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Seed bank spatial structure in semi-arid environments: beyond the patch-bare area dichotomy

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Abstract The prevalence of patchy structures in vegetation is a common feature in semi-arid ecosystems. Although the effect of patches on seed density is widely known, we still lack information on how patch features affect seed bank density and composition. Our aim was to answer two basic questions: (1) How do seed bank density and composition vary within and outside patch aboveground physical limits? and (2) Do patch characteristics affect soil seed bank density and composition? We sampled 50 shrub patches in a semi-arid gypsum system in Central Spain, measuring patch size, composition and structure, and seed bank at three locations per shrub (centre, edge and outside). We calculated the effect of interior patch location, patch composition and structure on seed density and composition. Patches acted both as seed sources, increasing seed density in neighbouring areas and as seed sinks by trapping seeds from bare areas. Patch structure (erect perennial cover) had the greatest effect on seed bank density, whereas patch size and microslope had the greatest influence on bare area density. Patch structure, composition and interior location explained the variation in seed bank composition. Patch effect extends to the surrounding bare matrix creating a seed bank gradient in density and composition. This effect is modulated by patch structure and composition and affects seed bank composition. Our results suggest that the spatial structure of gypsum community seed banks may act as a mechanism for a spatial storage effect contributing to the maintenance of high levels of diversity in semi-arid environments

Keywords Gypsum community · Mediterranean vegetation · Seed source effect · Seed trapping

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Introduction

A common feature of arid and semi-arid ecosystems is the prevalence of patchy structures in the vegetation (Aguiar and Sala 1997; Maestre and Cortina 2005). This pattern results in a two-phase mosaic with shrubby patches surrounded by a bare soil matrix which remains quite stable in time (Cipriotti and Aguiar 2005). Several mechanisms have been suggested to explain the existence and maintenance of

these structures, including a complex balance between competition and facilitation (Fowler 1986; Holzapfel and Mahall 1999). Plant performance in patches in these extreme habitats can be enhanced under canopies by increasing key resources such as water and nitrogen and by providing protection from herbivores (Pugnaire and Lázaro 2000; Bullock and Moy 2004). In fact, differences in habitat quality between bare soils and soils under canopies can have a great effect on plant populations and community dynamics.

In this sense the spatial patterning of the seed bank may also determine the existence of a patch structure itself (Aguiar and Sala 1994, 1999; Pugnaire and Lázaro 2000; Bisigato and Bertiller 2004). In fact, numerous works have shown that seed bank density and richness are much higher inside patches than in bare areas (Reichman 1984; Kemp 1989; Marone et al. 2004; Pugnaire and Lázaro 2000). This spatial structure is related to higher seed production within patches—seed source effect—and to the capability of patches to trap seeds from surrounding environments—trapping effect (Flores and Jurado 2003; Bullock and Moy 2004). As vegetated areas accumulate propagules in fertile islands, recruitment tends to occur there, reinforcing the existence of patchy structures (Franco and Nobel 1988).

Most previous works have studied differences in seed bank density between shrub and bare areas. However, few studies have focussed on the effect of clumped shrubby structures on seed bank composition (Aguiar and Sala 1997; Pugnaire and Lázaro 2000), or the role of patch properties (age, size and composition) on soil seed banks (Aguiar and Sala 1997; Moro et al. 1997). We hypothesize that seed bank density and composition are related to patch properties and that this relationship depends both on patch size, and patch composition and structure. We also hypothesize that seed bank density and composition in the bare soil matrix will be determined, at least partially, by the structure of nearby patches.

We specifically wanted to know to the effect of patches on seed bank structure and composition; and how some patch attributes including their aboveground composition may filter the composition and structure of the seed bank. This obviously implies the effect of seed source and trapping. Thus, we conducted a detailed survey in a semi-arid gypsum community in Central Spain to answer the following questions: (1) How do seed bank density and composition vary within and outside patch aboveground physical limits? and (2) Do patch characteristics affect soil seed bank density and composition?

