



On the importance of patch attributes, environmental factors and past human impacts as determinants of perennial plant species richness and diversity in Mediterranean semiarid steppes

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ABSTRACT

Richness and diversity of perennial plant species were evaluated in 17 *Stipa tenacissima* steppes along a degradation gradient in semiarid SE Spain. The main objective of the study was to evaluate the relative importance of historical human impacts, small-scale patch attributes and environmental factors as determinants of perennial plant species richness and diversity in *S. tenacissima* steppes, where vegetation is arranged as discrete plant patches inserted on a bare ground matrix. Partial least squares regression was used to determine the amount of variation in species richness and diversity that could be significantly explained by historical human impacts, patch attributes, and environmental factors together and separately. They explained up to 89% and 69% of the variation in species richness and diversity, respectively. In both cases, the predictive power of patch attributes models was higher than that of models consisting of abiotic characteristics and variables related to human impact, suggesting that patch attributes are the major determinants of species richness and diversity in semiarid *S. tenacissima* steppes. However, patch attributes alone are not enough to explain the observed variation in species richness and diversity. The area covered by late-successional sprouting shrubs and the distance between consecutive patches were the most influencing individual variables on species richness and diversity, respectively. The implications of these results for the management of *S. tenacissima* steppes are discussed.

Keywords

Diversity, partial least squares regression, semiarid, species richness, steppe, *Stipa tenacissima*.

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INTRODUCTION

Recent research has emphasized the prevalent role that biodiversity has for the proper functioning of Earth's ecosystems, as well as its intrinsic value (Ghilarov, 2000; Loreau *et al.*, 2001). Thus, understanding those factors affecting plant species richness and diversity is a crucial issue in current ecology and conservation biology. Efforts to determine the relationships between species richness and environmental attributes have substantially increased over the past decade, and nowadays there is a growing body of knowledge on the topic (e.g. Heikkinen, 1996; Pausas & Austin, 2001; Schaffers, 2002). Due to the multiple set of factors involved, it is important to follow a multivariate approach to understand patterns of plant species richness and diversity for a given ecosystem (Waide *et al.*, 1999). However, studies evaluating the dynamics of species richness and diversity over gradients

involving two or more environmental variables are not very common (Austin *et al.*, 1996; Pausas & Austin, 2001; Le Brocque & Buckney, 2003).

Environmental factors such as soil nutrient content, slope, aspect, and altitude have been shown to exert an important control on species richness and diversity on a great variety of ecosystems (El Ghani Monier, 1998; Schaffers, 2002; Le Brocque & Buckney, 2003). In addition to these factors, disturbances due to human activities may exert a strong influence on species richness and diversity patterns (Petraitis *et al.*, 1989). Incorporation of human impacts when assessing the determinants of species richness and diversity, despite its difficulty, is necessary (Waide *et al.*, 1999). The impact of human activities on ecosystem structure and processes may last for centuries and even millennia (Bruun *et al.*, 2001; Dupouey *et al.*, 2002). Thus, the evaluation of past human impacts may be especially important in areas where

human populations have been controlling ecosystem trajectories for centuries. Despite the importance of arid and semiarid ecosystems in global terms, and the relatively high levels of plant species richness and diversity that contain (Le Houérou, 2001), there is a lack of studies dealing with the relative importance of historical human impacts as determinants of species richness and diversity in these areas.

In the last decade we have assisted to an impressive development of biodiversity research (Loreau *et al.*, 2001). However, the relative importance of variables such as environmental factors, disturbance, and patch attributes as determinants of species richness and diversity, all of them affecting these ecosystem properties by separate (Bascompte & Rodríguez, 2001; Cardinale & Palmer, 2002; Le Brocque & Buckney, 2003), is still poorly known. With the aim of contributing to fill this gap, this study evaluates the importance of human impacts, patch attributes, and environmental factors as determinants of perennial plant species richness and diversity in semiarid steppes dominated by the perennial tussock grass *Stipa tenacissima* L. These steppes constitute one of the most representative vegetation types in the driest areas of the Mediterranean Basin, where they cover over 2.8 million ha (Le Houérou, 2001). *Stipa tenacissima* steppes result from the degradation of Mediterranean open forests and shrublands in N Africa and SW Europe, respectively (Rivas Martínez, 1987; Le Houérou, 2001), by human activities like grazing, harvesting, and repeated burning, which have been occurring in these steppes since millennia (Barber *et al.*, 1997). Thus, they can serve as a useful model to evaluate the effect of historical human impacts on current plant species richness and diversity, and to evaluate their relative importance against patch attributes and environmental factors, two major determinants of

