

Temporal and spatial patterns of seed dispersal of four shrubs in a Cistus-Erica shrubland from Central Spain

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Abstract

Background

Species of Mediterranean shrublands regenerate after fires from persistent (PSSB) or transient (TSSB) soil seed banks, which can affect postfire regeneration owing to the different importance of the current seed crop depending on soil seed bank types. However, seed dispersal in these shrublands has been little investigated. Here, we recorded temporal and spatial patterns of seed dispersal in four shrubs with different soil seed banks (persistent soil seed bank, PSSB; transient soil seed bank, TSSB), three of them are seeders (*Cistus ladanifer* [PSSB], *Salvia rosmarinus*, [TSSB] and *Erica umbellata* [PSSB]) and one is a resprouter (*Erica arborea* [TSSB]) in an old (> 40 year.) shrubland in Central Spain. A 15 x 10 m plot was chosen and divided into a 0.5 x 0.5 m grid, where plant cover and density were measured. At 106 quadrats, seed traps were set and periodically (1–2 monthly) monitored for three years.

Results

S. rosmarinus dispersed in late spring-early summer, *E. arborea* dispersed during the summer, and *C. ladanifer* and *E. umbellata* dispersed since early summer until nearly late spring of the next year. Globally, seeds were being dispersed all year round. Seed crop varied between years although species differed in the year their seed crop was largest, despite large differences in climate. Seed rain and cover of each species were poorly related. Semivariogram analysis showed that seed dispersal expanded beyond the cover of each species a few meters. No association between seed crop size and spatial dependence was ascertained. While species dispersal tended to be negatively related to one another, *E. arborea* seeds tended to dominate underneath the other species.

Conclusions

Seed dispersal was consistent with the type of soil seed bank and postfire regeneration strategy: *S. rosmarinus* dispersed before the fire season; *C. ladanifer* and *E. umbellata* dispersed mostly after the fire season, which is coherent with a bet-hedging strategy against seed predators; *E. arborea* dispersed before the rainy season. The dominance of *E. arborea* seeds underneath the other species suggests that this midsuccessional species might dominate when openings form due to the deaths of the seeders standing plants, which have lower longevity.

Background

Fire evolutionary pressures on dispersal patterns in fire-prone ecosystem would be expected to vary depending on the postfire regeneration strategy of the plant. Pressures by fire to select particular temporal or spatial patterns must have been stronger on species whose persistence depends solely on a seed bank rather than on resprouting (e.g., seeders, S+, as opposed to resprouters, R+, *sensu* (Pausas, Bradstock et al. 2004)). Seed dispersal in fire-prone ecosystems, like in those of Mediterranean-type areas, have been studied mostly in serotinous species, with a focus on how fire interacts with other biotic or abiotic factors to alter dispersal (Lamont, Connell et al. 1991; Saracino, Pacella et al. 1997; Parr, Andersen et al. 2007; Broncano,

Rodrigo et al. 2008; Groom 2010; Dunker, Bull et al. 2019). Few studies, however, have addressed dispersal temporal and spatial patterns between fires in non-serotinous species whose persistence rests on soil seed banks.

For species regenerating from a soil seed bank, the type of seed is important since it may condition the type of soil seed bank. Some seeds germinate readily once imbibed, others have physiological dormancy and require chilling (Baskin and Baskin 1998), and others need to be exposed to fire cues (heat or smoke) (Staden, Brown et al. 2000; Moreira, Tormo et al. 2010; Chamorro and Moreno 2019; Pausas and Lamont 2022). Recalcitrant seeds can persist for many years until germination is promoted by the appropriate cues, particularly those related to fire, and can form long-term persistent soil seed banks. In contrast, seeds that germinate readily or need just to be exposed to chilling may stay only for shorter periods in the soil and form transient soil seed banks (Pierce and Cowling 1991; Holmes and Newton 2004; Clemente, Rego et al. 2007).

In species that form persistent soil seed banks, the density and spatial patterns of emergences may reflect the long-term accumulation of seeds over the years plus that of the last crop before fire (Keeley 1977; Kilian and Cowling 1992; Zammit and Zedler 1993). In contrast, species that do not accumulate persistent soil seed banks, emergence after fire may mostly reflect inputs from the prefire crop (Musil 1991; Pierce and Cowling 1991). Thus, dispersing before the fire season can be utmost important (Le Maitre 1988; Harrington and Driver 1995; Wright and Clarke 2018). Fires before seed ripening and dispersal due to changes in fire seasonality can affect population persistence and alter the plant community (Miller, Tangney et al. 2019).

Yearly seed crops fluctuate largely within and between species and over the years (Herrera, Jordano et al. 1998) (Nathan and Muller-Landau 2000). This is partly determined by weather patterns during the year, with precipitation being an important driver in semiarid ecosystems like Mediterranean-type ones (Keeley 1977; Keeley 1987). Seed crop may differ among species owing to their sensitivity to the current weather, the timing of flowering and seed production, among other. Therefore, seed crop at a given year may vary among species of the same community. Furthermore, the size of the seed crop can affect spatial patterns (Gratzer, Pesendorfer et al. 2022). Therefore, total seed input and where seeds land may be subject to the vagaries of the climatic conditions during a given year. Until now, however, no study has addressed this temporal and spatial variability in fire-prone ecosystems in semiarid shrublands like the Mediterranean ones.

In addition to fire, other stressors may drive seed dispersal patterns. Granivorous ants are a main seed predator in this region (Bastida and Talavera 2002; Bastida, Talavera et al. 2009; Engelbrecht and García-Fayos 2012). Ants are active throughout the year until temperatures fall below 10°C (Retana and Cerdá 2000). Thus, seeder species with a permanent soil seed bank would be expected to delay dispersal well into autumn and winter, since there would be no benefit in dispersing when predators are most active, while their permanence is insured by a persistent seed bank. On the other hand, seeder species with transient soil seed banks would be expected to disperse before the fire season to benefit from the current seed crop in case of fire. If chilling would be required, this would just delay germination in time until late winter or early spring, which might compromise establishment (Luis, Verdú et al. 2008; Moreno, Zuazua et al. 2011), but would not affect dispersal temporal patterns. Non-seeder species with transient seed bank would be expected to disperse before the wet season.

Mediterranean seeder shrubs have small seeds that are dispersed alone or with their fruits or other floral structures by barochory. Dispersal spatial patterns are important in view of a future fire and future competition among species (Yeaton and Bond 1991). For instance, dispersing underneath the mother plant ensures spatial persistence, since these plants will be killed by fire, thus favoring the recolonization of space occupied prior to the fire. Yet, this would be more important for plants with persistent seed banks than for those with transient ones. In the latter case, greater occupancy of the space at any year might be important to reduce competition with the many more seedlings that might emerge in areas occupied by species with persistent seed banks. Additionally, seeders should avoid dispersing underneath resprouters, since resprouters will likely survive the fire (Parra and Moreno 2018) and might outcompete seedlings.

Dispersal spatial patterns (magnitude of seed patches and the importance of spatial relationships [i.e., how much seed rain can be explained by spatial relationships]) can vary with the size of seed crop (Gratzer, Pesendorfer et al. 2022). Yet, variability in species forming persistent seed banks might be greater than in those forming transient ones. The reason being that the soil seed bank would leverage in part the effects of a year with a low crop. In contrast, species with transient banks would be expected to vary less in their spatial relationships as a function of the yearly seed crop in order to maximize occupancy of open spaces after fire that will mostly rely on the last crop. Consequently, greater stability would be expected in the latter species than in the first ones. The pressure at any one year over resprouting species to ensure its colonizing capacity would be minimal since recruitment will occur over long periods of time, between fires; thus, what it is important is to expand the colonizable space to occupy empty spaces due to the death of the standing plants, as they occur over the years. Thus, pressures to maintain certain dispersal patterns with seed crop size would be minimal. All of the above rest on the assumption that primary dispersal is critical and that no other post dispersal mechanisms are as important but see (Broncano, Rodrigo et al. 2008; Warzecha and Thomas Parker 2014).

Here we studied the temporal and spatial patterns of seed dispersal of four species that were dominant in a *Cistus-Erica* shrubland of central Spain during a three-year period. Three of them are seeders (R-S+) (*C. ladanifer*, *S. rosmarinus* and *E. umbellata*) and the fourth is a resprouter (R + S-) (*E. arborea*). Despite their abundance in acidic shrublands of the Mediterranean Region, the temporal or spatial patterns of dispersal of these species have been little investigated. Dispersal in *C. ladanifer* occurs since early summer (June) over the next 10 months or longer (Bastida and Talavera 2002). Similar patterns were found for *C. monspeliensis*, *C. salviifolius* and *C. creticus* (Skourou and Arianoutsou 2004). These studies were carried out during one single year, so no information is available regarding the temporal variability of these patterns. Furthermore, seeds are predated by granivorous ants rather efficiently, decreasing seed density in the upper soil (Bastida and Talavera 2002; Bastida, Talavera et al. 2009). *S. rosmarinus* appears to have a short period of dispersal around late spring (Herrera 1986). Its seeds are prolifically predated by ants, unless they are moistened and glued to the soil by a mucilage secreted by the seed (Engelbrecht and García-Fayos 2012). No study is available regarding temporal patterns of dispersal of both *Erica* species.

