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Shrubs as a source of spatial heterogeneity —the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain

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ABSTRACT

The processes underlying the positive effect exerted by woody species on other plant species can be grouped into a physical effect due to the canopy itself (mainly amelioration of temperature and light extremes), and an edaphic effect (nutrient enrichment). Both groups of effects are present in the savanna-like systems originated by *Retama sphaerocarpa* in the Iberian Peninsula. The consequences of these shrubs for the spatial heterogeneity induced in the herbaceous community are not well known. The herbaceous community was sampled by means of radial transects around 20 adult shrubs, from the canopy centre to the open areas among the shrubs, both northwards and southwards. Floristic composition, diversity and pasture mean height change both along the inside–outside gradient, and from north to south. As a nutrient enriched environment, the centre of the understorey showed the lowest species richness and evenness, and the highest standing crop. In contrast, the environmentally stressful open areas showed the highest number of species and evenness, and the lowest standing crop. This general effect is only partially due to nutrient availability, and is not homogeneous around the shrub, as open area conditions penetrate into the understorey driving the herbaceous community towards that of open areas. An individual shrub effect is also suggested by our results. Different conditions are thus provided by *R. sphaerocarpa* understoreys, favouring different subsets of species from the general pool, and therefore defining shrub canopies as sources of spatial heterogeneity in the whole savanna-like system.

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1. Introduction

Pastures in the Mediterranean Basin, mainly dominated by annual species, are reported to have high diversity (Naveh and Whittaker, 1979; Rey Benayas and Scheiner, 2002). Spatial heterogeneity at different scales, from landscape to com-

munity patch, is at the core of this phenomenon (Blondel and Aronson, 2000). Besides historical climatic fluctuations and its transitional biogeographical situation, Marañón (1986) highlighted the importance of the complexity of mountain relief, the historical human disturbance and herbivory. Climatic variability also contribute to the coexistence of so many species (Espigares and Peco, 1995). Human transformation of Mediterranean forests into savanna-like systems for domestic herbivores could be one of the main processes involved in the genesis of spatial heterogeneity at an

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ecosystem scale. The opening of dense forests would turn the formerly continuous understorey conditions into a mosaic of open pasture and understorey conditions (where trees were preserved), thus increasing spatial heterogeneity due to the intermingling of situations.

In arid and semiarid ecosystems, trees and shrubs are known to exert an important influence upon the herbaceous layer (Vetaas, 1992; Belsky and Canham, 1994). Their deep roots exploit great volumes of soil in search of water and nutrients, which are accumulated and afterwards released into their surroundings (Belsky et al., 1989; Frost and Edinger, 1991; Rhoades, 1997). Additionally, hydraulic lift (Emerman and Dawson, 1996), rainfall concentration via stemflow (Haworth and McPherson, 1995), and microclimatic amelioration (Jackson et al., 1990; Ko and Reich, 1993), contribute to a higher microbial activity (Rhoades, 1997), making the understorey of woody species a site of high nutrient availability. Many plant and animal species take refuge in these sites (Archer et al., 1988), providing easily decomposable material that enhances the effects of woody plants. For these reasons they are usually known as 'fertility islands' (García-Moya and McKell, 1970).

The herbaceous layer responds to the spatial heterogeneity introduced by the woody plants adapting its species composition and abundance to the wide variety of microenvironments created (Pieper, 1990; Fuhlendorf and Smeins, 1997), often resulting in high beta-diversity (McNaughton, 1983; Belsky and Canham, 1994). Wild and domestic herbivores can further enhance the spatial heterogeneity, favouring some species and decreasing the abundance of others by differential consumption and dispersal. Their habitat selection also plays an important role in both ecosystem function and heterogeneity maintenance, via redistribution of nutrients in faeces (Gómez Sal et al., 1992; De Miguel et al., 1997).

