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

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Abstract

Background Mediterranean shrublands are composed of species that have different regeneration strategies after fire and soil seed bank types. However, differences over the years in seed dispersal temporal and spatial patterns of the various plants composing a community have been little investigated. Here, we studied the temporal and spatial patterns of seed dispersal in four shrubs of an old (> 40 years) shrubland in central Spain. Three of them are seeders (*Cistus ladanifer*, *Erica umbellata*, and *Salvia rosmarinus*), and one is a resprouter (*Erica arborea*); the first two have persistent soil seed banks, and the latter two, transient. A 15 × 10 m plot was chosen and divided into a 0.5 × 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 3 years.

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

Conclusions *S. rosmarinus* dispersed before the fire season, which is consistent with seeds avoiding fire while on the plant; *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, which is expected for a plant that germinates readily after imbibition. Seed dispersal in time was compatible with the type of soil seed bank and post-fire regeneration of the species. The evidence of such a relationship with spatial patterns was weak. The dominance of *E. arborea* seeds underneath most of the other species suggests that this mid-successional species might dominate when openings form due to the deaths of standing plants of the seeders between two fires, given their lower longevity.

Keywords Seed dispersal, Soil seed bank, Post-fire regeneration strategy, Seeder, Resprouter, Seed production, Barochory

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Resumen

Antecedentes Los matorrales mediterráneos están compuestos por especies que tienen diferentes estrategias de regeneración tras el fuego y bancos de semillas del suelo. Sin embargo, las diferencias a lo largo de los años en los patrones temporales y espaciales de dispersión de las semillas de las especies que componen una comunidad han sido poco investigadas. En este trabajo estudiamos los patrones temporales y espaciales de dispersión de semillas en cuatro especies arbustivas de un matorral viejo (> 40 años) del centro de España. Tres son semilladoras (*Cistus ladanifer*, *Erica umbellata* y *Salvia rosmarinus*) y una es rebrotadora (*Erica arborea*); los dos primeras tienen bancos de semillas persistentes, y las otras dos transitorios. Se seleccionó una parcela de 15 × 10 m que se dividió en una cuadrícula de 0.5 × 0.5 m, en la que se midió la cobertura y la densidad de plantas. En 106 de estos cuadrados se colocaron trampas de semillas y se monitorearon periódicamente (1–2 mensualmente) durante tres años.

Resultados *S. rosmarinus* dispersó a finales de primavera-principios de verano, *E. arborea* dispersó durante el verano y *C. ladanifer* y *E. umbellata* dispersaron desde principios del verano hasta casi finales de la primavera del año siguiente. Globalmente, hubo dispersión de semillas durante todo el año. La cosecha de semillas de una especie varió entre años, aunque las especies variaron en el año en que su cosecha fue mayor, a pesar de las grandes diferencias en el clima durante los tres años. La lluvia de semillas y la cobertura de cada especie estuvieron poco relacionadas entre sí en términos de la varianza explicada por los modelos. El análisis de semivariogramas mostró que la dispersión de semillas se expandió más allá de la cobertura de cada especie unos pocos metros. No se detectó asociación entre el tamaño de la cosecha de semillas y la dependencia espacial. Mientras que la dispersión de semillas tendió a estar relacionada negativamente entre las especies, las semillas de *E. arborea* tendieron a dominar mayoritariamente debajo de las otras especies.

Conclusiones *S. rosmarinus* dispersó antes de la temporada de incendios, lo que es consistente con que las semillas eviten el fuego mientras estén en la planta; *C. ladanifer* y *E. umbellata* dispersaron principalmente después de la temporada de incendios, lo que es coherente con una estrategia de apuesta contra los depredadores de semillas; *E. arborea* dispersó antes de la temporada de lluvias, lo que es consistente con una especie que germina fácilmente tras la imbibición. La dispersión de semillas fue compatible con el tipo de banco de semillas del suelo y la estrategia de regeneración tras el fuego de la especie. La evidencia de esta relación con el patrón espacial fue débil. El predominio de las semillas de *E. arborea* debajo de las otras especies sugiere que esta especie mediosucesional dominará cuando se formen claros debido a la muerte de las plantas en pie de las semilladoras, que son menos longevas.

Background

Fire evolutionary pressures on seed dispersal temporal and spatial patterns in fire-prone ecosystems must have varied depending on the post-fire 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+ (Pausas et al. 2004)). Seed dispersal in fire-prone ecosystems, like those of Mediterranean-type areas, has been studied mostly in serotinous species, with a focus on how fire interacts with other biotic or abiotic factors to alter dispersal after fire (Lamont et al. 1991; Saracino et al. 1997; Parr et al. 2007; Broncano et al. 2008; Groom 2010; Dunker 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.

Mediterranean seeder shrubs are dominated by Cistaceae, Lamiaceae, and Ericaceae, among others, and have small seeds that are dispersed alone or with their fruits or other floral structures by barochory (Paula et al. 2009).

Here, we will focus on four species that are dominant in the shrublands of central and western Spain. Three of them are seeders (R-S+) (*C. ladanifer*, *S. rosmarinus*, and *E. umbellata*), and the fourth is an obligate resprouter (R+S-) (*E. arborea*). Dispersal in *C. ladanifer* occurs from 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 et al. 2009). *S. rosmarinus* has 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 four species differ also in their seed type, response to fire cues, and soil seed bank type: *C. ladanifer*

has hard seeds, and its germination is promoted by a heat shock (Chamorro and Moreno 2019) and forms persistent soil seed banks that prolifically germinate after a fire (Quintana et al. 2004; Moreno 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), its viability in the soil is very low and forms transient seeds banks (Clemente et al. 2007). It germinates after a fire even if not in prolific numbers (Quintana et al. 2004; Moreno et al. 2011). *E. umbellata* seeds are soft but rather recalcitrant to germinate, its germination is either negatively affected by heat (Chamorro et al. 2018) or not (Vasques et al. 2012), but is positively affected by smoke (Moreira et al. 2010). Fire negatively affects seed density in the soil seed bank, particularly in the litter layer, but not so much in the deeper soil layers (Maia et al. 2016). Having seeds that remain in the deeper soil and are able to germinate 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 profusely after fires, even 2 or 3 years past the blaze (Quintana et al. 2004; Moreno et al. 2011; Céspedes et al. 2014). *E. arborea* germinates readily when moistened (Chamorro et al. 2017), heat either does not affect germination or reduces it (Mesléard and Lepart 1991; Valbuena and Vera 2002), and it does not germinate after a fire under Mediterranean conditions (Mesléard and Lepart 1991; Quintana et al. 2004; Moreno et al. 2011). We consider the soil seed bank of this species to be transient.