These species differ also in their seed type, response to fire cues and soil seed bank types: *C. ladanifer* has hard seeds, its germination is promoted by a heat shock (Chamorro and Moreno 2019), forms persistent seed banks in the soil that prolifically germinate after fire (Quintana, Cruz et al. 2004; Moreno, Zuazua et al.

2011). *S. rosmarinus* has soft seeds that imbibe readily when moistened, its germination can be enhanced by cold temperatures (Madeiras, Boyle et al. 2009), and viability in the soil is very low, hence it forms transient seeds banks (Clemente, Rego et al. 2007). It germinates after a fire even if not in prolific numbers (Quintana, Cruz et al. 2004; Moreno, Zuazua et al. 2011). *E. umbellata* seeds are soft but rather recalcitrant to germinate, its germination is either negatively affected by heat (Chamorro, Luna et al. 2018) or not (Vasques, Maia et al. 2012), but is positively affected by smoke (Moreira, Tormo et al. 2010). Fire negatively affects seed density in the soil seed bank, particularly in the litter layer, not so much in the deeper soil layers (Maia, Vasques et al. 2016). Remaining with capacity to germinate in the deeper soil is a sign of the capacity to form at least short-term persistent seed banks (Teketay and Granström 1995; Holmes and Newton 2004). The species germinates well after fires, even two or more years past the blaze (Quintana, Cruz et al. 2004; Moreno, Zuazua et al. 2011; Céspedes, Luna et al. 2014). *E. arborea* germinates readily when moistened (Chamorro, Luna et al. 2017). Heat either does not affect germination or reduces it (Mesléard and Lepart 1991; Valbuena and Vera 2002), and does not germinate after fire under Mediterranean conditions (Mesléard and Lepart 1991; Quintana, Cruz et al. 2004; Moreno, Zuazua et al. 2011). We consider the soil seed bank of this species to be transient.

Our goal was to determine whether seed temporal and spatial dispersal patterns were different between the three seeders and the resprouter species, and whether those of the seeders were linked to the fire season depending on the type of seed bank. Most fires are now lit by people, and occur during the summer; natural, lightning fires occur also during summer, with the largest area burned in recent decades centered in the month of July (Vázquez and Moreno 1998; Rodrigues, Jiménez-Ruano et al. 2023). Fires in these shrublands burn as high intensity crown fires that fully scorch the crowns. These fires have shown to kill non-dispersed seeds (Harrington and Driver 1995; Schmidt, Sampaio et al. 2005). Thus, if fire had selected dispersal, this should occur before the onset of the lightning season, assuming that current lightning patterns have been prevalent under Mediterranean climate conditions. For seeder species that rely on persistent soil seed banks, the time of dispersal might be secondary to other pressures, like predators. In this case, minimizing predator pressure might be more important than dispersing before the fire season. In contrast, resprouters recruit between fires; dispersal should occur before the onset of the rainy season in fall. We also expected higher dispersal underneath the mother plant in species with persistent than in transient soil seed banks. Additionally, we expected higher persistence of spatial patterns in transient than in persistent soil seed banks in relation to the yearly seed crop size. As for the resprouter, we expected high variability over the years following changes in seed crop size since colonization of empty spaces could occur over the years.

Methods

The study site was located at the Quintos de Mora Range Station, Montes de Toledo, Central Spain (39°23'N, 4°00' W). An old (> 40 years) shrubland was chosen in a south facing slope, at 700 m elevation. It was dominated by the shrubs *Cistus ladanifer* L. (Cistaceae), *Salvia rosmarinus* Spenn. (Labiatae) (former *Rosmarinus officinalis* L.), *Erica umbellata* Loebl. ex L., *Erica arborea* L. (Ericaceae), and *Phillyrea angustifolia* L. (Oleaceae). The first three species are seeders (S+), that is, they regenerate after fire from seeds, while the last two are resprouters, that is, they regenerate after fire by resprouting (R+). The soils are acidic, derived from quartzite; the mean annual temperature is 14.7°C and the mean annual precipitation is

689 mm (data from Los Cortijos meteorological observatory, 1971–2000, 10 km south from the area). We used data from this observatory plus the 12-months standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano, Beguería et al. 2010) to characterize the climatology and drought conditions, respectively, of the years of study.

In March 1997, a 15 x 10 m plot was chosen, and a 0.5 x 0.5 m grid established. Shrub density (No. m⁻²) and cover was measured for each species by the line-intercept method along the middle of each 0.5 x 0.5 m grid, with a total of 600 quadrats sampled. Plant cover was expressed as percentage of the intersected species within each quadrat. In *P. angustifolia*, an individual was considered if it sprouted from the soil without clear and visible connection to any other sprout.

Seed traps (106) were set in the middle of the 0.5 x 0.5 m quadrat following a systematic nested design. First, 40 plots were set at the upper left-hand-side corner of each 2 x 2 m. Then, 8 of these 2 x 2 m were randomly chosen and 7 locations within the original 0.5 x 0.5 m were randomly selected for a total of 8 x 7 = 56 additional locations. Finally, 10 additional locations were randomly selected within the original grid. The seeds traps consisted of an inverted funnel (12 cm diameter) placed in a bag within a pot with a hole to allow evacuating water. Seeds were collected periodically, every 1–2 months, depending on the season, from April 1997 until April 2000 (three years of observations). Bags were brought to the laboratory, cleaned, and seeds identified under a stereoscopic microscope. Seed counts in each trap were converted to seeds per square meter. In many instances, whole fruits fell into the traps; these were dislodged and seeds counted. In the case of *S. rosmarinus*, the fruit is dispersed as a unit, composed of four *nuculae*. We counted the *nuculae* as seeds. No significant seeds were collected for *P. angustifolia*; hence its seed production will not be treated further.

Temporal patterns

Differences in heterogeneity of the seed crop within a species across years were tested by the coefficient of variation (Gratzer, Pesendorfer et al. 2022). Additionally, differences in the seed crop between years for each species were tested by GLM repeated measures ANOVA. When sphericity was not met (Mauchly's test significant at $P \geq 0.05$), the Huynh-Feldt correction was used. *Post hoc* comparisons between years were corrected by Bonferroni for multiple comparisons.

The analysis of the temporal pattern of cumulative dispersal of each species was done considering the seed rain produced by the species during a 12-month period. The beginning and end of this period varied among species. The initial month was considered the one in which seed rain was null or minimum, since in some cases there a few seeds being dispersed over time. The periods used were January-December (*S. rosmarinus*), June-May of the following year (*C. ladanifer* and *E. umbellata*) and April-March of the following year (*E. arborea*). We summed all the seeds dispersed during the corresponding period and calculated the percentage that was accumulated over time. We then fitted non-linear functions to the cumulative seed rain over the selected period using the minimum Akaike's information criterion (AIC) for model selection. The model selected was:

$$y = \frac{A1 - A2}{1 + \left(\frac{x}{x_0}\right)^P} + A2$$

The relationships between seed rain among pair of species over the three years were studied by the non-parametric test of Spearman rank correlation coefficient (ρ), due all four species being not-normally distributed (Shapiro-Wilk test, $P < 0.001$).

Spatial patterns

The spatial relationship between standing species was investigated by calculating the Pearson correlation coefficient among pair of species using cover (%) values from all 0.5 x 0.5 quadrats ($n = 600$) in the plots. Plant density in each quadrat was transformed to presence/absence data and then we assessed the association between pair of species using the Pearson χ^2 test. Statistical significance was set in both analysis at $P \leq 0.05$.

For each species, we calculated omnidirectional, experimental semivariograms of annual and of 3-year accumulated seed rain up to a distance of 10 m, roughly half the maximum possible distance in the study plot (Rossi et al. 1992). Empirical semivariograms were modelled with spherical models, unless no clear autocorrelation was evident, when a pure nugget model was used, or when the spherical model fitted poorly. Maximum distance of autocorrelation (range, A_0) was extracted from the models and spatial dependence (SD, the variance explained by distance among samples) was calculated as the nugget-to-sill ratio (Robertson and Gross 1994). 3-year accumulated seed rain maps were generated by ordinary kriging.

The relationships between cover and total seed crop ($n = 106$ quadrats) of the respective species were studied by linear regression after $\text{Log}_{10} + 1$ transformation of the seed crop variable in all species except *S. rosmarinus*, which could not be made normal. In this case, the equivalent relationship was explored by the non-parametric Spearman rank correlation test.

The relationship between total seed crop ($n = 106$ quadrats) among pair of species was also studied by Spearman rank correlation. Since species were compared among themselves, yielding 6 comparisons, P -values of the correlation tests were corrected for multiple comparisons using the Benjamini-Hochberg test.

To determine the relationship between the size of the yearly seed crop and the range (A_0 , m) and spatial dependence (SD [%]) of the semivariograms obtained for each species and year, absolute values within each species were ranked from 1 to 3 from the largest to the smallest values. Lack of spatial dependence was ranked 3, since it was assumed that the range would be larger than what it was empirically obtained. Then a contingency test was run for all four species together to assess whether seed crop was significantly associated to either range (A_0) or spatial dependence (SD %).