These processes have been traditionally studied in the Mediterranean Basin savanna-like systems ('dehesas'), showing the effect of *Quercus* tree species upon the associated pastures: there is a sharp contrast both in species composition and soil fertility between open spaces and the internal regions of the understorey (González Bernáldez et al., 1969; Montoya and Mesón, 1982; Marañón and Bartolome, 1993). More recently, the effects of another woody species, the leguminous shrub *Retama sphaerocarpa* (L.) Boiss., have been studied. Besides quantifying the microclimatic and nutrient enrichment effects, and the associated increase in understorey vegetation productivity, Pugnaire et al. (1996a, b) and Moro et al. (1997a, b) show how this increase benefits the shrub, making the interaction reciprocally positive or mutualistic. Pugnaire and Lázaro (2000) also detected a change in the floristic composition of the herbaceous community from the centre towards the canopy border.

However, *R. sphaerocarpa* shrublands are savanna-like systems composed of a variable number of shrubs scattered in an herbaceous matrix (Gómez Sal et al., 1999), and in this context the spatial heterogeneity induced by shrub canopies is not well known. In a previous work López-Pintor et al. (2003) showed the different floristic composition of soil seed banks from the centre of shrub understoreys towards the open spaces among them. However, many factors besides initial floristic composition are involved in determining final

community structure, and they may change not only along a distance gradient, but also from north to south due to the asymmetry in solar radiation. The spatial integration of different-sized and potentially asymmetric patches would show an herbaceous layer with relatively high β -diversity.

Our objectives are to study the effect of *R. sphaerocarpa* canopy: 1) on soil properties, from the shrub centre to the open, and from the north to the south side; 2) on the herbaceous community changes induced along the entire gradient from the open spaces to the centre of the shrubs, and from the north to the south side; and 3) on the extent to which the changes in soil properties are related to the changes in the herbaceous community.

2. Material and methods

2.1. Study site

The study site was located in Uceda (Central Spain, 40°50'N, 3°27'W). Climate is continental Mediterranean, with mean annual temperature and precipitation of 13 °C and 500 mm, respectively. The study site is situated in a series of alluvial terraces where the former vegetation was Mediterranean woodland dominated by *Quercus ilex*, *Juniperus oxycedrus* and *Q. faginea*. These terraces were used as croplands and a source of wood by the nearby villages until they were acquired by the Spanish Army in 1981, when all traditional uses ceased. Since then, these old-fields have been recolonised mainly by *R. sphaerocarpa* (L.) Boiss., but also by *Q. ilex* and *J. oxycedrus*.

2.2. Sampling design

In the spring of 1997, 20 shrubs of similar size (mean diameter 340 cm, mean height 246 cm) were selected in a 0.7 ha old-field, with the north-south direction free from the influence of the nearby shrubs. For each individual, two radial transects were laid out from the canopy centre outwards, to the north and the south sides. Four positions were considered: inner, intermediate, border and completely outside the shrub understorey. In each position, one 25 × 25 cm quadrat was used to survey the percentage cover of every plant species. Maximum and mean heights of the herbaceous layer were also measured. Occasionally two quadrats were used at the intermediate position if the shrub size and shape suggested so, one nearer to the inner position, the other towards the border quadrat. A 10 × 10 cm soil sample, 8 cm deep, was taken from each quadrat to analyse the following soil variables: proportion of sand, silt and clay (Robinson pipette); pH; organic matter content (Walkley-Black method); total N (Kjeldahl method); P and K (Égner-Riehm method); and Na, Ca and Mg (percolation with ammonium acetate 1 N). Thirty-eight additional 50 × 50 cm quadrats were laid out in the old-field herbaceous matrix, as a further reference for no shrub conditions. The same data were obtained from them, including soil samples of identical characteristics. They were ranked according to their distance to each selected *Retama* individual for representation purposes.

2.3. Statistical analyses

To characterise the herbaceous community, a correspondence analysis (CA) was performed on the whole herbaceous species presence/absence data set to get a synthetic variable describing floristic composition. Species richness (S), Shannon–Weaver index (H') and evenness (E, derived from Shannon index) were also calculated for the radial transects data set. Mean height of the herbaceous layer was used as an indicator of standing crop. In addition, a principal components analysis (PCA) was performed upon the soil variables data set to obtain a synthetic variable to be used in further analysis.