Framing dispersal in a context of fire and soil seed bank type

For species regenerating from a soil seed bank, the type of seed is important since it may condition the type of soil seed bank it forms. 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 et al. 2000; Moreira 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 1991a, b; Holmes and Newton 2004; Clemente et al. 2007).

In species that form persistent soil seed banks, the density and spatial patterns of seedling emergence after a fire may reflect the long-term accumulation of seeds plus the input from the current year's seed crop (Keeley 1977;

Kilian and Cowling 1992; Zammit and Zedler 1993). In contrast, species that form transient soil seed banks, emergence after a fire may mostly reflect inputs from the prefire crop (Musil 1991; Pierce and Cowling 1991a, b). It has been shown that fires before seed ripening and dispersal due to fires early in the season can affect population persistence and alter the plant community (Miller et al. 2019). Thus, for the current year's seed crop to be effective after a fire, dispersal must occur before the fire season, and this will be of utmost importance for species forming transient soil seed banks, not so much for those forming persistent soil seed banks (Le Maitre 1988; Harrington and Driver 1995; Wright and Clarke 2018).

In addition to fire, other stressors may drive seed dispersion patterns. Granivorous ants are the main seed predators in this region (Bastida and Talavera 2002; Bastida et al. 2009; Engelbrecht and García-Fayos 2012). Ants are active throughout the year until temperatures fall below 10 °C in autumn and winter (Retana and Cerdá 2000). Thus, seeder species with a persistent 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 after a fire 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 maximally benefit from the current seed crop in case of fire. If chilling would be required, this would just delay the germination in time until late winter or early spring, which might compromise establishment (Luis et al. 2008; Moreno et al. 2011), but would not affect dispersal temporal patterns. Obligate resprouter species (R+S-) with transient seed soil seed banks would be expected to disperse before the wet season would start in autumn. Investing in dispersal before the fire season would be not selected since regeneration after a fire will rest only on resprouting.

Most fires are now lit by people and occur during the summer; natural, lightning fires occur during the summer, but with less temporal spread, 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. This type of fire has been shown to kill non-dispersed seeds (Harrington and Driver 1995; Schmidt et al. 2005). Thus, if fire had selected the timing of dispersal, this should occur before the onset of the lightning season, assuming that current lightning patterns have been prevalent under Mediterranean climate conditions.

Yearly seed crops fluctuate largely within and between species over the years (Herrera 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, 1987). Seed crops may differ among species owing to their sensitivity to the current weather and the timing of flowering and seed formation, among others. Therefore, seed crop size in a given year may vary among species of the same community. Furthermore, the size of the seed crop can affect seed dispersal spatial patterns (Gratzer, Pesendorfer et al. 2022). Therefore, total seed input and where seeds land may be subject to the vagaries of the weather during a given year.

Dispersal spatial patterns are important in view of a future fire and subsequent 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 since these sites were probably the most suitable ones. Yet, this would be more important for plants with persistent seed banks than for those with transient ones. In the latter case, greater exploration 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 that accumulate seeds over the years. Additionally, seeders, or species regenerating by seeding in general, should avoid dispersing underneath resprouters, since resprouters will likely survive the fire (Parra and Moreno 2018) and might outcompete seedlings.

While seed dispersion spatial patterns can vary with the size of the seed crop (Gratzer, Pesendorfer et al. 2022), interannual variability may depend on the soil seed bank of a species. This variability may be greater in species forming persistent seed banks than in those forming transient ones. The reason is that persistent soil seed banks would leverage in part the effects of a year with a low crop. In contrast, species with transient soil seed 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 year over resprouting species to ensure its colonizing capacity would be minimal, since recruitment will occur over long periods of time, between fires. For these species, what is most important is to expand the colonizable space to occupy the empty spaces that will emerge due to the death of the seeders' standing plants owing to their lower longevity. Thus, pressures to maintain certain dispersion spatial patterns with seed crop size would be minimal. All of the above rest on the assumption that primary dispersal is critical for determining emergence after a fire and that no other

post-dispersal mechanism is as important, although this may not apply to all species (Broncano et al. 2008; Warzecha and Thomas Parker 2014).

Objectives

Our goal was to study the seed temporal and spatial dispersal patterns over the course of 3 years in four Mediterranean species that dominate Mediterranean shrublands over acidic substrates. Until now, few studies have addressed dispersal at the level of the whole community in these shrublands. Additionally, we wanted to assess whether the patterns found would be compatible with a dispersal framework in which the type of soil seed bank could be important. Since the number of species in this community is limited, rigorous hypothesis testing is not possible given the variability in soil seed bank types and regeneration strategies. Nevertheless, addressing dispersal under such framework could provide insights as to what factors have selected dispersal patterns in these shrublands.

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). A 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* Loeff. ex L., *Erica arborea* L. (Ericaceae), and *Phillyrea angustifolia* L. (Oleaceae). The first three species are seeders (S+), that is, they regenerate after a fire from seeds, while the last two are resprouters, that is, they regenerate after a 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, period of observation 1971–2000, 10 km south from the area). We used data from this observatory plus the 12-month standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010) to characterize the climate and drought conditions, respectively, of the years of study.

In March 1997, a 15 × 10 m plot was chosen adjacent to an area used for experimental burning, and a 0.5 × 0.5 m grid established. Shrub density (individuals, m⁻²) was counted at each square of the grid and cover was measured for each species by the line-intercept method along the middle of each 0.5 × 0.5 m grid, with a total of 600 quadrats sampled. Plant cover was expressed as a percentage of the intersected species within each quadrat. In *P. angustifolia*, we considered as an individual all sprouts that had no clear and visible connection to any other.

Seed traps (106) were set in the middle of the 0.5×0.5 m quadrat following a systematic nested design. First, 40 plots were set at the upper left-hand-side corner of each 2×2 m. Then, 8 of these 2×2 m were randomly chosen, and 7 locations within the original 0.5×0.5 m were randomly selected for a total of $8 \times 7 = 56$ additional locations. This design was chosen to maximize sampling of the plot while having a range of distances between traps that would allow to rigorously apply geostatistical analysis (see later). Finally, 10 additional locations were randomly selected within the original grid. The seed traps consisted of a funnel (12 cm diameter) with a filter paper set onto a pot, with a hole to allow evacuating water, and fixed to the ground with a peg. Filters were sprayed with ant repellent, to avoid seed predation. Seeds were collected periodically, every 1–2 months, depending on the season, from April 1997 to April 2000 (3 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. The fruits of *P. angustifolia* are drupes that are dispersed by birds, and few of them fell into our traps; hence, its seed production will not be treated further.

