

Linking the spatial patterns of organisms and abiotic factors to ecosystem function and management: Insights from semi-arid environments

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Numerous theoretical and modeling studies have demonstrated the ecological significance of the spatial patterning of organisms on ecosystem functioning and dynamics. However, there is a paucity of empirical evidence that quantitatively shows how changes in the spatial patterns of the organisms forming biotic communities are directly related to ecosystem structure and functioning. In this article, I review a series of experiments and observational studies conducted in semi-arid environments from Spain (degraded calcareous shrubland, steppes dominated by *Stipa tenacissima*, and gypsum shrublands) to: 1) evaluate whether the spatial patterns of the dominant biotic elements in the community are linked to ecosystem structure and functioning, and 2) test if these patterns, and those of abiotic factors, can be used to improve ecosystem restoration. In the semi-arid steppes we found a significant positive relationship between the spatial pattern of the perennial plant community and: i) the water status of *S. tenacissima* and ii) perennial species richness and diversity. Experimental plantings conducted in these steppes showed that *S. tenacissima* facilitated the establishment of shrub seedlings, albeit the magnitude and direction of this effect was dependent on rainfall conditions during the first yr after planting. In the gypsum shrubland, a significant, direct relationship between the spatial pattern of the biological soil crusts and surrogates of ecosystem functioning (soil bulk density and respiration) was found. In a degraded shrubland with very low vegetation cover, the survival of an introduced population of the shrub *Pistacia lentiscus* showed marked spatial patterns, which were related to the spatial patterns of soil properties such as soil compaction and sand content. These results provide empirical evidence on the importance of spatial patterns for maintaining ecosystem structure and functioning in semi-arid ecosystems. Furthermore, they show how taking into consideration the small-scale spatial patterns of organisms and abiotic factors, their restoration can be improved.

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The presence of non-random patterns in the spatial distribution of organisms is the norm, rather than the exception, in most natural, semi-natural and human-dominated ecosystems (Perry 1995, Dale 1999, Perry et al. 1999, Webster and Boag 1992, Grundmann and Debouzie 2000). These patterns are determined by a combination of processes that include environmental heterogeneity (Ehrenfeld et al. 1997), biotic interactions (Callaway 1995), patterns of growth and propagule dispersal (Lechowicz and Bell 1991), availability of "safe sites" for establishment (Harper et al. 1965), and random factors (Halpern 1988). The understanding of these patterns is one of the core objectives of ecology as a science; therefore, it is not surprising that spatial pattern analysis has received substantial attention by ecologists in the last decades, and that numerous methods for quantifying spatial patterns have been developed (Dale 1999, Perry et al. 2002).

Research on the spatial patterns of organisms has not been limited to describe them and to infer the underlying formative processes. In recent decades there has been a growing body of theoretical and modeling studies highlighting the importance of the spatial patterns of organisms *per se* (i.e. independently of co-occurring community attributes such as cover, species richness and evenness) as drivers of ecosystem functioning, stability and dynamics (Pacala and Deutschman 1995, Tilman and Kareiva 1997, Bolker et al. 2003). However, and despite their recognized importance, relatively few studies have empirically examined how these patterns alter phenomena such as individual performance, population dynamics, species coexistence, and community structure (Schmid and Harper 1985, Bergelson 1990, Stoll and Prati 2001, Tirado and Pugnaire 2003, Monzeglio and Stoll 2005). Furthermore, even fewer studies have evaluated whether these spatial patterns are directly related to ecosystem functioning in natural communities (Pacala and Deutschman 1995, Maestre et al. 2005a, Kikvidze et al. 2005).

Being a priority in land management in a wide variety of biomes, the restoration of degraded ecosystems is especially important in arid and semi-arid areas, which are being degraded and desertified at a fast rate throughout the globe (Kassas 1995, Le Houérou 1996, Reynolds and Stafford Smith 2002, Reynolds et al. 2005). Despite the specific objectives of their restoration may differ depending on the degree of degradation, and on climatic, biotic and socio-economic constraints, restoration programs often aim to increase plant cover by directly introducing plant individuals, primarily woody species (Whisenant 1999, Pausas et al. 2004, Maestre and Cortina 2004a). This management action is crucial to stop further degradation, to combat desertification and to foster the recovery of the structure, composition and function of degraded ecosystems in these areas (Gao et al. 2002, Maestre and Cortina 2004b, Bastida et al. 2006). The importance of restoration programs is likely to increase in the near future due to their potential to fix atmospheric CO₂ and to reduce its concen-

tration at a global scale (Keller and Goldberg 1998, Lal 2001).