Statistical analyses were carried out with SPSS vs. 28 (IBM Corp., Armonk, NY, USA). Modeling and graphing of cumulative rain over time was done with OriginPro 2019 (OriginLab Corp., Northampton, MA, USA). Geostatistical analyses were done with the *gstat* package (Pebesma 2004; Gräler, Pebesma et al. 2016) in R version 4.1.3 (R Core Team 2022).

Results

The plot was dominated by *C. ladanifer* and *P. angustifolia*, followed by *E. arborea* and *E. umbellata*; the least abundant species was *S. rosmarinus* (Table 1). Note that *P. angustifolia* had a high cover but also a high density of individuals, signaling that these were of small size, a reason why few seeds were collected.

Table 1
Cover, density (mean, SE) and frequency (%) of the main species in the study *Cistus-Erica* shrubland at Quintos de Mora, Central Spain. Sampling unit was 0.5 x 0.5 m quadrats (n = 106).

Species	Cover (%)		Density (No. m ⁻²)		Frequency (%)
	Mean	SE	Mean	SE	
<i>Cistus ladanifer</i>	35.6	1.6	1.13	0.07	60
<i>Salvia rosmarinus</i>	8.5	0.9	0.40	0.03	31
<i>Erica umbellata</i>	15.2	1.2	0.92	0.06	51
<i>Erica arborea</i>	24.0	1.4	1.13	0.06	62
<i>Phillyrea angustifolia</i>	33.5	1.6	4.84	0.29	68

The climatology of the years of study was very different; the first two hydrological years (1996–1998) were rather wet, with both temperatures and, particularly, precipitations well above average, while the third one (1998–1999) was rather dry, particularly in the vegetatively active months, in which precipitation was nearly half of the long-term average, with temperatures being also higher than usual. This is well reflected in the SPEI, that showed the first two hydrological years well above average drought conditions, the reverse being for the third (Fig. 1).

Seed crop was very variable over the three years, with *E. arborea* being the species that fluctuated the most (CV = 93%), followed by *C. ladanifer* (CV = 55.2%), while *E. umbellata* (CV = 44.0%) and, particularly, *S. rosmarinus* fluctuated the least (CV = 22.4%) (Fig. 2). In absolute terms, the seed crop was highest in both *Erica*, which, in some years produced tens of thousands of seeds per square meter. *C. ladanifer* was also a prolific seed producer, with up to nearly thirty thousand seeds per square meter in some years. The species producing the least seeds was *S. rosmarinus*, not quite reaching one thousand seeds per square meter (Fig. 3). Averaged over the three years, *E. arborea*, despite the variability between years, was the largest seed producer, with *C. ladanifer* and *E. umbellata* producing about a third of such high number of seeds; *S. rosmarinus* produced the least of all, with two orders of magnitude less than *E. arborea*. These figures varied when correcting for the differences in cover and density. The relative rank persisted but the differences were attenuated, particularly due to the larger cover of *C. ladanifer* and the smaller one of *S. rosmarinus*. In terms of seeds produced per individual the values ranged from about 1000 in *S. rosmarinus* to 50-times higher in *E. arborea*, with the other species in between. When converting the figures to biomass it is worth noting that the largest effort was done by *C. ladanifer*, followed by *E. arborea*, the two other species being at a distance, with

S. rosmarinus being always the species that invested the least in seeds even after correcting for cover or density (Table 2).

Table 2

Average seed crop per year (mean $\pm$ SE) or after correcting it for the actual cover (assuming 100% cover for each species [100% Co]) or density (Per Indiv.) of each species based on data from Table 1. Similar results but expressed as biomass of the seed crop.

Species	Seed crop (No. m ⁻²)		Seed		Seed crop biomass (g m ⁻²)			
	Mean $\pm$ SE		100% Co	Per Indiv.	biomass (mg)	Mean	100% Co	Per Indiv.
<i>C. ladanifer</i>	18485	$\pm$ 690	51925	16359	0.2291	4.23	11.89	3.75
<i>S. rosmarinus</i>	535	$\pm$ 133	6293	1337	0.4600	0.25	2.89	0.62
<i>E. umbellata</i>	18148	$\pm$ 3647	119393	19726	0.0335	0.61	4.00	0.66
<i>E. arborea</i>	58126	$\pm$ 4580	242192	51439	0.0661	3.84	16.00	3.40

There were significant differences in seed crop among years for *C. ladanifer* ($F_{1.6, 168.6}=281.7$; $P < 0.001$), *E. umbellata* ($F_{2,210}=8.5$; $P < 0.001$), and *E. arborea* ($F_{1.2, 130.5}=77.0$; $P < 0.001$), but not for *S. rosmarinus* ($F_{1.4, 151.4}=1.6$; $P = 0.20$) (Fig. 3, Table SOM1). The timing for maximum seed crop over the years of each species varied among species. While *E. arborea* produced the largest seed crop in the first year, *E. umbellata* did so in the second, and *C. ladanifer* in the third, with *S. rosmarinus* not significantly varying over the three years studied (Fig. 3, Table SOM1).

Seed rain temporal dynamics were very different among species (Fig. 2, Fig. 4). Seed dispersal in *C. ladanifer* started in early summer (June) and lasted nearly a whole year. During this time, seed cumulative dispersal was nearly constant over time, with a pattern that was almost linear during most of the months, there being some variability among years (Fig. 4A). The cumulative seed rain of *S. rosmarinus* had a clear S-pattern and concentrated in spring and early summer (from April until June). There was very little variability in the cumulative temporal pattern of seed rain of this species (Fig. 4.B). The cumulative seed rain temporal pattern of *E. umbellata* was similar to *C. ladanifer*, being nearly constant over most of the dispersing period, which started in early summer (late June/early July) and lasted nearly ten months (Fig. 4C). This was the species with highest variability from year to year. The cumulative seed rain temporal pattern of *E. arborea* was also of an S-type, with little variability between years, and very much centered in the summer (Fig. 4.D). The temporal patterns of seed rain of *C. ladanifer* and *E. umbellata* were positively correlated among each other, while both were negatively correlated with *S. rosmarinus*. The temporal pattern of seed rain of *E. arborea* was uncorrelated to any of the other three species (Table 3). Taken all four species together, seed rain was continuous over the years, there being no period without seeds falling onto the ground (Fig. 5).

Table 3

Spearman rank correlation coefficient (ρ) among species for the temporal seed rain (No. m^{-2}) at each sampling over the three years ($n = 29$). Significant correlations ($\alpha \leq 0.05$) after correcting P-values for Benjamini-Hochberg test for multiple comparisons are marked in bold.

Species	<i>C. ladanifer</i>		<i>S. rosmarinus</i>		<i>E. umbellata</i>	
	ρ	P	ρ	P	ρ	P
<i>S. rosmarinus</i>	-0.45	0.018				
<i>E. umbellata</i>	0.51	0.006	-0.57	0.002		
<i>E. arborea</i>	0.30	0.120	-0.07	0.747	0.12	0.538

The relationship among plant cover (%) of the five species indicated that *C. ladanifer* was positively correlated with *S. rosmarinus* and *E. umbellata*, and negatively with *E. arborea* and *P. angustifolia*. *S. rosmarinus* was not correlated with any other species except as already indicated. *E. umbellata* was negatively correlated with both resprouters, while them both were positively correlated to one another. The absolute values of the correlation were never very high (Table 4). The association between species rooted within each quadrat showed that there were fewer significant relationships except the positive one between both *Erica* species and both resprouters (Table 3).

Table 4

Pearson correlation coefficient (r) and its statistical significance (P) for plant cover (upper-right panel) and Pearson χ^2 test (d.f. 1) for presence/absence data of rooted plants (lower-left panel) in 0.5×0.5 quadrats ($n = 600$) between all five dominant species in a *Cistus-Erica* shrubland at Quintos de Mora (Central Spain). Statistical significance ($P \leq 0.05$) is marked in bold.

Species	<i>C. ladanifer</i>		<i>S. rosmarinus</i>		<i>E. umbellata</i>		<i>E. arborea</i>		<i>P. angustifolia</i>	
	r/χ^2	P	r/χ^2	P	r/χ^2	P	r/χ^2	P	r/χ^2	P
<i>Cistus ladanifer</i>			0.098	0.016	0.129	0.002	-0.216	< 0.001	-0.155	< 0.001
<i>Salvia rosmarinus</i>	0.027	0.868			0.01	0.814	0.039	0.342	-0.069	0.092
<i>Erica umbellata</i>	3.566	0.059	0.03	0.863			-0.164	< 0.001	-0.148	< 0.001
<i>Erica arborea</i>	1.931	0.165	1.168	0.28	5.327	0.022			0.118	0.004
<i>Phillyrea angustifolia</i>	0.201	0.654	0.012	0.914	0.729	0.393	19.423	< 0.001		

Geostatistical analysis showed that overall cover or the cover of each species formed patches with ranges (A_0) of 1.4 m (total cover), 1.5 m (*C. ladanifer*, *E. umbellata* and *P. angustifolia*), 1.9 m (*E. arborea*), and 2.5 m (*S. rosmarinus*). Spatial dependencies were moderate (slightly > 50%) (Fig. SOM1, Table SOM2).

