RUNNING HEAD: Water infiltration and plant spatial patterns in drylands

RELATIONSHIPS BETWEEN PLANT SPATIAL PATTERNS, WATER INFILTRATION
CAPACITY AND PLANT COMMUNITY COMPOSITION IN SEMI-ARID
MEDITERRANEAN ECOSYSTEMS ALONG STRESS GRADIENTS.

Pueyo, Y.^{1*}, Moret, D.², Sáiz, H.¹, Bueno, C.G.³, Alados, C.L.¹

¹Instituto Pirenaico de Ecología (CSIC), Av. Montañana 1005, P.O. Box 13.034, 50080
Zaragoza, Spain. ²Departamento de Suelo y Agua, Estación Experimental de Aula Dei (CSIC),
P.O. Box 202, 50080 Zaragoza, Spain. ³Instituto Pirenaico de Ecología (CSIC), Avda.
Regimiento Galicia s/n, 22700 Jaca, Spain.

*Corresponding author: e-mail: ypueyo@ipe.csic.es; telephone:+34976369393 ext. 880044;
fax:+34976716019

Author contributions: YP and CLA conceived the study; all authors performed research; YP,
DM, HS and CGB prepared and analyzed data; and YP wrote the paper with assistance from all
authors.

Abstract

Water redistribution from bare soil to vegetation patches is a key feature of semi-arid ecosystems, and is responsible for their patchy vegetation patterns. The magnitude of water redistribution depends on the properties of the bare soil (which determine the amount of water run-off) and the capacity of vegetation patches to trap water run-on. We examined the relationships between plant spatial patterns, water infiltration into bare soil, and plant community composition in semi-arid sites with different hydro-physical properties (silty and gypseous soils) in NE Spain. We also studied the effect of two stressors, aridity and grazing, on water infiltration and plant spatial patterns. Our results indicate a negative correlation of bare-soil sorptivity (the capacity to absorb water by capillarity) and vegetation aggregation. There was a strong positive correlation between perennial grass cover and the spatial aggregation of vegetation, but aggregation was not associated with positive associations of different plant types. The aggregation of vegetation was positively correlated with species richness and the overall extent of vegetation cover. Grazing reduced water infiltration into silty soils, which are prone to compaction. In contrast, soil crust affected the hydrology of gypseous soils, especially in the most arid sites, where grazing increased infiltration, reducing surface sealing due to breaking of the soil crust. Together, our results suggest that biotic and abiotic factors affect the hydro-physical properties of soils in the semi-arid ecosystems of NE Spain, which is linked to the plant communities through the spatial distribution of plants.

Keywords: aridity, ecohydrology, infiltration, livestock grazing, soil compaction, soil crust, vegetation spatial aggregation, water run-off, water run-on.

Introduction

Water redistribution is fundamental to the function of ecosystems in arid and semi-arid regions (Shachak et al., 1998), and these are often called “source-sink” (Cerdeña, 1997; Imeson

and Prinsen, 2004) or “trigger-transfer-reserve-pulse” systems (Ludwig 2005). Spatially discontinuous vegetation cover plays a major role in the redistribution of water in these ecosystems (Cerdeira, 1997; Ludwig et al., 2005; Bautista et al., 2007). In particular, water infiltration is typically low in open (inter-patch) areas because of surface sealing by the soil crust and compaction; as a result, these areas have extensive water run-off and are considered “sources” of water run-off (Noy-Meir, 1973). In contrast, vegetation patches have loose particles near the soil surface and macropores created by roots that enhance water infiltration (Joffre and Rambal, 1993; Maestre et al., 2002; Bedford and Small, 2008; Segoli et al., 2008); hence these areas are considered “sinks” for water run-on (Bhark and Small, 2003; Ludwig et al., 2005; Arnau-Rosalen et al., 2008). Thus, water accumulates where there is existing plant growth and this promotes additional plant growth, a positive feedback loop (Rietkerk et al., 2004). This positive feedback loop has significant consequences for arid and semi-arid ecosystems, because it increases the capacity for greater biomass and biodiversity (Shachak et al., 1998; Aguiar and Sala, 1999), allows better recovery from perturbations, and increases the success of ecosystem restoration (Suding et al., 2004; Pueyo et al., 2009).

Thus, two coupled processes contribute to the accumulation of water in vegetation patches in these environments: water run-off from bare areas (source) and water run-on to vegetated sites (sink) due to the presence of vegetation. The surface properties of bare soil are responsible for water run-off (Rietkerk et al., 1997). In particular, the presence of surface crust (Tongway et al., 2001; Mills et al., 2009) obstructs soil pores and reduces infiltration (Eldridge et al., 2010). Soil compaction can also slow infiltration, limit water penetration to shallow layers, and enhance run-off and evaporative processes (Hamerlynck et al., 2002). In vegetation patches, the amount of water run-on depends on the capacity of the vegetation to increase water infiltration (Abrahams et al., 1995; Pockman and Small, 2010). This infiltration is affected by root characteristics (Callaway, 2007; Wainwright, 2009), the extent of physical-chemical soil

modification by roots, the biological activity of the root systems (Asbjornsen et al., 2011), and the interception of water run-on from the aerial parts of the plants (Bautista et al., 2007; Mayor et al., 2009).