The successful establishment of vegetation during the restoration of degraded arid and semi-arid areas is a challenging task due to the harsh climatic conditions, to the low soil resource levels, and to the scarce and unpredictable rainfall regimes that characterize these environments (Whisenant 1999). Important research efforts have been devoted in the last decades to overcome these limitations, and nowadays there are numerous techniques to aid plant establishment during restoration of arid and semi-arid environments (see Cortina et al. 2004 and Pausas et al. 2004 for reviews). Surprisingly, the use of the own spatial patterns of existing organisms and abiotic factors has often been neglected during the restoration of these areas (Padilla and Pugnaire 2006). Despite important floristic differences between regions, the physiognomy of semi-arid vegetation typically consist on a two-phase mosaic of discrete plant patches embracing different functional types – typically shrubs, perennial grasses and trees – surrounded by a bare ground matrix (Valentin et al. 1999). This spatial patterning is essential to maintain ecosystem composition and function (Noy Meir 1973, Tongway et al. 2004), and, indeed, is often a useful indicator of ecosystem degradation in arid and semi-arid areas (Wu et al. 2000, Bastin et al. 2002, Maestre and Cortina 2004b).

In this article I briefly review the results of a series of observational and experimental studies conducted over the last decade in three representative ecosystems of semi-arid areas of Spain: *Stipa tenacissima* steppes, gypsum outcrops dominated by biological soil crusts and degraded shrublands with very low perennial plant cover. These studies aimed to answer three basic questions: i) Is the spatial pattern of a community *per se* important as a driver of ecosystem structure and functioning?, ii) Can plant-plant interactions be employed to improve plant establishment during restoration?, and iii) Does the small-scale spatial pattern of abiotic factors determine the outcome of restoration actions? I do not intend to provide a comprehensive review of all the relevant research conducted on these topics, which have received considerable attention by ecologists and restoration practitioners in recent years. I rather aim to illustrate the relevance of the spatial pattern of organisms and abiotic factors for maintaining ecosystem structure/functioning and for improving restoration actions in semi-arid areas.

Ecosystem structure and the spatial pattern of *Stipa tenacissima* in semi-arid steppes

Stipa tenacissima L. steppes are one of the most important vegetation types in the driest areas of the Western Mediterranean Basin, where they cover 28000 km² in Northern

Africa (from Lybia to Morocco) and in the Iberian Peninsula (Le Houérou 2001). In their present state, these steppes are the result of a long-term human use of wooded steppes that included cutting, burning, fiber-cropping and overstocking, followed by abandonment (Cortina et al. 2007). The fiber from *S. tenacissima* has great strength and flexibility, and has been used to make ropes, sandals, baskets, mats, and other durable articles, and to produce high quality paper for centuries (Barber et al. 1997). In Spain there are historical records on the use of *S. tenacissima* by humans as early as 3500 BC. The intensification on its use 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 1960's (Barber et al. 1997). Because these activities, open shrublands containing *S. tenacissima* but dominated by species like *Pinus halepensis* Miller, *Quercus coccifera* L. and *Pistacia lentiscus* L. may have been degraded to *S. tenacissima* steppes, eventually supporting remnant shrub fragments (Cortina et al. 2007, Maestre and Cortina 2005).

Despite the long-lasting human activities that took place in *S. tenacissima* steppes are still influencing aspects of the composition and structure in these ecosystems, such as species richness and diversity (Maestre 2004), it must be noted that direct plantings of tussocks were not widespread (Yanes 1993, Barbet et al. 1997). Nowadays, most *S. tenacissima* steppes are commonly structured in a spotted or banded spatial configuration, with vegetation patterns resembling features of the "tiger-bush" vegetation described for semi-arid regions throughout the world (Fig. 1). It has been shown that these patterns are largely controlled by topography and the associated runoff fluxes (Sánchez 1995, Puigdefábregas et al. 1999). Thus, on moderate slopes and at the catchment scale, *S. tenacissima* tussocks tend to be aligned parallel to the contours to maximize their ability to trap runoff water generated in the bare ground areas during storm events (Puigdefábregas and Sánchez 1996, Webster and Maestre 2004, Maestre et al. 2005b). These inputs are critical for *S. tenacissima* growth (Puigdefábregas et al. 1999), and are also affected by the soil surface conditions in these areas (Cerdà 1997,



Fig. 1. View of different *Stipa tenacissima* steppes from Central and South-East Spain, showing the typical two-phase mosaic of bare ground areas and *S. tenacissima* tussocks and the presence of sprouting shrubs such as *Quercus coccifera* and trees like *Pinus halepensis*.

Maestre et al. 2002a), and by attributes of discrete plant patches such as cover and spatial pattern (Imeson and Prinsen 2004, Cammeraat 2004).

In a recent study conducted in 15 steppe sites of SE Spain, Maestre and Cortina (2006) evaluated the effects of different ecosystem attributes – 14 abiotic and biotic variables ranging from climatic to structural attributes of the vegetation – on the $\delta^{13}\text{C}$ of *S. tenacissima*, a surrogate of its water use efficiency (Lathja and Milchener 1994). These authors found that the $\delta^{13}\text{C}$ of *S. tenacissima* leaves was negatively related to its cover and positively related to the spatial pattern of perennial vegetation (Fig. 2a, b). The former relationship may be the result of the effects of perennial plant cover on the nutrient status of *S. tenacissima*. The $\delta^{13}\text{C}$ of *S. tenacissima* leaves increased with increases in their N concentration (Fig. 2c), which was indeed negatively related to perennial plant cover (Fig. 2d). The effect of total cover on the nutrient status of *S. tenacissima* sug-

gests the presence of intra- and inter-specific competition for belowground resources, a process already demonstrated in other steppes of SE Spain (Armas 2003, Ramírez 2006). Interestingly, the spatial pattern of perennial vegetation was not related to either total plant cover ($r = -0.371$, $p = 0.173$, $n = 15$) or leaf N concentration ($r = 0.435$, $p = 0.134$, $n = 15$). Therefore, the positive relationship between the $\delta^{13}\text{C}$ of *S. tenacissima* and the former variable suggests that an increase in the spatial aggregation of perennial vegetation, independently of its density, promotes an increase in the water use efficiency of this species. Albeit the Maestre and Cortina (2006) study cannot provide a full understanding of the mechanisms underlying the relationships observed, their results provide empirical evidence showing that the spatial pattern of vegetation *per se* may influence its own water use.

