and dynamics in semi-arid ecosystems, and may act as “hot spots” of understorey species diversity. Despite its importance, the relationships between shrub patch characteristics and understorey species richness, and the relative importance of these characteristics against other factors driving understorey species richness, are still poorly understood. We studied perennial species richness under the canopy of late-successional shrubs in semi-arid *Stipa tenacissima* steppes of SE Spain. The main aim of this study was to evaluate the relationship between shrub size and understorey richness, and to test if this relationship is modified by species identity. We also aimed to know the relative importance of shrub patch characteristics and abiotic factors as predictors of the distribution of understorey species under shrub canopies. Altitude and geographical co-ordinates were able to significantly explain the patterns of shrub occurrence and abundance in the study area. Understorey species richness was significantly related to the size of individual shrubs according to a simple power relationship for all evaluated species. Slope values of linear regressions with log-transformed data, ranging between 0.22 and 0.37, did not differ between species. Site characteristics, patch characteristics and patch species identity significantly explained the occurrence of species on patches. However, the relative importance of site characteristics was higher than that of patch characteristics and species identity in explaining these patterns. Our results agree with the general expectations of the theory of island biogeography and complement previous studies that emphasise the importance of late-successional shrubs in semi-arid *Stipa* steppes. Environmental management activities within these steppes should promote the conservation of remnant shrubs, as well as its introduction with restoration activities.

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Keywords: Island biogeography theory; Mediterranean; Species richness; Sprouting shrubs; *Stipa tenacissima*

1. Introduction

In arid and semi-arid areas, low rainfall does not allow for a continuous cover, and vegetation is typically patchy. One of the most dramatic and best-studied consequences of patchiness in vegetation is the formation of “resource islands” underneath the canopy of shrubs (Reynolds et al., 1999). Soil and microclimatic conditions are improved in these places as compared to adjacent areas without vegetation (Titus et al., 2002), and these changes favour the prevalence of facilitative inter-

actions between plant species (Callaway, 1995; Maestre et al., 2001; Pugnaire et al., 1996). In addition to their role in plant interactions, shrub patches strongly modify plant dispersal patterns by processes such as trapping of water-, wind- and bird-dispersed seeds (Aguar and Sala, 1999). Thus, they are a key element for community structure and dynamics in semi-arid ecosystems, and act as “hot spots” of diversity in these areas (Pugnaire and Lázaro, 2000). In these areas, characteristics of shrub patches like species identity, age, and size strongly influence seed banks, seedling recruitment, and community composition of understorey species (Facelli and Brock, 2000; Pugnaire and Lázaro, 2000). However, few studies so far have evaluated how patch characteristics affect patterns of understorey richness and diversity (Bascompte and Rodríguez, 2001; Gavilán et al., 2002), and the relative impor-

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tance of shrub patch characteristics against other abiotic factors driving the occurrence of understorey species is also poorly known (Gavilán et al., 2002). Increasing our knowledge on these links, and on the factors driving the distribution of shrub patches, will undoubtedly improve our understanding about ecosystem functioning in semi-arid degraded ecosystems, and will help to design adequate measures to manage, preserve and restore these ecosystems.

Steppes of the tussock grass *Stipa tenacissima* L. constitute one of the major vegetation types in the arid and semi-arid areas of the Mediterranean Basin (Le Houérou, 2001). They derive from the degradation of woody vegetation, which in the semi-arid areas of SE Spain is constituted by shrublands dominated by sprouting species such as *Quercus coccifera* L., *Pistacia lentiscus* L. and *Rhamnus lycioides* L. (Rivas Martínez, 1987). Due to the economic importance that the fibre obtained from *Stipa* species had during centuries, human populations have favoured the presence of *Stipa* steppes since millennia (Barber et al., 1997; Yanes, 1993). Activities like grazing, harvesting, and repeated burning, have promoted not only the expansion of these steppes at the expense of shrublands, but also the elimination of the remnant shrubs to avoid competition with *Stipa*, and to encourage its growth (Yanes, 1993).

Nowadays, sprouting late-successional shrubs in semi-arid *Stipa* steppes typically appear as isolated patches without symptoms of expansion and recovery, despite most part of human activities in these steppes finished with the development of industry and tourism that took place during the period 1950–1960 (Barber et al., 1997). According to the theory of island biogeography (IBT) of MacArthur and Wilson (1967), these patches may be treated as “islands” of woody vegetation within a sea of grassland vegetation. Following IBT, species richness in island habitats is related to the size of the “island” by a power relationship. This relationship has often been used to interpret plant diversity and colonisation patterns in fragmented temperate terrestrial landscapes (Cook et al., 2002; Holt et al., 1995; Yao et al., 1999), but it has barely been employed in harsh environments such as semi-arid areas (Sanchez and Parmenter, 2002).