A series of ANOVAs was performed to ascertain the effect of distance to canopy centre upon soil properties. Distance profiles were constructed for both floristic and soil gradients (CA and PCA first axes, respectively) according to sample position in relation to shrub centre to compare the pattern of change along them, and ascertain where the main discontinuities occurred. The hypothesis of spatial heterogeneity in the herbaceous community induced by aspect and distance to *R. sphaerocarpa* individuals was tested by means of a multivariate analysis of covariance on the variables floristic composition (CA first axis), S, H', E, and pasture mean height. Given the parallel effects on soil properties (see Section 3), that could be the real driving factor in the observed changes, the edaphic gradient (first PCA axis) was used as covariate in the

analysis. All variables were appropriately transformed when needed to meet the requirements of this analysis (square root or inverse transformations). Because the results of the CA suggested an individual effect of each shrub on pasture community, a MANCOVA was performed upon the community structural parameters, with shrub identity as independent factor and the first PCA axis of soil variables as covariate.

3. Results

The CA of floristic data gave as a result a first axis (CA1 henceforward) showing the entire gradient from the open spaces among shrubs (negative end) to the canopy centre (positive end) (Fig. 1a). At the negative end, the samples corresponding to the open spaces out from the influence of *R. sphaerocarpa* shrubs are mixed with the external samples of both north and south transects, although the latter are more abundant. Distance between the beginning and the end of transects in the CA ordination (i.e. length of arrows in Fig. 1b) is highly variable and independent of aspect. In spite of the general direction set by the first ordination axis, the change in floristic composition has a particular direction for many transects (different angles of arrows in Fig. 1b).

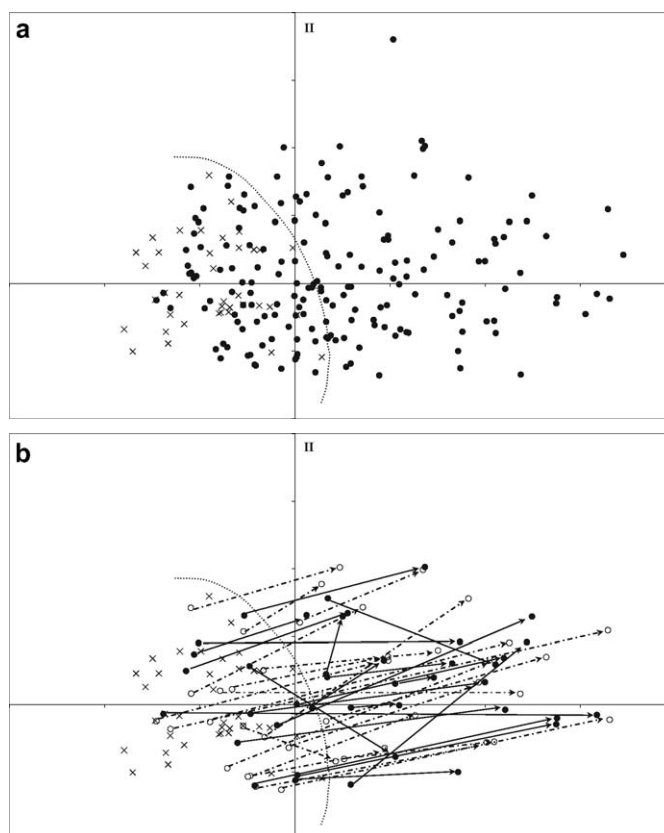


Fig. 1 – CA of floristic data. a) Solid dots indicate samples from the *R. sphaerocarpa* understorey transects; X indicate the old-field additional samples. b) Solid dots indicate samples from the north side of the understorey, the empty ones those from the south side of the understorey; X indicate the old-field additional samples. Arrows join the external sample of each transect with its corresponding innermost sample (solid lines for the north transects, dashed lines for the south transects). The intermediate positions of each transect have been omitted for clarity.

The PCA performed on soil physical and chemical variables produced a first axis (PCA1 henceforward) that accounted for 45.9% of total variance, and that was highly correlated with almost all variables ($r \geq 0.6$ except coarse sand, $r = -0.432$; $P < 0.0001$ in all cases; $N = 178$). The exceptions were pH ($r = 0.1702$, $P < 0.05$), and silt (no correlation at all). The second axis accounted for 13.1% of total variance, and was correlated with all soil variables, although r values were much lower (only N, organic matter, P and clay reached $r \geq 0.40$). This axis was considered redundant with the first and was not used in further analyses.