The geostatistical analysis of the seed rain that fell over the three years of study showed that the size of the patches of the seeds was larger than those of the plants, with ranges of 3.5 m in *C. ladanifer* and a strong spatial dependence, 2.9 m in *E. umbellata* and 4.4 m in *E. arborea*, although with reduced spatial dependencies (55% and 36%, respectively). The largest patches of seeds were found for *S. rosmarinus*, that showed a range (A_0) of 13.1 m and a moderate spatial dependence (66%) (Fig. 6, Table SOM3). Seed rain maps obtained by ordinary kriging showed that seed rain over the plot of *C. ladanifer* was widespread, there being some clusters of seed accumulation and few areas devoid of seed rain. In contrast, *S. rosmarinus* had its seed rain concentrated in one large area, much of the rest of the plot having little seed input. *E. umbellata* had a pattern of dispersal much concentrated on one half of the plot, there being distinct patches of concentration of seeds, while few seeds were dispersed over much of the other half of the plot. *E. arborea* had seed input over nearly the whole plot, the only areas being devoid of them being the larger patches that had not plants on them (Fig. 7).

The variability in spatial patterning over the years changed with the species and size of the seed crop (Fig. SOM2, Table SOM4): *C. ladanifer* was the species that presented more consistent spatial patterns over the years, with ranges of 3.4 m to 4.0 m and strong spatial dependence (> 79%). On the other side was *S. rosmarinus*, whose ranges were always much larger (9.7 to 11.7 m) and low spatial dependence (34%) at some years. *E. umbellata* had some years with ranges between 2.7 m and 4.0 m, and variable spatial dependence, including a very strong one, to others in which there was not spatial dependence (second year investigated) despite being the year with the largest seed crop. Patterning in space of *E. arborea* also fluctuated quite a bit, with one year having a range similar to 3-yr accumulated seed rain (4.0 m), and moderate spatial dependence (65%), and another one in which it produced a minimal seed crop without spatial structure (second year).

There was not a significant association between the yearly rank (1 to 3) of the year seed crop size and the ranks of either range (A_0 , m) or spatial dependence (SP [%]) as obtained in the relevant semivariograms for all four species analyzed together (Table 5).

Table 5
Contingency test of the ranks (1 to 3, from more to less) of the yearly seed crop and those of the range (A_0) and spatial dependence (SD [%]) of the semivariograms obtained for each of the four species and the three years studied.

Rank	Rank: Yearly seed crop		
	Pearson χ^2	d.f.	P
Range (A_0 , m)	1.5	4	0.827
Spatial dependence (%)	6.0	4	0.199

Dispersal in space of *C. ladanifer* tended to be negatively correlated with both Erica species, particularly with *E. arborea*. Dispersal in space of *S. rosmarinus* was uncorrelated with the other three species. Dispersal in space of both Erica species was negatively correlated among each other (Table 6).

Table 6
Spearman rank correlation coefficient (ρ) among species for accumulated seed rain (No. m^{-2}) during the three years of study at each sampling position ($n = 106$). Significant correlations ($\alpha \leq 0.05$) after correcting P-values for Benjamini-Hochberg test for multiple comparisons are marked in bold.

Species	<i>C. ladanifer</i>		<i>S. rosmarinus</i>		<i>E. umbellata</i>	
	ρ	P	ρ	P	ρ	P
<i>S. rosmarinus</i>	-0.13	0.166				
<i>E. umbellata</i>	-0.29	0.002	0.05	0.610		
<i>E. arborea</i>	-0.43	< 0.001	0.01	0.902	-0.35	< 0.001

In general, for the three seeder species there was a significant relationship between cover of the species and its total seed crop over the three years studied at the scale of the 0.5 x 0.5 quadrats ($n = 106$) (Table 7). Nonetheless, when significant relationships were detected, the correlation coefficients were not very large. No significant correlation was detected for *E. arborea* cover and its seed crop (Table 7).

Table 7
Linear relationship (*C. ladanifer*, *E. umbellata* and *E. arborea*) (r , F) or Spearman correlation (*S. rosmarinus*) (ρ) between cover (%) of each species and total seed crop ($\text{Log}_{10} + 1$ transformed in the first three species) that fell over the three years of study ($n = 106$). Statistical significance ($P \leq 0.05$) is marked in bold).

Species	Independent var./Var.1	Dependent var./Var. 2	r/ρ	$F_{1,106}$	P
<i>C. ladanifer</i>	Cover (%)	Seed crop Yr1-Yr3	0.47	28.66	< 0.001
<i>S. rosmarinus</i>	Cover (%)	Seed crop Yr1-Yr3	0.47		< 0.001
<i>E. umbellata</i>	Cover (%)	Seed crop Yr1-Yr3	0.54	43.92	< 0.001
<i>E. arborea</i>	Cover (%)	Seed crop Yr1-Yr3	< 0.10	0.20	0.655

Dispersal in either open spaces (no rooted plant within the 0.5 x 0.5 quadrat) or underneath particular species or combination of two of them was dominated by *E. arborea*, which produced that largest seed inputs in all areas but underneath *E. umbellata*, which was dominant in spaces where it was the sole rooted plant (Table 7). If we consider only the seeders species, *E. umbellata* dominated in open spaces and underneath its own space and on spaces shared with *C. ladanifer*. In contrast, *C. ladanifer* dominated seed input in quadrats where it dominated and where *S. rosmarinus* or *P. angustifolia* did so (Table 8).

Table 8

Mean seed crop (seeds m⁻²) per year the fell onto the traps located in 0.5 x 0.5 quadrats that either had no rooted individual (open space) or had individuals of one or two species. Note that we did not differentiate between one or more individuals per quadrat. No data was shown for the rest of combinations (13.4%) due to low numbers for any of them. Note that *Phillyrea angustifolia* did not produce seeds during the whole study period but was very abundant in the plot. In bold is shown the species that dominated the most underneath any species or where no plant was rooted.

Rooted species	Freq. (%)	Mean annual seed crop (seeds m ⁻²)			
		<i>C. ladanifer</i>	<i>S. rosmarinus</i>	<i>E. umbellata</i>	<i>E. arborea</i>
No rooted plant	32.0	19234	720	22905	47438
<i>C. ladanifer</i>	6.6	22486	788	5520	33076
<i>S. rosmarinus</i>	6.6	12415	1294	1488	74450
<i>E. umbellata</i>	6.6	24442	34	46793	22052
<i>E. arborea</i>	2.8	17375	718	3284	32124
<i>P. angustifolia</i>	13.2	16970	504	9528	74960
<i>C. ladanifer</i> / <i>E. umbellata</i>	5.6	24243	69	29882	33564
<i>E. umbellata</i> / <i>E. arborea</i>	3.8	13805	413	39646	74897
<i>E. arborea</i> / <i>P. angustifolia</i>	8.5	16970	504	9528	74960

Discussion

Our results document that seed dispersal temporal and spatial patterns were very different among the species of this shrubland. Our findings confirm in part the hypothesis that there is a relationship between the type of seed bank formed by a species and its temporal pattern of dispersal. We found that *C. ladanifer* has a staggered dispersal, starting in summer and lasting for nearly a whole year. These results confirm earlier findings either with this species (Bastida and Talavera 2002) or with other species of the same genus (Skourou and Arianoutsou 2004). Such a temporal dispersal pattern suggests that it is driven by factors not related to fire. Indeed, dispersing during nearly a whole year, much of which took place of in the cool months, suggests that evading predator pressure might have been behind the selection of this pattern, as suggested by (Bastida and Talavera 2002; Bastida, Talavera et al. 2009). The fact that its seeds are hard and persist in the soil for years insures regeneration after fire. Under such setup, the largest pressure on seed dispersal would be in ensuring the largest soil seed bank possible, not on dispersing at a particular time of the year in anticipation of fire, since fires may not occur for years to decades. Thus, escaping predator pressure seems to be the most pressing factor for ensuring regeneration after fire.

Albeit more variable over the years, *E. umbellata* dispersed its seeds in a very similar way to *C. ladanifer*, the dispersal of both being highly correlated in time. Unlike *C. ladanifer*, its seeds are much smaller and soft, and the need of fire cues to germinate is unclear, while it is negatively affected by heat, one study reported a significant effect of smoke in promoting germination (Moreira, Tormo et al. 2010). Fires of low severity tend

to produce low emergence and cover along the years (Reyes and Casal 2008; Fernández and Vega 2014), in contrast to others of greater fire severity (Fernández and Vega ; Moreno, Zuazua et al. 2011). This species has generally low initial germinability, a trait that is often related to persistent soil seed banks (Holmes and Newton 2004). Their persistence in the soil seed bank has not been investigated but it is probably long enough to be able to germinate even three years after fire (Moreno, Zuazua et al. 2011; Céspedes, Luna et al. 2014). All of this is consistent with being at least short-term persistent in the soil seed bank. Thus, the strategy of escaping predators fits with this pattern. Additionally, studies in vitro simulating various seasons have shown that south populations tend to germinate more readily than northern ones, which postpone their germination until past winter-type conditions, suggestive of physiological controls. Indeed, in postfire environments the species tends to germinate in spring (Quintana, Cruz et al. 2004) or can even miss germinating during the first year after fire (Céspedes, Luna et al. 2014). Therefore, this species would gain little by dispersing prior to the fire season while it would be more exposed to its predators. Delaying dispersal until fall and winter would ensure that physiological dormancy might be broken, thus leaving the seeds ready to germinate when a next fire occurs due to the stimulatory effects of smoke.