We hypothesise that, in *Stipa* steppes, the number of understorey perennial species will be related to individual shrub size as predicted by IBT. Since species-specific traits may strongly influence both the dispersal patterns and the availability of safe sites for the establishment of seedlings (Dunne and Parker, 1999; Fulbright et al., 1995; Russell and Schupp, 1998), we also hypothesise that this relationship is modulated by shrub species identity. The main objectives of this study were: (i) to evaluate if abiotic factors determine the abundance of late-successional shrubs in semi-arid *Stipa* steppes, (ii) to evaluate the relationships between the size of isolated shrubs and the number of perennial understorey species, (iii) to explore if this relationship is modified by the identity of the shrub, and (iv) to evaluate the relative importance of shrub size, species identity and abiotic characteristics as determinants of understorey species occurrence.

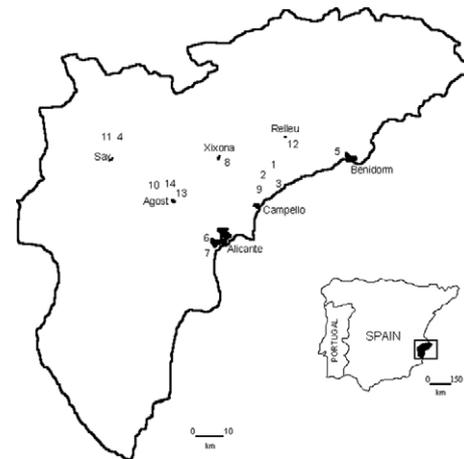


Fig. 1. Map of the study area showing the location of the study sites (numbers) and of some cities in the province of Alicante (SE Spain). Legend of sites as follows: 1 = Aguas; 2 = Campello 1; 3 = Campello 2; 4 = Colominas; 5 = Finestrat; 6 = Foncalent 1; 7 = Foncalent 2; 8 = Xixona; 9 = Marquesa; 10 = Palomaret; 11 = Peñarrubia; 12 = Relleu; 13 = Ventós 1; and 14 = Ventós 2.

2. Materials and methods

2.1. Study area

Our study was conducted at 14 experimental sites representative of semi-arid *S. tenacissima* steppes under varying degradation stages. All the sites were located in the province of Alicante, in SE Spain (Fig. 1). The climate of the study area is Mediterranean semi-arid, with average annual precipitation values ranging from 220 to 388 mm, and average annual temperature ranging from 16 °C to 18 °C. With the aim to reduce climatic variability associated with orientation, all the sites were located in south-facing slopes, with orientation values ranging between 140° and 240° and slope values range between 4° and 29°. The vegetation is an open steppe dominated by *S. tenacissima*, with total cover values ranging between 17 and 51%.

2.2. Field survey

Field survey was performed from July to November 2002. Within each site, we located a 30 m × 30 m plot starting on the upper edge of the hillslope. We located all late-successional sprouting shrubs existing in the plots, which are expected to be a remnant of mature shrubland vegetation (Rivas Martínez, 1987). Late successional sprouting shrubs and trees that were not present in more than two sites, such as *Rhamnus alaternus* L. and *Osyris lanceolata* Hochst. & Steud., as well as early successional shrubs, such as *Globularia alypum* L., *Anthyllis cytisoides* L. and several species of camephytes, were not considered for this study. In practice, six species were selected for this study: *Quercus coccifera* (hereafter referred as *Quercus*), *Rhamnus lycioides* (hereafter referred as *Rhamnus*), *Pistacia lentiscus* (hereafter referred as *Pistacia*), *Juniperus oxycedrus* L. (hereafter referred as *Juniperus*), *Erica multiflora* L. (hereafter referred

as *Erica*), and *Ephedra fragilis* Desf. (hereafter referred as *Ephedra*).

For all selected shrubs, we measured the maximum crown diameter in the horizontal, and the diameter orthogonal to this. With these data we estimated shrub size by using the formulae of the ellipse. All the perennial species located underneath shrub canopy were counted, and this value was considered as our estimate of species richness. At each site, we also measured the following environmental variables: altitude, slope, azimuth, mean annual rainfall and UTM co-ordinates. The altitude and UTM co-ordinates were obtained in situ with a global positioning system device (model GPS 76, Garmin, Olathe, Kansas, USA). The slope and azimuth were obtained with a clinometer (model PM-51360 PCB, Suunto, Vantaa, Finland) and a compass (model A-10, Suunto), respectively. The mean annual rainfall (period 1960–1990) at each site was obtained from the nearest meteorological station according to the database provided by Pérez (1994).

2.3. Statistical analyses

We evaluated the role of measured environmental variables as determinants of the number and area covered by shrub patches from all species by using forward stepwise linear regressions. Before these analyses, the values of slope, UTM N co-ordinates, number of sprouting shrubs, and the area covered by them were log-transformed to achieve normality in their distribution. To avoid problems when transforming the last two variables (some of the sites had no shrubs), we added one as a constant to all sites before log-transforming them.