Temporal patterns

Differences in the 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 first month of the period was considered the one in which seed rain was null or minimum, since in some cases there were a few seeds being dispersed over time. The periods used were January to December (*S. rosmarinus*), June to May of the following year (*C. ladanifer* and *E. umbellata*), and April to 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 (power, exponential, and logistic, with 3, 4, and 5 parameters) to the cumulative seed rain over the

selected period. The model selected based on Akaike's Information Criterion (AIC) was:

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

$A1$, $A2$, x_0 and P are parameters of the model. The relationships between seed rain among pair of species over the 3 years were studied by the non-parametric test of Spearman rank correlation coefficient (ρ), due to 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 pairs of species using cover (%) values from all 0.5×0.5 quadrats ($n=600$) in the plots. Plant density in each quadrat was transformed to the 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 analyses at $P \leq 0.05$.

For each species, we calculated omnidirectional, experimental semivariograms of annual and 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 modeled with spherical models, unless no clear autocorrelation was evident, when a pure nugget model was used or when the spherical model fitted poorly. The 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 (Robertson and Gross 1994). To better ascertain where the seeds were landing over the years, 3-year accumulated seed rain maps were generated by ordinary kriging.

The relationships between the 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 pairs of species was also studied by Spearman rank correlation. 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 were done with Origin-Pro 2019 (OriginLab Corp., Northampton, MA, USA). Geostatistical analyses were done with the *gstat* package (Pebesma 2004; Gräler 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).

The climate 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 the average drought conditions, the reverse being for the third (Fig. 1).

Seed crop was very variable over the 3 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 3 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).

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* ($F_{1,2, 130.5}=77.0; P\leq 0.001$), but not for *S. rosmarinus* ($F_{1,4, 151.4}=1.6; P=0.20$) (Fig. 3, Additional file 1: Table S1). 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 3 years studied (Fig. 3, Additional file 1: Table S1).

Seed rain temporal dynamics were very different among species (Figs. 2 and 4). Seed dispersal in *C. ladanifer* started in early summer (June) and lasted nearly a whole year. During this time, accumulated seed rain 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 was concentrated in spring and early summer (from April to June). There was very little variability in the cumulative temporal pattern of seed rain of this species (Fig. 4B). 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 10 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. 4D). The temporal patterns of seed rain of *C. ladanifer* and *E. umbellata* were positively correlated among each other, while both were negatively

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 0.5×0.5 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

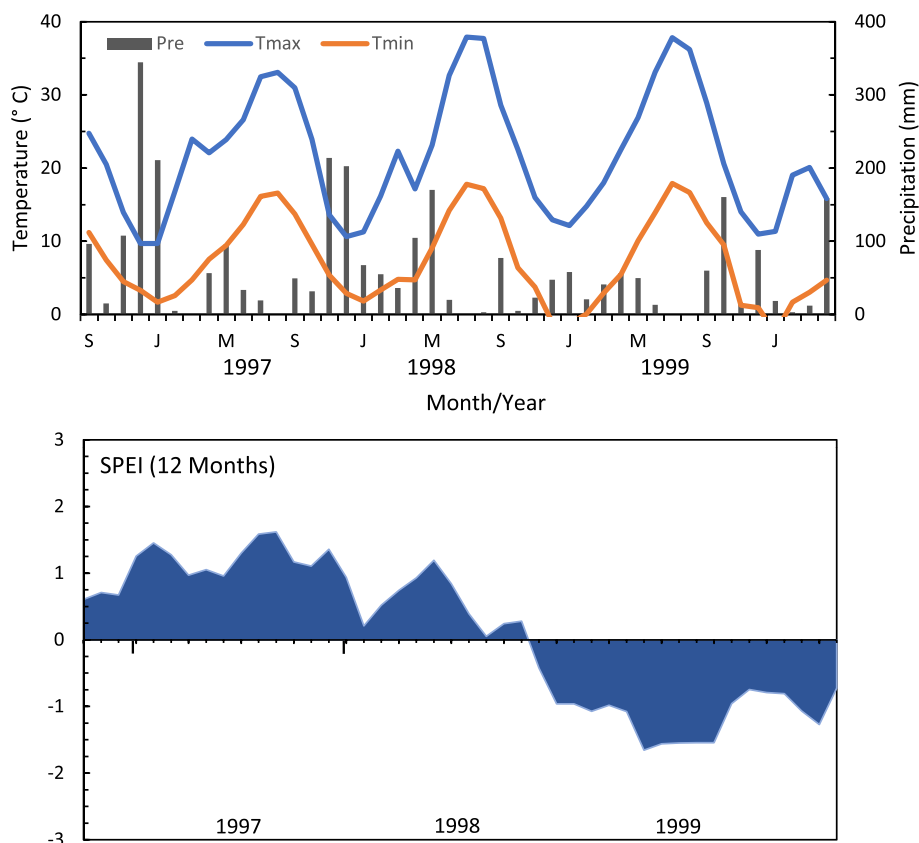


Fig. 1 Maximum and minimum temperature (T_{max} , T_{min}) and precipitation (PRE) from Los Cortijos meteorological observatory (top) and 12 months Standardized Precipitation-Evapotranspiration Index (SPEI)(bottom) for the $1^{\circ} \times 1^{\circ}$ cell of the study area (bottom) during the years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

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).

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 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 for the positive one between both *Erica* species and both resprouters (Table 3).

Geostatistical analysis showed that 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%) (Additional file 1: Fig. S1, Table S2).

The geostatistical analysis of the seed rain that fell over the 3 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, Additional file 1: Table S3). 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.