S. rosmarinus showed a very different temporal pattern since it dispersed mostly in late spring and early summer, a time that would be compatible with anticipating the fire season. This is consistent with being a seeder that has soft seeds that do not persist for long in the soil, and thus forms transient soil seed banks. Anticipating fires every year would allow this species to have their seeds in the soil and be more prone to escaping the blaze than if they had been in the canopies. Yet, survival in the canopy and soil during the passage of fire has not been investigated. Such early dispersal before the autumn rainy season would likely entail a high predation risk by ants, which are very efficient at doing so unless the seeds are moistened, in which case a mucilage is secreted by the seed that allows it to attach to the soil particles and largely reduces the risk of predation by these animals (Engelbrecht and García-Fayos 2012). Seed predation is also high in the plant, since whole calyx sections are cut and transported by the ants, which further adds to the pressure to disperse them (Engelbrecht and García-Fayos 2012). Late spring or early summer rains might reduce predator pressure on this species while providing the opportunity to remain in the soil until the rainy season.

The resprouter *E. arborea* had a pattern of dispersal similar to *S. rosmarinus*, although more delayed towards the summer and early fall. This would allow the seeds to be dispersed before the autumn rainy season, when they could germinate readily once moistened. By shifting the dispersal timing more towards the middle of the summer it reduces predation risk. Still, the period of risk of seed predation by ants was high, but no study has investigated this yet.

The fact that dispersal of *C. ladanifer* and *E. umbellata* occurred much along the year and the, to some extent, separation in time between *S. rosmarinus* and *E. arborea* led to a system in which there was a continuous seed input into the soil, a finding that had not been described yet for this type of shrublands, and contrasts with the marked seasonality of this habitat. What role does such continuous input of seeds on the predators is unknown but deserves further investigation.

Our results also document that the factors behind producing smaller or larger seed crop were idiosyncratic for each species. Of the four species investigated, the largest seed crop was obtained in a different year for

three of them (*C. ladanifer*, *E. umbellata* and *E. arborea*), with one (*S. rosmarinus*) virtually not varying over the years. This is surprising given the large variability in the climate of each of the years investigated.

Provided that the last seed crop may contribute to the regeneration of the population after fire, more so for the species whose seeds do not persist for long in the soil seed bank, this can have variable implications for each of the species. Since *S. rosmarinus* disperses mostly before the fire season, the current crop could affect the postfire population emerging during a fire occurred in that season. However, since *C. ladanifer* and *E. umbellata* disperse most of their seeds after the fire season, the effect of the current year seed crop after fire will be negligible, assuming that seeds stored in the canopy will be killed. Instead, it will be the seed crop of the previous years the ones that would play a role in the subsequent recruitment after fire. This can have important implications because a fire in a dry year, in which the seed crop might have been compromised (but see the high resilience of *C. ladanifer* to drought) (Chamorro, Parra et al. 2016) might benefit from the seed crop of the previous year that may or may not have been subject to negative climatic pressures. This uncoupling between the current year seed production and the population emerging after fire can be advantageous to overcome the limitations imposed by the vagaries of climate, and issue that had not been noted until now and should be considered in how changes in fire seasonality can affect the plant community (Miller, Tangney et al. 2019).

We documented that seed input into the soil varied very greatly among species and reached thousands of seeds per square meter. These figures for one single year are much larger than the number of seedlings that emerge after fire in the case of the three seeders. The maximum/minimum values of emergences after fire observed at adjacent stands or in similar old stands in this area are: 274/61 (No. m⁻²) for *C. ladanifer*, 20/6 for *R. officinalis* and 156/13 for *E. umbellata* (Quintana, Cruz et al. 2004; Moreno, Zuazua et al. 2011; Parra and Moreno 2018). Seed inputs at any year for *C. ladanifer* and *E. umbellata* can also exceed those reported in the soil seed bank (e.g., *C. ladanifer* [1600–3572 No. m⁻²] (Ferrandis, Herranz et al. 1999; Torres, Céspedes et al. 2013); *S. rosmarinus* [20 No. m⁻²] (Céspedes, Torres et al. 2012); *E. umbellata* [877 No. m⁻²] (Maia, Vasques et al. 2016)). These results confirm similar findings from other Mediterranean-type shrublands that suggest that large losses of seeds occur after dispersal and that emergence after fire may in part reflect seed inputs from the current year (Keeley 1977; Zammit and Zedler 1988; Pierce and Cowling 1991; Meney, Nielssen et al. 1994). In contrast, annual seed input in *S. rosmarinus* was half of what has been reported at an old stand with a large seed bank [3061 No. m⁻²] (Clemente, Rego et al. 2007). It must be noted, however, the large rate (55%) of non-viable seeds in this species, and the reduced viability (< 3%) when buried during one year, in contrast to species of *Cistus* most of whose seeds remained viable (> 70%) after three years burial (Clemente, Rego et al. 2007).

We demonstrate that dispersal in space was dominated by *E. arborea*, which ruled in squares that had on them any of the other species or combinations of them except in the case of *E. umbellata*. In this case, *E. umbellata* dominated underneath itself. Being *E. arborea* of much larger size than *E. umbellata*, and the positive relationship between standing individuals of both species hint at a displacement of the second by the first. Moreover, *E. arborea* does not germinate after fire, but between fires. The life cycle of the seeder species is in the range of maximum 15–30 years, which means that, even if few germination events occur, the likelihood that one *E. arborea* will occupy open spaces is high, given its overall seed dominance in space.

This suggest that this shrubland will not be stable over the years and that, with succession, little by little, *E. arborea* will be taking over the stand (Santana, Porto et al. 2011). While we did not collect sufficient seeds of *P. angustifolia*, the fact that it was abundant in terms of spatial occupancy and number of single individuals suggest that birds (Herrera 1995) are dispersing them from adjacent areas. The positive association with standing plants of *E. arborea* and not with the rest of the species suggests that birds are perching on this species. *P. angustifolia* is also a mid-successional species and suggests that the old stand is well on its way of becoming dominated by these two species. In case of fire, both species resprout rather well, with few losses even under severe drought conditions (Parra and Moreno 2018). Thus, even though if abundant germination might occur from the other three species, a fire will but deter for some time the successional vector of change that tends to make these two resprouters dominant.

Our results document that although standing plants were well-structured in space, with very small patches, the patches formed by the total seed input during the three years where much larger, indicating for each species the rain shadow that dispersal can produce, that amounted to a very few meters. *S. rosmarinus* was different from the other three species: while the patches produced by the standing plants were the largest, those produced by the fallen seeds where much larger, which is surprising given that it was the species that produced the least seeds. Inspection of the seed map suggests that these larger patches might correspond to conglomerates of single patches of plants, rather than specific patches of the rain shadow produced by the individual standing plants. This patterning was consistent over the years which lends support to our hypothesis that *S. rosmarinus* would be the one that would change the least over the years to ensure the greater space in case a fire would occur. Notwithstanding, *C. ladanifer* presented also patches that changed little over the years, unlike we had hypothesized. In contrast, the two *Erica* species, which were also large seed producers, had spatial patterns that changed very much and presented similar patterns among the two over the years despite the large differences in seed crop. Overall, we did not find support for a relationship between seed crop size and spatial patterning at the level of the whole community. The fact that we studied only three years necessarily limits the generalizations that can be made from this study, and more years (Gratzer, Pesendorfer et al. 2022) are needed to establish the relationships here depicted in Mediterranean shrublands for the first time.

Conclusions

Seed dispersal temporal and spatial patterns differed among the three species of seeders investigated and were related to the type of soil seed bank they form. *C. ladanifer* and *E. umbellata* (persistent soil seed banks) dispersed during long periods since early summer into the winter and next spring, indicative of a strategy that might have been selected to reduce the pressure of predators. *S. rosmarinus* (transient soil seed bank) dispersed during a short period before the summer, consistent with completing dispersal before the summer season. The resprouter *E. arborea* (transient soil seed bank) dispersed during the summer before the rainy season. Dispersal patterns in space produced seed rain shadows that exceeded in a few meters those of the plant cover. Spatial patterns of seed dispersal varied with seed crop size. We found support for a conserved spatial pattern over the years for *S. rosmarinus*, independent of seed crop size, but we did not find support for an overall relationship between spatial patterning and seed crop size for this community. The dominance of *E. arborea* in the seeds falling where the other species were rooted suggests that, as seeder

plants die without fire, this species might take over the stand, together with *P. angustifolia*, both of them midsuccessional resprouters.

Declarations

Availability of data and materials

The data used here are available upon reasonable request to the corresponding author.

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JMM designed the study and obtained funding. EZ carried out research. IT, AP, CMF conducted data analysis and modelling. JMM implemented the analysis and drafted the manuscript. IT, CLM, AP contributed editorial

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Competing interests

The authors declare that they have no competing interests.

Additional information

Supplementary Information

Additional file SOM1.

