

RESEARCH ARTICLE

Functional traits explain both seedling and adult plant spatial patterns in gypsum annual species

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Abstract

1. Ecological processes such as seed dispersal or plant–plant interactions and environmental constraints such as climate or soil heterogeneity are known to influence establishment, and thus the spatial patterns of plant communities and populations. In this study, we hypothesized that key functional traits such as the specific leaf area (SLA), reproductive ratio (reproductive/vegetative biomass), seed mass and maximum plant height would influence the spatial patterns of individual species in annual, gypsophilous plant communities, and that these effects would be modulated by both the soil surface structure (biocrust) and climate (precipitation) conditions.
2. We mapped the spatial patterns of all plants found in six 1×1 m plots (more than 1000 individuals per plot) in both the seedling (autumn) and adult stages (spring) under two biocrust experimental conditions (intact vs. disturbed biocrust) during two consecutive years which were contrasted in term of precipitation (dry year and wet year). To assess the spatial patterns of seedlings and adults, we fitted four different spatial point pattern models (i.e. Poisson, inhomogeneous Poisson, Poisson cluster and inhomogeneous Poisson cluster processes) to each of the 242 populations of the 26 most abundant species that had more than 15 individuals per plot.
3. Most seedling populations exhibited clustered spatial patterns that persisted in the adult stage, which suggests that short-distance dispersal is an adaptive trait for soil specialists such as gypsophilous plants. One-third of the populations fitted an inhomogeneous model best but the physical structure of the biocrust was not related to them. More importantly, we found a connection between the functional strategies of species and the spatial distribution of plants. In particular, during the dry year, irrespective of the biocrust conditions, species with a high SLA and high Rep/Veg mainly exhibited clustered spatial patterns, whereas low SLA and low Rep/Veg were associated with random distributions. Species with heavy and light seed masses had random and clustered patterns, respectively. In both the dry and wet years, species with lower maximum heights had clustered patterns, whereas taller species exhibited random patterns. In addition, species with heavier seeds and greater maximum heights had the largest cluster sizes.

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4. Our results confirm that the spatial patterns of seedlings and adult plants are significantly determined by the functional strategy of each species.

KEYWORDS

biological soil crust, gypsophyte, maximum plant height, point pattern analysis, reproductive/vegetative biomass ratio, seed dispersal, seed mass, specific leaf area

1 | INTRODUCTION

Ecological processes are known to leave recognizable footprints on the spatial patterns of plants. Observed spatial patterns can be tested against theoretic expectations based on the effects of species dispersal, fine-scale abiotic factors and biotic interactions on the realized spatial patterns of plants (McIntire & Fajardo, 2009). The point-to-point spatial relationships among plants, known as the 'plant's eye perspective' (Murrell et al., 2001), have been successfully used to infer dispersal, abiotic heterogeneity and interspecific relationships at fine spatial scales of perennial plants (Chacón-Labela et al., 2016; Jara-Guerrero et al., 2015; Pauchard et al., 2016; Pescador et al., 2014, 2020). Seed dispersal profoundly affects the spatial structure of plants at population and community levels (Cousens et al., 2008; Wang & Smith, 2002). The initial dispersal pattern provides the biological template that allows subsequent ecological processes to act, such as germination, herbivory, pathogen infection, facilitation and competition, thereby leading to the realized distribution of seedlings and then adults (Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995). Depending on the relative strengths of all these processes, the initial dispersal pattern will disappear, mainly due to non-random thinning (Chacón-Labela et al., 2014; Kenkel, 1988), or the initial pattern of the seedlings will be retained by the adult plants (e.g. Lara-Romero et al., 2016; Schupp & Fuentes, 1995; Seidler & Plotkin, 2006). It is well known that species adapted to restrictive soils (i.e. serpentines, gypsum soils) usually behave as island edaphisms showing limited seed dispersal. This ensures that offspring will remain in the same or similar environmental conditions as the mother plants (Friedman & Stein, 1980), thereby minimizing the risk of dispersal to unsuitable habitats.

Fine spatial heterogeneity is known to affect the spatial signal of plant distribution (Pescador et al., 2020). Specifically, biological soil crusts (BSCs) are important sources of spatial heterogeneity in gypsum habitats (Escudero et al., 2015; Ortiz et al., 2023). BSCs act as environmental biotic filters during soil seed bank formation (Peralta et al., 2016), seed germination and seedling establishment (Escudero et al., 2007; Romão & Escudero, 2005) to determine the realized annual plant community structure and composition at fine spatial scales (Luzuriaga et al., 2012; Peralta et al., 2019; Sánchez et al., 2022). BSCs also affect ecosystem functions by limiting soil evapotranspiration and increasing the availability of resources beneath them (Berdugo et al., 2014; Delgado-Baquerizo et al., 2013). Consequently, BSCs are the primary source of fine-scale heterogeneity for annual plant communities in gypsum soils, and they are expected to leave deep signals in the spatial patterns of coexisting annual plant species.