In a series of 17 steppe sites located along a degradation gradient in SE Spain, Maestre and Cortina (2004b) found

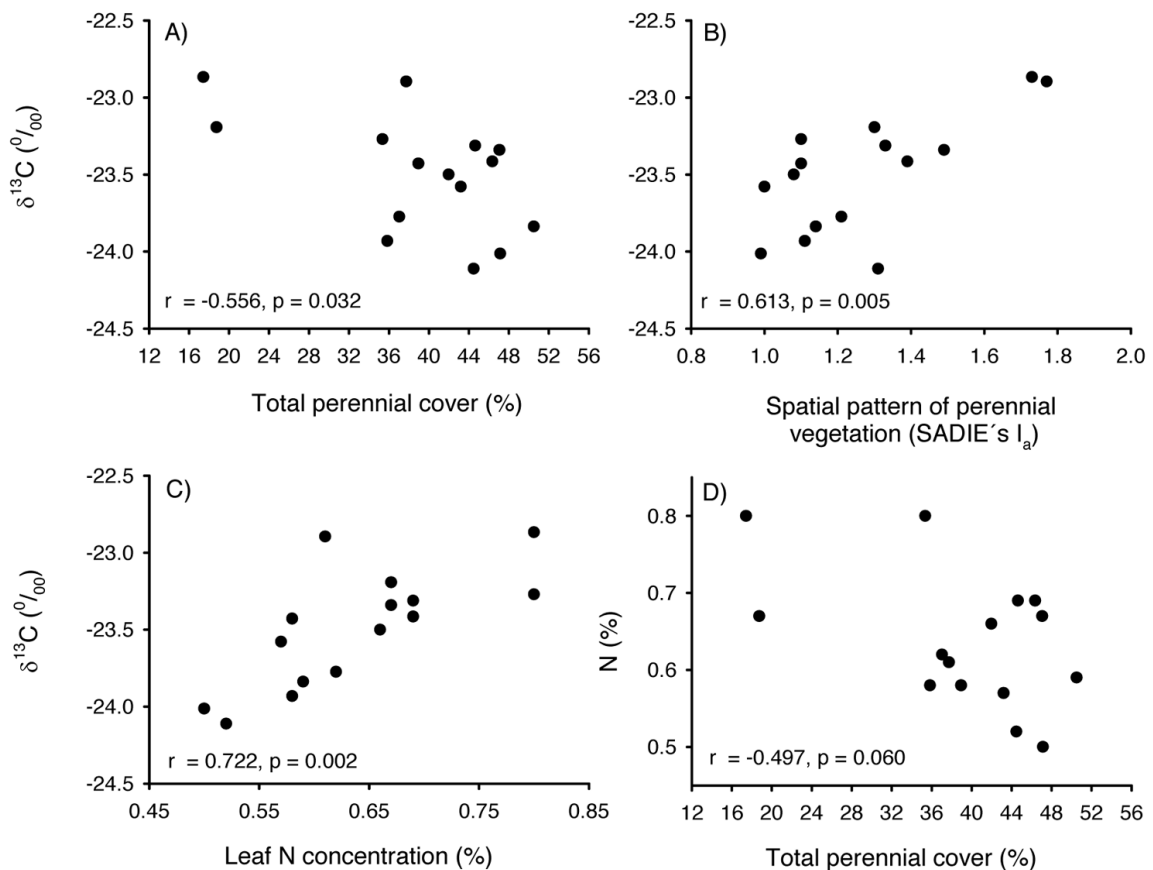


Fig. 2. Relationships between the $\delta^{13}\text{C}$ of *Stipa tenacissima* and total perennial plant cover (A), the spatial pattern of perennial vegetation (B) and leaf N content (C), and between total plant cover and leaf N content (D). Plant spatial patterns were measured using SADIE analysis (Perry et al. 1999), in 15 steppes from SE Spain. As I_a increases, the spatial pattern of vegetation becomes more aggregated. Results of correlation analyses (Pearson correlation coefficient) are also shown. Adapted from data presented in Maestre and Cortina (2006).