External biotic and abiotic factors can also affect the redistribution of water to vegetation patches. For example, livestock trampling increases soil compaction, thereby reducing water infiltration (Schlesinger et al., 1990; Castellano and Valone, 2007; Dunne et al., 2011) and potentially increasing water flow to vegetation patches (Stavi et al., 2009). However, modest trampling (associated with light stocking rates) can increase water infiltration because it leads to removal of the topsoil crust (du Toit et al., 2009). Second, the difference between the soil moisture beneath vegetation patches and bare soil is larger as aridity increases (D'Odorico et al., 2007; Thompson et al., 2010). Thus, as aridity increases, soil crusts become stronger, water infiltration rates are reduced (Lavee et al., 1998), and this increases the amount of run-off directed towards vegetation patches.

In arid and semi-arid ecosystems, plant patchiness is an indication of “source-sink” water redistribution (Imeson and Prinsen, 2004; Rietkerk et al., 2004). Theory suggests that, when the amount of water redistribution from bare soil to vegetation patches increases, that vegetation biomass will be concentrated in patches and plant spatial pattern will be more marked (Rietkerk et al., 1997; Pueyo et al., 2008). The relationship between plant spatial pattern and hydrological processes in patchy environments is well known (Tongway et al., 2001), but there is insufficient empirical support for this relationship in many ecosystems in order to verify underlying assumptions (Bautista et al., 2007). In addition, it is uncertain whether plant spatial pattern is associated with ecosystem capacity for high productivity and diversity (Maestre and Escudero, 2009; Kéfi et al., 2010).

The present study had several major objectives (Fig. 1a). The first objective was to examine the relationship between plant spatial pattern and water infiltration in bare soil (I_a , an

indicator of water run-off) and plant community composition (*1b*, in order to identify the capacity of the predominant vegetation to concentrate water run-on and create an aggregated vegetation pattern). We also investigated the associations of plant spatial patterns with other indicators of ecosystem health, such as plant species richness and plant cover (*1c*). Our second objective (2 in Fig. 1a) was to assess the effect of aridity and livestock grazing on water infiltration and plant spatial patterns in sites with contrasting hydro-physical soil properties (silty and gypseous soils).

We predicted that vegetation would be more aggregated in ecosystems where bare soil has a lower capacity for water infiltration, because more of the water will move to vegetation patches through run-off, and plants will fail to establish in the bare soils. To assess the relationship between plant community composition and plant spatial pattern, we identified the predominant plant types associated with an aggregated spatial pattern of vegetation and their spatial associations with other plant types. With respect to the second objective, we hypothesized that water infiltration of bare soil will be greater and vegetation will be less aggregated under mildly arid conditions than under severely arid conditions, because of differences in the soil crust and soil compaction. We also hypothesized that grazing would have a different effect on water redistribution in soils that are prone to compaction (e.g. silty soils) and in soils that are influenced by the presence of crust (e.g. gypseous soils). In the former, we expect that grazing would increase soil compaction, leading to decreased water infiltration of bare soil, increased water redistribution to vegetation patches, and to more aggregation of vegetation. In the later, we expected that the trampling associated with grazing would remove surface crust (Heady and Child, 1994), leading to increased water infiltration of the bare soil, and to less aggregation of vegetation. In addition, the presence of highly specialized flora (gypsophytes) in gypsesous soils might partially uncouple the relationship of plant spatial pattern with eco-hydrology by other ecological mechanisms determining plant spatial patterns. Gypsophytes have certain traits (e.g.

mucilaginous seed coats) that allow them to attach to and germinate in the intact soil crust (Escudero et al., 1999). However, many gypsovags (regionally common species that can occur in gypseous soils but are not specialized for this soil type) lack these traits, so these plants may find more suitable conditions for their establishment beneath the canopy of other plants rather than in the bare soil, leading to a more aggregated pattern than gypsophytes.

Materials and Methods

Study area

This study was conducted in the Middle Ebro Valley (NE Spain, 41°31'N 0°37'W; Fig. 1b), a region with semi-arid Mediterranean climate, average annual temperature of 15°C (at 250 m a.s.l., Zaragoza station, n=50 yr), and average annual precipitation of 353 mm yr⁻¹. The Middle Ebro Valley is an ideal location for investigation of the relationship between water infiltration processes and plant spatial patterns in semi-arid environments, because this region has a variety of ecosystems with different soil types, different plant communities, and significant climatic gradients. Silty and gypseous soils, which have markedly different hydro-physical properties, are predominant in this region. The bare areas of silty soils have very low water infiltration because of high soil compaction (Pueyo et al., 2009; Moret et al., 2011), so rainfall generates a large amount of water run-off. On the other hand, gypseous soils are highly permeable (Desir, 2002) but tend to develop physical and biological soil crusts, hampering water infiltration and seed establishment (Escudero et al., 1999; Pueyo et al., 2007).

The landscape has low hills and flat-bottomed valleys and the elevation ranges from 127 m to ~ 800m a.s.l in the study area. Most of the vegetation on the hills is shrubland (with species such as *Rosmarinus officinalis* L.) and gypsophytes (e.g. *Helianthemum squamatum* (L.)Pers) occur in gypsum outcrops. *Lygeum spartum* L. steppe and scarce scrub of *Salsola vermiculata* L. and *Artemisia herba-alba* Asso are predominant in the uncultivated bottom valleys (Braun-Blanquet and Bolòs, 1957). Land use in the area is based on a traditional agro-pastoral system

that involves dry cereal croplands and extensive sheep (*Rasa aragonesa*) production (Pueyo, 2005).