Methods

Study area

The study was carried out in Chinchón, 60 km SE of Madrid, in Central Spain (40°10′ N, 3°27′ W, 720 m). The climate is semi-arid Mediterranean with an annual rainfall of 415 mm and almost no rainfall in summer. Mean daily temperature ranges from 0.6°C to 9.6°C in January and from 15.4°C to 32.7°C in July (data from the Aranjuez thermopluviometric station). Soils are classified as Calcic Gypsisols, developed over gypsum parental rocks with a gypsum content over 50% (Monturiol and Alcalá del Olmo 1990).

The area is characterized by a succession of small hills with steep slopes. Gypsum outcrops are covered by a sparse shrub community, dominated by genuine gypsophytes (*Centaurea hyssopifolia* Vahl., *Lepidium subulatum* L., *Helianthemum squamatum* (L.) Dum. Cours.) and a complete set of endemic specialists. Shrubs usually aggregate into patches, where a rich annual community develops. The intershrub area is usually covered by a lichenic crust, which hosts a sparse annual community.

Sampling design

A total of 50 shrubby multi-specific patches were randomly selected on a homogeneous gypsum southeast exposed slope covering one hectare. Small patches with only one or two shrub species in their canopy were not considered. We measured patch size (maximum length and width), microslope, and total cover in percentage for each perennial species in the patch as well as for the whole patch (some patches have a cover under 100%). Perennial species were classified as erect or creeping depending on their growth form (Appendix 1). All perennials were long-lived except *Helianthemum squamatum*, a very short-lived erect perennial (unpub. data), which was included in a third category.

Three locations were established in each patch—two inside the patch (in the centre and on the edge) and a third outside the patch on crusted soil. Bare soil

samples were taken at 15 cm from the patch edge. As this distance represented 75% of average patch radius, the area was considered to accurately represent the bare soil area close to the patch. Three soil cores were extracted from each location following a regular scheme and thoroughly merged before analyses (Fig. 1). Soil cores were 3 cm deep and 1.85 cm diameter, since the first 2 cm accumulate most of the seed bank in arid environments (Childs and Goodall 1973). Samples were taken in August 2003 after all seeds had been shed and prior to autumn emergence; thus, the seed bank included both the transient and persistent seed bank (Caballero et al. 2005).

The resulting soil samples were placed in 10 × 10 cm plastic cells in a greenhouse in a sterile substrate of vermiculite and peat (2:1). About 10 additional cells were filled with the sterile mixture to detect contamination. Emerged seedlings were identified and removed. After 5 months, the soil in the cells was crumbled to enhance seedling emergence and monitoring continued for another 3 months. After 8 months, the cells were watered with a gibberellic acid (GA3) solution (1,000 ppm) to break endogenous dormancy and seedling emergence was monitored for another 2 months (see Caballero et al. 2003 for details).

Numerical analysis

Seed bank density

Seed density was log-transformed to fit normality. To test for the effect of "within-patch location" on seed
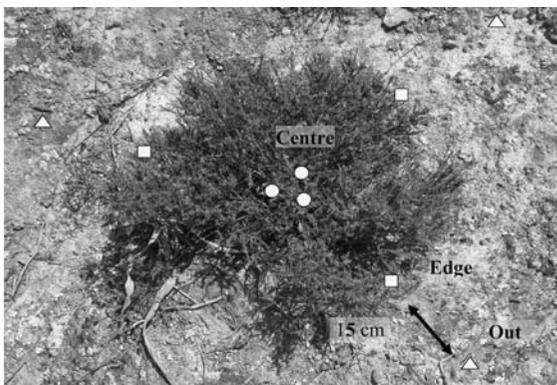

Fig. 1 Sampling design on a gypsum patch. Three soil cores extracted from each of the three locations were merged before analyses (○, centre; □, edge; and △, out)

density, this variable was pair-wised compared between locations (centre, edge, out) using paired Student's t tests. The correlation between seed bank density and the different locations in the patch was tested using Pearson's r. As species richness was not normal, comparisons between locations were based on Wilcoxon's Z.

A linear model was built to test the effect of patch features on seed density. As significant differences in density were observed between the within-patch locations, we expected the parameters influencing seed density to differ between these locations. Thus, separate analyses were performed for our response variable for each of the three patch locations. The included predictors were: microslope, patch size (two variables: width and patch area approached as an ellipsoid), cover of perennial species, cover of erect perennials, cover of creeping perennials, richness of perennials in the patch, and patch aboveground composition (eight variables: cover of the seven most abundant perennials: *Centaurea hyssopifolia*, *Helianthemum squamatum*, *Herniaria fruticosa* L., *Koeleria castellana* Boiss. & Reuter, *Lepidium subulatum*, *Teucrium pumilum* L., *Thymus lacaitae* Pau and cover of the remaining perennials).