The initial seed dispersal patterns may vary throughout ontogeny depending on species specific strategies. Functional traits may promote different plant competitiveness or stress tolerance capacities (Garnier et al., 2016; Westoby et al., 2002), which have been observed to modify the community functional structure under different stress levels in perennial (Luzuriaga et al., 2020) and annual plant communities (López-Rubio et al., 2022) in gypsum systems. In this study, we explore, for the first time to our knowledge, the relationship between functional traits and spatial patterns of seedlings and adults of the species that conform local assemblages and in two climatically contrasting years. This will allow to improve our knowledge about the role of functional traits during the species assembly at very fine spatial scales. Key plant functional traits such as seed mass, maximum plant height, specific leaf area (SLA) and reproductive/vegetative biomass ratio (reproductive ratio, hereinafter) are clearly connected to the main ecological processes that determine community and population assembly. For example, large-seeded species have competitive (Freckleton & Watkinson, 2001; Rees, 1995) and establishment advantages (Freckleton & Watkinson, 2001; McConaughay & Bazzaz, 1987; but see Tracey & Aarssen, 2019) compared with small-seeded species. The initial seedling size is positively correlated with seed size (Leishman et al., 2000), and larger seedlings are usually favoured under competitive or drought conditions (Leishman & Westoby, 1994). The maximum plant height is also related to competitive advantage (Garnier et al., 2016; Westoby et al., 2002), seed dispersal distance (Thomson et al., 2011), stress resistance in water-limited environments (Dovrat et al., 2019) and the capacity of species to establish on hard BSCs (Peralta et al., 2019). Species with high SLA and reproductive ratios are associated with more efficient use of resources (Moravcová et al., 2010; Wang et al., 2018), and ultimately with greater competitive ability (Kraft et al., 2015; Pérez-Ramos et al., 2019). Coexisting annual species exhibit broad variability in all of these functional traits (Peralta et al., 2019) as well as in their soil preferences (from opportunistic to specialized gypsophytes; see Luzuriaga et al., 2015, 2018). In fact, it is well known that variations in trait values (i.e. 'limiting similarity hypothesis'; Abrams, 1983, 1996), as well as variation in phylogenetic relatedness among neighbours (Chaves et al., 2021) is a critical mechanism for allowing fine scale coexistence. Annual plant communities in gypsum habitats are excellent models for evaluating the effects of functional traits on the spatial patterns of plants. These diverse communities (around 120 species; Luzuriaga et al., 2018) usually form very rich species assemblages (around 38 species per 0.25 m² in rainy years; Luzuriaga et al., 2012, 2015) of small-sized individuals (10.5 cm tall in average) with short and synchronized

life cycles (from autumn to spring). Thus, every individual can be mapped at very fine spatial scales in a relatively small area over time from the seedling stage until they are reproductive individuals. Furthermore, annual plant communities restart their life cycle every year from the soil seed bank, so we could evaluate the effects of different climatic conditions on the spatial pattern of each species. We measured the afore mentioned functional traits for each species, fully mapped their spatial patterns, and fitted spatial point process models to elucidate dispersal limitation and the responses to environmental heterogeneity (e.g. Baddeley et al., 2015; Jara-Guerrero et al., 2015; Lin et al., 2011; Shen et al., 2009). These analyses were conducted separately for the seedling and adult stages in each species during two consecutive years (a dry year and a wet year) in two contrasting experimental set ups: intact BSC versus artificially disturbed BSC plots located in gypsum soils in central Spain.

Here, we use spatial pattern analyses as a valuable tool to understand the role of specific functional traits in species assembly processes, in an experimental setup where we manipulated the spatial heterogeneity of the BSC—known to be a crucial environmental filter for annual plant communities—during two consecutive years with contrasting climate conditions. In particular, we tested the following hypotheses (see Table 1, for detailed explanations): (1) The responses of species to dispersal limitation and spatial heterogeneity will be correlated with their functional traits (Murren, 2012; Reich et al., 2003); (2) Limited dispersal will occur around the mother plants, which would be reflected in aggregated spatial patterns at least in the seedling stage; (3) The heterogeneity of BSCs at fine spatial scales should be reflected in the spatial distribution of individual plants.