According to IBT, the size of individual shrubs can be related with the number of perennial understorey species that contains by using a single power function of the type $S = cA^z$, where S is the number of species, and A is the shrub size. To obtain values of z comparable with published studies, we calculated the slope of the linear relationship $\log S = \log c + z \log A$. To avoid problems when transforming the number of species (some of the shrubs had no understorey species), we added one as a constant to all shrub clusters before data transformation. We tested for significant differences in slope (z) and intercept values between species by using the F test implemented in the program Statgraphics Plus 2.1 for Windows (Magnistics Inc., Rockville, USA). Due to the low number of individuals of *P. lentiscus* found (only three shrubs in the 14 study sites), they were removed from these and subsequent analyses. All regression analyses were conducted with the software SPSS 9.0 (SPSS Inc., Chicago, Illinois, USA).

To evaluate the relative importance of patch characteristics, species identity, and site characteristics as determinants of understorey species occurrence, we used canonical correspondence analysis (CCA; Ter Braak 1986) coupled with the variation partitioning method of Borcard et al. (1992). For these analyses, the matrix of perennial species occurrences (binary variable) constituted our response matrix. The patch characteristics matrix were confirmed by the size of the shrub patch, the number of understorey species present on it, and

the interaction between them. The site characteristics matrix was formed by the following environmental variables: altitude (in m), slope (in degrees), azimuth (in degrees), mean annual rainfall for the 1961–1990 period at the nearest meteorological station (in mm), and UTM North (N) and East (E) co-ordinates. For this matrix, all the shrub patches within the same site received the same values. The species identity matrix was formed by five dummy variables defining the identity of the overstorey species forming the patch. As a first step, the response matrix was analysed by detrended correspondence analysis (DCA) to evaluate the length of the ecological gradients (Ter Braak, 1986). According to the guidelines given by Borcard et al. (1992) and Legendre and Legendre (1998), CCAs and partial CCAs were performed to quantify the amount of variation that could be explained by the different fractions defined by the three constraining matrices. For each of these analyses, the sum of all canonical eigenvalues, divided by the sum of all eigenvalues, gives the fraction of variation that each fraction explains (Borcard et al., 1992). A Monte Carlo permutation test (999 permutations) on both first and the sum of all canonical axes (Ter Braak and Šmilauer, 1998) was carried out in order to establish if the relationships between matrices in the CCAs were significant. The CCAs were performed only with those shrub patches containing at least one understorey species (165 patches of a total of 256), and without transforming data nor downweighting rare species. All CCAs were performed with the software Canoco 4.0 for Windows (Ter Braak and Šmilauer, 1998).

3. Results

The number of sprouting late-successional shrubs and the area covered by them differed substantially between sites (Table 1). The number of shrubs was positively and significantly related only to the altitude of the study sites, which explained a substantial amount of the variation in these data ($R^2 = 0.544$; $F = 14.30$; $df = 1.12$; $P = 0.003$). The area covered by them was positively related with altitude and the UTM E co-ordinates, both variables explaining an important amount of variation in the data ($R^2 = 0.832$; $F = 27.30$; $df = 2.11$; $P < 0.001$).

A power function satisfactorily described the relationship between understorey species richness and shrub size for all evaluated species (Fig. 2). When data from all species were used, we obtained a close fit ($R^2 = 0.59$; $S = 3.11A^{0.46}$; $P < 0.001$). When individual species were fitted by separate, the best fits were obtained for *Ephedra* ($R^2 = 0.61$; $S = 5.32A^{0.32}$; $P < 0.001$) and *Juniperus* ($R^2 = 0.62$; $S = 2.31A^{0.64}$; $P < 0.001$). Lower, but still significant, fits were obtained for *Quercus* ($R^2 = 0.39$; $S = 4.73A^{0.29}$; $P = 0.039$), *Erica* ($R^2 = 0.28$; $S = 2.45A^{0.53}$; $P < 0.001$), and *Rhamnus* ($R^2 = 0.32$; $S = 5.72A^{0.26}$; $P = 0.010$). Slope values obtained for individual species after linear regressions of log-transformed data varied between 0.22 and 0.37 (Table 2), but they did not differ statistically (F test for comparison of slopes;

Table 1
Number (N) of individuals of the evaluated shrub species, and area covered by them (A, in m²), in the study sites

Site	<i>Ephedra fragilis</i>		<i>Erica multiflora</i>		<i>Juniperus oxycedrus</i>		<i>Pistacia lentiscus</i>		<i>Quercus coccifera</i>		<i>Rhamnus lycioides</i>		Total	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A
Aguas	2	15.43	0	0	0	0	0	0	3	56.01	1	0.79	6	72.23
Campello 1	0	0	10	4.28	3	1.75	0	0	0	0	2	4.01	15	10.04
Campello 2	1	0.66	0	0	0	0	0	0	0	0	0	0	1	0.66
Colominas	0	0	51	17.30	11	14.37	0	0	3	36.36	1	0.24	66	68.27
Finestrat	2	2.21	0	0	0	0	0	0	0	0	3	5.71	5	7.92
Foncalent 1	1	0.91	0	0	0	0	0	0	0	0	0	0	1	0.91
Foncalent 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xixona	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marquesa	5	0.93	0	0	0	0	0	0	0	0	2	3.13	7	4.06
Palomaret	0	0	0	0	4	8.26	1	6.03	1	6.03	1	2.27	7	17.89
Peñarrubia	0	0	110	43.18	18	16.67	1	5.72	3	19.60	0	0	140	85.17
Relleu	4	3.86	0	0	3	4.04	0	0	0	0	7	8.58	14	16.48
Ventós 1	0	0	0	0	0	0	0	0	1	5.42	1	4.70	2	10.12
Ventós 2	0	0	0	0	0	0	1	12.88	0	0	1	2.54	2	15.42