Seed bank composition

The relative importance of some environmental variables (patch location, patch aboveground composition and patch physical attributes) in seed bank composition was evaluated by constrained ordination techniques (ter Braak 1986). To select an appropriate ordination technique, the seed matrix was submitted to Detrended Correspondence Analysis (DCA; ter Braak 1988), with detrending by segments and non-linear rescaling of the axes. Since the length of the extracted gradient was 1.873 s.d. units, a Redundancy Analysis (RDA) was conducted (see ter Braak 1986).

Several 'environmental' matrices were considered for constraining the main data set (seed count data): (1) a location matrix with three dummy variables depending on location in the patch (centre, edge and out); (2) a matrix which comprised structural features including patch size (patch width and area), microslope, cover of erect perennials, cover of creeping shrubs, cover of perennials and number of perennial species per patch; and (3) a set related to patch composition including individual species cover. As a

first step, the total variation explained (hereafter TVE) independently by each data set was calculated as the sum of all canonical extracted axes using each of these matrices as the constraining data matrix (Borcard et al. 1992). A Monte Carlo permutation test was performed to determine the accuracy of the relationships (999 randomizations) between the two data sets. The sum of all canonical eigenvalues or trace was used to build the F-ratio statistic (ter Braak 1990; Legendre and Anderson 1999). The relationship between the two data sets was considered significant when $P < 0.05$, adjusted for multiple comparisons by the Bonferroni correction (Legendre and Legendre 1998). If the corresponding RDA model was significant, a forward stepwise procedure was carried out to select a reduced model including only the significant variables for each matrix. Explanatory variables were incorporated one at a time and step by step in the order of decreasing eigenvalues after partialling out the variation accounted for by the variables already included. The process was brought to an end when the new variable was not significant ($P > 0.05$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 999 randomizations. Variance partitioning with RDA was performed to evaluate the relative importance of these three explaining data sets after adjusting the variability of other data sets considered as covariables (Legendre and Legendre 1998). This procedure has been called partial RDA (ter Braak 1988). In this case, the question is not only whether correspondence between data sets exists, but also what fraction of the seed composition information can be explained by the covariable data set and by the constraining matrix. These analyses were conducted using CANOCO for Windows v. 4.0 (ter Braak and Šmilauer 1997).

Results

Seed bank density and richness

A total of 3,368 seedlings of at least 38 taxa emerged from the seed bank samples. The number of seedlings per sample ranged from 0 to 147, with a mean of 20.26 seedlings. The number of species in the seed bank ranged from 0 to 15, with a mean of 5.56 species.

Seed density was significantly lower in the outer (bare soil) areas (5,070 seeds/m^2) than on the patch edge (23,908 seeds/m^2) or in the centre (25,063 seeds/m^2) (Table 1), with no significant differences between edge and centre locations. Seed bank density was highly correlated between locations in the same patch (Fig. 2). Patch location had a strong effect on species richness, which was much higher in the centre and edge locations (8 and 6.8 species, respectively) than outside the patch (1.9 species). The Wilcoxons' Z test (Table 1) showed significant differences in species richness between all three locations.
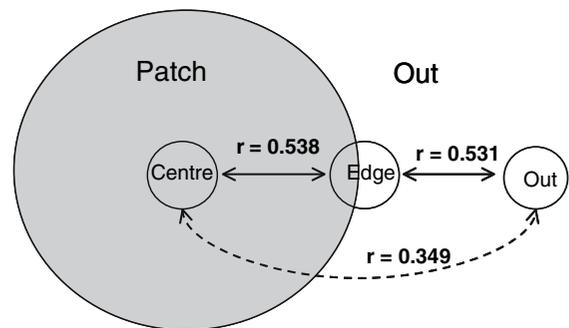

Fig. 2 Pearson's correlation of seed bank densities amongst patch locations. Discontinuous lines indicate $P < 0.05$, whereas continuous lines stand for $P < 0.01$ after Bonferroni correction