2 | MATERIALS AND METHODS

2.1 | Study area

The experiment was conducted in a flat zone on the top of a gypsum hill in El Espartal (Valdemoro, Madrid, Central Spain, 40°11'11.5"N 3°37'47.0"W—permit Ref. 10/058764.9/15 Comunidad de Madrid) (Figure S1). The mean annual precipitation was 365 mm year⁻¹ and the mean annual temperature was 15°C (www.aemet.es). The vegetation in this area is dominated by perennial shrubs (30% cover) and many are gypsum specialists, such as *Helianthemum squamatum* (L.) Dum. Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl, and *Gypsophila struthium* L. in Loefl., *Launaea fragilis* (Asso) Pau, as well as some generalists, including *Thymus zygis* Loefl. ex L., *Retama sphaerocarpa* (L.) Boiss. and *Macrochloa tenacissima* (L.) Kunth. These perennials are scattered in a well-developed BSC matrix dominated by lichens (e.g. *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt and *Psora decipiens* (Hedw.) Hoffm) (Luzuriaga et al., 2012). The area is seasonally covered by a very rich annual plant community (up to 38 species per 0.25 m² in rainy years; Luzuriaga et al., 2012) with high plant densities (up to 1200 plants m⁻²). The annual community comprises tiny plants (mean height = 9.7 ± 8.0 cm) that complete their whole life cycle from

TABLE 1 Tested hypotheses and expectations.

Expectation	Explanation
HYPOTHESIS 1: Species responses to dispersal limitation and spatial heterogeneity are correlated with their functional traits (Murren, 2012; Reich et al., 2003)	
a. Large-seeded species will show aggregated spatial patterns more frequently than small-seeded ones	The effects of wind or water on seed dispersal differs for large or small seeds
b. Short species (low MPH values) will have more aggregated patterns than tall species	Due to lack of efficient dispersal mechanisms, mother plant height determines dispersal distance in most of our species
c. Species with more efficient resource usage (high SLA and Rep/Veg), will have random patterns at fine spatial scales more frequently than conservative species (low SLA and low Rep/Veg)	Efficient species would be less affected by environmental heterogeneity than conservative ones
HYPOTHESIS 2: Limited seed dispersal will occur around the mother plants, which would be reflected in aggregated patterns at least in the seedling stage	
a. Most species will show aggregated spatial patterns in our system	Most annual plants in our system lack specialized structures for seed dispersal
b. Gypsum specialists (gypsophytes) behave as edaphic island specialists	Germination in a favourable microenvironment (i.e. near mothers) outweighs the negative effects associated with high plant densities for specialists (Ward, 2016)
HYPOTHESIS 3: The heterogeneity of BSCs at fine spatial scales should be reflected in the spatial distribution of individual plants	
a. Plots with intact biocrust will have species with inhomogeneous spatial patterns	Intact biocrusts create microenvironmental heterogeneity for seed accumulation and germination
b. Plots with disturbed biocrust will have species with random patterns	Disturbed biocrusts will be more homogeneous in terms of microenvironmental conditions

October to April. The most abundant annuals are *Asterolinon linum-stellatum* (L.) Duby in DC, *Bromus rubens* L., *Micropyrum tenellum* (L.) Link, *Helianthemum salicifolium* (L.) Mill., and *Ziziphora hispanica* L., and the strict gypsophytes include *Chaenorrhinum reyesii* (C. Vicioso & Pau) Benedí and *Campanula fastigiata* Dufour ex DC.

2.2 | Experimental design

Six plots measuring 1 × 1 m were randomly distributed in a flat area of around 0.4 ha avoiding small holes or depressions, where the main microtopographic differences were created by the BSC (Figure S1).

One plot was extended to 1.20×1 m to ensure at least 1000 individuals were present per plot. In three of the plots, the BSC was kept intact and in the other three plots the BSC was thoroughly destroyed with a mallet and the remaining small fragments and powder were left on the soil surface ('disturbed BSC', see [Figure S1](#)) thereby maintaining the total soil seed bank. We monitored every plant that emerged in each plot in two consecutive years. The autumn precipitation was 33% below average in the first year and 35% above average in the second year, which we designated as the 'dry year' and 'wet year', respectively ([Figure S1](#)). Although differences in precipitation between both study years are remarkable, we are aware that other non-measured environmental differences may be associated with each study year. In each year, we sampled twice to register the spatial patterns of plants in the seedling stage (in December) and adult stage (April).

2.3 | Data collection

We mapped every plant that emerged for each species (28,330 individuals) in the six plots during two consecutive years (two complete life cycles). We identified the species and traced the rooting point of each plant in DIN-A3 transparent vinyl (polyvinyl chloride, PVC) sheets. We used a mobile transparent methacrylate structure suspended 10 cm above the plot to avoid plant and biocrust damage. In total, 216 PVC sheets were recorded and converted into digital images with a photo-scanner (Epson Expression 10000XL; Seiko Epson Corp.). Images were assembled in a unique picture per plot with Adobe Photoshop CS3 software (Adobe Systems). We recorded the coordinates of every point (i.e. the rooting point of each plant) in ArcGIS 10.1 software (ESRI, 2011) using an interactive pen display (Wacom DTU-2231).