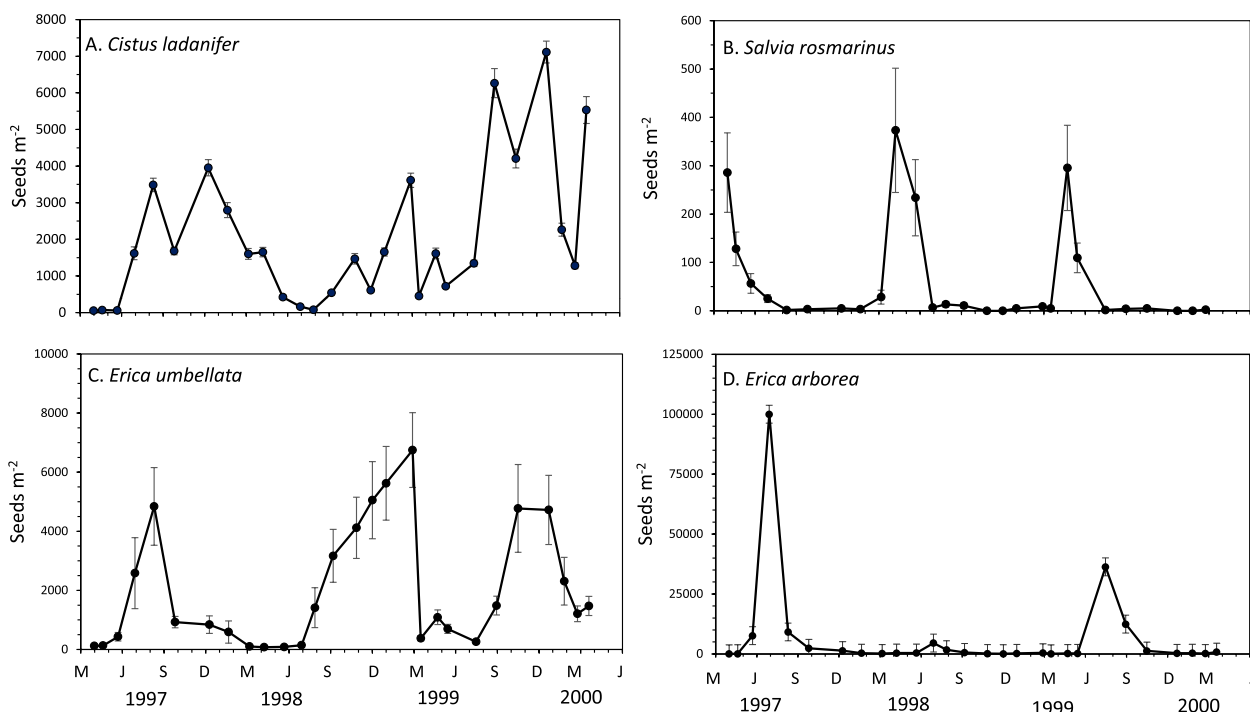


Fig. 2 Temporal pattern of seed rain (mean \pm SE) of **A** *Cistus ladanifer*, **B** *Salvia rosmarinus*, **C** *Erica umbellata*, and **D** *Erica arborea* over the course of the years studied in an old shrubland at Quintos de Mora Range Station (central Spain) ($n=106$ seed traps). Note the different scales for each species as well as their different abundances (see Table 1)

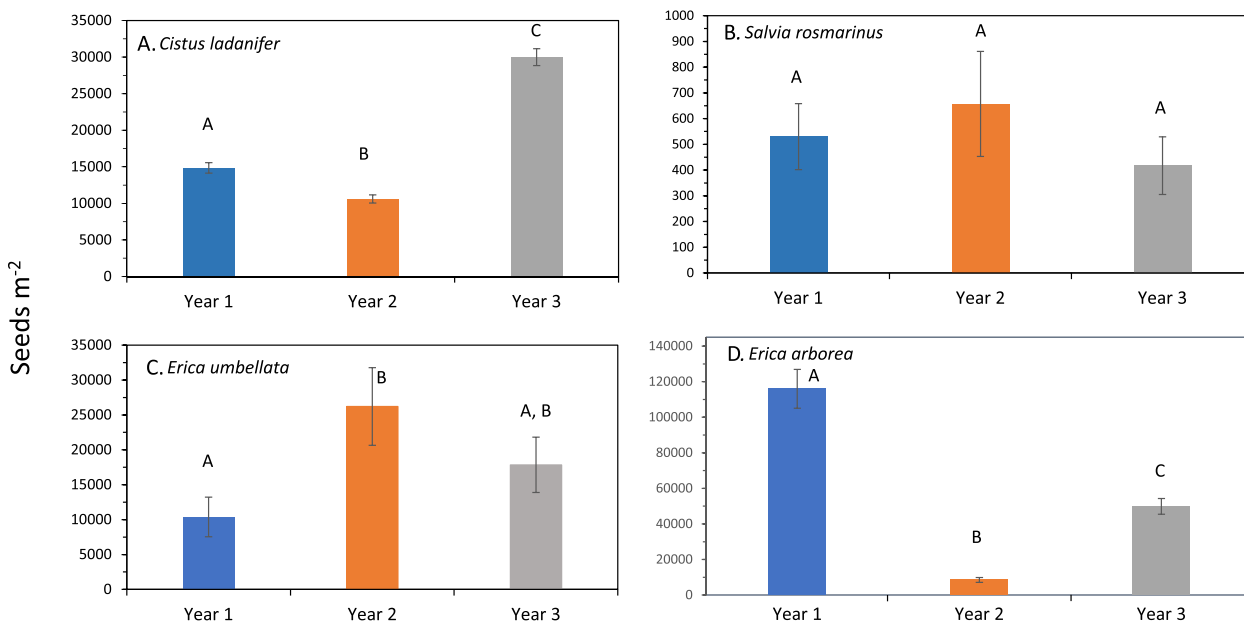


Fig. 3 Annual seed crop (mean \pm SEM) in **A** *Cistus ladanifer*, **B** *Salvia rosmarinus*, **C** *Erica umbellata*, and **D** *Erica arborea* over the course of the 3 years studied in an old shrubland at Quintos de Mora Range Station (central Spain) ($n=106$ seed traps). Note the different scales for each species as well as the different abundances (see Table 1). A year was considered from April (traps were set 1 month earlier) until March. Within a graph, significant differences among years are indicated with different letters (see text)

Table 2 Average seed crop per year (mean ± 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, after multiplying seed crop by seed biomass. Seed biomass data were provided by Dr. D. Chamorro