The PCA analysis reproduced the previous ordination of samples according to their floristic composition, thus suggesting a shrub effect on soil properties. Therefore, to test the hypothesis of differences in soil physical and chemical parameters induced by distance to shrub centre and aspect, a series of ANOVA analyses was performed. The results (Fig. 2) showed no effect of distance to *R. sphaerocarpa* individuals on soil physical parameters and P concentration. The effect is just significant for pH and Mg, and highly significant

for N, organic matter, Na, K and Ca. Overall, their mean values depict the inner region of the understorey as a nutrient-enriched environment. No significant differences were found for any soil parameter between the north and south sides of the understorey.

Distance profiles were constructed for both floristic and edaphic gradients (CA1 and PCA1) according to sample position in relation to shrub centre (Fig. 3). Globally, the distance profile for floristic composition showed a slightly more abrupt descent in the intermediate zone of the understorey than the one for soil properties, but overall the pattern was rather similar (Fig. 3a). In the northward transects the change in floristic composition followed rather closely the change in soil properties (Fig. 3b). The main discontinuity occurred in the transition from the intermediate zone towards the understorey periphery. In contrast, in the southward transect the main change in floristic composition occurred in the intermediate zone, whereas the change in soil properties followed the same pattern as in the northward transect (Fig. 3c).