2.4 | Functional plant traits

We measured functional traits related to the leaf economics spectrum (SLA and reproductive/vegetative ratio), reproduction trade-offs (seed mass), and establishment of size hierarchies (maximum plant height) ([Tables S1](#) and [S2](#)). Functional traits were estimated based on at least 10 healthy undamaged individuals per species, which were randomly collected during the spring outside sampling plots surrounding our study area (see [Peralta et al., 2019](#) for more details). All traits were measured according to the protocols described by [Cornelissen et al. \(2003\)](#) and [Pérez-Harguindeguy et al. \(2013\)](#).

2.5 | Characterization of spatial patterns and dispersal limitation

We recorded 61 annual plant species in our experiment in both study years, but we only considered 242 spatial patterns for 26 species

with at least 15 individuals per plot and sampling dates ([Tables S3](#) and [S4](#)). To characterize the spatial pattern, we used Ripley's K function ([Ripley, 1976](#)): $\lambda K(r)$, where λ is the pattern intensity (i.e. density), which is the expected number of points within a circle of radius r around an arbitrary point in a homogeneous point pattern. Note that using the cumulative K function for fitting cluster processes provides better estimates of their parameters than other non-cumulative functions such as the pair correlation function ([Baddeley et al., 2015](#)). We fitted models for the following four different spatial point processes that are commonly used in spatial ecology studies (for mathematical details, see [Jara-Guerrero et al., 2015](#); [Figure S2](#)): (1) The Poisson process (PP) model assumes that the spatial locations of points (i.e. either individual seedlings or adults) are independent of each other and that their intensity is constant across the plot, where this pattern is considered the result of random processes in a homogeneous environment ([Lin et al., 2011](#); [Shen et al., 2009](#)); (2) The inhomogeneous Poisson process (IPP) assumes independence between points but recognizes the existence of variations in intensity across the plot, where this variation is usually assumed to be related to microhabitat spatial heterogeneity ([Wiegand et al., 2007](#)); (3) The Poisson cluster process (PCP) assumes both constant intensity and the aggregation of points due to limited dispersal ([Shen et al., 2009](#)), where it is considered that the aggregated pattern is generated in a two-step process: a PP of cluster centres (i.e. plants aggregated around mother plants) with intensity ρ is created first, before each mother plant then produces a number of offspring according to a Poisson distribution, which are located around the mothers according to a radially symmetric Gaussian distribution with mean zero and standard deviation σ , and this is usually employed as a measure of the aggregation ([Jara-Guerrero et al., 2015](#); [Seidler & Plotkin, 2006](#); [Shen et al., 2009](#)). (4) The inhomogeneous Poisson cluster process (IPCP) assumes that the spatial pattern is created by dispersal limitation (i.e. similar to a PCP), but the intensity varies in response to habitat heterogeneity ([Wiegand & Moloney, 2014](#)).

To select the model that best fitted the spatial pattern of each species, we employed Akaike's information criterion based on the sum of residuals and the number of parameters in different models ([Jara-Guerrero et al., 2015](#); [Webster & McBratney, 1989](#)). K -functions were estimated using translation edge correction ([Ohser, 1983](#)). All functions were estimated up to a radius of 250 mm with steps of 1 mm. K functions, and model fitting and selection were calculated in R (R Core Team, 2021) using functions from the R packages `SPATSTAT` ([Baddeley et al., 2015](#)), `ECESPA` ([de la Cruz, 2008](#)) and `SELECTSPM` ([de la Cruz, 2015](#)).

2.6 | Statistical analyses

We fitted a Poisson generalized linear model to analyse the effects of the BSC treatments (intact vs. disturbed), year (wet autumn vs. dry autumn), life stage (seedling vs. adult) and their interactions on the frequency of the observed spatial point pattern types (i.e. frequency of the best fit models). We conducted nonparametric Kruskal–Wallis tests to evaluate whether species trait values determined the best

fit spatial process depending on the year and BSC treatment. For the patterns that were fitted best by PCP ($n = 156$), we fitted a multiple linear regression model to examine the effects of the four functional traits, BSC treatment, and abundance of individuals on the aggregation parameter σ (which is related to the mean cluster size). We log-transformed σ to normalize the data. It should be noted that in all of these statistical analyses, we ignored species with IPCC patterns because they comprised less than 1% of the cases (only two IPCC patterns, see Table S4). All statistical analyses were performed in R software version 4.0.5 (R Core Team, 2021). Kruskal–Wallis tests were performed with the *kruskal.test* function in the *STATS* package. Multinomial linear models were fitted with the *multinom* function in the *NNET* package. Linear models were fitted with the *lm* function in the *STATS* package and tested with the *Anova* function in the *CAR* package.