Species	Seed crop (No. m ⁻²)			Seed biomass (mg)	Seed crop biomass (g m ⁻²)		
	Mean ± SE	100% Co	Per Indiv		Mean	100% Co	Per Indiv
<i>C. ladanifer</i>	18,485 ± 690	51,925	16,359	0.2291	4.23	11.89	3.75
<i>S. rosmarinus</i>	535 ± 133	6293	1337	0.4600	0.25	2.89	0.62
<i>E. umbellata</i>	18,148 ± 3647	119,393	19,726	0.0335	0.61	4.00	0.66
<i>E. arborea</i>	58,126 ± 4580	242,192	51,439	0.0661	3.84	16.00	3.40

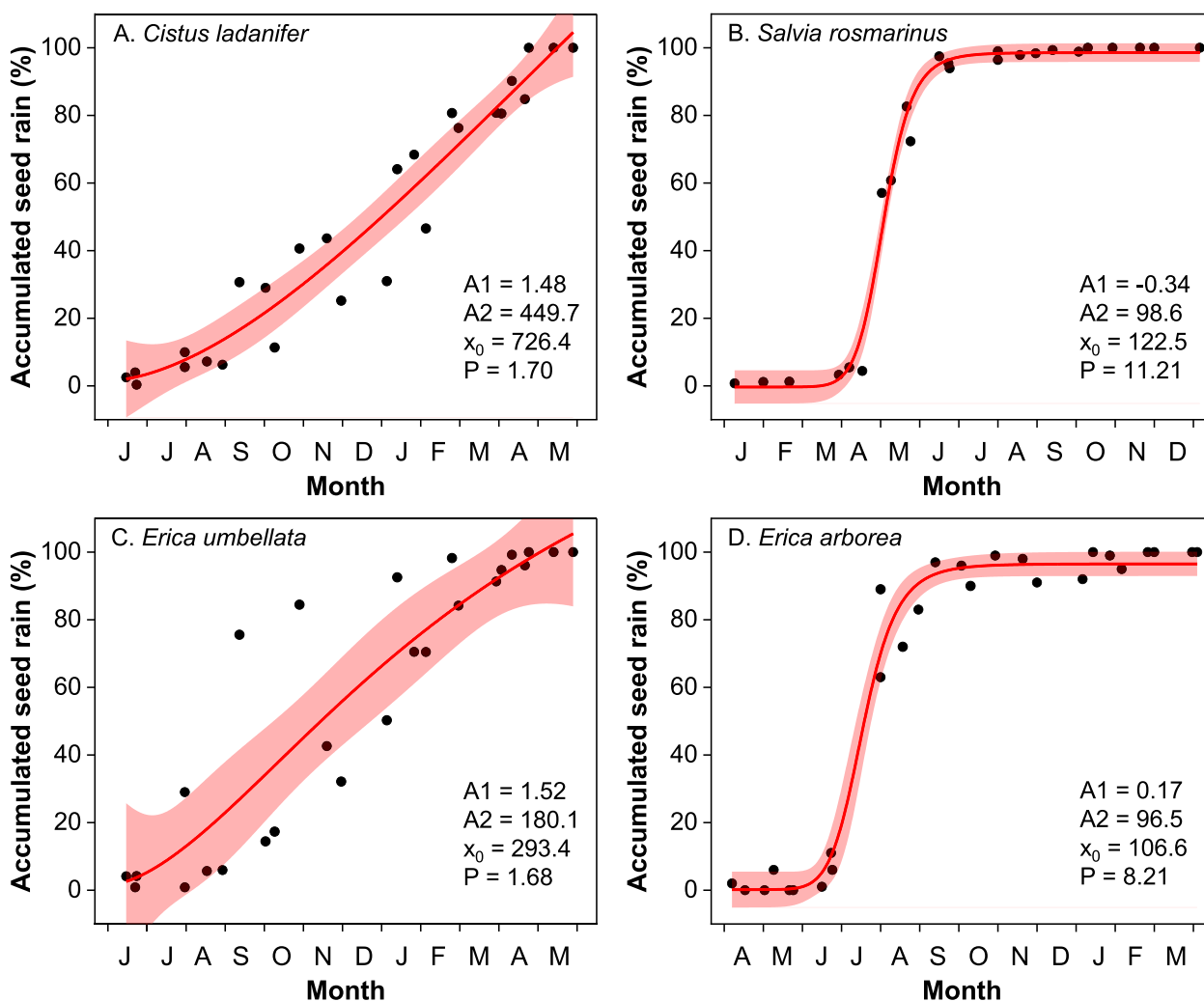


Fig. 4 Cumulative seed rain of **A** *Cistus ladanifer*, **B** *Salvia rosmarinus*, **C** *Erica umbellata*, and **D** *Erica arborea* during the 3 years studied. Seed dispersal starts in January for *S. rosmarinus*, in April for *E. arborea*, and in June for *C. ladanifer* and *E. umbellata*. Modeling 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

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 (Additional file 1: Fig. S2, Table S4): *C. ladanifer* was the

Table 3 Spearman rank correlation coefficient (ρ) among species for the temporal seed rain (No. m^{-2}) at each sampling over the 3 years ($n=29$). Significant correlations ($\alpha \leq 0.05$) after correcting P -values for the 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