Field surveys

Field surveys were conducted in gypseous and silty soils in locations with different levels of aridity and grazing. In particular, we selected two locations on gypseous and silty soils in the most arid region and in a less arid region of the study area. Each location included nearby ungrazed and grazed areas (Fig. 1b, Table 1). Topography and types of human activities (e.g. livestock grazing) were similar among the field sites. Farmers did not use the ungrazed areas because they were inaccessible or located within a natural reserve. Grazed areas had livestock densities less than 0.7 head ha⁻¹ year⁻¹ (Pueyo, 2005). In May and June of 2010, the hydro-physical properties of the soils, plant spatial patterns and plant community composition were assessed at each study site.

Hydro-physical soil properties

The saturated hydraulic conductivity (*K*) and sorptivity (*S*) of soils were measured at eight sampling points per site (*n*=64) before and after removal of the surface crust (top 1 cm of soil), by use of a tension disc infiltrometer (base radius, *R* =50 mm) (Perroux and White, 1988). Measurements were taken in open unvegetated areas. We applied a thin layer of commercial sand (grain size, 80-160 µm) to ensure good hydraulic contact of the disc and soil. The maximum infiltration time was 15 min. Flow readings, which are based on the decrease in the level of the water reservoir, were recorded automatically every 5 s by use of a ±0.5 psi pressure transducer that was installed at the bottom of the reservoir (Casey and Derby, 2002) and connected to a datalogger (CR1000, Campbell Sci.). We calculated *K* and *S* using transient cumulative infiltration based on the method of Vandervaere et al. (2000), which only uses the cumulative water infiltration curve and the initial and final soil water content. The initial soil water content was estimated using soil core samples (diameter = 50 mm, length = 50 mm). All

soil samples were dried at 50 °C for 48 h and weighed to calculate the initial volumetric water content. The final soil water content was based on samples taken from the upper few centimeters of soil just after the disc infiltrometer was removed from the soil surface.

The three-dimensional steady state infiltration flux, q_{3D} (mm s⁻¹), was estimated based on K and S as described by Haverkamp et al. (1994), $q_{3D} = K + \frac{\gamma S^2}{R(\theta_f - \theta_o)}$, where γ is a constant (0.75) (Angulo-Jaramillo et al., 2000), and θ_o and θ_f indicate the initial and final soil volumetric water content, respectively.

Plant spatial patterns and community composition

We measured plant spatial patterns at two levels to identify the main factors involved in the formation of the spatial patterns: the overall spatial patterns of vegetation cover (with no consideration of individual plants and species) and the spatial pattern of individual plants.

Overall vegetation cover is a good indicator of aboveground biomass (Flombaum and Sala, 2007), so the spatial pattern of vegetation cover is equivalent to the plant spatial pattern predicted by mechanistic models that describe the spatial pattern of vegetation biomass without consideration of species (Rietkerk et al., 2002; Pueyo et al., 2008). In those mechanistic models, the presence of vegetation biomass in patches indicates a water concentration mechanism due to plant-water infiltration feedback. Thus, we established six 250-m linear transects at each site (n = 48) to investigate the spatial pattern of vegetation cover. The presence of plant species or bare soil was recorded every 20 cm using the point intercept method (Goodall, 1952). The presence of vegetation cover was assigned to transect points where plants were present. Detrended fluctuation analysis (DFA) was used to quantify the spatial pattern of vegetation cover. This procedure provides a one-dimensional index of the spatial autocorrelation of vegetation (Alados et al., 2003). For each 250-m linear transect x , every recorded point i was assigned a value of +1 if vegetation cover was present ($x(i) = +1$), and a value of -1 if there was no vegetation ($x(i) =$

-1). This binary data sequence was transformed into a cumulative sequence, y ,
 as $y(s) = \sum_{i=1}^s x(i)$, where s is the displacement of the sequence after s steps. The sequence has a
 total length of N . In DFA this cumulative sequence is divided in N/b non-overlapping boxes,
 where b is the number of intercept points inside each box. A regression line was calculated for
 each box of size b (i.e., $y_b(s)$ was regressed on s), and the average of the residual variance for
 each b was calculated as $F^2(b) = \sum (y_b(s) - \hat{y}_b(s))^2 / N$. This procedure was repeated for
 different b values (4, 8, 16, . . . and 256 points) along the first 1024 points in each transect
 (N=1024). The scale of the relationship was calculated as $F(b) \propto b^\alpha$, where α values near 0.5
 indicate a random distribution and values greater than 0.5 indicate long-range autocorrelation
 (i.e. vegetation aggregated in patches). DFA α value is independent of the abundance of
 vegetation cover from 10 to 90%. Peng et al. (1992), Alados and Weber (1999) and Alados et al.
 (2003) provide more details about the DFA procedure. DFA was computed with DRASME 2009
 software (freely available at <http://www.ipe.csic.es/conservacion/Services.html>).

We analysed the spatial pattern of individual plants using one 100-m transect per site ($n =$
 8) to identify the effect of interactions among individual plants on the observed vegetation
 patterns. We recorded the location and species of every individual plant using the line intercept
 method (Bonham, 1988) along the transects. The cover data was converted to a point pattern by
 assigning the location of each plant in the central point of the cover of each individual
 overlapping the line. Ripley's K -function was used as the one-dimensional point pattern to
 characterize the spatial pattern of the one-dimensional mapped points of individual plants along
 the transect (Cowling, 1998; Dale, 1999), $\hat{K}(d) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1, j \neq i}^n w_{ij}^{-1} k_{ij}$, where A is the length of the
 transect, n is the number of points recorded in the transect, k_{ij} is 1 if the distance between points i

220 and j are $\leq d$, and 0, otherwise. $w_{ij}=1/p_{ij}$ is a weight for edge effects, where $p_{ij} = \frac{e+d}{2d}$ and e is
221 the distance from point i to the overlapping end of the transect.