3 | RESULTS

We found an average of 27.5 ± 4.6 plant species and 2060 ± 1018.4 individuals per plot (1×1 m). We fitted 242 spatial patterns for the 26 species with more than 15 individuals per plot and sampling dates (Tables S3 and S4). The spatial patterns of most species were best described by a PCP (64%) and IPP (31%). We only found nine PPs (3.7%) and two patterns best described as IPCCs (<1%) (some examples of these patterns are shown in Figure S2). BSC treatments, year, life stage or their interactions did not significantly affect the frequency of each spatial pattern in our study system (Table S5). Around 65% of the seedling spatial patterns were maintained throughout the life cycle of plants (Figure 1), but 17.2% of the spatial patterns shifted from clustered (PCP) in the seedling stage to less aggregated patterns (IPP) in the adult stage. By contrast, 15% of the spatial patterns shifted from random (PP and IPP) to more clustered patterns (PCP and IPCC) throughout the life cycle. This trend was very similar in both study years.

We found that the seedling and adult spatial patterns in each species were highly correlated regardless of the BSC treatment and year. Furthermore, the functional traits of species determined the spatial patterns of plants, especially in dry conditions. In the dry year, we found significant effects of all functional traits on the spatial patterns of many species (Table 2; Figure 2). In particular, species with high SLA and high reproductive ratios exhibited predominantly clustered spatial patterns (PCP), whereas species with lower SLA and lower reproductive ratios had random distributions (PP and IPP). Species with heavier seeds had random patterns (PP), whereas those with smaller seeds tended to have clustered patterns (PCP). This trend was also observed under the disturbed BSC treatment (Figure 2). We found that species with lower maximum heights had aggregated spatial patterns (PCP), whereas taller species had random patterns (PP and IPP) in both study years and under the intact BSC treatment. Finally, in the plants best described by PCP, cluster size was not affected by the disturbed BSC treatment (Table 3). Nevertheless, species with heavier seeds and

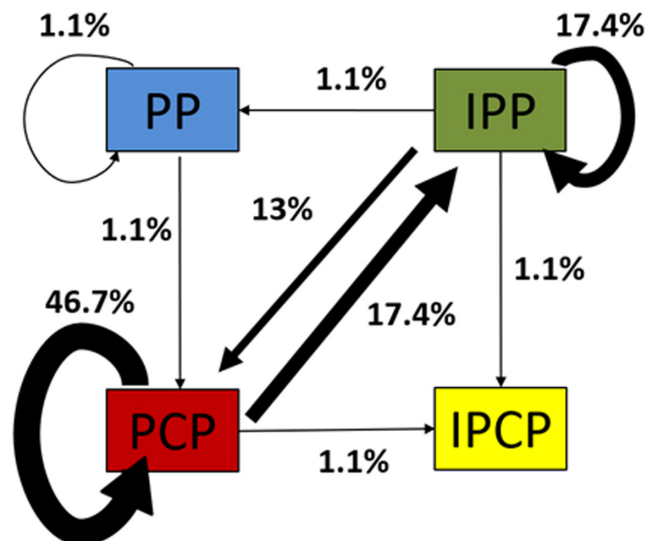


FIGURE 1 Percentage number of point patterns that remained constant or shifted to another spatial pattern type during the seedling to adult stage transition considering both study years together. Only populations with more than 15 individuals per plot in both life stages were considered ($n = 92$). The arrow thickness is proportional to the proportion of patterns. PP, Poisson; IPP, inhomogeneous Poisson; PCP, Poisson cluster; and IPCC, inhomogeneous Poisson cluster.

higher maximum heights had larger cluster sizes (higher σ parameter values).

4 | DISCUSSION

The key determinants of the spatial patterns of annual plants on gypsum soils are dispersal limitation and fine-scale heterogeneity to a minor extent. Our results showed that individuals from most species had clustered spatial patterns (PCP models), which agrees with the lack of specialized dispersal mechanisms (i.e. atelechory; sensu Ellner & Shmida, 1981), and with the presence of mucilaginous seed coats that anchor seeds to the soil in the vicinity of mother plants (i.e. myxospermy sensu Engelbrecht & García-Fayos, 2012) (Table S3). In fact, previous studies that analysed the similarity between the standing vegetation and the soil seed bank in ephemeral plant communities on gypsum soils found evidence of limited dispersal (Olano et al., 2005; Caballero et al., 2008; Peralta et al., 2016; López-Rubio et al., unpublished data). This strategy is interpreted as a method for increasing the likelihood of success by occupying the same microenvironments as the mother plant (Friedman & Stein, 1980), or for avoiding the extremely low probability of success associated with larger-dispersal distance in these special habitats (Ellner & Shmida, 1981; García-Fayos et al., 2013). Remarkably, the dominant spatial patterns for the three strict gypsophytes were clustered (Table S3). These results support our hypothesis that gypsophytes behave as edaphic island specialists which use short-distance dispersal as an adaptive trait to ensure appropriate soil conditions for the following plant cohort.