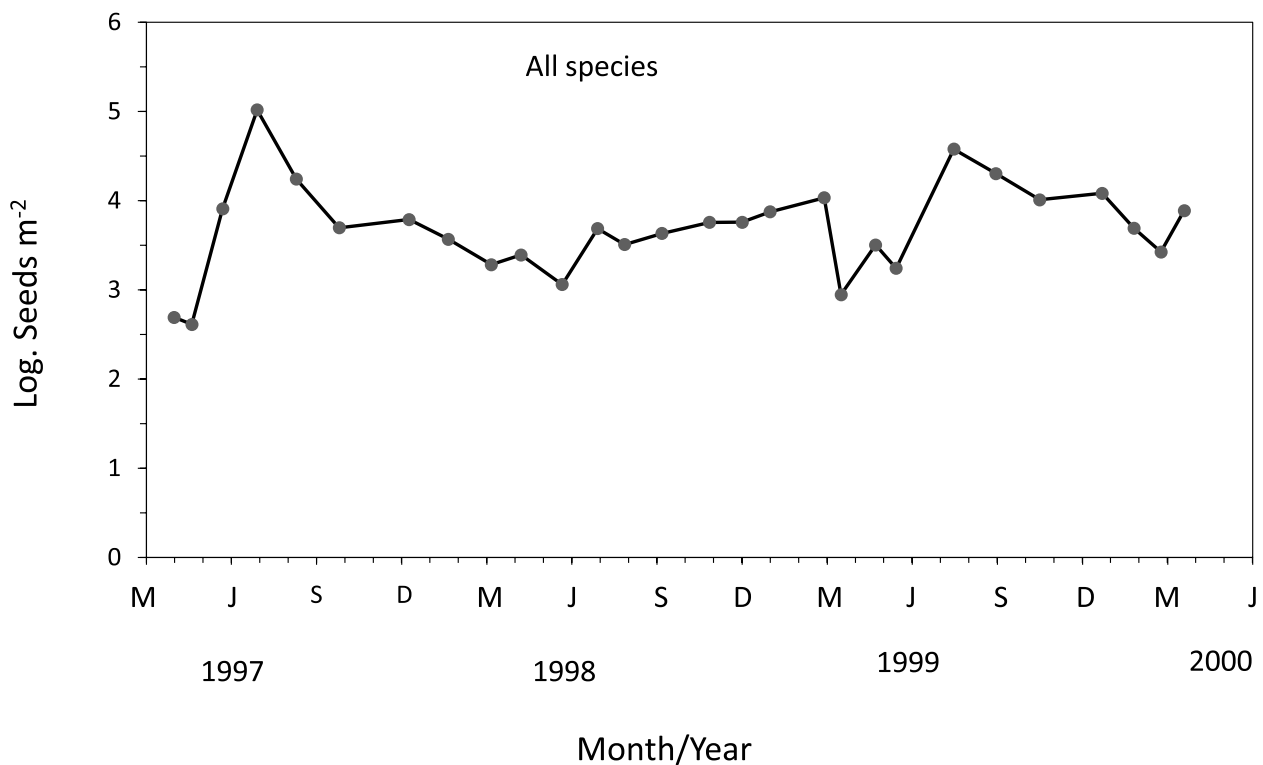


Fig. 5 Total seed rain (*C. ladanifer*, *S. rosmarinus*, *E. umbellata*, and *E. arborea*) (log seeds m^{-2}) during the 3 years studied at an old shrubland in Quintos de Mora Range Station (Toledo, Spain)

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 the 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			0.010	0.814	0.039	0.342	-0.069	0.092
<i>Erica umbellata</i>	3.566	0.059	0.030	0.863			-0.164	<0.001	-0.148	<0.001
<i>Erica arborea</i>	1.931	0.165	1.168	0.280	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		

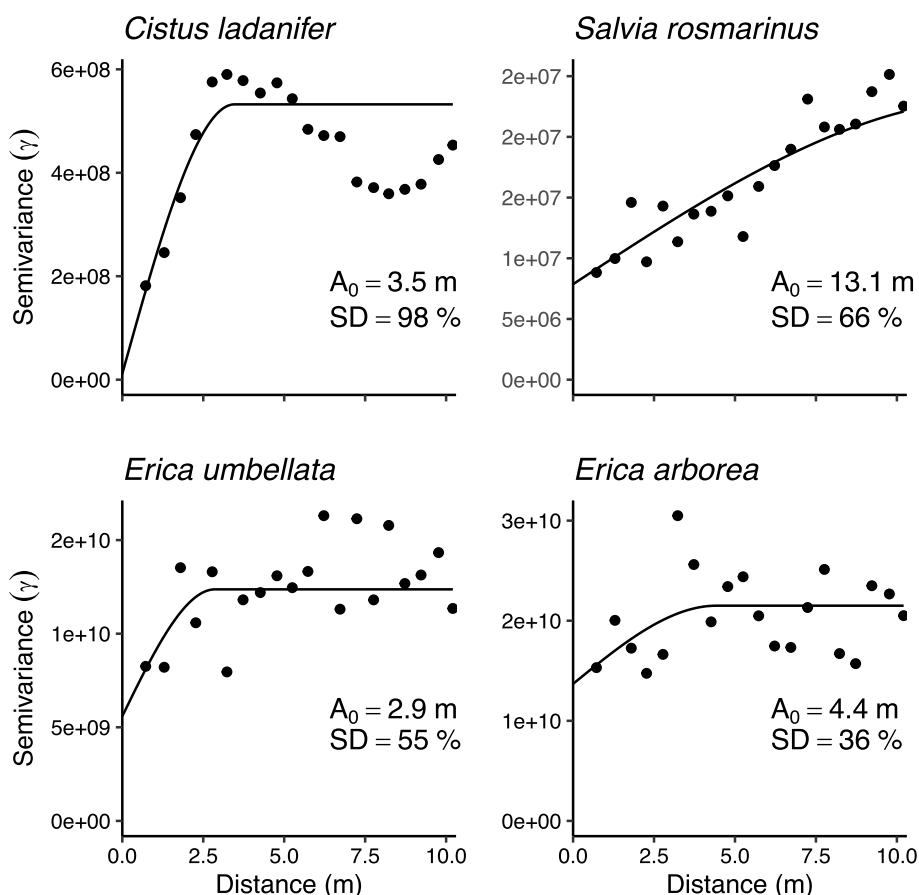


Fig. 6 Semivariograms (semivariance as a function of distance) fitted to the total number of seeds fallen at 0.5×0.5 m quadrats ($n=106$) during the 3 years of study in a *Cistus-Erica* shrubland at Quintos de Mora Range Station (central Spain). Top left: *Cistus ladanifer*; top right: *Salvia rosmarinus*; bottom left: *Erica umbellata*; bottom right: *Erica arborea*

species that presented more consistent spatial patterns over the years, with ranges of 3.4 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 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 1 year having a range similar to 3-year 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).

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).

In general, for the three seeder species, there was a significant relationship between cover of the species and its total seed crop over the 3 years studied at the scale of the 0.5×0.5 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).