Table 1 Pairwise comparison of seed bank density (log transformed) and richness for the three patch locations considered

	Seed bank density			Seed bank richness	
	t	df	P	Z	P
Edge-centre	−1.684	49	−0.099	−2.62	0.009
Edge-out	11.938	49	<0.001	−6.021	<0.001
Centre-out	12.467	49	<0.001	−5.938	<0.001

Students' t showed significant differences between seed density outside of the patch (Out) and the two undershrub inside locations (Centre and Edge). Wilcoxons' Z test showed differences in seed bank richness between all locations

Table 2 Linear models for seed density for the three patch locations

Position	Predictor information			Model information		
	Predictors	Sign	P	r^2	F	P
Centre				0.092	4.861	0.032
	Erect perennial cover	+	0.032			
Edge				0.266	17.434	<0.001
	Erect perennial cover	+	<0.001			
Out				0.412	10.759	<0.001
	Microslope	−	0.010			
	Minimum diameter	+	0.002			
	Lepidium subulatum	+	0.008			

Only significant predictors after a forward stepwise procedure were included

All linear models were highly significant for each location (Table 2). Erect perennial species cover was found to have a significant positive effect on seed bank density at the centre and edge locations. However, at the outer location patch width and cover of *Lepidium subulatum*, a dominant erect shrubby Cruciferae, had a positive effect on seed bank density, whilst microslope had a negative effect.

Seed bank composition

The three environmental data sets used in our RDA models explained significant fractions of the total variation in seed bank composition (Table 3). The model for the within-patch location included two of the three dummy variables and accounted for 14.9% of the variance. The reduced model for patch structure included only one of the seven parameters (erect perennial cover) and accounted for 7.3% of

total variance. Finally, the reduced model for patch composition included two of the eight species (*Lepidium* and *Centaurea* cover), which accounted for 7.2% of total variance.

Partial RDA (Fig. 3) indicated that the effect of patch location was not dependent on the effect of patch aboveground composition ($F_{rat} = 13.287$, $P < 0.001$) or patch structure ($F_{rat} = 13.941$, $P < 0.001$). However, patch composition and patch structure shared an important amount of their TVE (5.8%). Whilst patch structure explained a small, but significant part of TVE when controlled by patch composition (1.5%, $F_{rat} = 2.426$, $P = 0.037$), no significant portion of TVE was explained by patch composition when controlled by patch structure (1.4%, $F_{rat} = 1.131$, $P = 0.542$). Total variance explained by the three data sets was 23.6%, which is quite high considering the heterogeneity and diversity of the seed bank.

Table 3 Results of the reduced RDA model after a stepwise forward procedure

Variables	Predictors	Reduced model				
		λ	P	% TVE	F_{rat}	P
Within patch position (3 v)				14.9	12.828	0.001
	Out	0.14	0.001			
	Centre	0.01	0.007			
Physical features of patch (7 v)				7.3	11.700	0.001
	Erect perennial cover	0.07	0.001			
Patch composition (8 v)				7.2	5.723	0.001
	Lepidium subulatum*	0.04	0.001			
	Centaurea hyssopifolia*	0.03	0.001			

λ indicates the eigenvalue, F_{rat} is the F-ratio statistic and P is the significance level (999 randomizations). Only significant parameters were included

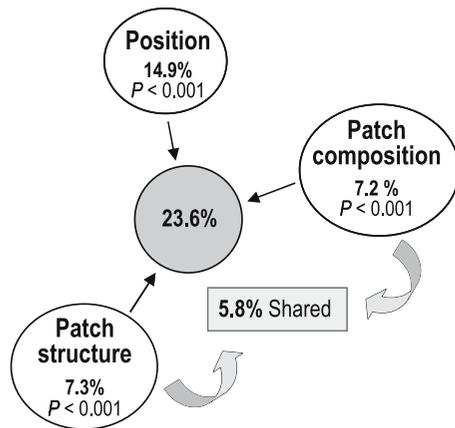* This effect continued even after removing these species' seeds from analyses

Fig. 3 Results of pRDA test, with the percentage of total variation explained by each feature and the significance level. Patch composition and patch physical traits effects are not independent