TABLE 2 Results of Kruskal–Wallis tests to determine the effect of each functional trait (seed mass, maximum height, SLA, and reproductive ratio) on the best spatial process model adjusted for each year (a) and for each BSC treatment (b). Seedlings and adults were considered together. IPCC models were extremely rare in our study (<1%), and thus they were excluded.

	Seed mass			Maximum height		SLA		Reproductive ratio	
	df	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Year									
Dry year, <i>n</i> = 97	2	7.9	0.02*	5.8	0.05*	7.1	0.03*	8.5	0.01*
Wet year, <i>n</i> = 143	2	0.9	0.6	8.7	0.01*	1.2	0.5	0.2	0.9
BSC treatment									
Intact BSC, <i>n</i> = 113	2	1.0	0.6	9.9	0.007**	1.9	0.4	3.5	0.2
Disturbed BSC, <i>n</i> = 127	2	7.2	0.03*	5.2	0.07	4.8	0.09	1.9	0.4

Significant results are shown in bold and indicated with asterisks: ***p* < 0.01; **p* < 0.5.

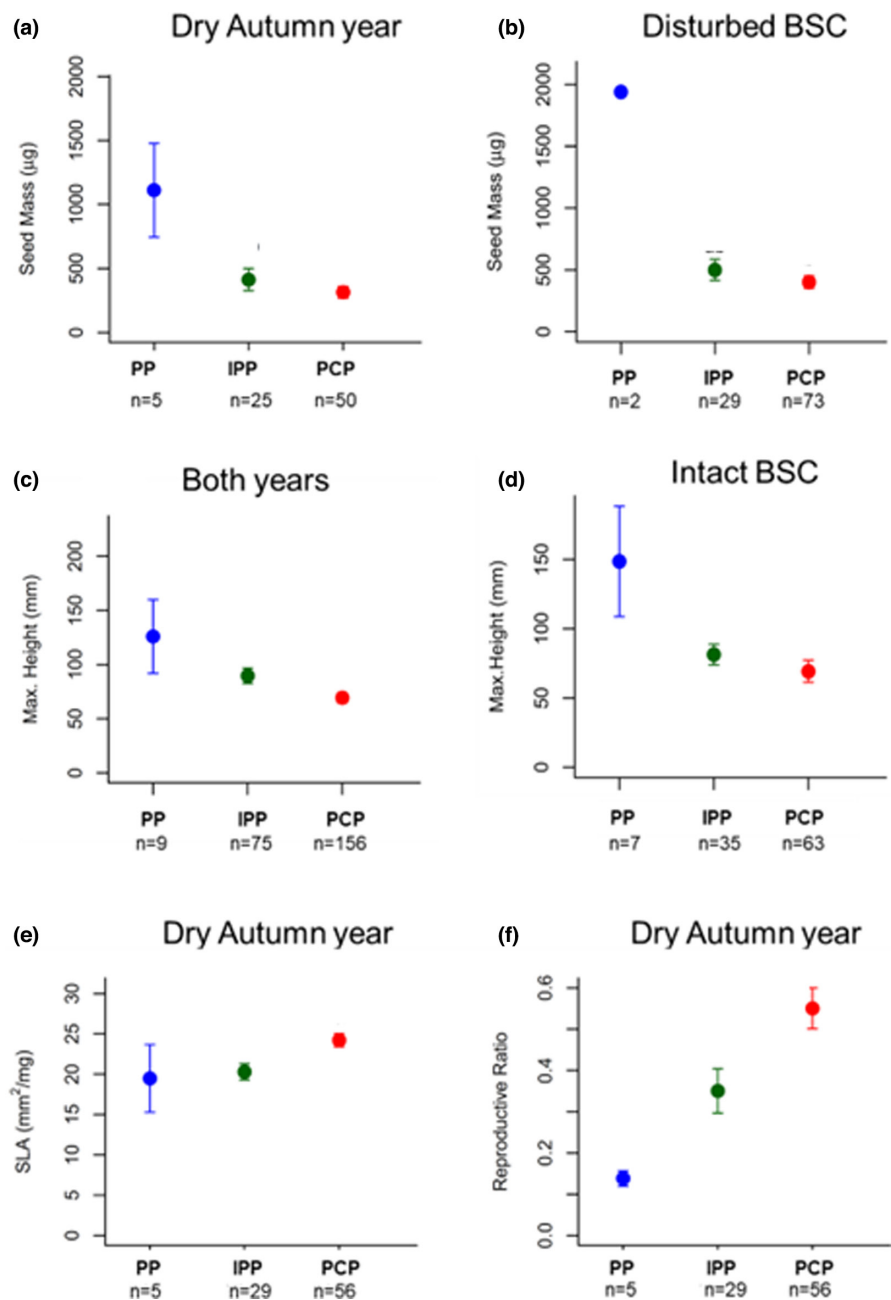


FIGURE 2 Mean values and standard deviations (vertical bars) of the functional traits for species with each point pattern type: Poisson (PP), inhomogeneous Poisson (IPP), and Poisson cluster (PCP). IPCC patterns are not included because they were less than 1% of the cases in our study. Significant differences in the mean seed mass (a, b), maximum plant height (c, d), SLA (e), and reproductive ratio (f) are shown (see Table 2).