222 The bivariate extension of Ripley's K function was used to measure the degree of
223 association between two plant types, $\hat{K}_{12}(d) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} k_{ij}$, where 1 and 2 are the two plant
224 types. The expected $\hat{K}(d)$ under spatial randomness is $2d$ in the univariate and the bivariate
225 spatial patterns. We calculated the difference between expected and the observed values using
226 Ripley's $\hat{L}(d)$, using $\hat{L}(d) = \frac{\hat{K}(d)}{2} - d$. $\hat{L}(d) = 0$ when the points are randomly distributed,
227 $\hat{L}(d) > 0$ when points are aggregated, and $\hat{L}(d) < 0$ when the points are uniformly distributed
228 (Dale, 1999).

229 Plant species composition was quantified using species richness (number of species per
230 transect). Plant type composition was assessed by classifying plant species based on growth form
231 (Cornelissen et al., 2003), and assignment to one of three groups based on the potential role in
232 soil water infiltration: (i) annual plants, (ii) dwarf shrubs and shrubs, and (iii) perennial grasses.
233 Annual plants would not have a significant role in water infiltration because they do not have
234 well-developed root systems and only form sparse patches that cannot intercept water run-off
235 (Bautista et al., 2007). Dwarf shrubs and shrubs promote water infiltration into the soil
236 (Tongway et al., 2001; Bhark and Small, 2003), while perennial grasses would be even more
237 efficient in the trapping of water run-on than shrubs, because of the density of their aerial parts
238 and their ability to create channels and macropores under the canopy (Abrahams et al., 1995;
239 Eldridge et al., 2010; Pockman and Small, 2010).

240 Plant species richness and the frequency of plant types were calculated for each of the
241 250-m linear transects ($n = 48$). In addition, the percent of bare soil in each transect was used as
242 an indicator of a site's susceptibility to degradation (Kirkby et al., 1990). At the gypseous sites,

the percent of gypsophytes and gypsovags in each transect were calculated because these plants are surrogates for unmodified and modified conditions on gypseous soils, respectively (Pueyo et al., 2007).

Statistical analysis

Spearman's rank correlation test was used to assess the significance of relationships between the hydro-physical properties of soil and the spatial pattern of vegetation cover. Linear mixed-effects models, with sampling locations as a random factor were used to assess the relationship between the spatial pattern of vegetation cover and the composition of the plant community.

Randomization test were used to assess the significance of the univariate and bivariate $\hat{L}(d)$. *Complete Spatial Randomness* (CSR) was the null model for the univariate $\hat{L}(d)$. *Independence* of the bivariate patterns was the null model for the bivariate $\hat{L}(d)$; this is equivalent to the CSR but, when the bivariate spatial pattern is randomized, the spatial pattern of each variable must be retained. We generated random spatial patterns by randomly shifting one entire spatial pattern relative to the other (Wiegand and Moloney, 2004). Analyses of point patterns and comparisons with null models were performed with MATLAB R2010b.

We used linear mixed-effects models for the analysis of the effects of soil type, aridity and grazing on the hydro-physical properties of soils and on the traits of plant communities, with soil type, aridity and grazing as fixed factors and sampling location as a random factor. We examined the effect of random effects on the model as described by Zuur et al. (2007). Data were arcsine-root transformed to achieve normality (when necessary). Analyses were performed using the nlme library of R (R_Development_Core_Team, 2010).

Results

Hydro-physical soil properties, plant community composition, and plant spatial pattern

First, we examined the relationship of plant spatial pattern (DFA) with the hydro-physical soil properties. The results indicate that the spatial aggregation of vegetation (DFA) was negatively correlated with soil sorptivity (S_{crust} ; Spearman's $\rho = -0.71$, $p = 0.047$, Fig. 2a). In other words, the vegetation was less aggregated at sites where the sorptive forces of bare soil (namely, the water infiltration capacity in unsaturated soils) were high. Interestingly, when the soil crust was removed, there was no significant relationship between vegetation spatial aggregation (DFA) and soil sorptivity (S_{1-10} ; Spearman's $\rho = -0.09$, $p = 0.823$, Fig. 2b). Although removal of the soil crust had little on DFA, it had a significant effect on soil sorptivity, indicating the importance of soil crust in the hydrology of these ecosystems.

Our results also indicate that the spatial aggregation of vegetation (DFA) was not correlated with the hydraulic conductivity of the intact soils (K_{crust} , Spearman's $\rho = -0.59$, $p = 0.120$) nor with the hydraulic conductivity of soil without surface crust (K_{1-10} , Spearman's $\rho = -0.07$, $p = 0.867$). In addition, the vegetation spatial aggregation (DFA) and infiltration flux in bare soil that had an intact soil crust were not significantly correlated ($q3D_{\text{crust}}$; Spearman's $\rho = -0.62$, $p = 0.102$). Removal of the soil crust further reduced the correlation of vegetation spatial aggregation (DFA) and infiltration flux of bare soil ($q3D_{1-10}$; Spearman's $\rho = -0.07$, $p = 0.867$).