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Figures

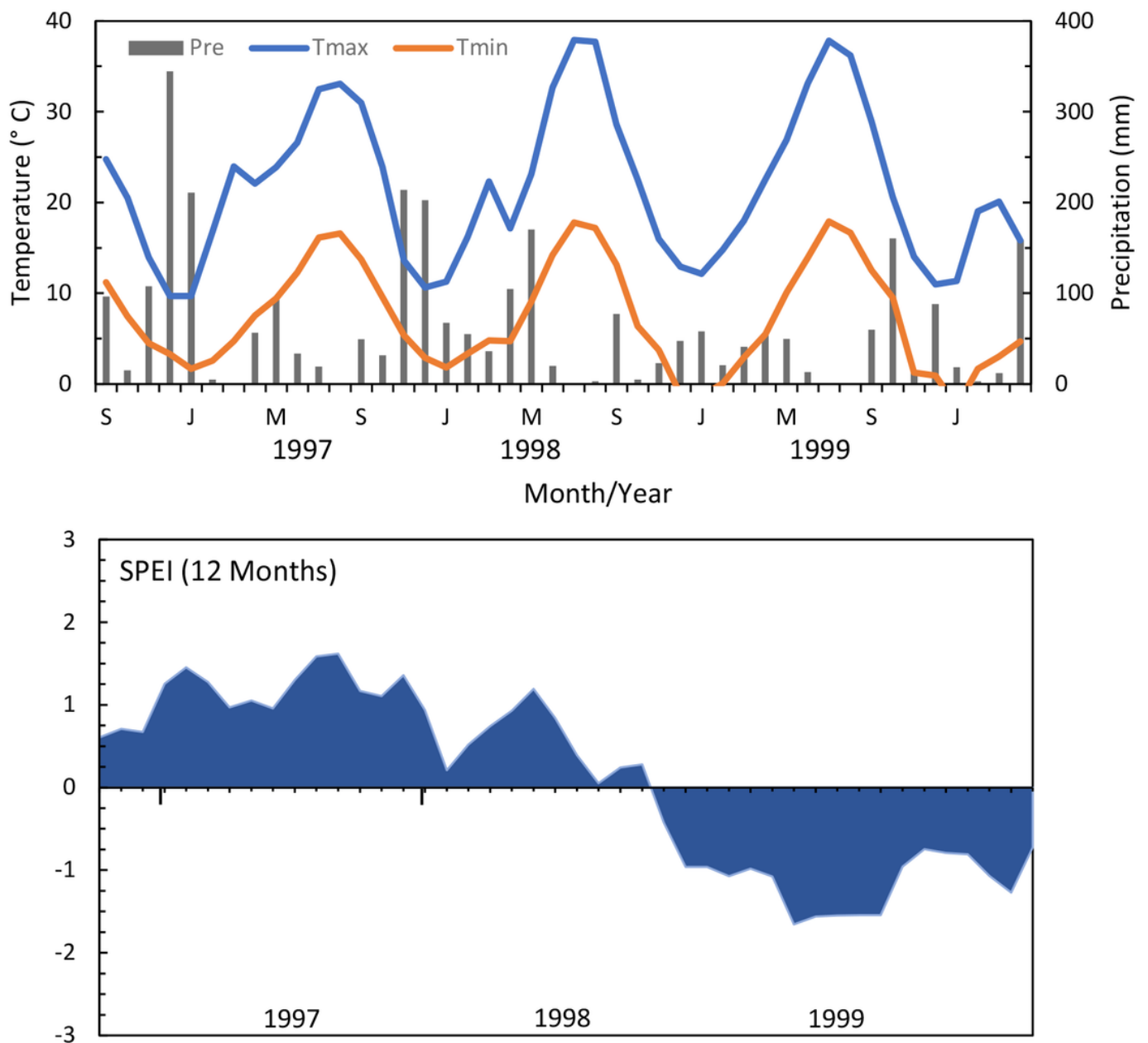


Figure 1

Maximum and minimum temperature ($T_{\max}$, $T_{\min}$) and precipitation (PRE) from Los Cortijos meteorological observatory (top), and 12-months Standardized Precipitation-Evapotranspiration Index (SPEI)(bottom) for the $1^{\circ} \times 1^{\circ}$ cell of the study area (bottom) during the years of study of seed dispersal of four shrubs of a *Cistus-Erica* shrubland at Quintos de Mora Range Station (Central Spain).

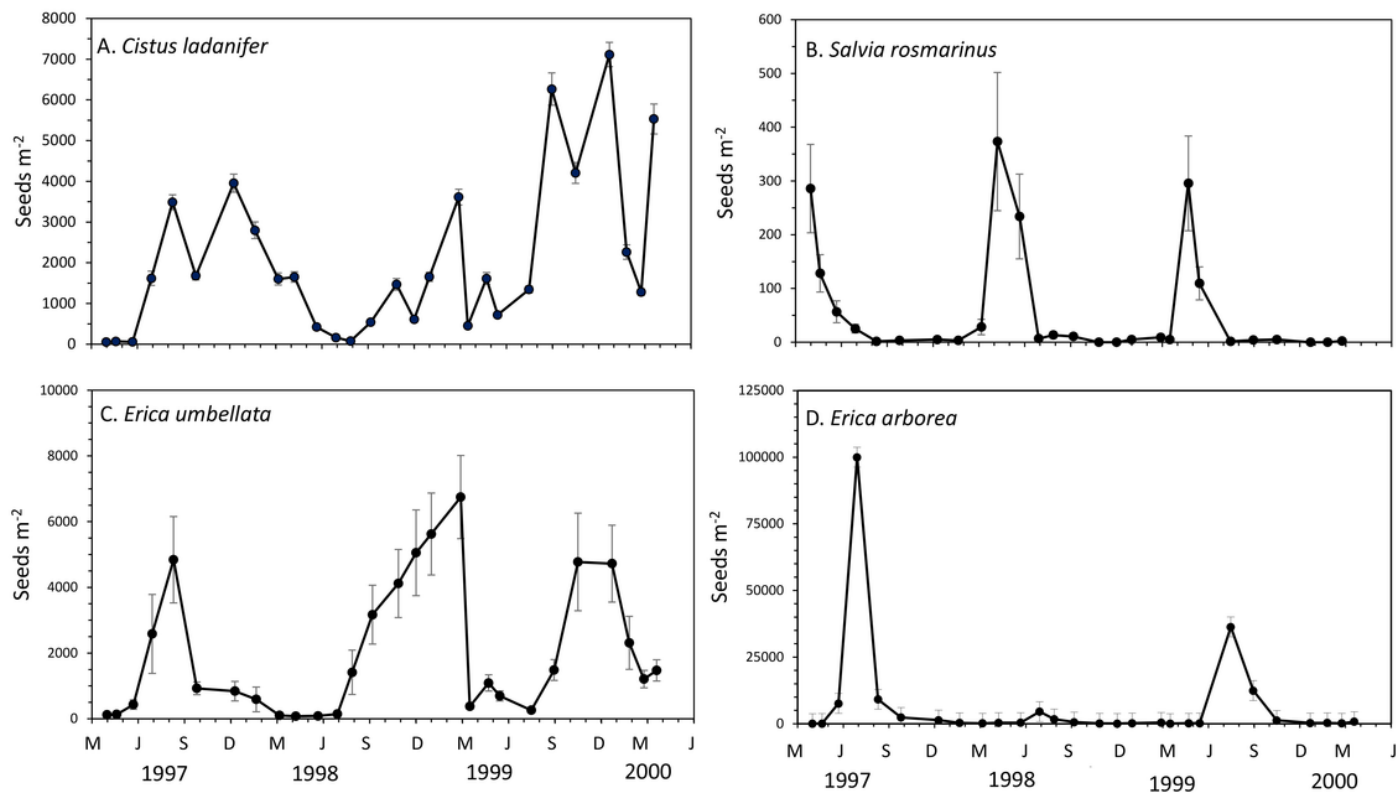


Figure 2

Temporal pattern of seed rain (mean $\pm$ SE) of A) *Cistus ladanifer*, B) *Salvia rosmarinus*, C) *Erica umbellata*, and D) *Erica arborea* over the course of the years studied in an old shrubland at Quintos de Mora Range Station (Central Spain) ($n=106$ seed traps). Note the different scales for each species as well as their different abundances (see Table 1).