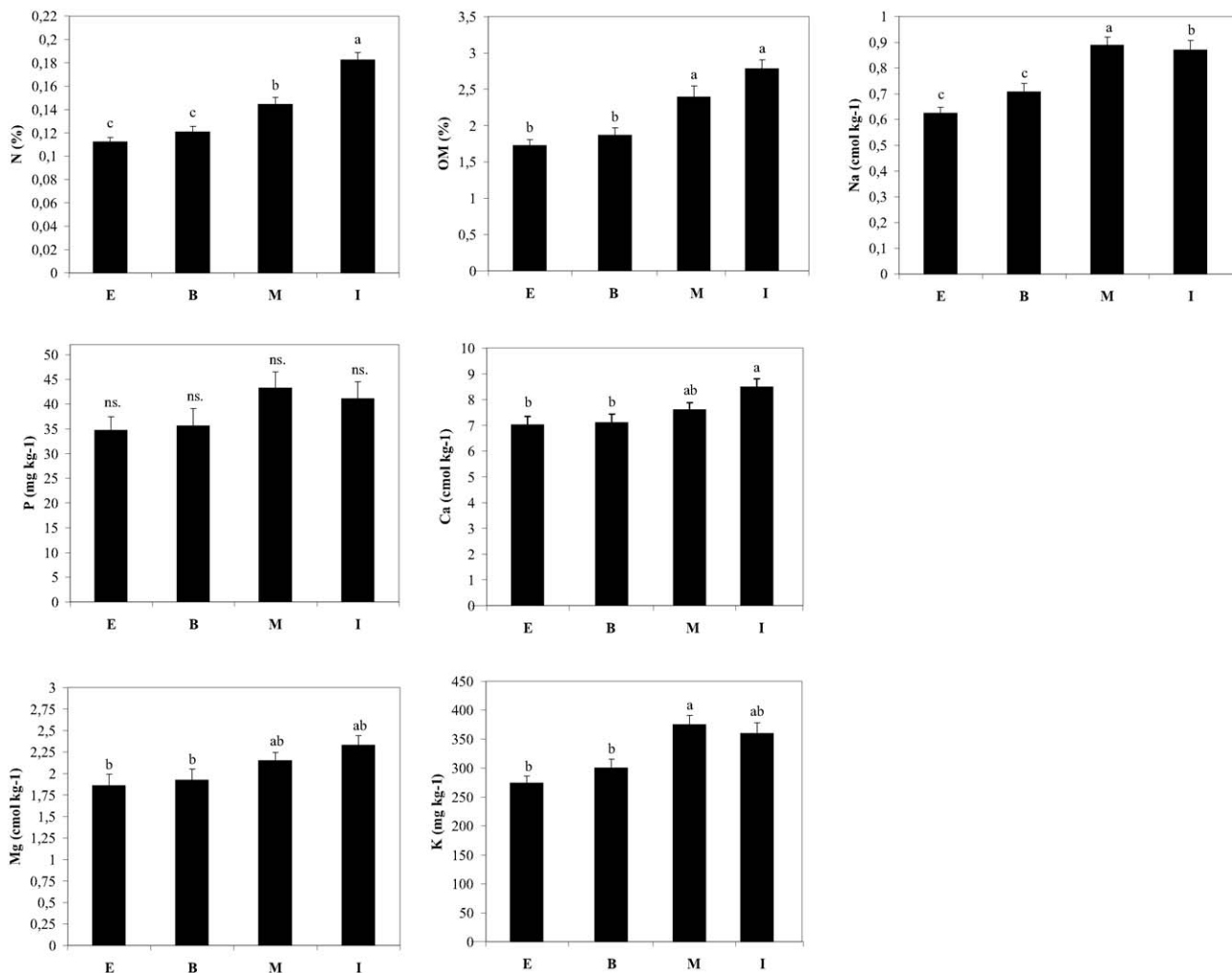


Fig. 2 – Mean \pm 1 S.E. for those soil variables whose values change with distance to shrub centre. Different letters associated with the means denote significant differences (LSD test, $P < 0.05$). ns = non significant differences; E = external position; B = border; M = intermediate position; I = inner position.

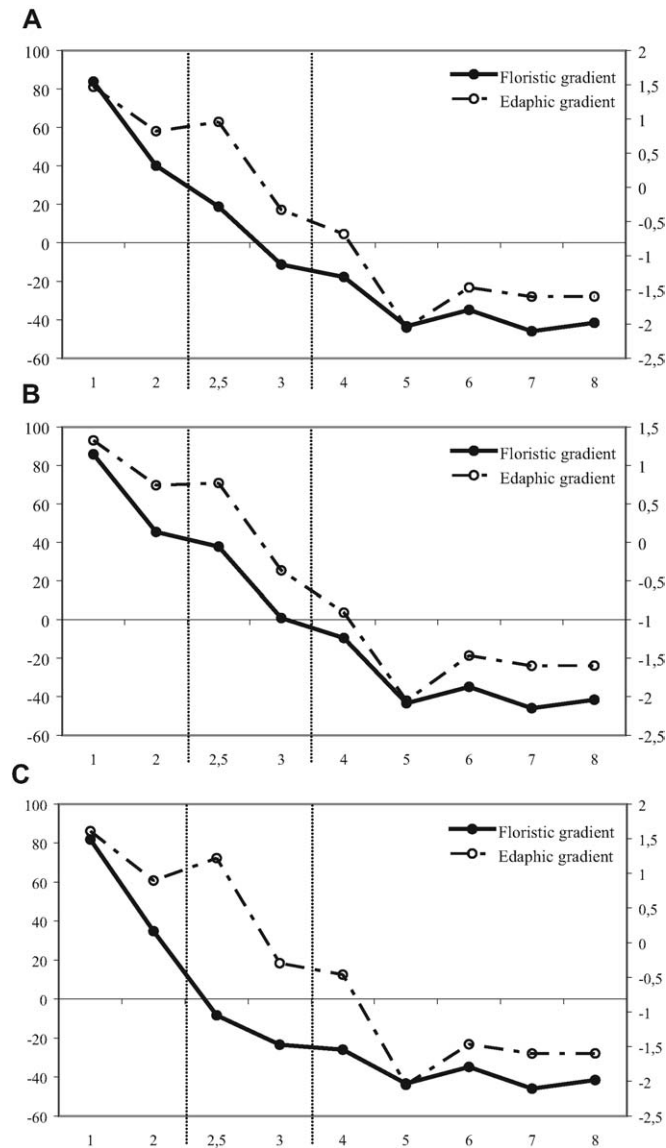


Fig. 3 – Distance profiles of floristic composition (first CA axis) and soil gradients (first PCA axis) for: a) total; b) north side; c) south side. Numbers in x-axis represent distance ranked from 1 (shrub centre) to 4 (external position of transects), and from five to eight old-field samples at increasing distance from the shrubs. Dashed lines indicate the zone corresponding to understorey periphery and canopy limit. Values for CA are to be read in the main axis; values for PCA in the secondary one.