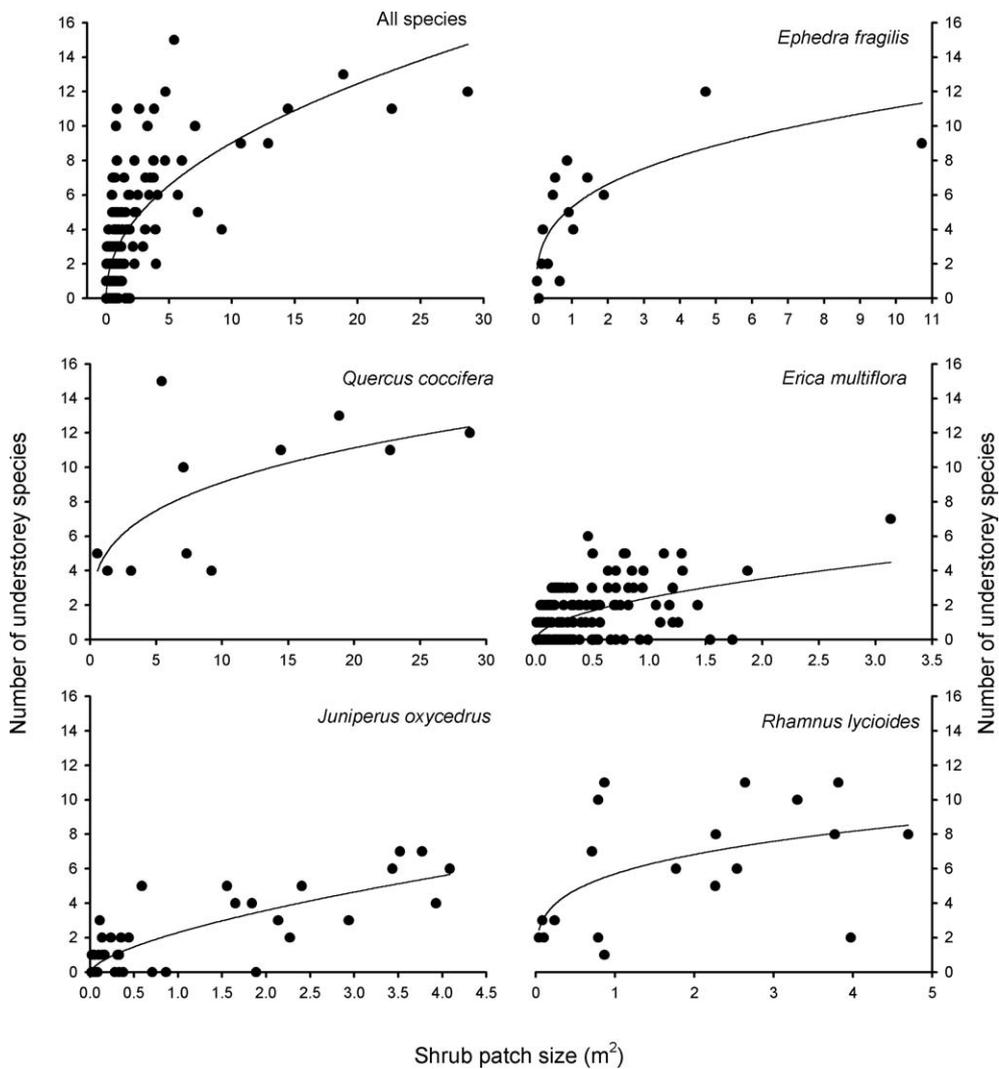


Fig. 2. Relationships between the individual shrub size and the number of perennial understorey species. Note the differences in the x-axis scale between the evaluated species. Solid lines represent significant ($P < 0.05$) power functions fitted to data. Details of the equations fitted are provided in the text.