Next, we investigated the relationship of the dominance of different plant types with vegetation spatial aggregation (DFA). Our results indicate that the abundance of perennial grasses and the extent of spatial aggregation had a strong positive relationship ($F_{1,43} = 14.89$, $p < 0.001$; Fig. 3a). The abundances of annuals ($F_{1,43} = 1.041$, $p = 0.3132$), dwarf shrubs and shrubs ($F_{1,43} = 0.3205$, $p = 0.5742$), were unrelated to the extent of vegetation spatial aggregation.

In gypseous soils, the extent of vegetation spatial aggregation was positively associated with the abundance of gypsophytes ($F_{1,21} = 7.84$; $p = 0.011$; Fig. 3b) and strongly associated with the abundance of gypsovags ($F_{1,21} = 18.011$; $p < 0.001$; Fig. 3c).

There was a significantly positive association of vegetation spatial aggregation and plant species richness ($F_{1,43} = 19.26$, $p < 0.001$, Fig. 3d); i.e., an aggregated vegetation pattern was associated with more plant species in the plant community. Furthermore, plant spatial aggregation and the abundance of bare soil were strongly and negatively related ($F_{1,43} = 8.79$, $p = 0.005$; Fig. 3e); i.e., an aggregated vegetation pattern was associated with small proportions of bare soil in the ecosystems.

Calculation of univariate Ripley's $\hat{L}(d)$ indicated that individual plants were highly aggregated at all sites (Table 3). The univariate $\hat{L}(d)$ for perennial grasses indicate that most of the sites had an aggregated distribution, although individuals were less aggregated at the mildly arid silty sites (spatial pattern not significantly aggregated at small scales; Table 2). Calculation of the bivariate Ripley's $\hat{L}(d)$ between perennial grasses and other plant types indicated aggregation, but in most of cases these relationships were not statistically significant (Table 3).

At gypseous sites, gypsophytes exhibited a univariate random spatial distribution (Fig. 4a and b) whereas gypsovags were strongly aggregated (Fig. 4c and d). Interestingly, the bivariate Ripley's $\hat{L}(d)$ indicated that gypsophytes and gypsovags were segregated spatially at the GVN site at short scales (marginally significant; Fig. 4e). At the GVV site gypsophytes and gypsovags had an independent bivariate pattern (Fig. 4f).

Effects of soil type, aridity and grazing on the hydro-physical properties of soils, plant community composition and plant spatial patterns.

Our results indicate that soil type and grazing combined to influence the infiltration flux in bare soils ($q3D_{\text{crust}}$). In particular, grazing reduced the infiltration flux in silty sites and increased the infiltration flux in gypseous sites (Table 3, Fig. 5a and b). Grazing significantly

reduced the infiltration flux into bare soils after removal of the crust ($q3D_{1-10}$, Table 3, Fig. 5c and d), indicating the presence of soil compaction due to livestock trampling. There was also an interaction of soil and grazing on $q3D_{1-10}$ (Table 3, Fig. 5c and d). Grazing reduced the infiltration flux into bare soil without crust more at silty sites than at the gypseous sites.

Grazing and soil combined to affect the abundance of perennial grasses. In particular, grazing uniquely decreased the abundance of perennial grasses at silty sites (Table 3, Fig. 6a and b). The interaction effect of aridity and grazing also had a significant effect on the abundance of perennial grasses: grazing reduced the abundance of perennial grasses mainly in the most arid sites (Table 3, Fig. 6a and b).

At gypseous sites, there was an interaction of aridity and grazing on the abundance of gypsophytes (Table 3, Fig. 6c). Grazing reduced the abundance of gypsophytes at the most arid sites, but increased their abundance at mildly arid sites. On the other hand, grazing had a limited effect on gypsovags species (Table 3, Fig. 6c). Our experimental design did not allow statistical evaluation of the effect of aridity on the abundance of gypsophytes and gypsovags, although the interactive term aridity $\times$ grazing suggested a decrease in the abundance in gypsovags in the most arid sites for grazed and ungrazed treatments (Table 3).

Soil type, aridity and grazing had no effect on the extent of vegetation spatial aggregation (DFA ; Table 3). In addition, the interactions of grazing with aridity and grazing with soil type were not significant. Our experimental design did not allow assessment the effect of the interactions of soil type with aridity, soil type with grazing and aridity with grazing on dependent variables.

Discussion

The present study examined the relationship between plant spatial pattern, water infiltration capacity of soils and the predominant plant types in semi-arid Mediterranean ecosystems. We found that the extent of spatial aggregation of vegetation was related to soil

sorptivity, a key physical property that indicates the water infiltration capacity of bare soil. In particular, the vegetation was more aggregated at sites where the sorptive forces were less pronounced. This supports the hypothesis that less water infiltration into bare soil leads to more water redistribution to vegetation patches and less plant establishment in bare soil, which appears to be a driving force for the characteristic plant spatial patterns of semi-arid ecosystems. This relationship has been generally accepted based on theoretical studies, but there has been little field evidence to support it. Many previous studies have evaluated the hydro-physical properties of soils in vegetation patches and bare soil (Bhark and Small, 2003; Bochet et al., 2006; Arnau-Rosalen et al., 2008; Bedford and Small, 2008; Mayor et al., 2009). These studies are fundamental to understanding the relationship between plant spatial patterns and water redistribution processes. The present study examined this phenomenon at a broader scale, in ecosystems with two different soil types, different levels of aridity and different impact of livestock grazing.