ecosystem functioning and biodiversity in semiarid environments (Aguiar & Sala, 1999). Previous studies have described the floristic composition of *S. tenacissima* steppes (Aidoud, 1990; Aidoud & Touffet, 1996; Hensen, 1999), and related it to soil properties and bioclimatic characteristics (Costa *et al.*, 1988; Hanifi-Halima & Loisel, 1997). However, none of them has evaluated the importance of past human impacts, patch attributes and environmental factors as determinants of present-day species richness and diversity in these ecosystems.

METHODS

Study area

Our study was conducted at 17 experimental sites located in the provinces of Alicante and Murcia, in SE Spain (Table 1). Site selection was performed according to three criteria: (i) to capture a wide range in degradation status (ii) to capture the rainfall variability, and (iii) to reduce between-site variability associated with vegetation type, slope aspect and soil type. All the sites were located in South-facing slopes, with slopes varying between 4° and 29°. They share soil type (*Lithic Calciorthid*; Soil Survey Staff, 1990) and climate (Mediterranean semiarid; FAO, 1989), with average annual precipitation and temperature values ranging from 212 to 388 mm, and from 16 to 18 °C, respectively. Vegetation in the study system is arranged as a two-phase mosaic of discrete plant patches inserted on a bare ground matrix (see Appendix S1 in Supplementary Material). It is dominated by *S. tenacissima*, with late-successional shrubs, such as *Quercus coccifera* L., *Rhamnus lycioides* L. and *Pistacia lentiscus* L., present at the less degraded sites. At the more degraded sites these shrubs

Table 1 Environmental factors, species richness and diversity of the experimental sites. ELE = elevation (m above sea level), RAI = Mean annual rainfall (1960–90; Pérez, 1994), ASP = Aspect (°), SLO = Slope (°), UTM = UTM co-ordinates, SPE = Species richness, DIV = Species diversity (Shannon's H index, bits)

Site*	ELE	RAI	ASP	SLO†	UTM	SPE	DIV†
Aguas (Ag)	441	387.7	168	13.6 ± 0.4	731431 E 4267459 N	31	1.7 ± 0.2
Albatera (Al)	355	277	228	24.8 ± 0.6	683000 E 4235820 N	34	2.0 ± 0.1
Campello (Ca)	349	220.2	140	14.8 ± 0.8	728411 E 4264059 N	28	0.9 ± 0.1
Colomina (Co)	726	315.4	198	9.8 ± 0.3	692176 E 4273892 N	35	1.1 ± 0.2
Etasa (Et)	205	385.7	290	23.5 ± 0.9	720469 E 4261970 N	22	0.8 ± 0.1
Finestrat (Fi)	212	317.7	160	22.8 ± 0.6	745052 E 4271046 N	27	1.5 ± 0.1
Foncalent1 (Fn)	80	301.5	220	4.4 ± 0.2	712879 E 4245495 N	24	0.8 ± 0.1
Foncalent2 (Ft)	63	301.5	100	23.5 ± 0.3	713572 E 4246605 N	23	0.8 ± 0.1
Fortuna (Fo)	99	294	220	14.1 ± 0.7	666166 E 4215166 N	16	1.2 ± 0.1
Jijona (Ji)	240	385.7	180	24.8 ± 0.3	720312 E 4263831 N	23	1.0 ± 0.1
La Nuzza (Ln)	102	220.2	160	27.8 ± 0.6	730961 E 4260414 N	23	0.9 ± 0.2
Marquesa (Ma)	85	220.2	178	23.8 ± 0.3	727972 E 4259533 N	22	0.7 ± 0.04
Palomaret (Pa)	540	302.2	190	23.5 ± 1.8	703116 E 4261639 N	28	1.6 ± 0.1
Peñarrubia (Pe)	769	369.1	180	22.5 ± 0.3	690160 E 4273578 N	36	1.3 ± 0.1
Relleu (Re)	395	387.7	125	10.8 ± 0.3	735591 E 4269506 N	33	1.4 ± 0.1
Ventós1 (Ve)	468	302.2	270	26.3 ± 0.6	707768 E 4259748 N	28	1.3 ± 0.1
Ventós2 (Vn)	550	302.2	240	24.5 ± 0.3	707506 E 4260684 N	29	1.1 ± 0.2