Table 2

Linear regressions fitted to the relationship between the log-transformed values of shrub size (A) and number of understorey species (S). Different superscript letters together the interception of the regression model indicates significant differences between the different species (F test, $P < 0.05$)

Species	Model	R^2	ANOVA		
			F	df	P
All species	$S = 0.55 + 0.33A$	0.462	222.74	1.259	<0.001
<i>Ephedra fragilis</i>	$S = 0.77^b + 0.37A$	0.605	19.91	1.13	0.001
<i>Erica multiflora</i>	$S = 0.42^a + 0.22A$	0.215	46.20	1.169	<0.001
<i>Juniperus oxycedrus</i>	$S = 0.50^a + 0.30A$	0.463	31.90	1.37	<0.001
<i>Quercus coccifera</i>	$S = 0.74^b + 0.25A$	0.402	6.06	1.9	0.036
<i>Rhamnus lycioides</i>	$S = 0.78^b + 0.23A$	0.390	8.84	1.19	0.008

$F = 0.95$; $df = 4.9$; $P = 0.434$). However, interceptions significantly differed between species (F test for comparison of interceptions; $F = 13.5$; $df = 4.9$; $P < 0.001$).

The length of the extracted gradients in the matrix of understorey species, as obtained by DCA ($l_1 = 4.079$, $l_2 = 4.184$), was large enough to carry out a CCA-type constrained ordination. The CCAs performed with site characteristics, patch characteristics and patch species identity as constraining matrices were significant, suggesting that they were able to explain the distribution of perennial species under the canopy of shrubs (Table 3). The CCA biplot using the species identity matrix showed that *Ephedra* and *Quercus* were positively related with both the first and second axes, and that *Erica* and *Juniperus* were negatively related with both of them (Fig. 3A). It is also interesting to note how, when present in the understorey, shrub species that are able to form patches showed a general trend towards association with other species rather than with conspecific individuals. That is the case, for instance, for *Ephedra*, closely related to *Rhamnus*, and for *Erica* and *Juniperus*, more related to *Quercus* than to conspecifics. All environmental variables defining site characteristics, excepting the UTM E co-ordinates, were negatively related with the first axis of the ordination (Fig. 3B). The UTM E co-ordinates are strongly related with this axis, and largely determine the separation of most chamaephytes from the rest of species. The presence in the understorey of some shrub species, such as *Cistus clusii*, *Erica*, and *Juniperus* is related mainly with altitude. All variables defining patch characteristics were positively related with both the first and the second axis of the ordination (Fig. 3C). The scatter of the species found in the centre of the ordination diagram suggests that a good number of them were not particularly related to any of evaluated shrub patch characteristics. However, the occurrence of species such as *Rubia peregrina*, *J. oxycedrus* and *Pistacia lentiscus* increased when increasing the size of shrub patches. On the other hand, species such as *Globularia*

alypum and *Fumana ericoides* were more associated with the number of understorey species.

Partial CCA models were significant in all cases, suggesting that site characteristics, patch characteristics, and species identity explained significant non-overlapping fractions of variation in the matrix of understorey species occurrence (Fig. 4). Despite significant, the amount of variation of the understorey matrix explained by site characteristics alone was higher than that of patch characteristics and species identity, which explained similar amounts of variation each.

4. Discussion

Geographical co-ordinates and altitude were able to significantly explain the patterns of variation in the number and area covered by sprouting shrubs in semi-arid degraded *Stipa* steppes. Since the former variables are strongly related with differences in rainfall and temperature within the study area (Pérez, 1994), our results suggest that current shrub abundance in these steppes is mainly controlled by climatic conditions.

We found that the richness of perennial understorey species is strongly related to the size of shrubs according to a single power relationship. Similar relationships between shrub size and understorey richness have been found in Mediterranean shrubs like *Retama sphaeocarpa* (Pugnaire et al., 1996; Pugnaire and Lázaro, 2000). Such relationships may arise from the effects of shrub size on soil resources and microclimate, which are likely to be non-linear (Puigdefábregas et al., 1999), and on the deposition of wind- and bird-dispersed seeds (Aguiar and Sala, 1999; Herrera, 2002). Within individual shrub canopies, soil resources and microclimate show complex spatial patterns (Halvorson et al., 1994; Moro et al., 1997), and their interaction promote the apparition of different niches that increase in number and availability as shrub

Table 3

Summary of CCA models using presence/absence of understorey species data as the main matrix, and data sets based on site characteristics, patch characteristics, and species identity as constrained matrices. λ = eigenvalues for first (λ_1), second (λ_2), and third (λ_3) axis; Sum λ = the sum of all constrained axes; TVE = total variation explained (in percentage); Axis 1 = F -ratio statistic (P value) computed using the first canonical axis as reference (999 randomizations); All axes = F -ratio statistic (P value) computed using the trace or sum of all canonical axis as reference (999 randomizations)

Constraining matrix	λ_1	λ_2	λ_3	Sum λ	TVE	Axis 1	All axes
Patch characteristics (3 variables)	0.336	0.114	0.062	0.513	7.35	8.153 (0.001)	4.255 (0.001)
Site characteristics (6 variables)	0.431	0.226	0.175	1.079	15.46	10.394 (0.001)	4.816 (0.001)
Species identity (5 variables)	0.343	0.115	0.101	0.628	9.00	3.952 (0.001)	3.952 (0.001)