Our results indicate that plant spatial patterns were correlated with soil sorptivity, but this correlation was not equally evident for soil hydraulic conductivity. Early in a rainfall event, the sorptive forces of dry soil have the most effect on the rate of water infiltration. As the soil becomes saturated with water, the infiltration process becomes more strongly influenced by gravity, and this depends on the hydraulic conductivity of the soil (Angulo-Jaramillo et al., 2000). Thus, our results suggest that sorptive forces before saturation are more relevant for water run-off and plant spatial pattern. This interpretation is supported by the presence of individual rainfall events in semi-arid ecosystems that are often not large enough to saturate the soil.

Our study sites were predominantly flat; hence the run-off water moves slower than it would in steep areas. Consequently, water infiltration in vegetation patches would be considerable, and water and sediment losses by run-off are likely to be small. On steep slopes, some previous studies indicate that the hydro-physical properties of the soil have less effect on

plant spatial pattern, but this requires further study. For example, in semi-arid sloped areas of southern Spain, the properties of bare soil had little effect on water run-off, sediment losses, or plant spatial pattern (Bautista et al., 2007). Run-off and infiltration patterns on slopes are mostly dependent on the ability of vegetation to trap water and sediments, and this is influenced by plant spatial patterns and plant functional type (Puigdefabregas, 2005), both of which are largely independent of the hydro-physical properties of soils in such regions (Bautista et al., 2007).

In our study, the predominance of perennial grasses and the spatial pattern of vegetation were strongly correlated, suggesting that the type of plant can have a significant effect on the spatial pattern of vegetation (see also Abrahams et al., 1995; Pockman and Small, 2010). The capacity for clonal growth allows perennial grasses to quickly and efficiently benefit from the plant-water infiltration feedback (Pueyo et al., 2010). Furthermore, perennial grasses have superficial root systems that allow the trapping of run-on water (Cammeraat et al., 2010). However, these root systems also exert strong below-ground competition for space with seedlings and forbs (Jurena and Archer, 2003; Alados et al., 2006), and this might explain the weak spatial association of grasses with other plant types. Thus, the presence of aggregated vegetation cover is not always associated to positive interactions among individuals of different plant types.

In this study, we also examined the relationship between vegetation spatial pattern and vegetation indicators of ecosystem health. The water redistribution that occurs in source-sink systems concentrates water and resources efficiently, and thereby increases productivity and diversity (Shachak et al., 1998; Aguiar and Sala, 1999; Tongway et al., 2001). In Mediterranean ecosystems, vegetation patches, which are considered “islands of fertility”, are essential for sustaining ecosystem diversity and productivity (Maestre et al., 2009). In our study, sites with more aggregated vegetation spatial patterns were more diverse and had greater vegetation cover. Thus, our results would support the view that patchy spatial patterns are beneficial to the

ecosystem. However, causal relationships cannot be proven in observational studies. Thus, in our case, the presence of greater plant species richness in sites with more aggregated patterns could be also attributed to the greater overall vegetation cover. In any case, our observations of positive association of plant spatial pattern, plant species richness and vegetation cover suggests that an aggregated spatial pattern of vegetation indicates good ecosystem health in semi-arid Mediterranean ecosystems.

The second objective of this study was to examine the effects of abiotic and biotic stressors on the hydro-physical properties of soils, plant community composition, and plant spatial patterns. As we predicted, grazing reduced water infiltration in soils that were prone to compaction (silty soils). At these sites, water infiltration rates with crust ($q3D_{crust}$) and without crust ($q3D_{I-10}$) were higher at the ungrazed sites. On the contrary, the hydrology of gypseous soils was strongly influenced by the presence of soil crust. In these cases, water infiltration rates with crust were higher at grazed areas (where the crust was removed by trampling), but water infiltration rates without crust were slightly lower at grazed areas. Although some studies have shown that biological crust, rather than the physical soil crust increase water infiltration (Eldridge et al., 2010), the present results and other studies reported that removal of soil crust increased infiltration (Eldridge et al., 2000). This topic is controversial, and there appear to be contrasting results in the literature (West, 1990; Eldridge and Greene, 1994; Maestre et al., 2002), because the effect of biological soil crust on infiltration depends on the hydrophobic or hydrophilic nature of the predominant crust species (Eldridge et al., 2010).

In the gypseous plant communities of the Middle Ebro Valley, we found that gypsophytes were distributed randomly, but that gypsovags were strongly aggregated. In addition, gypsophytes were more abundant in ungrazed arid sites, where the hydrology was mostly controlled by the soil crust. These results are in accordance with the observation that gypsophytes are adapted to germinate in intact gypseous soils (Escudero et al., 1999), and can

establish and maintain large abundances even under restrictive conditions, whereas gypsovags appear to aggregate in the rare locations that allow establishment. However, previous studies of the establishment patterns of the gypsophyte *Helianthemum squamatum* suggest an intricate spatio-temporal pattern in seedling establishment, survival, and mortality (Escudero et al., 2005; De la Cruz et al., 2008). This suggests that the spatial patterns of adult gypsophytes might result from antagonistic forces at the time of establishment and also during subsequent growth stages.