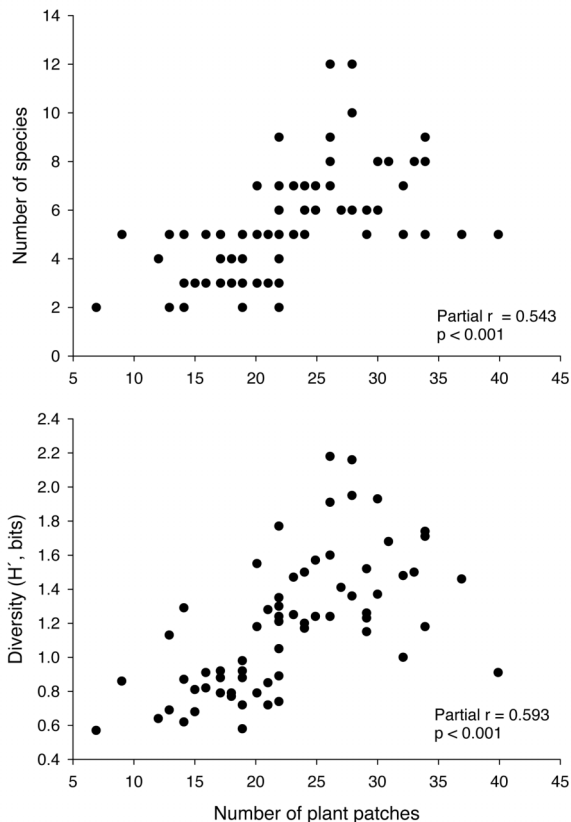


Fig. 3. Relationships between the number of discrete plant patches and the richness and diversity of perennial vascular plants in semi-arid steppes of SE Spain. Results of partial correlation analyses, where the effect of plant cover is controlled, are shown in the lower right margin of each graph. Adapted from data summarized in Maestre and Cortina (2004b).

a strongly significant and positive relationship between the number of discrete plant patches (*S. tenacissima* constituted between the 38% and 94% of the total plant cover) – a simple indicator of the spatial patterning of vegetation – and both the number and diversity of perennial plant species in 30 m-long transects (Fig. 3). This relationship, which was maintained even when controlling for plant cover – a key vegetation attribute that could confound it –, indicates that the spatial patterning of *S. tenacissima* tussocks is an important attribute for maintaining the structure of these ecosystems.

Positive effects of *S. tenacissima* tussocks on the diversity and richness of vascular plants in semi-arid steppes may be related to facilitative processes mediated by their effects on microclimate and soil properties. Recent studies have thoroughly described the effect of these tussocks on their own microenvironment through microclimatic amelioration (Maestre et al. 2001, 2003a), the improvement in the soil structure and depth (Bochet et al. 1999, Puigdefábregas et al. 1999), and the increase in soil moisture (Puigdefábregas

and Sánchez 1996, Maestre et al. 2001), water infiltration (Cerdà 1997, Maestre et al. 2002a), and carbon storage and nitrogen (Martínez-Sánchez et al. 1994, Sánchez 1995, Bochet et al. 1999) in relation to adjacent areas devoid of vascular plants. Therefore, *S. tenacissima* creates the so-called “resource islands” (Reynolds et al. 1999), a phenomenon commonly described in shrub species from arid and semi-arid areas throughout the world (Whitford 2002).

Through the creation of resource islands, *S. tenacissima* modifies the small-scale distribution and performance of a wide variety of taxa. In semi-arid steppes of SE Spain, Maestre (2003a, b) and Maestre et al. (2002a) have described how *S. tenacissima* tussocks modify the small-scale spatial patterning of soil lichens, cyanobacteria and mosses, with mosses dominating in the vicinity of the tussocks and cyanobacteria and lichens dominating the bare ground areas located between them. Interestingly, a significant negative relationship between the cover of cyanobacteria, which dominate bare-ground areas, and the infiltration rate was found (Maestre et al. 2002a), suggesting that the effect of *S. tenacissima* on these organisms could modify the source-sink process described above on its own benefit. Regarding vascular plants, it has been found that the vicinity of *S. tenacissima* tussocks holds more diversity and abundance of annual plants than the adjacent open ground areas (Sánchez 1995). Observational studies have reported positive spatial interactions between the spatial patterns of *S. tenacissima* and those of species such as *Anthyllis cyrisoides* (Webster and Maestre 2004, Maestre et al. 2005b), as well as higher survival of seedlings and adults of woody species in the vicinity of *S. tenacissima* tussocks than in open ground areas (García-Fayos and Gasque 2002). The implications of plant-plant interactions involving *S. tenacissima* for the restoration and management of these ecosystems will be discussed below.

Biotic attributes and ecosystem functioning in communities dominated by biological soil crusts

Biological soil crusts (BSC), composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi and lichens, are a major biotic component of arid and semi-arid ecosystems world-wide (West 1990, Belnap and Lange 2001). These crusts frequently cover soil surfaces (Fig. 4) and exert a strong influence on critical ecosystem processes like infiltration, carbon sequestration and nutrient cycling (Beymer and Klopatek 1991, Evans and Ehleringer 1993). They also influence the distribution and abundance of plants and animals (Prasse and Bornkamm 2000, DeFalco et al. 2001, Shepherd et al. 2002). Despite important advances in our knowledge of the structure, composition, physiology and biogeography of biological soil crusts (reviewed by Belnap & Lange 2001), little is known on the

A)



B)



Fig. 4. A) View of biological soil crusts dominating the spaces between plants in non-disturbed gypsum outcrops from central Spain, B) Close up view of the lichens forming the crust; the main species in this picture are *Fulgensia subbracteata* (yellow thalli) and *Toninia sedifolia* (grey and black thalli).

effects of small-scale habitat variation on the spatial patterns of their components (Maestre 2003a, b, Martínez et al. 2006), and on the influence of these patterns on ecosystem functioning.