Dispersal in either open spaces (no rooted plant within the 0.5×0.5 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

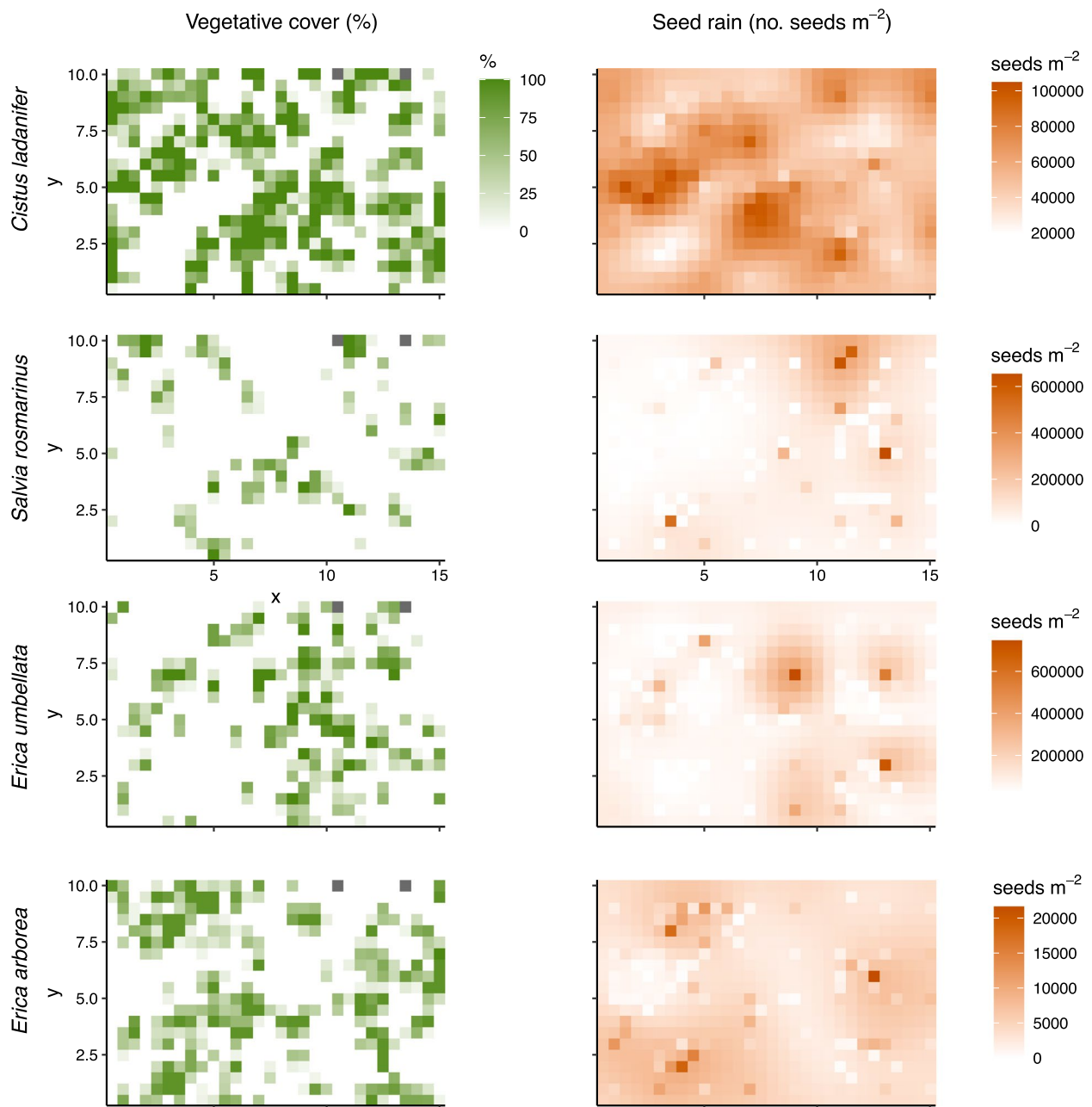


Fig. 7 Plant cover (left) and 3-year accumulated seed rain (right) maps at each 0.5×0.5 m over the whole plot (15×10 m) obtained by ordinary kriging in a *Cistus-Erica* shrubland at Quintos de Mora Range Station (central Spain). Top to bottom: *Cistus ladanifer*, *Salvia rosmarinus*, *Erica umbellata*, and *Erica arborea*

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).

Discussion

Our results document that seed dispersion temporal and spatial patterns were very different among the species dominant in this shrubland. 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

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

2002) or with other species of the same genus (Skourou and Arianoutsou 2004). Such a temporal dispersion pattern suggests that it is driven by factors not related to fire. Indeed, dispersing during nearly a whole year, much of which took place 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 et al. 2009). The fact that its seeds are hard and persist in the soil for years insures regeneration after fire. Under such a setup, the largest pressure on seed dispersal would be in ensuring the largest soil seed bank

Table 6 Spearman rank correlation coefficient (ρ) among species for accumulated seed rain (No. m^{-2}) during the 3 years of study at each sampling position ($n=106$). Significant correlations ($\alpha \leq 0.05$) after correcting P-values for the 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

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 (Log10+1 transformed in the first three species) that fell over the 3 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

Table 8 Mean seed crop (seeds m^{-2}) per year that fell onto the traps located in 0.5×0.5 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 and 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. The species that dominated the most underneath any species or where no plant was rooted is shown in bold

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	19,234	720	22,905	47,438
<i>C. ladanifer</i>	6.6	22,486	788	5520	33,076
<i>S. rosmarinus</i>	6.6	12,415	1294	1488	74,450
<i>E. umbellata</i>	6.6	24,442	34	46,793	22,052
<i>E. arborea</i>	2.8	17,375	718	3284	32,124
<i>P. angustifolia</i>	13.2	16,970	504	9528	74,960
<i>C. ladanifer</i> / <i>E. umbellata</i>	5.6	24,243	69	29,882	33,564
<i>E. umbellata</i> / <i>E. arborea</i>	3.8	13,805	413	39,646	74,897
<i>E. arborea</i> / <i>P. angustifolia</i>	8.5	16,970	504	9528	74,960

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. This response is compatible with that expected for a species with a persistent soil seed bank.

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 for fire cues to germinate is less clear. While it is negatively affected by heat, one study reported a significant effect of smoke in promoting germination (Moreira et al. 2010). Fires of low severity tend to produce low emergence and cover over the years (Reyes and Casal 2008; Fernández and Vega 2014), in contrast to others of greater fire severity (Fernández and Vega 2016; Moreno 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 3 years after a fire (Moreno et al. 2011; Céspedes et al. 2014). All of this is consistent with being at least short-term persistent in the soil seed bank. 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 post-fire environments, the species tends to germinate in spring (Quintana et al. 2004) but, depending on precipitation patterns, can even miss germinating during the first year after fire (Céspedes et al. 2014). Therefore, this species would gain little by dispersing prior to the fire season when 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. Thus, the strategy of escaping predators fits with this pattern, and is compatible with having a persistent soil seed bank.

S. rosmarinus showed a very different temporal pattern of seed release, 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 late in 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, to some extent, the 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 contrasts with the marked seasonality of this habitat. What role does such continuous input of seeds play on their predators is unknown but deserves further investigation.