TABLE 3 Results obtained by generalized lineal models for the σ parameter (i.e. cluster size) in the Poisson cluster (PCP) models ($n = 156$) to test the effects of the independent variables: BSC treatment (intact vs. disturbed), year (dry autumn vs. wet autumn), life stage (seedlings vs. adults), plant abundance, seed mass, maximum plant height, SLA, and reproductive ratio. σ was log transformed. Estimated values of the levels are indicated in brackets. df, degrees of freedom.

	df	Estimate	F	p-value
Intercept	1	7.9	140.7	<0.001***
BSC (disturbed)	1	0.2	0.6	0.4
Year (wet year)	1	-0.5	4.05	0.05*
Stage (seedlings)	1	-0.2	0.4	0.5
Abundance	1	-0.001	6.7	0.01*
Seed mass	1	0.001	7.0	0.01**
Maximum height	1	0.004	3.3	0.07
SLA	1	-0.01	0.04	0.84
Reproductive ratio	1	-0.09	0.04	0.84
Residuals	124			

Significant results are shown in bold and indicated with asterisks: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.5$.

Seed dispersal appeared to determine the spatial structure of adults in 65% of the populations analysed in this study, regardless of BSC disturbance and the yearly contrasting environmental conditions. Indeed, most of the initial clustered patterns detected in the seedling stage were maintained in the adult stage, which contradicts the usual findings in other plant communities, especially forests where the initial clustered pattern of seedlings becomes random or overdispersed in the adult life stages due to the important roles played by density-dependent processes (Chacón-Labela et al., 2014; He & Duncan, 2000; Kenkel, 1988). The maintenance of a clustered pattern throughout the life cycle is consistent with our hypothesis that germination in a favourable microenvironment (i.e. near mother plants) outweighs any possible costs associated with high plant densities (Ward, 2016). In fact, only a relatively small percentage of the studied populations (18%) shifted from a clustered pattern to a random pattern, thereby demonstrating that density-dependent mortality also occurs but it is not the norm in these Mediterranean gypsum soils.

Spatial environmental heterogeneity explained a significant proportion (32%) of the observed patterns (IPCP and IPP models). We suggest that the effect of soil chemical heterogeneity on plant spatial patterns at such very fine spatial scales must be negligible as evidenced in other studies (Pescador et al., 2020) and that the effect of soil microtopography was experimentally removed by selecting flat zones where the main meaningful differences in surface relief were due to the BSC, which was manipulated in our system. However, contrary to our expectations, the observed effect of spatial heterogeneity was not mediated by the physical structure of the BSC, which implies that other unmeasured fine-scale environmental properties affected the spatial patterns of annuals in both the seedling and adult stages. It should be noted that the BSC disturbance

treatment disaggregated the BSC and modified it into tiny fractions that remained in the soil. Consequently, the microscopic portions of lichens, algae, fungi and bacteria that comprised the BSC were active and probably maintained similar chemical and metabolic properties to the intact BSC in the soil surface (Delgado-Baquerizo et al., 2013; Escudero et al., 2007). Similarly, Ortiz et al. (2023) also found that intact and disturbed BSCs had restrictive effects on plant establishment and beneficial effects on growth for most annual plants in average water availability conditions. However, studies have shown that intact BSCs are more beneficial than disaggregated BSCs for plant development in extremely water-limited conditions (Peralta et al., 2019; Sánchez et al., 2022). In this study, both years were not extremely dry (Figure S1c), so it is not surprising that although the disturbed BSC had a meaningful effect, its influence was not significantly different from that of the intact BSC.