Grazing and aridity altered the composition of our plant communities. Specifically, grazing reduced the abundance of perennial grasses in silty sites, and in the most arid conditions. However, other abiotic factors might also affect the vegetation response to aridity. For example, in soils with low infiltration capacity (silty soils), salinity and aridity are intrinsically associated, because the increased evaporation at high temperature increases both of these. Thus, the individual effects of salinity and climatic aridity cannot be disentangled along aridity gradients, and salt accumulation at the most arid sites must be considered an additional water stress for vegetation, because it reduces the osmotic potential of the soil (Callaway, 2007). Nevertheless, we found no differences in the intrinsically aggregated pattern of vegetation cover across sites. In other words, the abiotic and biotic stressors in the area did not cause appreciable changes in the plant spatial patterns of those semi-arid ecosystems, which showed a strong tendency to spatial aggregation in all the external conditions examined.

In our study, aridity had little effect on plant spatial patterns or on the infiltration capacity of bare soil. Climatology models predict that arid and semi-arid regions of the world, and more specifically in the Mediterranean area, will become increasingly arid in the future years due to an increase of temperature and decrease of rainfall (IPCC, 2007). The eco-hydrological consequences of climate change on semi-arid ecosystems still needs to be studied, but studies of ecosystems along stress gradients, such the present study serve as a first approach to understand the possible response of plant communities to increased aridity.

On the other hand, the influence of soil type on the effects of grazing suggests that the complexity of grazing behaviour should be incorporated into theoretical models of arid ecosystems, since traditionally, such models only consider the amount of biomass consumed by animals (Rietkerk et al., 1997). In addition, to ensure the use of appropriate conservation strategies, we suggest that management policies consider the differential effects of grazing on gypseous soils.

In conclusion, our study of the relationships of plant spatial pattern, hydro-physical properties of soil, and the composition of plant communities underscores the importance of the plant-water infiltration feedback on the function of Mediterranean semi-arid ecosystems. Other factors, such as adaptations that allow plants to become established in bare soil, may also influence plant spatial pattern and these also require further investigation. Grazing, aridity, and soil type affect the eco-hydrological behavior of ecosystems in multiple ways and these often interact with one another. Our results indicate that gypseous environments have a unique response to abiotic and biotic external stress because of the presence of specialized flora and because of the important role of soil crust in controlling soil hydrology.

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659 Table legends

660 Table 1. Location, abbreviation, climatic conditions (annual rainfall, P, mean annual

661 temperature, T, and aridity index $T/P \times 100$), stocking rate of grazed areas, gypsum and

662 CaCO_3 content, pH and Electrical conductivity (EC) for the field sites.

663 Table 2. Univariate spatial patterns of all individuals, and of perennial grasses, and bivariate

664 spatial patterns of perennial grasses vs. other plant life forms at each of the study sites. +,

665 aggregated pattern; -, over-dispersed pattern; 0, pattern not significantly different from

666 random; 0/+, pattern only significantly aggregated at certain scales, and not significantly

667 different from random at most scales; ND, insufficient data for analysis (< 50 points).

668 Significance was tested with 5% and 95% confidence limits obtained with a

669 randomization test (39 replicates; see Methods section for details).

670 Table 3. Fixed effects of the mixed linear-effect models for soil hydro-physical and plant

671 community properties with soil type, aridity, grazing and their interactions as independent

672 factors. $q3D_{crust}$, total degrees of freedom (d.f.) = 63, residual d.f. = 58; $q3D_{1-10}$, total d.f.

673 = 62, residual d.f. = 57; *Perennial grasses frequency* and *DFA* total d.f. = 47, residual d.f.

674 = 41; *Gypsophyte frequency* and *Gypsovags frequency*, total d.f. = 23, residual d.f. = 20.

675 All p values less than 0.005 are shown in bold.

676 **Figure legends**

677 Figure 1. a) Schematic diagram of the hypothesized relationships between the soil properties and

678 plant communities, and the influence of external factors. Numbers refer to the objectives

679 described in the Introduction. This study considered the intrinsic hydro-physical

680 properties of the bare soil, but not the modifications of soils that occur under the

681 vegetation patches; b) Study area and location of field sites.

682 Figure 2. Relationship of plant spatial pattern (DFA) with a) sorptivity of intact soils (S_{crust}), and

683 b) sorptivity of soil after removal of the soil crust (S_{1-10}). Black points indicate the mean

values per field site on the x-axis ($n = 8$) and the y-axis ($n = 6$) and bars indicate standard errors.

Figure 3. Relationship of plant spatial pattern (DFA) with a) the abundance of perennial grasses, b) the abundance of gypsophytes at gypseous sites, c) the abundance of gypsovags at gypseous sites, d) plant species richness, and e) abundance of bare soil cover. Black points ($n = 48$) represent pairs of x and y values for each transect. The significance of the relationships was corrected by inclusion of location in the regressions (field site = 4) as a random factor (see text; 12 transects per location). Lines represent regressions for each location.

Figure 4. Ripley's L functions (solid line) for the univariate pattern of gypsophytes at a) GVN and b) GVV, univariate pattern of gypsovags at c) GVN and d) GVV, and bivariate pattern of gypsophytes vs. gypsovags at e) GVN and f) GVV. Dotted lines indicate 5% and 95% confidence limits from randomization tests (39 replicates; see Methods section for details). At GHN and GYN there were too few gypsophytes for calculation of Ripley's L function (<50 points per 100-m transect).

Figure 5. Effect of grazing on infiltration flux of intact soil ($q3D_{crust}$) in a) silty sites and b) gypseous sites, and on infiltration flux after removal of the soil crust ($q3D_{1-10}$) c) in silty sites and d) in gypsesous sites. Dots and bars indicate means ($n = 16$) and standard errors.