Given the significant effect of aspect on a previous MANCOVA with distance and aspect as factors (Wilks' Lambda = 0.8979, $P = 0.00319$), and the different behaviour of northward and southward transects, separate MANCOVA analyses were performed for each one. For both transects the results were significant (Wilks' Lambda = 0.4298 for the northward transect, Wilks' Lambda = 0.3157 for the southward transect; $P = 0.00000$ in both cases). Distance to shrub centre showed significant effects on floristic composition, S, H', and herb height for the northward and southward transects, and on evenness only for the former (Fig. 4a). These effects were independent of the influence that *R. sphaerocarpa* canopy exerts on soil properties. The pattern of change for

all variables was similar in both transects. Species richness, evenness and Shannon index increased from the canopy centre towards the open areas. Pasture mean height followed the opposite pattern, increasing towards the canopy centre, and to the northward side. Although marginally non significant, the trend followed by E and H' was the opposite, being higher to the southward side (Fig. 4b). The main differences between the northward and southward transects were evident in the covariate (PCA1): it was only significant for the northward transect (Wilks' Lambda = 0.847, $P = 0.0176$), and only for floristic composition ($F = 11.155$, $P = 0.0012$).

The MANCOVA used to test the individual effect of each *R. sphaerocarpa* shrub suggested by the initial CA confirmed