In a recent study, Maestre et al. (2005a) related biotic attributes of BSC (spatial pattern, cover, species richness and species evenness) to different surrogates of ecosystem functioning (total C and N, aggregate stability, bulk density and soil respiration) using structural equation modeling in two study sites located in central and SE Spain. Both the biotic attributes of BSC and the surrogates of ecosystem functioning showed an important degree of variation within the studied areas (Maestre et al. 2005a, Martínez et al. 2006). In the site located in Alicante, spatial pattern was positively and directly related to respiration, and negatively related to soil bulk density (Fig. 5). However, the magnitude of this relationship was lower than that between at-

tributes such as cover and species richness on the same surrogates of ecosystem functioning. In the other site, spatial pattern was not significantly related to any of the surrogates of ecosystem functioning evaluated.

These results represent, to our knowledge, one of the first empirical evidences of a direct relationship between the spatial pattern of a community and surrogates of ecosystem functioning, and add new empirical evidence on the importance of the spatial pattern of a community as a driver of ecosystem functioning. They also suggest that this importance may depend on co-occurring community attributes like total cover and diversity.

Small-scale spatial heterogeneity of soil properties and ecosystem restoration in degraded shrublands

In semi-arid environments, germination and subsequent establishment of plants is strongly controlled by soil water availability (Veenendal et al. 1996, Escudero et al. 1999). This availability shows a strong degree of heterogeneity owing to large spatial and temporal variations in rainfall patterns (Le Houérou et al. 1988), and to complex spatial redistribution of rainwater once it arrives to the soil surface (Tongway and Ludwig 1994, Seghieri et al. 1997). Such redistribution is strongly influenced by soil surface properties like compaction, physical crusts and rock fragments, which have a prevailing role in runoff and infiltration dynamics in these areas (Valentin and Bresson 1992, Valentin 1994). Therefore, the spatial pattern of surface soil properties, which often is quite complex (Bromley et al. 1997, Seghieri et al. 1997, Maestre and Cortina 2002), should be critical for seedling establishment in semi-arid degraded areas holding a low vegetation cover.

In a recent study, Maestre et al. (2003b) evaluated the effects that the small-scale spatial patterns of abiotic factors had on the establishment of the shrub *Pistacia lentiscus* L. in a degraded area in Southeastern Spain. These authors randomly introduced a total of 205 one-year-old seedlings in a 0.28-ha (100 m × 28 m) experimental plot apparently homogeneous, and followed seedling survival during the three years after planting. After this time, only 36% of the seedlings survived. This mortality did not occur randomly throughout the plot, as clearly defined areas of high and low survival emerged after the first summer in the field (Fig. 6). Surface soil variables showed complex small-scale spatial patterns in the studied plot. Interestingly, variables such as bare soil cover, sand content, and soil compaction were strongly and significantly related to seedling survival, suggesting that the small-scale pattern of these variables controlled the spatial pattern of seedling survival (Fig. 7, Maestre et al. 2003b).

These results have strong implications to improve the restoration of degraded semi-arid ecosystems. Attempts to

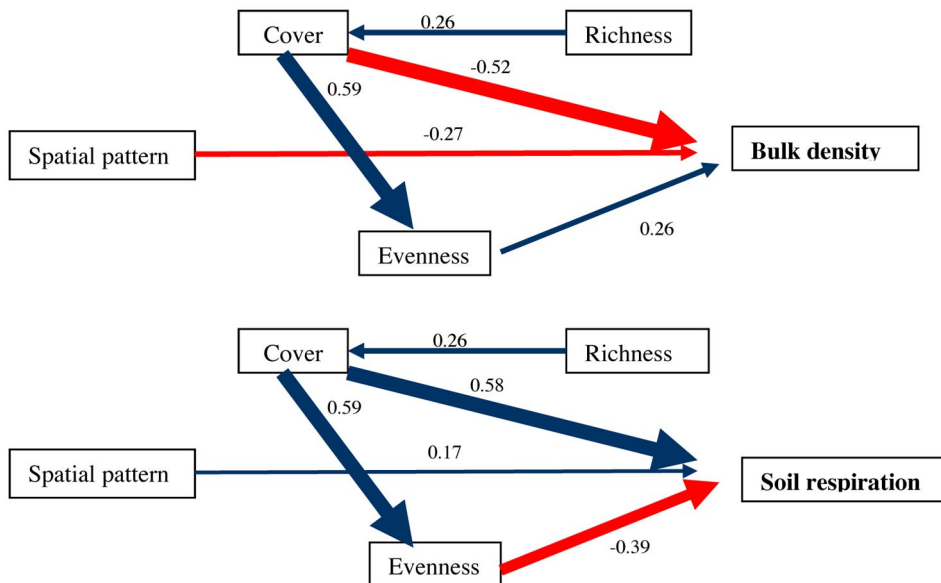


Fig. 5. Structural model showing the relationships between the attributes of biological soil crusts and different surrogates of ecosystem functioning in a gypsum area from Alicante (SE Spain). Only significant paths are shown. The breadth of the arrow is proportional to the standardized path coefficient, which is indicated by the corresponding number. Positive and negative relationships are in blue and red, respectively. Adapted from Maestre et al. (2005a).