*The code in brackets is the name given to the experimental site in Fig. 1. †Mean ± SE ($n = 4$).

are replaced by others like *Artemisia herba-alba* L. and *Salsola genistoides* L. Both species composition and vegetation structure of the experimental sites is representative of semiarid *S. tenacissima* steppes (Costa *et al.*, 1988).

Field survey

Within each site, a 30 m × 30 m plot starting on the upper edge of the hillslope was located. All perennial species within this plot were counted, and it was used as my estimator of species richness. Only perennial species were considered because the occurrence of annual plants in *S. tenacissima* steppes is generally very variable both seasonally and annually. At each site a 24-m transect starting in the upper left corner of the plot was established along the contour. Four 30-m parallel transects, separated by 8 m, were run perpendicular to and down slope from the 24-m transect for the estimation of perennial plant species diversity using Shannon's diversity index (H, Greig-Smith, 1983). It was estimated by using the point sampling method, with a sampling frequency of 50 cm along each 30-m transect. These transects were also used to sample patch attributes. According to Tongway & Hindley (1995), I considered as a patch those long-lived features that are able to retain water, sediments, and seeds coming from runoff fluxes, and that are surrounded by bare ground soil. In the study area, patches include *S. tenacissima* tussocks, other herbaceous species, shrubs, and dead shrub branches resting in the soil surface. In each transect a continuous record of patch and interpatch zones was collected; when a patch was located, its width at right angles to the transect line was measured. Clumps of grasses, or of grasses and small shrubs growing closely together or connected with litter bridges were considered as a single patch (Tongway & Hindley, 1995). The variables used to describe patch attributes were: patch width density (m/10 m of transect), number of patches (n/10 m of transect), cover of patches (%) and average distance between consecutive patches (m). The area occupied by sprouting shrubs (*P. lentiscus*, *Q. coccifera*, *R. lycioides*, *Ephedra fragilis* Desf., *Erica multiflora* L., and *Juniperus oxycedrus* L.), which are expected to be remnants of mature shrubland vegetation (Rivas Martínez, 1987), was also included as another patch attribute. The maximum crown diameter in the horizontal direction, and the diameter orthogonal to this, were measured in each individual shrub; with these data shrub size was estimated as the volume of an ellipsoid. Individual areas were summed to obtain the total cover of sprouting shrubs at each 30 m × 30 m plot.

The following abiotic variables were also measured at each plot: altitude, slope, aspect, soil organic matter at 0–10 cm depth, mean annual rainfall, and UTM co-ordinates. The altitude and UTM co-ordinates were obtained *in situ* with a Global Positioning System device. The slope and aspect were obtained with a clinometer and a compass, respectively. The mean annual rainfall and temperature (1960–90 period) were obtained from the nearest meteorological station according to the database provided by Pérez (1994). Soil organic matter was estimated with the loss-on-ignition method after burning in a furnace for two hours at 550 °C.

Assessment of human impacts

The fibre from *S. tenacissima* has great strength and flexibility, and for this reason has been used for making ropes, sandals, baskets, mats, and other durable articles (Barber *et al.*, 1997). It has also been widely used to produce high quality paper, especially in the United Kingdom (American Paper & Pulp Association, 1965). In Spain there are historical records on the use of *S. tenacissima* by humans as early as 3500 BC. The intensification started during the occupation of the Iberian Peninsula by the Carthaginians (480 BC) and, with differences in the intensity of this use over different historical periods, lasted until the 1960s. At this time, the rapid industrialization of the country promoted a drastically cessation of human activities in *S. tenacissima* steppes (Barber *et al.*, 1997).