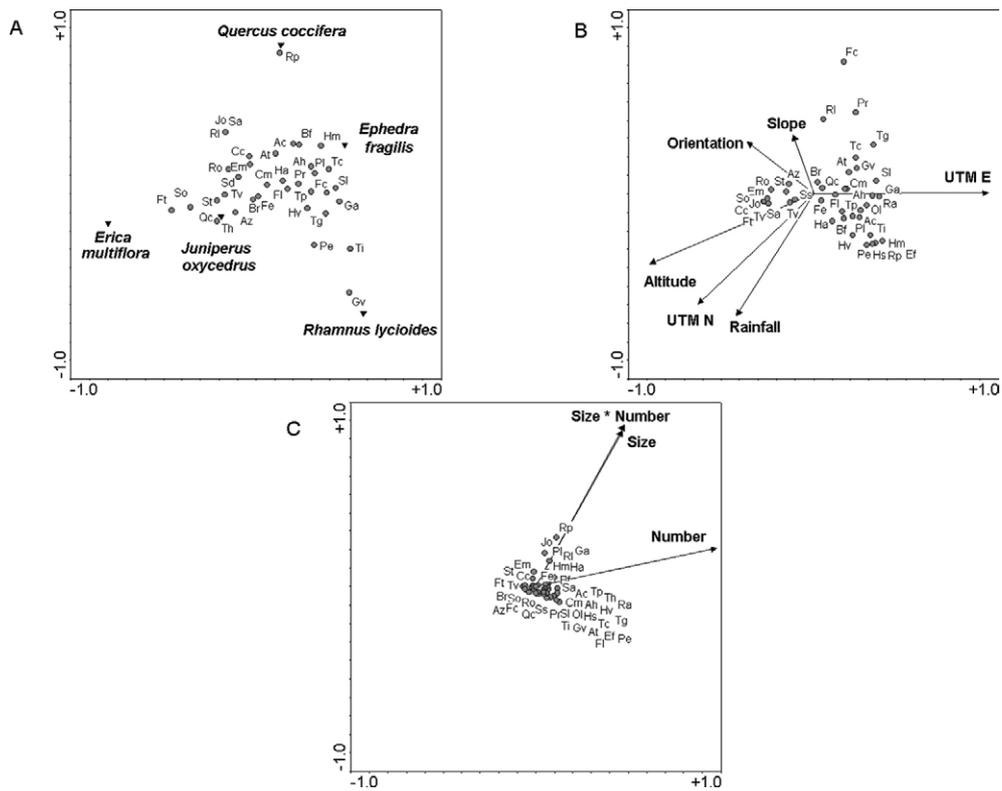


Fig. 3. First two axes of CCA ordination diagrams based on species identity (A); site characteristics (B); and patch characteristics (C). Species abbreviations are described in the Appendix 2.

size increases (Pugnaire et al., 1996). This increased habitat availability, together with the amelioration of the harsh climatic conditions typically found in semi-arid environments, favour the presence of facilitative interactions between plants (Callaway, 1995), which also increase in strength with the increase in the size of the benefactor canopy (Callaway and Walker, 1997).

The relationships species-area found agree with the general expectations of IBT, and suggest that shrubs are acting

as “islands” within a sea of grass-dominated vegetation. However, this affirmation should be treated with caution because no data from for the inter-patch zones were collected. The number of species, as well as their density and biomass, is much higher under the canopy of the shrubs than in inter-shrub areas (F. T. Maestre, personal observation), in a similar way as reported in other semi-arid environments (Vetaas, 1992). Thus, substantial differences in the relationship species-area between shrub and inter-shrub areas are likely to exist, and we expect the increase in the number of species per increase of unit area to be much higher in the former habitat.

It is interesting to note that the relationship between shrub size and species richness was not affected by the identity of the species forming the patch. We would have expected to find higher slopes in the relationships involving shrub species acting as bird perches (e.g., Juniperus and Rhamnus), which are likely to receive more seed inputs than those that do not act as perches (e.g., Erica). The lack of differences found may be due to the behaviour of birds, but also to the low proportion of zoochorous species in the steppes studied (it varied between 9 and 21% of the total number of perennial species present in the 30 m × 30 m plots). This result also suggests that, in the study area, the different sprouting shrubs may be functionally equivalent (sensu Zamora, 2002), at least regarding their effects on understorey species richness. Such an equivalence can emerge when the relevant traits driving the outcomes of the ecological interactions are common to several species (Zamora, 2002). However, as the causes and