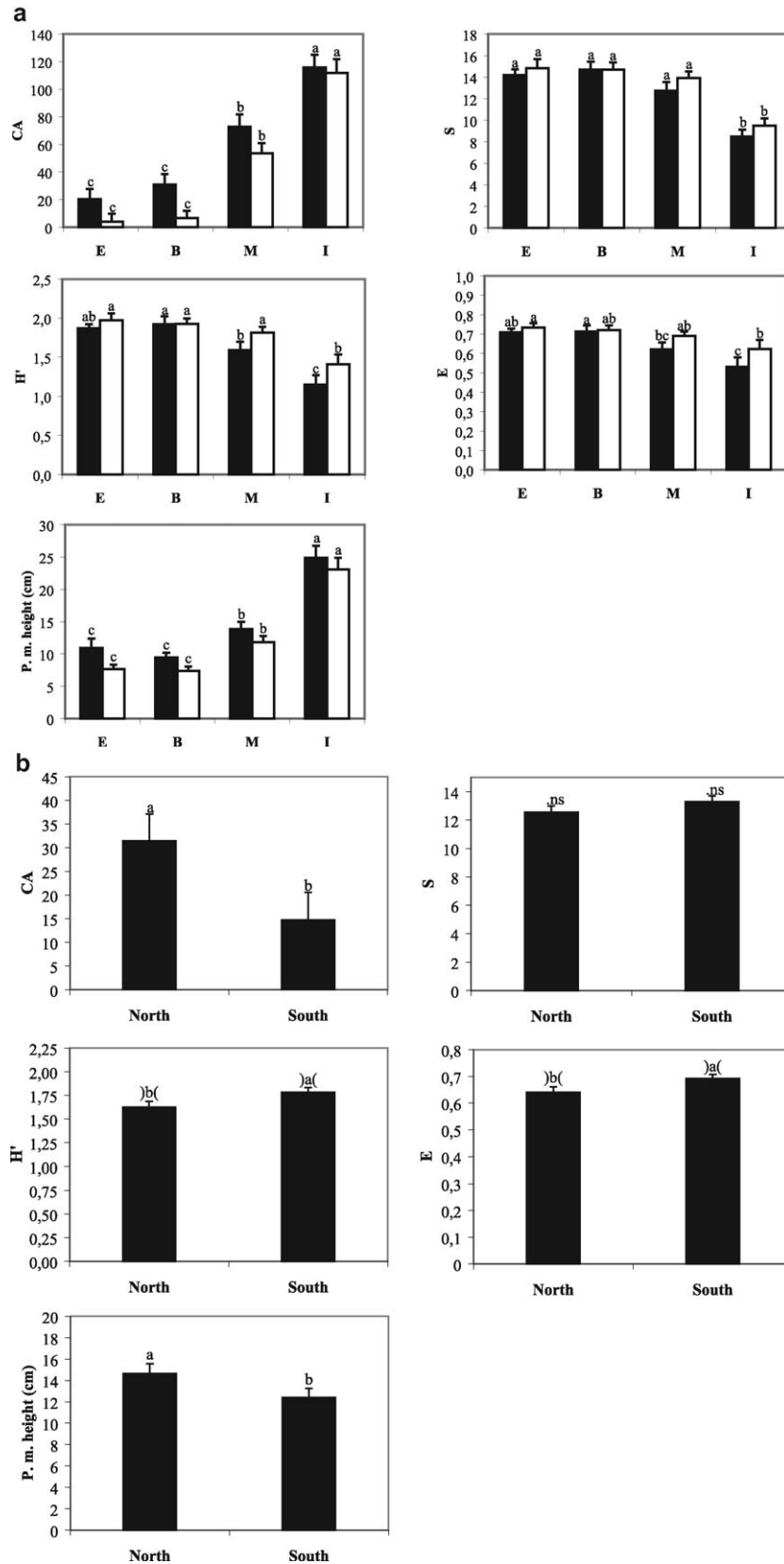


Fig. 4 – Mean ± 1 S.E. for each community structural parameter: a) distance gradient from the shrub centre to the open areas (solid bars for the north side, empty bars for the south side); b) aspect (north vs. south side). Different letters associated with the means denote significant differences (LSD test, $P < 0.05$). Letters inside brackets show marginally non significant differences. ns = non significant; E = external position; B = border; M = intermediate position; I = inner position; P.m. height = pasture mean height.

our hypothesis (Wilks' Lambda = 0.2159, $P = 0.00000$), being significant for all the community parameters. In this case the covariate was highly significant for all of them ($P < 0.001$).

4. Discussion

Overall, our results are further evidence of shrubs as sources of spatial heterogeneity. They show the role of *R. sphaerocarpa* in structuring the herbaceous community, as there is a clear change in floristic composition, diversity and mean height from the understory centre to the open spaces among the shrubs.

Changes in herbaceous communities caused by woody species influence have been reported throughout the world (e.g. Joffre et al., 1988; Vetaas, 1992; Belsky et al., 1993; Ko and Reich, 1993; Belsky, 1994; Jackson and Ash, 1998). The mechanisms invoked to explain them can be generally grouped into two categories of canopy effects: an edaphic effect (improved nutrient and water content), and a physical effect (mainly amelioration of climatic extremes, redistribution of rainfall, and light quality/intensity modification). For a thorough revision of the mechanisms involved see Callaway (1995).

Previous studies of Pugnaire et al. (1996b), Moro et al. (1997a, b) and Pugnaire and Lázaro (2000) focused on facilitative effects of *R. sphaerocarpa* on its understory vegetation from the canopy border to its centre. Both the edaphic and the physical effects were present. They found a progressive increase in soil organic matter, nitrogen content and mineralisation rates, an improvement in water status of understory vegetation, as well as a reduction in temperature and light intensity. The community responds to this gradient changing its floristic composition, decreasing the number of species and increasing production.

As far as they can be compared, these results are consistent with ours. According to our expectations, the gradient in soil chemical variables extends beyond the canopy border into the open spaces, with a smooth decrease in N, organic matter and exchangeable cations. Following this gradient, the community properties change. The nutrient enriched centre of the understory, with a high amount of litter, lower temperatures and light intensity (Pugnaire et al., 1996b; Moro et al., 1997a, b) shows the lowest values for species richness, evenness and Shannon–Weaver index. These characteristics would define a microenvironment of relatively high competition levels, to which the shade-tolerant, nitrophilous or even ruderal species present, lacking functional traits to protect them from high radiation intensity and evapotranspiration (López-Pintor et al., 2003), would be well adapted. In contrast, the open spaces among the shrubs, with high solar radiation intensity, greater temperature extremes, and lower nutrient availability, have the highest values of species richness, evenness and Shannon index. In this stressful environment the species display functional traits that enable them to cope with high light intensity, evapotranspiration and vertebrate herbivory (López-Pintor et al., 2003): hairy/woolly leaves, small body size or prostrate growth form, all of them disadvantageous inside the canopy. Towards the understory periphery conditions are not so extreme in terms of light and