I used the following variables as surrogates of past human impacts on the experimental sites: human population in the nearest town at several historical periods (1787, 1887 and 1950), distance to the nearest town, and distance to the nearest traditional road. Population dates were selected because they represent the first modern census available in Spain (1787), and two moments of special human pressure on *S. tenacissima* steppes in the study area, due to the lack of woody fuel (1887) and to the socio-economic situation following the Spanish Civil War (1950) (Servicio del Esparto, 1950; López *et al.*, 1992). Both the distances to the nearest town and to the nearest traditional road (pathways used to drive the livestock and to have access to rural areas with century-long use; Pérez & Terés, 1991) were used as indices of the likelihood of local population having access to the study sites.

Population data for each of the three periods were obtained from official statistics (Anonymous, 1889; Instituto Nacional de Estadística, 1987, 2003). The distances to the nearest town and to the nearest traditional road were obtained using digitized maps at scale 1:50,000 available from the Regional Government (Anonymous, 1998). The UTM co-ordinates of the nearest city and traditional road were obtained for each site using the digitized cartography. From these, and the UTM co-ordinates of the experimental plots obtained with the GPS, the Euclidean distance between each experimental site and both the nearest city and traditional road was calculated.

Statistical analyses

To evaluate the importance of patch attributes, environmental factors, and human impacts as determinants of present-day species richness and diversity, I used partial least squares regression (PLS). PLS is a regression calibration technique that is useful when there are few replicates, many predictors or when predictors show high collinearity (Næs & Martens, 1989). PLS reduces a set of explanatory variables into a few components that have maximum covariance with the dependent variable. To determine the number of PLS components to be included in the model, a cross-validation procedure is performed. PLS is run as many times as there are observations in the data set (n), leaving out one observation in turn. The regression model based on the $n - 1$

observations is used to predict the value of the response variable in the excluded observation. The sum of squares of differences between these 'leave-one-out predictions' and the observed values of the dependent variable produce the root mean square error (RMSE). The lower the RMSE, the higher the predictive power of the PLS model. To select the number of significant components to be included in the model, I followed the cross-validation test described in Umetrics (2002).

I performed separate PLS analyses for species richness and diversity as dependent variables, but using in both cases three matrices: patch attributes, environmental factors and human impacts. With the aim to evaluate how the predictive power of each matrix was modified by the presence of the other matrices, additional analyses were performed with pairs of matrices and with the sum of the three matrices. The latter analysis was also used to evaluate the relative importance of individual variables as predictors of species richness and diversity. In this analysis, the variable influence (VIP) is computed as described in Umetrics (2002). Explanatory variables with VIP values larger than one are the most relevant for explaining the variation observed in the dependent variable.

Prior to PLS analyses, I transformed explanatory variables in order to achieve normality on their frequency distributions. The area covered by sprouting shrubs, the distance between consecutive patches, and the distance to the nearest traditional road were log transformed. For the first variable, a constant (1) was added to the original value before transformation. The number and cover of patches were transformed with a power function (x^3); slope was also transformed with a power function (x^4). Population data could not be fitted to a normal distribution after several transformations, and were not transformed. The other explanatory variables, and the dependent ones, were not transformed because they were normally distributed (Kolmogorov-Smirnoff test; $P > 0.05$). The relationships between the explanatory variables used in PLS analyses were evaluated with correlation analysis. Since some variables were not normally distributed, the Spearman rank correlation coefficient was used. Significance values were corrected for the number of paired comparisons by using the procedure described in Hochberg (1988). Due to the high number of comparisons (136) and to the low number of replicates (17), I used a significance level of $\alpha = 0.10$ in these analyses. All PLS analyses were performed with both dependent and explanatory variables centred and standardized (Umetrics, 2002) using the software SIMCA-P for Windows, version 10.0.2 (Umetrics AB, Umeå, Sweden). Data transformations and correlation analyses were performed with the software SPSS for Windows 9.0 (SPSS Inc, Chicago, IL, USA).