Discussion

Our results showed that seed bank density and richness are much higher in patches than in bare areas, as found by Reichman 1984, Kemp 1989, Marone et al. 2004, Pugnaire and Lázaro 2000. Nevertheless, density under canopies is highly correlated to density in bare areas, suggesting the relevance of the so-called seed source effect. The plants in the patch, including many annuals which make up 92% of the total seed bank, disperse their seeds mainly in the vicinity of their mothers and to a lesser extent in the surrounding bare area. This implies that the patch effect extends beyond its canopy limits. In fact, most arid plants have short-range dispersal (Chambers and McMahon 1994). This may be due to the prevalence of mucilaginous seeds, a very common trait in gypsum communities (Escudero et al. 1997) and other arid and semi-arid environments (Gutterman 1994). Seed anchorage on the soil surface close to source patches may explain the relation between the size and composition of the seed bank inside and outside the patches.

However, the seed bank distribution of several crust inhabiting annual specialists such as *Campanula fastigiata* Dufour ex A. DC. and *Chaenorhinum reyesii* (C. Vicioso & Pau) Benedí highlights the strength of the seed trapping effect. These two plants, which are very abundant in gypsum crusts and rarely emerge under shrubs (Olano et al. 2005), reach their

highest seed bank densities on canopy edges (Appendix 1). We may expect seed trapping in semi-arid environments to allow species to recruit in favourable abiotic environments. However, this may have detrimental effects on poorly competitive species such as these gypsum crust soil specialists, which cannot withstand the combined effect of competition and litter accumulation under shrub canopies (Aguiar and Sala 1994). Our results suggest that, at least in the case of some annual specialists, patches act as genuine sinks.

Aboveground cover structure was a more relevant predictor of seed bank density than patch size. Shrub architecture has a major role in the creation and maintenance of these islands of fertility (Escudero et al. 2004) as well as in the diversity and complexity of their annual plant community. The inclusion of patch size in the density model for the outer location can be interpreted as a result of increased seed rain in the vicinity of larger patches due to a higher surface/perimeter ratio.

Seed bank composition is affected by several independent factors. Patch location causes the segregation of the seed bank community particularly between the patch and exterior areas. Simultaneously, canopy patch structure and composition influence seed bank composition. The strong overlap between patch composition and erect perennial cover can be more easily explained by traits related to patch architecture than by the effect of individual species. In this sense, Bullock and Moy (2004) found that plant patches modify the spatial patterns of wind-dispersed seeds, although they did not suggest which patch traits are implied.

Thus, patches play a complex role in seed bank patterning which shapes population and community dynamics. Patches can act both as seed sources and seed sinks (Soriano et al. 1994). Moreover, the spatial heterogeneity generated by patches on seed banks is more complex than simple dichotomy between patch and bare areas. The patch effect extends to the surrounding bare matrix creating a seed bank gradient not only in density (Aguiar and Sala 1994), but also in composition. This obviously implies certain variability in bare areas which is partially controlled by patches in the vicinity. Furthermore, not all patches are equivalent, especially in those communities where the composition and structure of vegetated areas is highly variable, and seed bank composition is

related to some patch attributes. Some of these variables such as the dominance of erect shrubs are partly related to patch size and seem to be primarily caused by patch dynamics. In these gypsum environments, initial patches are dominated by creeping plants, whereas erect shrubs are later successional elements which usually only occur in larger, more diverse patches (Romao 2003). This means that differences in seed bank density and composition may also be related to patch dynamics. These results agree with previous findings that reported the strength and constancy of the spatial structure in gypsum environment seed banks (Caballero et al. 2005).

Finally, seed bank patterning may help to explain the high diversity of gypsum annual plant communities (Izco 1974). A Mediterranean-type climate allows little opportunity for seasonal niche-partitioning, a key factor in explaining the high diversity of annual communities in other arid environments (Guo 1998). Therefore, other mechanisms are needed to explain this high diversity. Seed banks have been considered basic for ensuring stable coexistence in unpredictable environments (Harper 1977). Seed banks promote diversity through a storage effect (Chesson 2000a), and may act as a temporal buffer against competition effects by accumulating surplus seed production in ''good years'' to cope with unfavourable conditions that decrease survival and seed production in ''bad years.'' Simultaneously, heterogeneity at different spatial levels of different life stages is another mechanism for this storage effect (Chesson 2000b). Therefore, our results suggest that the strong spatial structure of gypsum community seed banks may also act as a spatial buffer, making up for the lack of heterogeneity due to seasonality. Moreover, the recently demonstrated relationship between seed bank and emergence (Olano et al. 2005) would give additional support to this storage effect hypothesis.