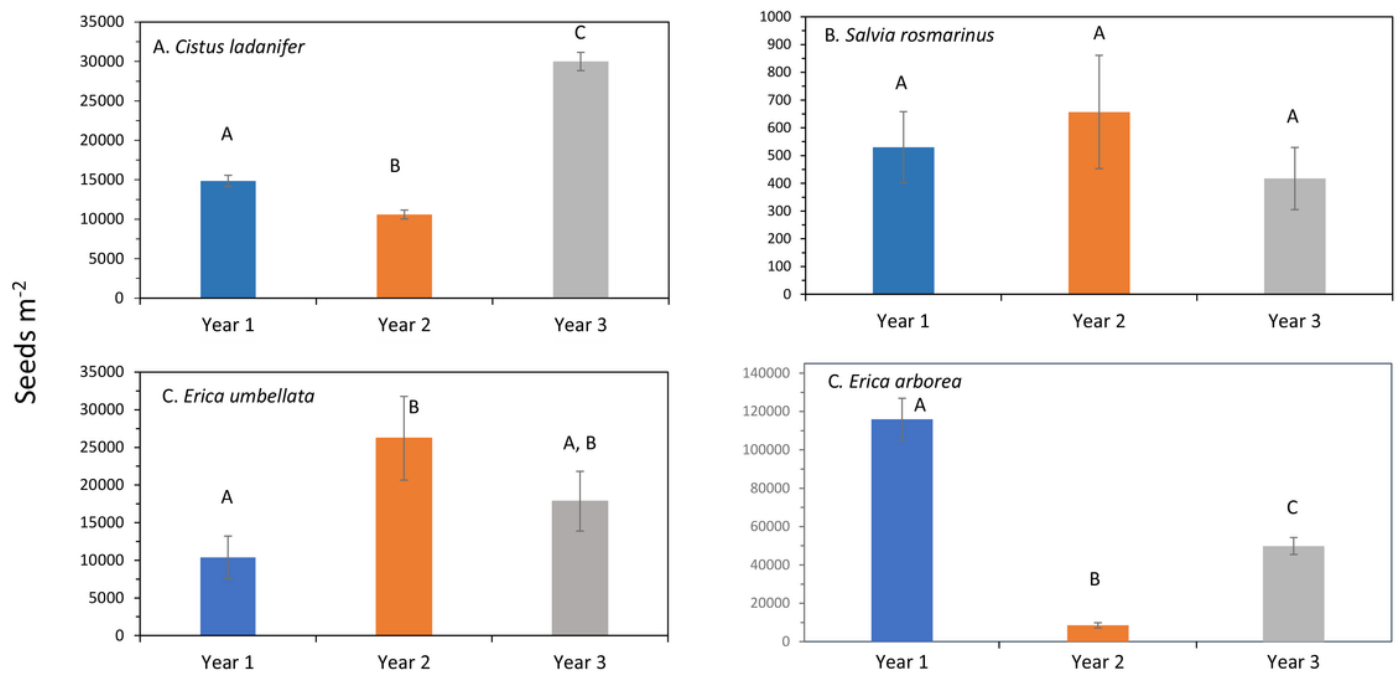


Figure 3

Annual seed crop (mean $\pm$ SEM) in A) *Cistus ladanifer*, B) *Salvia rosmarinus*, C) *Erica umbellata*, and D) *Erica arborea* over the course of the three years studied in an old shrubland at Quintos de Mora Range Station (Central Spain) (n=106 seed traps). Note the different scales for each species as well as the different abundances (see Table 1). A year was considered from April (traps were set one month earlier) until March.

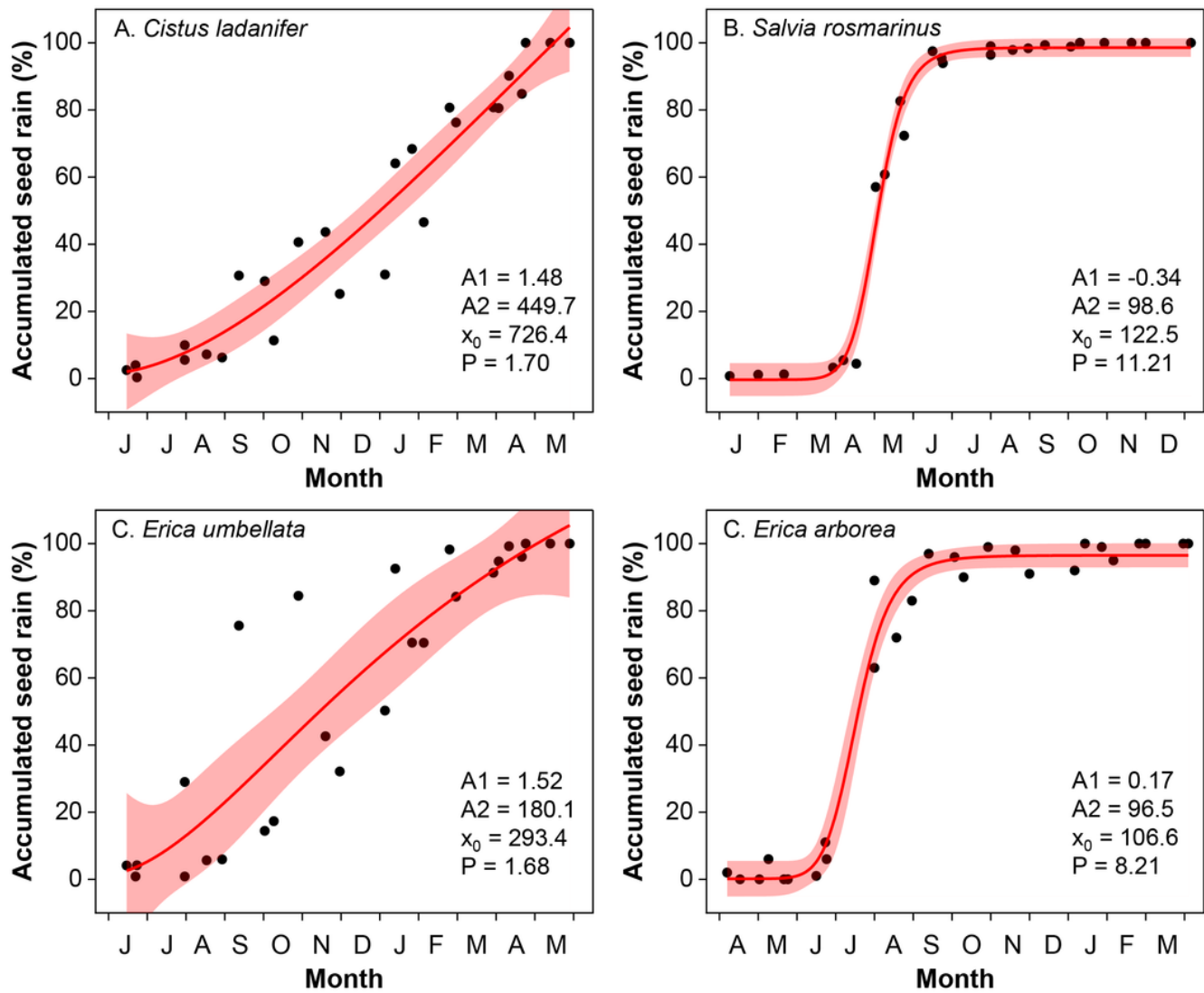


Figure 4

Cumulative seed rain of A) *Cistus ladanifer*, B) *Salvia rosmarinus*, C) *Erica umbellata*, and D) *Erica arborea* during the three years studied. Seed dispersal starts in January for *S. rosmarinus*, in April for *E. arborea*, and in June for *C. ladanifer* and *E. umbellata*. Modelling was done by fitting a logistic function ($y = A2 + (A1 - A2)/(1 + (x/x_0)^P)$), where $A1$, $A2$, x_0 , and P are parameters of the model selected based on the minimum AIC.

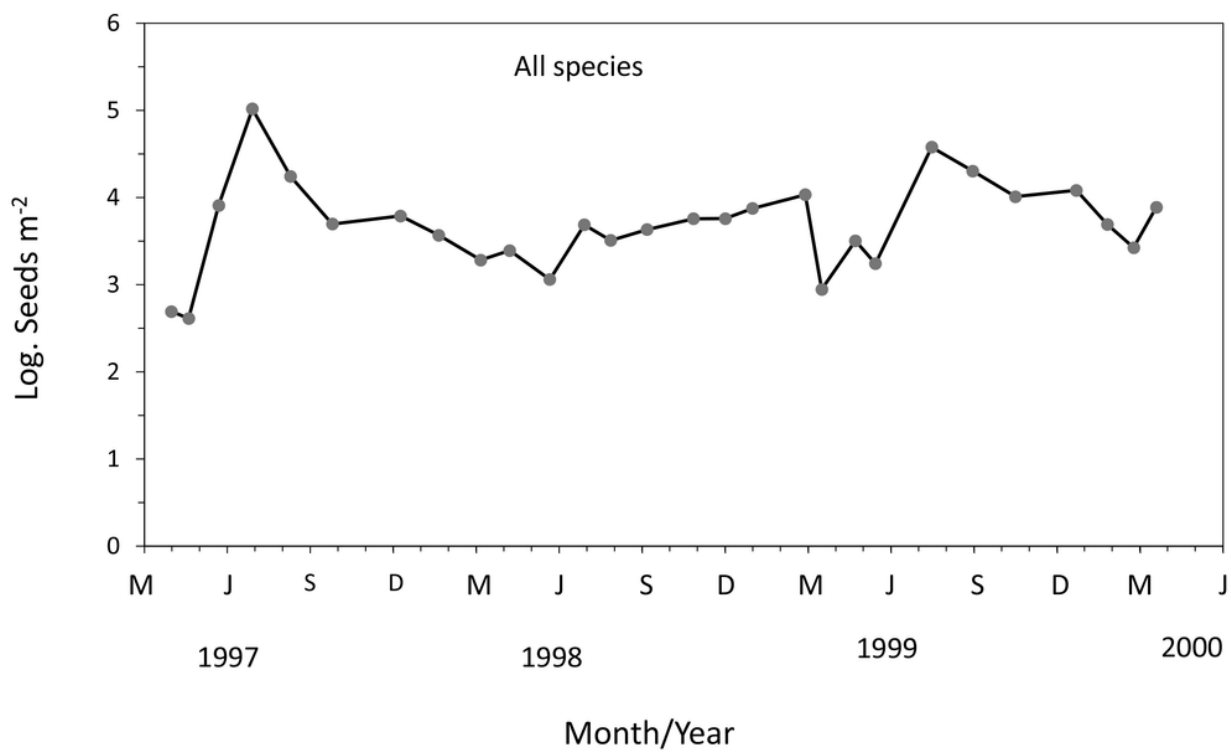


Figure 5

Total seed rain (*C. ladanifer*, *S. rosmarinus*, *E. umbellata* and *E. arborea*) (log seeds m⁻²) during the three years studied at an old shrubland in Quintos de Mora Range Station (Toledo, Spain).