restore them with plantings of woody species using regular grids have been often ineffective (Maestre and Cortina 2004a). Against uniform plantings, restoration of these areas should be based on the introduction of vegetation according to natural vegetation patterns, with the aim of recover previous landscape processes (Ludwig et al. 1999). Such restoration efforts can be improved by incorporating knowledge on the spatial pattern of those soil properties affecting seedling establishment. Areas of potential high mortality could be defined beforehand by performing an analysis of the spatial distribution of those variables more related with seedling survival before planting. Alternatively, the results presented suggest that restoration success could be improved reducing the amount of bare soil cover at the moment of planting, something that can be easily and cheaply done by placing stones or branches over the surface of the planting hole.

Plant-plant interactions and ecosystem restoration in *Stipa tenacissima* steppes

As mentioned above, *S. tenacissima* steppes derive from the degradation of open shrublands and woodlands by human activities carried out during centuries. Remnants of native,

late-successional, sprouting shrubs like *Pistacia lentiscus* L. and *Quercus coccifera* L. play key functional and structural roles in semi-arid *S. tenacissima* steppes from SE Spain. They enhance ecosystem functioning (Maestre and Cortina 2004b), are a major determinant of plant diversity (Maestre 2004, Maestre and Cortina 2005), and supply shelter and food for wild and game animals (López and Moro 1997). *Stipa tenacissima* steppes are often degraded through their distribution range in SE Spain (Maestre and Cortina 2004b), and increasing shrub cover and density in these ecosystems through direct planting is often a target objective when restoring them (Cortina et al. 2007).

While facilitation has been documented in a wide variety of environments (Callaway 1995), it is by far most common in arid and semi-arid ecosystems (Flores and Jurado 2003). Despite the *a priori* potential and attractiveness of facilitation as a restoration tool, and the large number of studies emphasizing its importance as a driver of community structure and ecosystem dynamics, it has been largely neglected in the restoration projects carried out in semi-arid areas for decades (Padilla and Pugnaire 2006).

The spatial patterning of *S. tenacissima* tussocks modifies the distribution of soil properties and microclimatic conditions, and observational studies suggest that these changes may facilitate the establishment of some BSC components and vascular plants. In order to evaluate the