Appendix

Appendix 1 Species seed density per location and frequency in patches

Species	Family	Life forms	Growth forms	Seed bank density (seeds/m^2)			% Freq. in patches
				In	Edge	Out	
Campanula fastigiata	Campanulaceae	a		10,789	13,517	5,035	100
Asterolinon linum-stellatum (L.) Duby in DC	Primulaceae	a		6,027	5,630	694	100
Centaurium gypsicola (Boiss. & Reut.) Ronninger	Gentianaceae	b		5,109	2,406	322	90
Vulpia unilateralis (L.) Stace	Poaceae	a		3,447	3,274	521	92
Galium sp.	Rubiaceae	a		1,736	1,686	99	68
Desmazeria rigida (L.) Tutin	Poaceae	a		1,686	1,042	25	58
Herniaria fruticosa	Caryophyllaceae	p	Creeping	1,835	744	0	54
Campanula erinus L.	Campanulaceae	a		446	1,860	99	10
Helianthemum squamatum	Cistaceae	p		1,190	818	99	68
Chaenorhinum reyesii	Scrophulariaceae	a		744	918	248	28
Teucrium pumilum	Lamiaceae	p	Creeping	1,017	595	25	48
Filago pyramidata L.	Asteraceae	a		645	694	50	46
Unidentified 1				694	446	174	50
Bellardia trixago (L.) All.	Scrophulariaceae	a		347	174	50	22

Appendix 1 Species seed density per location and frequency in patches

Species	Family	Life forms	Growth forms	Seed bank density (seeds/m^2)			% Freq. in patches
				In	Edge	Out	
Euphorbia sulcata De Lens ex Loisel.	Euphorbiaceae	a		124	322	74	28
Thymus lacaitae	Lamiaceae	p	Creeping	174	223	0	22
Centaurea hyssopifolia	Asteraceae	p	Erect	248	74	0	20
Neatostema apulum (L.) I. M. Johnston	Boraginaceae	a		124	124	25	16
Coris mospeliensis L.	Primulaceae	p	Creeping	223	25	0	10
Helianthemum salicifolium (L.) Miller	Cistaceae	a		99	99	25	12
Linum strictum L.	Linaceae	a		124	74	0	14
Reseda stricta Pers.	Resedaceae	a		149	50	0	16
Teucrium capitatum L.	Lamiaceae	p	Erect	99	99	0	12
Hippocrepis ciliata Willd.	Fabaceae	a		74	74	0	10
Thesium divaricatum Jan ex Mert. & W.D.J. Koch in Röhl	Santalaceae	p	Creeping	74	50	0	8
Trisetum loeflingianum (L.) C. Presl	Poaceae	a		50	74	0	6
Bupleurum semicompositum L.	Brassicaceae	a		74	0	0	4
Lepidium subulatum	Brassicaceae	p	Erect	74	0	0	4
Odontites viscosa (L.) Clairv.	Scrophulariaceae	a		25	50	0	6
Erophila verna (L.) Chevall.	Brassicaceae	a		0	25	25	2
Helianthemum hirtum (L.) Mill.	Cistaceae	p	Erect	50	0	0	2
Holosteum umbellatum L.	Caryophyllaceae	a		0	50	0	4
Koeleria castellana	Poaceae	p	Creeping	25	0	25	4
Unidentified 2				0	0	25	2
Launaea pumila (Cav.) Kuntze	Asteraceae	p	Erect	0	25	0	2
Sherardia arvensis L.	Rubiaceae	a		25	0	0	2
Taeniatherum caput-medusae (L.) Nevski	Poaceae	a		25	0	0	2
Valerianella coronata (L.) DC.	Valerianaceae	a		0	25	0	2

Taxa are ordered by total seed abundances. Life-forms are classified into p (perennials), b (biennials) and a (annuals). Perennials are classified as creeping and erect growth forms

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