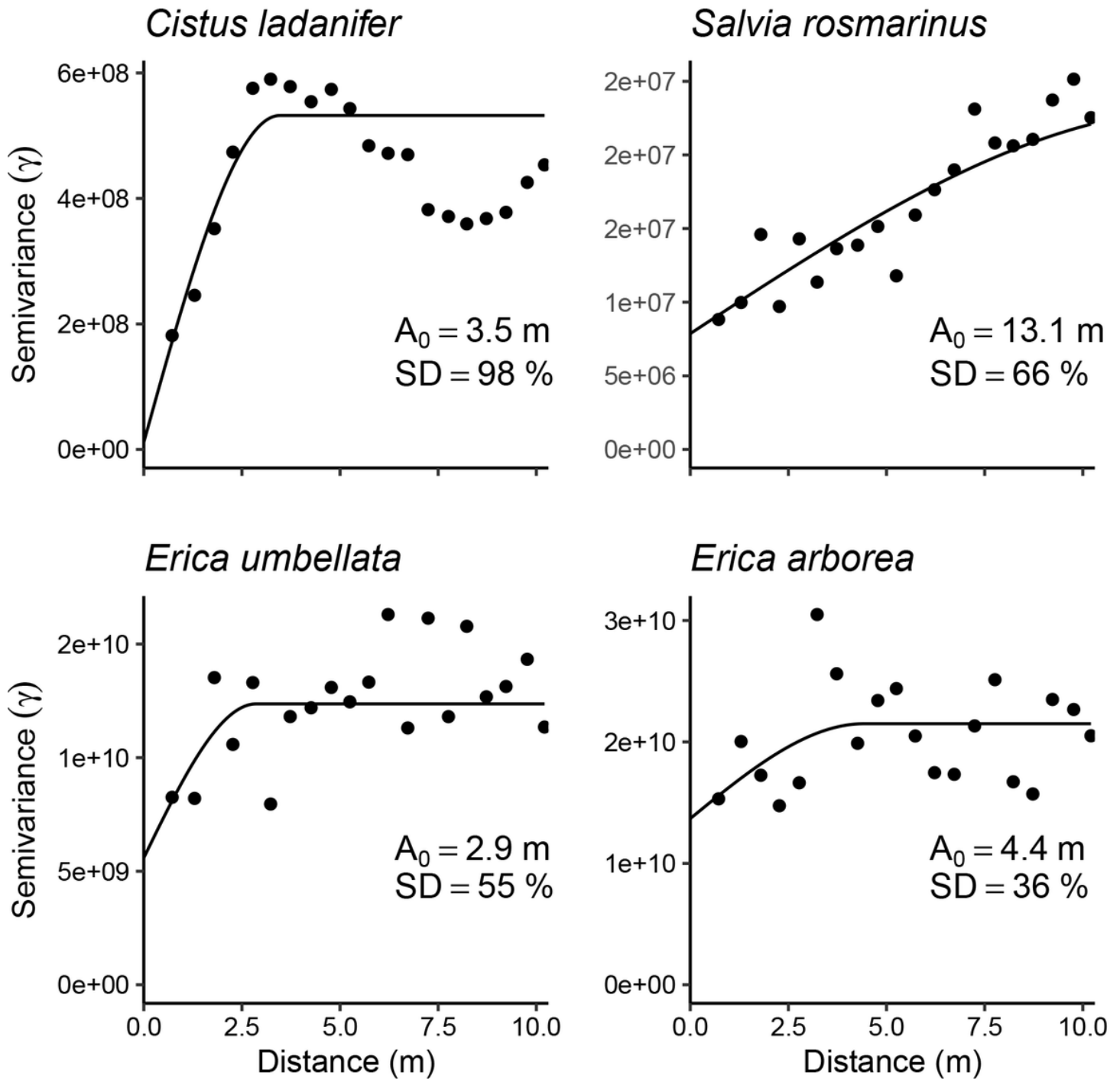


Figure 6

Semivariograms (semivariance as a function of distance) fitted to the total number of seeds fallen at 0.5 x 0.5 m quadrats (n=106) during the three years of study in a *Cistus-Ericashrubland* at Quintos de Mora Range Station (Central Spain). Top left: *Cistus ladanifer*; Top right: *Salvia rosmarinus*; Bottom left: *Erica umbellata*; Bottom right: *Erica arborea*.

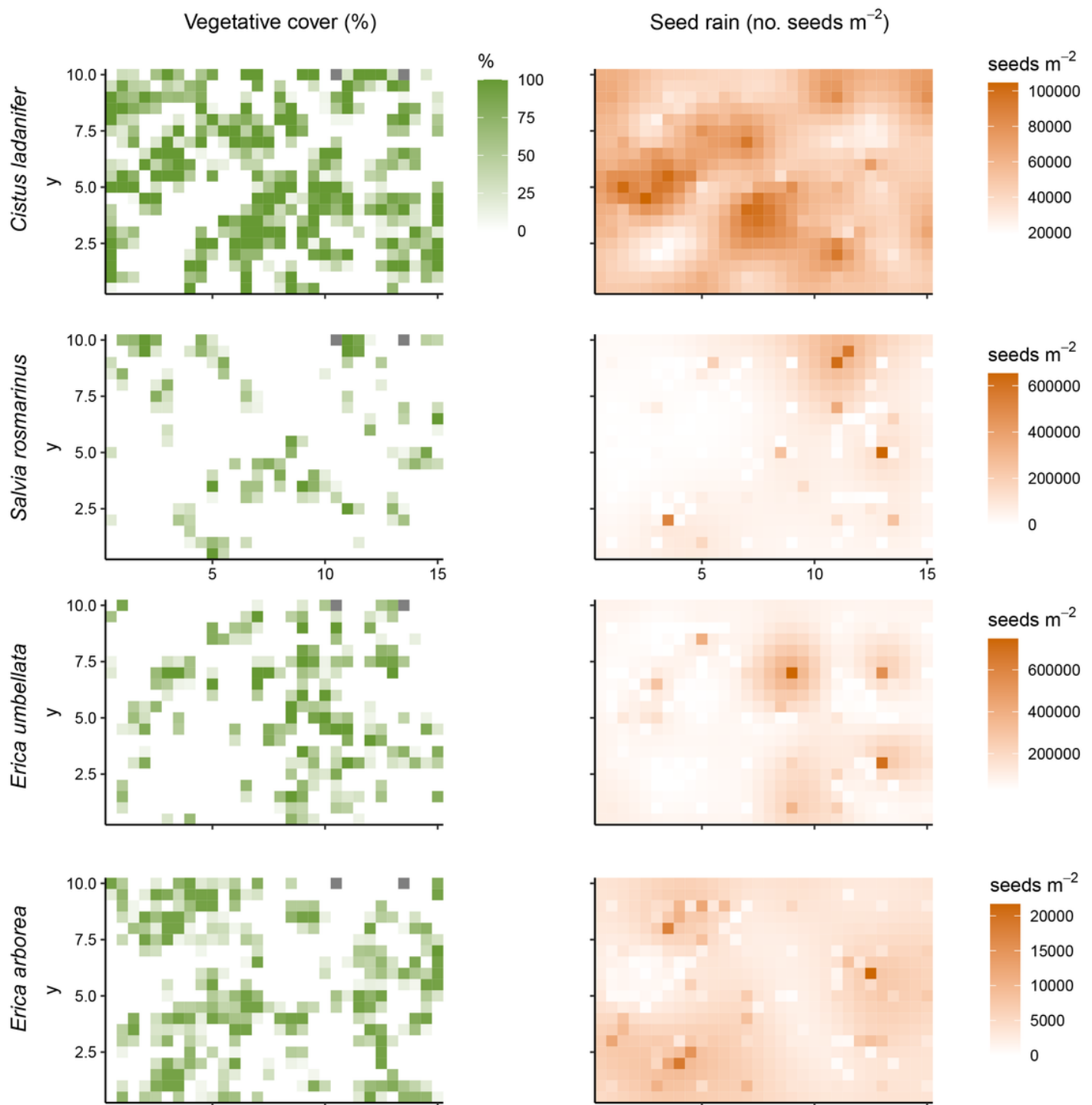


Figure 7

Plant cover (left) and three-year accumulated seed rain (right) maps at each 0.5 x 0.5 m over the whole plot (15 x 10 m) obtained by ordinary kriging in a *Cistus-Erica* shrubland at Quintos de Mora Range Station (Central Spain). Top to bottom: *Cistus ladanifer*, *Salvia rosmarinus*, *Erica umbellata*, *Erica arborea*.

Supplementary Files

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