temperature, and also in terms of competition due to the lower nutrient levels. We see then intermediate values of species richness, evenness and Shannon index. According to its intermediate nature, the species present include some from the open spaces and some others from the inner understory (Pugnaire and Lázaro, 2000; López-Pintor et al., 2003).

However, as the MANCOVA analyses reveal, this gradient inside–outside is not homogeneous all over the understory. A point at a given distance from the shrub centre is not necessarily equivalent to any other point at the same distance, which is related to the spatial asymmetry of the canopy physical effects. Other authors have found effects of the relative position of woody species on their surrounding vegetation, either herbaceous or woody (e.g. Montoya, 1982; Joffre et al., 1988; Rhoades, 1997; Schenk and Mahall, 2002). Solar radiation and wind were the main physical factors responsible for their results. In our case, if the values for the community parameters in the north–south gradient are compared to those of the inside–outside gradient, it is clear that the trend in the north side is similar to that of the inner parts of the understory. Consistently, the trend in the south side resembles that of the outer canopy and open areas. The understory would be 'invaded' in its southward side by the external conditions, mainly through higher light intensity and the associated higher temperatures and evapotranspiration, inducing a change in the herbaceous community characteristics towards those of the open areas.

This penetration of external conditions would place a constraint in the benefits the understory vegetation can obtain from the edaphic effects provided by the nurse plant. The results for the covariate highlight how in the south side there is no apparent contribution of the edaphic effect to the organisation of the herbaceous community, in spite of no difference in nutrient content between the north and south gradients. This is further illustrated by the distance profiles, which show the different behaviour imposed by aspect: floristic composition in the southward transect changes rather independently of the edaphic gradient. Belsky et al. (1989) found a similar pattern in Kenyan savannas: completely independent trajectories for the changes in floristic composition and edaphic variables from the tree trunks to the open areas. In contrast, the northward transect showed a close relationship between the floristic and edaphic changes in both analyses. The year-round asymmetry in the distribution of solar radiation in extratropical latitudes would turn the microclimatic amelioration exerted by the canopies asymmetric, giving rise to a weak and a strong side in them. In the weak side, the constraints imposed by the relatively lower water availability (Swank and Oechel, 1991), and higher photo-inhibition and photo-damage (Long et al., 1994; Horton et al., 1996) could limit nutrient uptake by the understory vegetation. In contrast, the milder situation in the strong side would enable the maximum benefit from the nutrient enrichment to be attained. This would be another example of the importance of the complex interaction between facilitation, interference and abiotic factors in the structuring of plant communities described by Callaway (1998).

In addition to the general heterogeneity introduced by *R. sphaerocarpa* understoreys in the shrubland studied, the different floristic gradients associated with different indivi-

duals (Fig. 1) should be taken into account. Other authors have reported differential effects of woody species upon their understoreys (Gross et al., 1995; Wezel et al., 2000), and even among individuals of the same species (Rhoades and Sandford Jr., 1994). Differences in canopy shape and biomass distribution could be behind the varying behaviours found in our study. However, the effect of the initial heterogeneity at the scale of 20–100 m in the former crop field (Robertson et al., 1993) may also be an overriding factor.

In conclusion, *R. sphaerocarpa* understoreys are an important source of spatial heterogeneity in the savanna-like systems this species generates. Through their physical and edaphic effects on their surroundings they provide habitat for herbaceous species adapted to environmental conditions very different from those of the open areas, increasing their abundance and the overall species richness. However, the increase in spatial heterogeneity varies between individuals and systematically due to the asymmetry in the physical effects of their canopies, making the herbaceous community in the southward side different from that of the northward side.

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