RESULTS

Perennial species richness and diversity ranged from 16 to 36 species, and from 0.7 to 2 bits per 30 m × 30 m plot (Table 1). The experimental sites showed important differences in all the evaluated patch attributes (Fig. 1). Correlation analyses indicated the relationships between the variables defining patch attributes, environmental factors and human impacts (see

Table 2 Summary of PLS models fitted to perennial species richness and diversity. The number of significant PLS components (N), the mean square error of prediction (RMSE), and the coefficient of determination (R^2) are shown for each model

Dependent variable	Matrix of explanatory variables	N	RMSE	R^2
Species richness	Environmental factors (EF)	1	3.423	0.634
	Patch attributes (PA)	2	2.420	0.829
	Human impacts (HI)	1	4.330	0.415
	EF + PA	1	2.588	0.791
	EF + HI	1	3.432	0.632
	PA + HI	2	2.237	0.854
	EF + PA + HI	2	1.961	0.888
Diversity	EF	*	—	—
	PA	2	0.215	0.685
	HI	*	—	—
	EF + PA	1	0.254	0.530
	EF + HI	*	—	—
	PA + HI	2	0.212	0.694
	EF + PA + HI	1	0.260	0.505

*The PLS model was not significant ($P > 0.05$).

Appendix S2 in Supplementary Material). Significant relationships were found between the number of patches and the average distance between consecutive patches (-0.74), and between their cover and width (0.89). The area covered by sprouting shrubs was related to elevation (0.83), and rainfall showed a positive correlation with the UTM North co-ordinate (0.70). The population at the different periods was highly correlated (correlation coefficients ranging from 0.79 and 0.92). The population in 1950 was negatively correlated with the cover of patches (-0.75), and positively correlated with the distance to the nearest town (0.79), as was the population in 1787 (0.76).

PLS analyses showed how the three evaluated matrices were able to explain significant amounts of the variation found in species richness (Table 2). The predictive power of the model consisting of patch attributes was quite high ($R^2 = 0.83$), and was higher than that of the models consisting of abiotic characteristics ($R^2 = 0.63$) and variables related to human impacts ($R^2 = 0.42$). When patch attributes were included, the inclusion of abiotic characteristics and human impacts slightly reduced and increased the predictive power of the model, respectively. However, the most parsimonious PLS model for species richness was that consisting of the three matrices together. Only PLS models consisting of patch attributes were able to explain significant amounts of the variation observed in species diversity (Table 2). The most parsimonious PLS model for this variable was that consisting of patch attributes and human impacts. The addition of environmental factors to this model increased its prediction error and reduced its predictive power.

The percentage of the total area covered by sprouting shrubs was the variable that most influenced species richness (Table 3). This area was positively related to species richness, as was elevation, the UTM North co-ordinate and the total cover of patches. Variables related to human population at the different historical