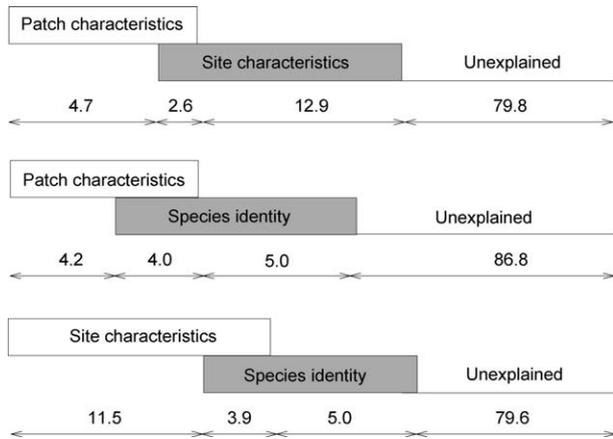


Fig. 4. Graphical summary of partial CCAs performed to quantify the amount of variation in the understorey species matrix explained by the fractions defined by the constraining matrices (represented by the bars). Overlapping fractions indicate shared explained variation. The numbers located in the bottom of each bar represent the amount of variation in the understorey species matrix explained by each fraction. All individual fractions of variation were significant ($P = 0.001$). Not drawn at scale.

shrub traits underlying the relationships shrub size-understorey richness were not specifically studied, the possible equivalence suggested by our results needs to be considered with caution.

The prevalence of site characteristics over shrub patch characteristics and identity as a determinant of observed understorey occurrences may be the consequence of the overriding role that environmental conditions play in the patterns of plant recruitment and establishment in semi-arid areas (Whitford, 2002). In Mediterranean environments, post-germination summer drought is a critical period for the establishment of perennial species, and often promote that dispersal patterns differ from those of recruitment, since favourable microsites for seed deposition and germination may not be those for seedling growth (Rey and Alcántara, 2000). Despite the dominance of site characteristics, patch characteristics and species identity accounted for significant fractions of the variation in species occurrence under the canopy of shrubs. The CCA diagrams showed that the size of shrub patches per se was related to the occurrence of late-successional species in the understorey like *Juniperus* and *Pistacia*. Thus, the presence of these fleshy-fruited species may require the presence of shrub patches of a certain size to attract birds that disperse their seeds (Herrera, 2002), which are absent in very disturbed sites. On the other hand, the lack of a clear relationship between the shrub species forming the patch and understorey conspecifics, as showed by CCAs, suggests that dispersal is a crucial process for their recruitment in semi-arid *Stipa* steppes (Rey and Alcántara, 2000).

The results presented here provide some indirect evidence that could help to understand the reasons promoting the lack of late-successional shrubs in these steppes, despite the cessation of human activities since decades (Barber et al., 1997). Maestre et al. (2001) suggest that it may be the consequence of several mechanisms, including the relative scarcity of remaining individuals, current soil and microclimate conditions, competition with established vegetation, and the lack of appropriate dispersers and dispersal sites. Recent studies demonstrate that the microsite provided by *Stipa* is able to facilitate their establishment, and that shrub establishment is not limited by current soil fertility conditions (Maestre et al., 2001,2002). The number of birds that are able to disperse shrub seeds is also usually high in semi-arid steppes (Germán López, personal communication). Based on the results obtained in this study, we hypothesise that both the lack of late-successional shrubs of appropriate size and climatic constraints are limiting the recovery of late-successional shrub vegetation in semi-arid *Stipa* steppes. New studies are needed to test this assumption, and to evaluate in more detail the dynamics of remnant shrub patches in these steppes.

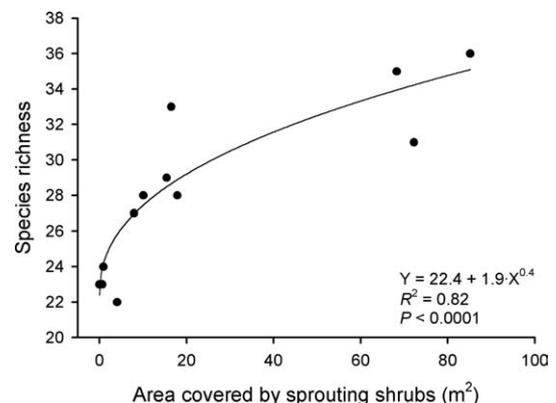
In the steppes studied, the area covered by sprouting shrubs was related to local species richness according to a power relationship (Appendix 1). It has also been recently shown that its importance as a determinant of this local richness in semi-arid *Stipa* steppes is higher than that of abiotic factors, past human impacts and ecosystem attributes like plant cover

(Maestre, 2004). Other studies have highlighted the importance of sprouting shrubs for improving ecosystem functionality and resilience, both in *Stipa* steppes (Maestre and Cortina, 2004), and in other degraded semi-arid ecosystems (Vallejo et al., 2000). Our results complement these findings, and emphasise the importance that these shrubs may have in the functioning and dynamics of semi-arid *Stipa* steppes towards their influence as reservoir of perennial species diversity. The conservation of remnant shrubs, and the increase of the number and area covered by them, should be a priority within the management of these steppes, and would help substantially to accelerate successional processes in these areas. Traditional restoration procedures carried out in semi-arid *Stipa* steppes have mostly been based on regular plantings of *Pinus halepensis* Miller performed with methods that, such as mechanically-built terraces, eliminate existing vegetation before planting (Serrada, 1990). Such a restoration should be replaced by non-aggressive techniques like those proposed by Maestre et al. (2001,2002), who suggest to use the microsite provided by *Stipa* tussocks as a suitable place for the introduction of seedlings of late-successional sprouting shrubs.