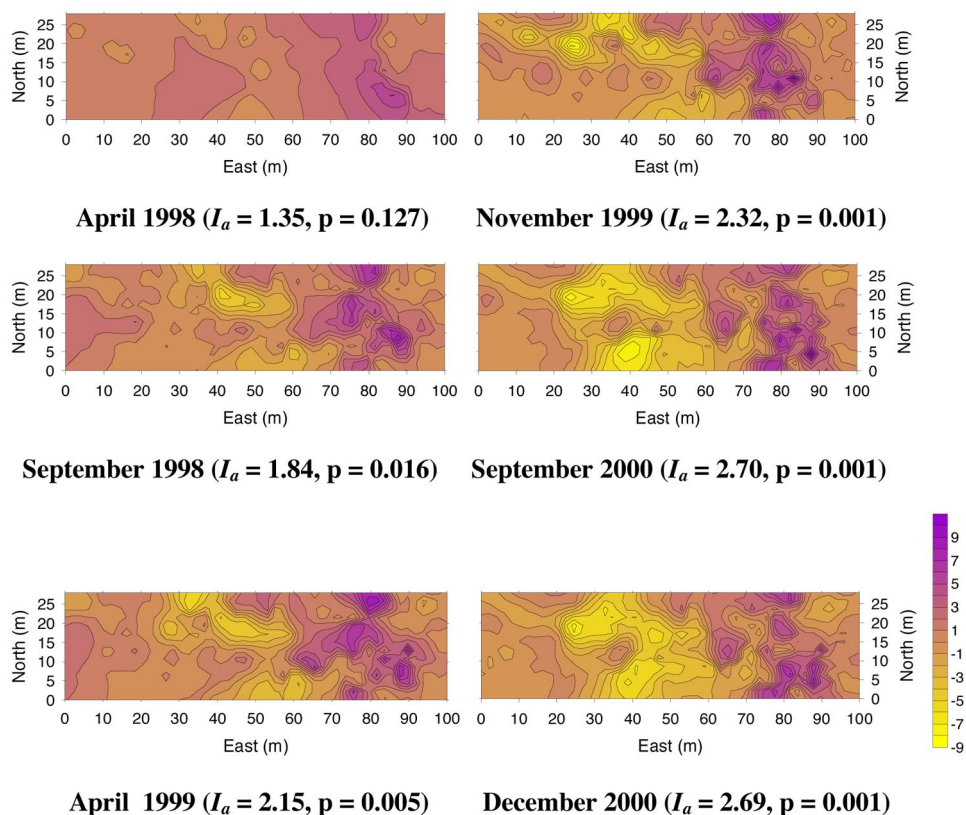


Fig. 6. Maps showing the small-scale spatial pattern of survival (estimated with the SADIE's index of aggregation, Perry et al. 1999) of 205 randomly-introduced *Pistacia lentiscus* seedlings in a 100 × 28 m experimental area from SE Spain. The maps show the distribution and evolution of patches (high survival areas, in purple) and gaps (low survival areas, in yellow) during the three years after planting. Values of I_a (SADIE's index of aggregation) significantly higher than 1 indicate that the overall spatial pattern of survival in the plot is aggregated. Adapted from Maestre et al. (2003b).

potential of these changes to improve the restoration of *S. tenacissima* steppes, a series of experimental plantings in steppes located in the province of Alicante (SE Spain) have been conducted (Table 1). In these experiments, seedlings of different shrub species were introduced under the canopy of *S. tenacissima* tussocks and in bare ground areas devoid of vascular plants. The results obtained were mainly dependent on the climatic conditions of the first year after plantation, the species considered and the presence of *S. tenacissima*. This species facilitated the establishment of the introduced seedlings in most cases where mortality was not complete. The amelioration of harsh climatic conditions through shade, as well as the increase in soil fertility, has been identified as the main drivers of this facilitation (Maestre et al. 2003a). However, this effect was not universal, and net competitive interactions between *S. tenacissima* and the introduced seedlings were observed under low rainfall conditions. Similar results have been observed in semi-arid *Pinus halepensis* plantations when introducing shrubs like *Pistacia lentiscus* under the canopy of *P. ha-*

lepnis and in the bare spaces between pines (Maestre and Cortina 2004a).

In semiarid steppes of SE Spain, it has been observed that *S. tenacissima* increases soil water availability after main rainfall events, and that this effect is maintained for some time thanks to the reduced evaporation caused by the shading of its canopy (Maestre et al. 2001, 2003a). However, and at the same time, manipulative experiments have demonstrated that competition for water between *S. tenacissima* and the introduced shrubs is intense (Maestre et al. 2003a). I argue that, in strongly water-limited environments, we should expect facilitation only when neighbors increase the water status of the target plant (the species being facilitated) when compared to bare ground areas without vegetation. As plant water status is strongly linked to the availability of water in the soil, it is likely that a threshold level in water availability will define the transition from net negative to net positive effects of *S. tenacissima* on the introduced shrubs (Maestre and Cortina 2004c; Armas and Pugnaire 2005).

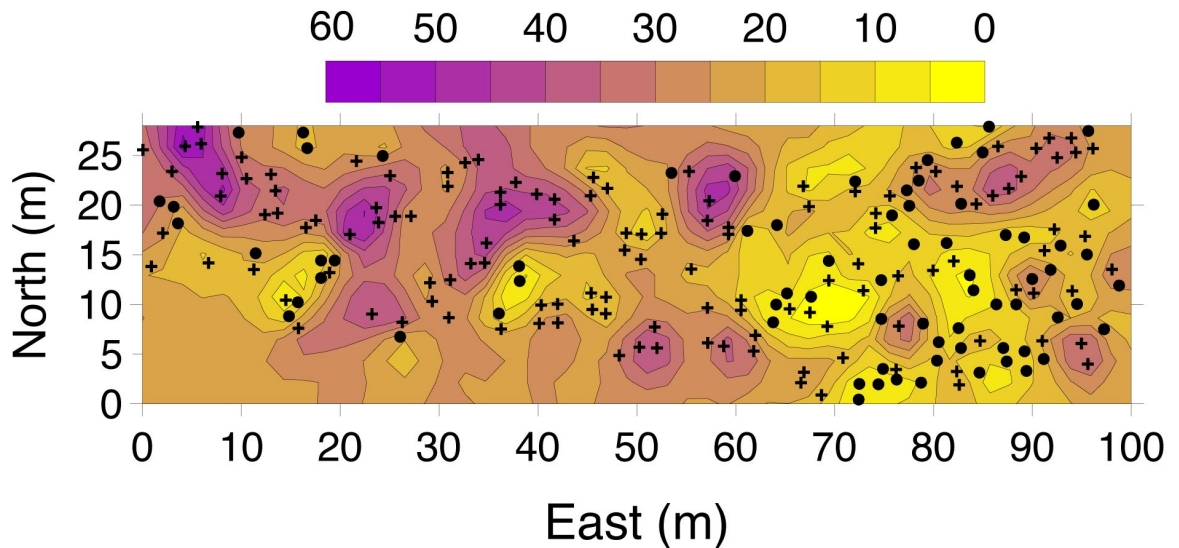


Fig. 7. Small-scale spatial distribution of the amount of bare soil covering planting holes (in %) and of seedling survival three years after planting. Crosses (+) and circles (•) are dead and alive seedlings, respectively. There is a significant negative relationship between the amount of bare soil and the survival of seedlings (logistic regression; $p < 0.001$). Elaborated from Maestre et al. (2003b).