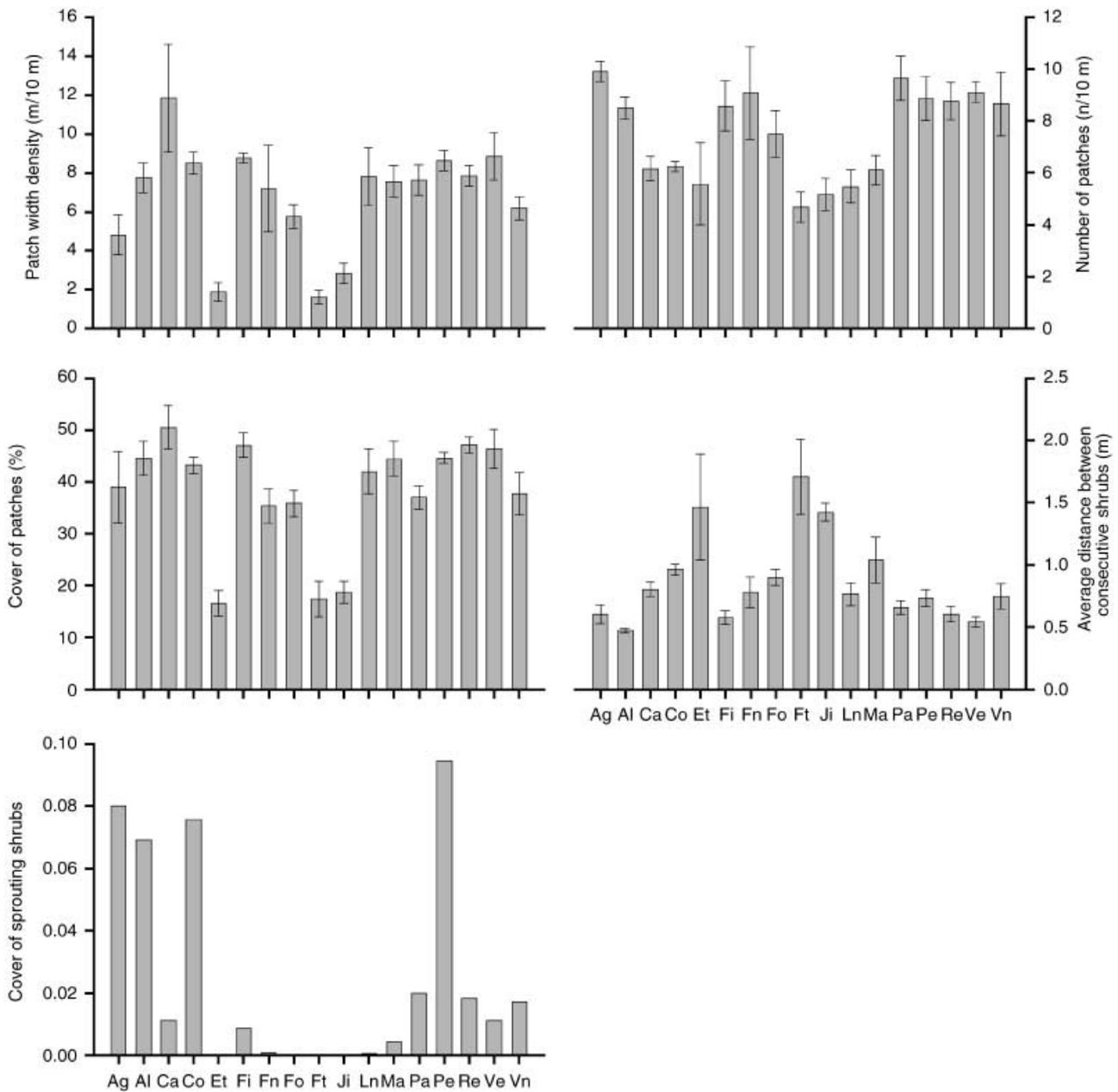


Figure 1 Patch attributes of the experimental sites. Patches include *S. tenacissima* tussocks, other herbaceous species, shrubs, and dead shrub branches resting in the soil surface. In all cases except the area covered by sprouting shrubs, data represents means \pm SE ($n = 4$). Abbreviations of the experimental sites correspond to those presented in Table 1.

periods evaluated were among the most influencing variables, and were negatively related to species richness. The distance between consecutive patches was the variable that most influenced diversity, and was negatively related to it. The number of patches and the percentage of the total area covered by sprouting shrubs were the variables following in importance, and were positively related to diversity. It is interesting to note that environmental factors such as slope and organic matter were not included among the most influencing variables by the PLS models fitted to both species richness and diversity.

DISCUSSION

The significant correlations found between the explanatory variables, and the low number of replicates compared to the number of explanatory variables available in the data set employed, justify the use of PLS in this study. The high correlation found between population variables is expected, as well as the correlation between some patch attributes like the number and the average distance between two of them. The positive correlation between rainfall and the UTM North co-ordinate reflects the latitudinal

Dependent variable	Explanatory variable	VIP	Coefficient
Species richness	Area covered by sprouting shrubs	1.724	0.245
	Elevation	1.561	0.221
	Population in 1887	1.171	-0.100
	Population in 1950	1.155	-0.087
	Population in 1787	1.130	-0.109
Diversity	UTM North co-ordinate	1.067	0.069
	Distance between consecutive patches	2.087	-0.187
	Number of patches	1.948	0.174
	Area covered by sprouting shrubs	1.873	0.168
	Elevation	1.197	0.107

Table 3 Influence (VIP) and coefficient of the variables used in the PLS model with species richness and diversity as dependent variables and all the variables from the three matrices (abiotic characteristics, patch attributes and human impacts) as explanatory ones. Only the most influencing variables (VIP > 1) are shown

variation of rainfall in the study area (Pérez, 1994). Among the correlations that were significant, that between elevation and the area covered by sprouting shrubs is the most noticeable, since the altitudinal range evaluated does not limit the distribution of any of the sprouting shrubs measured in the study area (Rivas Martínez, 1987). The underlying causes of this relationship can not be elucidated from this study; it may be the consequence of complex interactions between small-scale differences in climate, land-use history, vegetation structure, and composition of faunal communities, which play a prevalent role on the dispersion of these species (Herrera, 2002).