In agreement with our hypothesis, we also found connections between the spatial distributions of plants and their functional traits. For example, the maximum plant height and seed mass strongly determined the spatial patterns in both study years. Here, we should remark that both traits were positively correlated among the studied species (Table S2); thus, species with higher maximum plant heights showed larger seed sizes as well. Atelochorous species (i.e. those lacking dispersal mechanisms) dominate our study system (Table S3), so the maximum height determines the average distance of seed dispersal from the mother plant (Thomson et al., 2011), which may explain why shorter species (maximum height ~5 cm) with smaller seed sizes formed clustered spatial patterns and taller species (from 8 to 16 cm) with larger seed sizes generated random homogeneous or inhomogeneous spatial patterns (PP and IPP models). Indeed, among the species that formed clustered spatial patterns, taller species had larger cluster sizes than shorter species. Another complementary explanation could be based on the different effects of seed predators and secondary dispersers on heavy and light seeds. Small seeds usually survive longer in soil seed banks (Peco et al., 2003), probably because they enter the soil more readily (Luzuriaga et al., 2005), thereby joining the soil seed bank immediately after falling from the mother plant (Baskin & Baskin, 1998; Chambers et al., 1991; Thompson, 1987) and avoiding seed losses due to ant predation or secondary seed dispersal. However, large seeds are not trapped as readily by soil particles (Gutterman, 2002; Leishman et al., 2000; Leishman & Westoby, 1994), and thus they remain exposed to secondary dispersal, but especially to ants (Gutterman, 1994). Ant predation is considered one of the main drivers of seed loss in Mediterranean habitats (Azcarate & Peco, 2006), and has also been documented in these gypsum habitats (Azcarate et al., 2021) and they preferably select larger seeds (Azcarate et al., 2005). Thus, the random distributions of individuals from large-seeded species may reflect the random likelihood of each seed avoiding ant predation. However, large-seeded species usually produce a smaller number of seeds due to the trade-off between seed mass and seed number (Reekie & Bazzaz, 2005), and thus the low number of individuals may hinder the formation of well-defined clumps, and we might have detected random patterns simply due to numerical reasons.

A remarkable effect of functional traits related to the plant economics spectrum was also found in our study. We found that opportunistic species with more efficient functional strategies for adaptively exploiting resources, such as high SLA (Garnier et al., 2004; Wright et al., 2004) and high reproductive ratios (Moravcová et al., 2010; Wang et al., 2018), exhibited clustered homogeneous spatial patterns (i.e. not affected by environmental heterogeneity: PCP), especially in the dry year. We should highlight that SLA and reproductive ratios were positively correlated across all the studied species (Table S2). Opportunistic species can cope with a wide range of resource availability conditions, so they may have germinated and established in microsites where the seeds were primarily dispersed, usually around the mother plant, thereby generating clustered patterns. By contrast, conservative species (low SLA and reproductive ratios) mainly had non-clustered heterogeneous spatial patterns (IPP), which probably reflected the underlying microenvironmental variation related to differences in water retention on the BSC soil surface, irrespective of the physical integrity of the BSC. However, in the wet year, functional traits were not associated with differences in the spatial patterns of species, probably because higher rainfall and subsequent water run-off events promoted secondary seed dispersal to blur the previous spatial patterns, while germination was more successful in the favourable water availability conditions. In this point, we should remark that this study was performed in two climatically contrasting years; however, we cannot discard other confounding factors associated to the environmental variability of each year.

In summary, our study confirmed that the ecological processes that dominate plant population dynamics, that is, the realized spatial patterns of seedlings and adult plants are significantly determined by the functional strategies of each species. These patterns were strongly correlated throughout ontogeny, thereby suggesting that limited seed dispersal and establishment close to the mother plants is a key strategy for annual plant species and particularly for gypsumophytes in semiarid gypsum systems. Environmental heterogeneity explained almost one-third of the observed spatial patterns but in contrast to our expectations, the effect of the physical structure of the BSC was not significantly different from that of the disturbed BSC.

AUTHOR CONTRIBUTIONS

Adrián Escudero and Marcelino de la Cruz conceived the ideas and designed methodology; Ana L. Peralta collected the data; Ana L. Peralta and Marcelino de la Cruz analysed the data; Arantazu L. Luzuriaga led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this article are available at the Dryad public repository under the following link:

After publication: <https://doi.org/10.5061/dryad.59zw3r2cm>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Mean trait values of the 46 dominant species evaluated in this study: Seed mass (μg), Specific Leaf Area (SLA, mm^2/mg), Reproductive/vegetative biomass ratio (Rep/Veg) and Maximum plant height (mm).

Table S2: Correlation coefficients (Spearman's ρ) and p -values of pairwise species trait correlations: Seed mass, Specific Leaf Area (SLA), Reproductive/vegetative biomass ratio (Rep/Veg) and Maximum plant height. Bold numbers indicate significant correlations ($p < 0.05$).

Table S3: List of the 26 species with at least 15 individuals per plot and sampling date.

Table S4: Number of best fit spatial point patterns for species with at least 15 individuals per plot and sampling date in each 1×1 m experimental plot according to the biocrust treatment (intact biocrust vs. disturbed biocrust), life stage (seedling vs. adult), and year (dry autumn vs. wet autumn).

Table S5: Multinomial tests for the effects of Biocrust treatment (intact vs. disturbed), year (dry autumn vs. wet autumn), life stage (seedling vs. adult), and their interactions on the frequencies of realized spatial point pattern processes (PP, IPP, and PCP). IPCP models were very rare in our study ($<1\%$), and thus they were excluded.

Figure S1: Sampling location in El Espartal (Valdemoro, Madrid, Spain).

Figure S2: Example of a 1×1 m plot, where each single individual was marked and identified at species level in vinyl (PVC) sheets.

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