Concluding remarks

Spatial heterogeneity in the distribution of vegetation and soil resources is a hallmark of semi-arid ecosystems worldwide, and a large set of field studies have demonstrated that the spatial pattern of vegetation influence ecosystem structure and functioning through the formation of “resource islands” underneath the canopy of plant patches (see review by Whitford 2002). However, the relative importance of spatial pattern against other co-occurring community attributes as a driver of ecosystem functioning in these ecosystems is largely unknown. Using examples drawn from *S. tenacissima* steppes and BSC-dominated communities, I have illustrated that the spatial pattern *per se* of a biotic community is an important driver of ecosystem structure and functioning. However, major gaps in our knowledge of the functional role of spatial patterns remain. Two important steps towards filling them up would be the realization of: (i) cross-ecosystem studies to evaluate the generality of the results observed so far, and (ii) experiments manipulating in a factorial fashion the biotic attributes of communities (richness, diversity and spatial pattern).

Both the analysis of spatial pattern of those abiotic factors associated with mortality clumps and positive plant interactions have an enormous potential to improve the restoration of semi-arid degraded ecosystems, especially under conditions of moderate abiotic stress. Their use in restoration would allow to incorporate the own ecosystem structure and functional processes into their active man-

agement, an issue as largely advocated by ecologists as rarely employed in practice (Wallace et al. 1980, Whisenant 1999). Both techniques have also ecological, economical and technical advantages against other techniques currently being recommended to restore degraded ecosystems in drylands (Cortina et al. 2004, Pausas et al. 2004). They do not require the use of heavy machinery, the purchase of special material (e.g. tree shelters) and the use of special nursery protocols (e.g. mycorrhizal inoculation, seedling preconditioning). They do not destroy existing vegetation, nor modify soil conditions and hydrological processes critical for proper ecosystem functioning (Ludwig et al. 2004), as techniques that employ heavy machinery do. When using facilitation as an aid in restoration, however, we must take into account that the rainfall registered during the first year after planting is critical for the success of plantations in semi-arid environments (Cortina et al. 2004), and that, under conditions of very low rainfall, neighbors may reduce, rather than enhance, the establishment of the introduced seedlings.

Advancing in our understanding of the functional role of the spatial pattern of biotic populations and communities, and of the abiotic factors driving them, will undoubtedly lead to the establishment of successful conservation, monitoring and restoration programs in semi-arid environments. The challenges of building the necessary bridges between scientists and land managers to incorporate this ecological knowledge into management practices are enormous, so is the need for urgent action to understand and manage semi-arid ecosystems worldwide.

Table 1. Results of experimental plantings evaluating the effect of *Stipa tenacissima* on the survival of one-year-old seedlings of Mediterranean woody shrubs. In all cases, the seedlings were planted using hand-made 25 × 25 × 25 cm planting holes. YE = Planting year, SP = Species, SI = Name of the experimental site, ST = survival of seedlings planted in the vicinity of *S. tenacissima* tussocks (in %), SO = survival of seedlings planted in open ground areas devoid of vascular plants (in %), DU = duration of the study (in months), RA = rainfall accumulated during the first year after planting (mm), SO = source of data.

YE	SP	SI	ST	SO	DU	RA	SO
1998	<i>Quercus coccifera</i>	Aguas	5	7	12	212	Maestre et al. (2001)
		Ballestera	13	4	12	132	
		Campello	20	2	12	197	
	<i>Pistacia lentiscus</i>	Aguas	10	3	12	212	
		Ballestera	16	15	12	132	
		Campello	17	9	12	197	
	<i>Medicago arborea</i>	Aguas	85	78	12	212	
		Ballestera	69	30	12	132	
		Campello	85	77	12	197	
1999	<i>Quercus coccifera</i>	Aguas	0	0	12	264	Maestre et al. (2002b)
		Ballestera	0	0	12	150	
		Campello	0	0	12	193	
	<i>Quercus coccifera</i> *	Aguas	0	0	12	264	
		Ballestera	0	0	12	150	
		Campello	0	0	12	193	
1999	<i>Quercus coccifera</i>	Aguas	0	0	24	264	Maestre (2002)
		Ballestera	0	0	24	150	
		Campello	0	0	24	193	
	<i>Pistacia lentiscus</i>	Aguas	8	6	24	264	
		Ballestera	0	3	24	150	
		Campello	3	0	24	193	
2001	<i>Pistacia lentiscus</i>	Aguas	57	32	15	225	Maestre et al. (2003a)
		Ballestera	4	0	15	149	
2003	<i>Pistacia lentiscus</i> †	Albatera	0	0	17	133	Maestre et al. (2006)
		Jijona	72	72	17	125	
		Lanuza	56	23	17	134	
		Marquesa	83	67	17	156	
		Finestrat	40	60	17	171	
		Fontcalent	47	88	17	109	
		Palomaret	13	0	17	139	
		Peñarrubia	0	0	17	187	
		Relleu	89	65	17	150	
Ventós	0	0	17	102			

* Seedlings inoculated with sporal inoculum of *Pisolithus tinctorius* in the nursery.

† Rainfall values from this experiment correspond to the first eight months after planting.

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