Determinants of species richness and diversity

The results obtained suggest that patch attributes are the most important determinant of species richness and diversity in semiarid *S. tenacissima* steppes. The prevalence of these attributes agrees with previous studies showing a positive relationship between patch attributes like number, size and size heterogeneity and woody species richness in prairie ecosystems (Bascompte & Rodríguez, 2001). In semiarid environments, discrete plant patches modify the availability of resources as compared to the surrounding bare ground matrix. Plant patches have high soil nutrient contents and microbial activity, ameliorate harsh climatic conditions, improve soil moisture conditions, and may also provide shelter against herbivores (Callaway, 1995). In addition, they trap seeds transported during runoff events, blown by wind, or deposited by birds, and provide 'safe sites' for seed germination and seedling establishment (Aguar & Sala, 1999; Montaña *et al.*, 2001). All these processes lead to the prevalence of positive interactions between plant species within the patches (Callaway, 1995), which are of great importance in the establishment and maintenance of species diversity at higher spatial scales (Naeem *et al.*, 2002). The results presented here suggest that facilitation could be an important force driving species richness in semiarid steppes, but can not provide direct evidence for this.

Within variables defining patch attributes, the area covered by late-successional sprouting shrubs showed a positive relationship with both species richness and diversity, and was the most important explanatory variable for the former. These findings suggest that sprouting shrubs are playing a key role in maintain-

ing plant species richness in *S. tenacissima* steppes at the plot scale, despite their low cover in absolute terms (Fig. 1). They also complement previous studies showing a significant and positive relationship between individual shrub size and perennial understorey species richness in semiarid areas (Pugnaire & Lázaro, 2000). As discussed above, facilitative mechanisms may mediate the relationship found between species richness and the area covered by sprouting shrubs. Particular features of shrubs that could foster such facilitative interactions include their role as frugivorous birds feeders, the high levels of soil resources usually found under its canopy, and the improvement of harsh environmental conditions through shrub canopy shading (Moro *et al.*, 1997; Herrera, 2002). The distance between consecutive patches was the most important explanatory variable for species diversity, followed in importance by the number of patches. It has been already mentioned the role of plant patches as 'safe sites' for seed germination and seedling establishment, as well as the prevalence of facilitative interactions within them. In addition, seed dispersal and establishment in semiarid areas with sparse plant cover, and in *S. tenacissima* steppes, decrease with the distance to seed sources, which are also concentrated in plant patches (Gasque, 1999; Montaña *et al.*, 2001). The negative effect of increasing the distance between consecutive patches on species diversity may be mediated by local seed dispersal limitations. They are likely to occur in *S. tenacissima* steppes given the dispersal characteristics of the species that contain (Hensen, 1999), and to the short runoff lengths typically found in these steppes (Puigdefábregas *et al.*, 1999). Similar negative effects on species diversity may be achieved by reducing the number of patches, which reduces both the amount of seed sources and of suitable sites for seed germination and seedling establishment.

PLS analyses suggest that environmental factors alone explain a substantial amount of the variation observed in species richness. Among the variables included in this group, elevation was the most important and showed a positive relationship with species richness. The results obtained here agree with previous studies showing the importance of altitude as a predictor of plant species richness over a wide variety of ecosystems at higher spatial scales (Srutek & Kolbek, 1994; Heikkinen, 1996). However, and given the relatively small altitudinal gradient evaluated (~700 m), it is likely that the relationship found may be promoted by small-scale changes in climate associated to elevation.