Acknowledgements

We thank J. Huesca, C. Martínez and V. Valverde for their help during fieldwork and A. Bonet, S. Hättenschwiler and two anonymous referees for discussions and improvements on earlier versions of the manuscript. This work was supported by FPU and Fulbright fellowships of the Spanish Ministerio de Educación, Cultura y Deporte awarded to F. T. Maestre and by the research project FANCB (REN2001-0424-C02-01/GLO), funded by the Spanish Ministerio de Ciencia y Tecnología.

Appendix 1. Relationships between the area covered by late-successional sprouting shrubs and the number of perennial species richness in the 30 m × 30 m experimental plots. Details of the power equation fitted appear in the lower right corner of the figure



Appendix 2. Taxa recorded under the canopy of shrub patches. Presented frequency values represent the occurrence of the species (in percentage) under the canopy of shrub patches ($n = 256$). A “Yes” in the matrix column indicates that the species is also present outside the shrub patch

Abbreviation	Full species name	Life form	Frequency	Matrix
Ac	<i>Anthyllus cytisoides</i>	Nanophanerophyte	3.5	Yes
Ah	<i>Asparagus horridus</i>	Nanophanerophyte	5.1	Yes
At	<i>Atractylis humilis</i>	Hemicryptophyte	3.1	Yes
Az	<i>Helianthemum oranifolium</i>	Chamaephyte	3.1	Yes
Bf	<i>Bupleurum fruticosens</i>	Chamaephyte	5.9	Yes
Br	<i>Brachypodium retusum</i>	Hemicryptophyte	30.5	Yes
Cc	<i>Cistus clusii</i>	Nanophanerophyte	3.1	Yes
Cm	<i>Coronilla minima</i>	Chamaephyte	2.3	Yes
Ef	<i>Ephedra fragilis</i>	Nanophanerophyte	1.2	Yes
Em	<i>Erica multiflora</i>	Nanophanerophyte	2.0	Yes
Fc	<i>Fagonia cretica</i>	Chamaephyte	2.7	Yes
Fe	<i>Fumana ericoides</i>	Chamaephyte	14.5	Yes
Fl	<i>F. laevis</i>	Chamaephyte	3.9	Yes
Ft	<i>Fumana thymifolia</i>	Chamaephyte	2.3	Yes
Ga	<i>Globularia alypum</i>	Chamaephyte	4.7	Yes
Gv	<i>Galium valentinum</i>	Hemicryptophyte	0.4	Yes
Ha	<i>Helianthemum appeninum</i>	Chamaephyte	8.2	Yes
Hm	<i>Helianthemum marifolium</i>	Chamaephyte	2.7	Yes
Hs	<i>Helichrysum stoechas</i>	Chamaephyte	0.8	Yes
Hv	<i>Helianthemum violaceum</i>	Chamaephyte	3.9	Yes
Jo	<i>Juniperus oxycedrus</i>	Mesophanerophyte	0.8	Yes
OI	<i>Osyris lanceolata</i>	Nanophanerophyte	1.2	Yes
Pe	<i>Picris echioides</i>	Hemicryptophyte	3.1	Yes
Pl	<i>Pistacia lentiscus</i>	Mesophanerophyte	4.3	Yes
Pr	<i>Phagnalon rupestre</i>	Chamaephyte	1.6	Yes
Qc	<i>Quercus coccifera</i>	Mesophanerophyte	0.4	Yes
Ra	<i>Ruta angustifolia</i>	Chamaephyte	1.2	Yes
Rl	<i>Rhamnus lycioides</i>	Nanophanerophyte	1.6	Yes
Ro	<i>Rosmarinus officinalis</i>	Nanophanerophyte	7.0	Yes
Rp	<i>Rubia peregrina</i>	Phanerophyte	0.4	No
Sa	<i>Sedum album</i>	Chamaephyte	0.8	Yes
Sl	<i>Sideritis leucantha</i>	Chamaephyte	3.5	Yes
So	<i>Stipa offneri</i>	Hemicryptophyte	21.9	Yes
Ss	<i>Sedum sediforme</i>	Chamaephyte	5.9	Yes
St	<i>Stipa tenacissima</i>	Hemicryptophyte	41.0	Yes
Tc	<i>Teucrium capitatum</i>	Chamaephyte	4.7	Yes
Th	<i>Thapsia villosa</i>	Hemicryptophyte	0.4	Yes
Ti	<i>Teucrium carolipau</i>	Chamaephyte	2.7	Yes
Tg	<i>Teucrium gnaphalodes</i>	Chamaephyte	1.2	Yes
Tp	<i>Teucrium pseudochamaeopythis</i>	Chamaephyte	2.7	Yes
Tv	<i>Thymus vulgaris</i>	Chamaephyte	12.1	Yes

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