Figure 6. Mean abundance (% cover; $n = 6$ per bar) and standard errors of perennial grasses at a) silty sites and b) gypseous sites; c) mean abundance (% cover; $n = 6$ per bar) and standard errors of gypsophytes at gypseous sites; d) mean abundance (% cover; $n = 6$ per bar) and standard errors of gypsovags at gypseous sites.

Table 1.

Abbreviation	Location	Soil type	Aridity	Grazing	Annual rainfall (mm)	Mean annual temperature (°C)	Aridity index (°C mm ⁻¹)	Stocking rate (head ha ⁻¹ yr ⁻¹)	Gypsum content (%)	CaCO ₃ content (%)	pH	EC (mS cm ⁻¹)
SVN	Planerón	Silty	Very high	No	319	15.4	4.83	-	7.02	10.63	8.21	2.00
SVY	Planerón	Silty	Very high	Yes	319	15.4	4.83	0.32	41.04	6.28	8.09	2.17
SHN	Jubierre	Silty	High	No	376	14.7	3.91	-	0.24	25.07	8.71	0.09
SHY	Jubierre	Silty	High	Yes	378	14.7	3.89	0.23	0.23	25.72	8.54	0.65
GVN	Lomaza	Gypsum	Very high	No	339	14.8	4.37	-	62.39	7.68	8.02	2.22
GVY	Lomaza	Gypsum	Very high	Yes	347	14.8	4.27	0.35	43.17	11.23	7.97	2.22
GHN	Leciñena	Gypsum	High	No	462	13.6	2.94	-	49.32	14.78	7.86	1.93
GHY	Leciñena	Gypsum	High	Yes	470	13.5	2.87	0.66	45.83	21.29	7.91	2.03

Note: Site SVY was not classified as gypseous because gypsum was only present as inert rocks (from an upland gypseous hill) in a silty matrix (Moret et al., 2011).

Table 2.

		Site							
Pattern		GVN	GVY	GHN	GHY	SVN	SVY	SHN	SHY
Univariate	All	+	+	+	+	+	+	+	+
	Perennial grasses	<i>ND</i>	+	+	+	<i>ND</i>	<i>ND</i>	0/+	0/+
Bivariate	Perennial grasses vs. other plant types	<i>ND</i>	0/+	0	0	<i>ND</i>	<i>ND</i>	0/+	0

Table 3.

Dependent variable	Explanatory variable	Value	SE	t-value	p-value
q3D _{crust}	Intercept	0.011	0.002	5.186	<0.001
	Soil (Gypsum)	0.007	0.002	3.023	0.003
	Aridity (VeryHigh)	0.004	0.002	1.541	0.128
	Grazing (Ungrazed)	0.004	0.003	1.436	0.156
	Soil (Gypsum):Grazing (Ungrazed)	-0.008	0.003	-2.465	0.017
	Aridity (VeryHigh):Grazing (Ungrazed)	-0.002	0.003	-0.616	0.540
q3D ₁₋₁₀	Intercept	0.018	0.006	2.846	0.006
	Soil (Gypsum)	0.018	0.007	2.507	0.015
	Aridity (VeryHigh)	0.011	0.007	1.536	0.130
	Grazing (Ungrazed)	0.049	0.009	5.557	<0.001
	Soil (Gypsum):Grazing (Ungrazed)	-0.031	0.010	-3.076	0.003
	Aridity (VeryHigh):Grazing (Ungrazed)	-0.014	0.010	-1.360	0.179
Perennial grasses freq.	Intercept	0.675	0.234	2.885	0.006
	Soil (Gypsum)	-0.082	0.270	-0.305	0.812
	Aridity (VeryHigh)	-0.321	0.270	-1.187	0.446
	Grazing (Ungrazed)	0.096	0.041	2.321	0.025
	Soil (Gypsum):Grazing (Ungrazed)	-0.278	0.047	-5.855	<0.001
	Aridity (VeryHigh):Grazing (Ungrazed)	0.172	0.047	3.627	<0.001
Gypsophytes freq.	Intercept	0.308	0.018	17.330	<0.001
	Grazing (Ungrazed)	-0.084	0.025	-3.348	0.003
	Grazing (Ungrazed):Aridity (VeryHigh)	0.165	0.025	6.561	<0.001
	Grazing (Grazed):Aridity (VeryHigh)	-0.060	0.025	-2.374	0.028
Gypsovags freq.	Intercept	1.098	0.042	26.316	<0.001
	Grazing (Ungrazed)	-0.054	0.060	-0.921	0.368
	Grazing (Ungrazed):Aridity (VeryHigh)	-0.405	0.060	-6.870	<0.001
	Grazing (Grazed):Aridity (VeryHigh)	-0.500	0.060	-8.305	<0.001
DFA	Intercept	0.851	0.432	19.707	<0.001
	Soil (Gypsum)	-0.023	0.050	-0.456	0.728
	Aridity (VeryHigh)	-0.136	0.050	-2.722	0.224
	Grazing (Ungrazed)	-0.015	0.024	-0.594	0.556
	Soil (Gypsum):Grazing (Ungrazed)	-0.024	0.029	-0.832	0.410
	Aridity (VeryHigh):Grazing (Ungrazed)	0.036	0.029	1.249	0.219

a)

b)

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

a)

b)

c)

d)

Figure 6