It is also interesting to note that elevation showed a high correlation with the area covered by sprouting shrubs, the most influencing variable explanatory variable. Despite the wide differences in slope among the study sites (4–29°), this variable was not selected among the most important predictors of species richness and diversity. This was initially unexpected due to the prevailing role of slope as a controlling factor of soil moisture content in semiarid areas (Gómez-Plaza *et al.*, 2001), which ultimately affects species richness (El Ghani Monier, 1998; Pausas & Austin, 2001). The results obtained suggest that soil moisture is not an important driver of species richness in the study area or, most likely, that other site features like patch attributes may override gravity effects in controlling soil moisture and their possible effects on species richness (Puigdefábregas *et al.*, 1999). The lack of importance of rainfall is also noticeable, and may be due to the fact that our climatic database failed to reflect accurately the variation in rainfall at local scale.

Past human impacts explained a significant amount of the variation observed in species richness, although its importance was lower than that of patch attributes and environmental factors. The lack of significant correlations between surrogates of these impacts and the most influencing variables defining patch attributes, and the increase in the predictive power of PLS models already containing patch attributes and environmental factors when adding past human impacts, suggest that such impacts are constraining present-day species richness and diversity in semiarid *S. tenacissima* steppes. As far as I know, the results presented here provide the first evidence of the importance of historical human influence as a determinant of current species richness and diversity in semiarid ecosystems. They also agree with previous studies showing the importance of such influence as a determinant of current plant species richness in temperate steppes and woodlands (Peterken & Game, 1984; Honnay *et al.*, 1999; Bruun *et al.*, 2001). Historical human influence on present ecosystem structure and function may have been largely underestimated, given the large areas influenced by human activities in the past that support now unmanaged seminatural ecosystems. The results presented here and those from previous studies suggest that past human impacts are relevant to current species richness and diversity, and should be considered when evaluating determinants of biodiversity in ecosystems located in areas supporting human populations for centuries. However, in practice is often difficult to obtain accurate estimators of past human impacts due to the lack of detailed and quantitative historical information, especially at scales such as employed in this study. The approach followed has several drawbacks that merit some discussion. It is very difficult, if not impossible, to know if all the important variables related to human impacts are available for analysis (Bruun *et al.*, 2001). It is also very difficult to obtain reliable information on punctual impacts (e.g. a human-induced fire or an episode of illegal fibre cropping) that may affect ecosystem structure and function for centuries, and which are not usually registered in the available written sources. The direct causes underlying the effects of past human impacts on current species richness and diversity in *S. tenacissima* steppes can not be elucidated from the results obtained in this study. However, I hypothesize that a major influ-

ence of such impacts in current species richness and diversity has been the progressive elimination of late-successional shrubs by activities like wood harvesting for fuel and repeated burning to avoid shrub competition with *S. tenacissima* and to encourage its growth (Barber *et al.*, 1997). As discussed above, sprouting shrubs may be acting as keystone species (*sensu* Naeem *et al.*, 2002) regarding the maintenance of species richness in semiarid *S. tenacissima* steppes, and their elimination in ancient times may still be constraining current species richness and diversity.

Implications for the management of semiarid *Stipa tenacissima* steppes

Results show that the area covered by late-successional shrubs is a key determinant of species richness in degraded *S. tenacissima* steppes. Thus, the conservation of remaining shrub patches, and the increase of their area, should gain priority in management to maintain and enhance plant biodiversity in these ecosystems. Among the actions that could be taken to increase late-successional shrub cover, planting of seedlings of species like *P. lentiscus*, *R. lycioides* and *Q. coccifera* seem the most efficient (Maestre *et al.*, 2003). These plantings should take advantage of shrub seedling establishment facilitation by *S. tenacissima* tussocks (Maestre *et al.*, 2001), and thus seedlings should be introduced in the microsite provided by *S. tenacissima*. An increase in the cover of late-successional shrubs would not only be a useful management tool to maintain and increase plant biodiversity in *S. tenacissima* steppes. It would also help to increase overall ecosystem resilience against disturbances such as grazing and fire (Lloret & Vilà, 1997), to improve soil nutrient status (Caravaca *et al.*, 2003), and to provide suitable habitat and food for a great number of wild and game animals, especially birds (López & Moro, 1997).

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI057/DDI057sm.htm>

Appendix S1. View of two experimental sites.

Appendix S2. Matrix of Spearman rank correlation coefficients between the explanatory variables.

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