Our results also document that the factors behind producing smaller or larger seed crops 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 post-fire population emerging during a fire that 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's seed crop after a fire will be smaller, assuming that seeds stored in the canopy will be killed. Instead, it will be the seed crops of previous years the ones that would play a role in the subsequent recruitment after a 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 et al. 2016), might benefit from the seed crop of the previous year that may or may not have been subject to negative climate pressures. This uncoupling between the current year's seed production and the population emerging after a fire can be advantageous to overcome the limitations imposed by the vagaries of climate, an issue that had not been noted until now and should be considered in how changes in fire seasonality can affect the plant community (Miller 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 et al. 2004; Moreno 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 et al. 1999; Torres et al. 2013); *S. rosmarinus* [20 No. m^{-2}] (Céspedes et al. 2012); *E. umbellata* [877 No. m^{-2}])(Maia 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 1991a, b; Meney 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 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 for 1 year, in contrast to species of *Cistus* most of whose seeds remained viable (>70%) after 3 years burial (Clemente et al. 2007).

We found that dispersion 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 given the positive relationship between the density of standing individuals of both species hint at a displacement of the second by the first. Moreover, *E. arborea* does not germinate after a fire, but between fires. The life cycle of the seeder species is in the range of a maximum of 15–30 years, which means that, even if few germination events occur, the likelihood that one *E. arborea* will occupy the open spaces is high, given its overall seed

dominance in space. This suggests that this shrubland will not be stable over the years and that, little by little, *E. arborea* will be taking over the stand (Santana et al. 2011). While we did not collect sufficient seeds of *P. angustifolia*, the fact that this species was abundant in terms of spatial occupancy suggests 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 to 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 abundant germination might occur from the other three species, a fire will 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 (i.e., space explained large portions of the spatial variability of seed dispersion), with very small patches, the patches formed by the total seed input during the 3 years were much larger, indicating for each species the rain shadow that dispersal can produce, which amounted to a very few meters. *S. rosmarinus* was different from the other three species: the patches produced by the standing plants were the largest, and those produced by the fallen seeds were even larger, which is surprising given that it was the species that produced the least seeds. Inspection of the seed dispersion 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 plants. This patterning was consistent over the years which lends support to the contention that *S. rosmarinus* would be the one that would change the least over the years to ensure the greatest space in case a fire would occur. Notwithstanding, *C. ladanifer* presented also patches that changed little over the years, unlike what we initially expected. 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 3 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. *C. ladanifer* and *E. umbellata* 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 seed predators. In contrast, *S. rosmarinus* dispersed during a short period before the summer, consistent with the idea of completing dispersal before the summer season. The resprouter *E. arborea* dispersed during the summer and fall before the rainy season. These temporal patterns were compatible with the type of soil seed bank of these species. Nevertheless, the validity of these findings must be taken with care, given the limited sample of species that were investigated. Dispersion patterns in space produced seed rain shadows that exceeded a few meters of the plant cover. Spatial patterns of seed dispersion 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. Thus, the evidence for the role of soil seed bank type on spatial patterns was weak. The dominance of *E. arborea* in the seeds falling where the other species were rooted suggests that, as seeder plants die in the period between two consecutive fires, this species might take over the stand, together with *P. angustifolia*, both of them being mid-successional resprouters.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-023-00213-3>.

Additional file 1: Table S1. Results of the repeated measures ANOVA for the seed crop of each of the three years studied and for each of the four species. When sphericity could not be assumed (significant Mauchly's test) the Huynh-Feldt correction was applied. Letters (A, B, C) denote the results of the *post hoc* pair-wise comparison, corrected by Bonferroni for multiple comparisons. Years sharing the same letter were not significantly different. **Table S2.** Year, model, range (A_0 , m), spatial dependence (SD, %) and weighted sum of squared errors (SSErr) of the variograms fitted to plant cover measured on 0.5 x 0.5 quadrats of a 10 x 15 m plot (n=600) of total plant cover, *Cistus ladanifer*, *Salvia rosmarinus*, *Erica umbellata* and *Erica arborea* growing in an old Cistus-Erica shrubland in Quintos de Mora Range Station (To, Spain). **Table S3.** Model, range (A_0 , m), spatial dependence (SD, %) and weighted sum of squared errors (SSErr) of the variograms fitted to the total seed rain fell during the three years of study on 0.5 x 0.5 quadrats (n=106) of a 10 x 15 m plot of *Cistus ladanifer*, *Salvia rosmarinus*, *Erica umbellata* and *Erica arborea* growing in an old Cistus-Erica shrubland in Quintos de Mora Range Station (To, Spain). **Table S4.** Year, model, range (A_0 , m), spatial dependence (SD, %) and weighted sum of squared errors (SSErr) of the variograms fitted to seed rain that fell on 0.5 x 0.5 quadrats (n=106) of a 10 x 15 m plot of *Cistus ladanifer*, *Salvia rosmarinus*, *Erica umbellata* and *Erica arborea* growing in an old Cistus-Erica shrubland in Quintos de Mora Range Station (To, Spain). **Fig. S1.** Semivariograms (semivariance as a function of distance) fitted to the plant cover (%) measured at the 0.5 x 0.5 m quadrats of the 15x10 m plot in a Cistus-Erica shrubland at Quintos de Mora Range Station (Central Spain). Top row: Total plant

cover (left), *Cistus ladanifer* (right); Middle row: *Salvia rosmarinus* (left), *Erica umbellata* (right); Bottom row: *Erica arborea* (left), *Phillyrea angustifolia* (right). **Fig. S2.** Semivariograms (semivariance as a function of distance) fitted to the seeds fallen at 0.5 x 0.5 m quadrats (n=106) during each of the three years of study (Year 1: Ap. 1997- Mar. 1998; Year 2: Ap. 1998-Mar. 1999; Year 3: Ap. 1999- Mar. 2000) in a Cistus-Erica shrubland at Quintos de Mora Range Station (Central Spain) for *Cistus ladanifer* (top row), *Salvia rosmarinus* (middle-upper row), *Erica umbellata* (middle lower row), and *Erica arborea* (bottom row).

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Authors' contributions

JMM designed the study and obtained funding. EZ carried out the research. IT, AP, and CMF conducted the data analysis and modeling. JMM implemented the analysis and drafted the manuscript. EZ, IT, CLM, and AP contributed editorial input to the manuscript. All authors read and approved the manuscript.

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Availability of data and materials

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

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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