



# Temporal and spatial differentiation in seedling emergence may promote species coexistence in Mediterranean fire-prone ecosystems

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Mediterranean ecosystems are hotspots of species richness where fire is one of the key processes influencing their structure, composition and function. Post-fire seedling emergence constitutes a crucial event in the life cycle of plants and species-specific temporal and spatial patterns of seedling emergence have been hypothesized to contribute to the high diversity in these ecosystems. Here we study the temporal and spatial patterns of seedling emergence observed for the four dominant species (*Cistus albidus*, *Ulex parviflorus*, *Helianthemum marifolium*, *Ononis fruticosa*) after an experimental fire in a Mediterranean gorse shrubland. In a first analysis we compared the timing of emergence of each species using the Kaplan-Meier method. The spatial component of seedling emergence and the spatiotemporal relationship between different cohorts of the same species were analyzed using recent techniques of spatial point pattern analyses. We found a bimodal temporal pattern of emergence. Emergence of Cistaceae species (*H. marifolium* and *C. albidus*) occurred predominantly early after the fire while Fabaceae (*O. fruticosa* and *U. parviflorus*) emerged mainly during the following autumn. Individually, all species showed an aggregated spatial pattern and, when testing for pair interactions, we found that the clusters of individual species were spatially segregated. Additionally, the clusters of individual species showed an internal spatial structure where seedlings of different cohorts were spatially segregated. Theoretical models predict that these patterns will promote species coexistence. We identified a number of mechanisms that all have the potential to contribute to the observed pattern formation. However, the potential interaction among these mechanisms are complex and not easy to predict. Our analyses take a significant step forward in studying seedling emergence in fire prone ecosystems since, to our knowledge, this is the first time that both spatial and temporal patterns of all dominant species have been studied together.

Mediterranean ecosystems are hotspots of species richness where exceptional concentrations of biodiversity occur (Mooney et al. 2001). However, the patterns and processes that promote such high diversity are still not fully understood (Keeley et al. 2005). One of the main factors influencing Mediterranean ecosystems is fire. On evolutionary time scales, fire plays a significant role, by influencing their structure, composition, and function (Naveh 1975, Bond and Keeley 2005). Post-fire seedling emergence constitutes one of the crucial events in the life cycle of plants (Harper 1977), often proving decisive in the performance and success of well-adapted species in fire-prone Mediterranean communities.

Mechanisms that minimize risk during the seed-to-seedling transition will be under strong selection pressure (Meyer et al. 1997), and natural selection should favour seed germination patterns that increase the probability of successful seedling establishment (Daws et al. 2002). Specific germination requirements can provide fine temporal niche partitioning in Mediterranean fire-prone com-

munities, because germination requirements are often far more restrictive than requirements for vegetative growth and reproduction (Facelli et al. 2005). Spatial niches may also arise due to spatial seedling patterning if seedlings show intraspecific aggregation and interspecific segregation. Intraspecific aggregation is a mechanism known to promote coexistence in plant communities (Stoll and Prati 2001). Thus, a detailed understanding of spatial and temporal patterns of seedling emergence for the various species in a community is critical in assessing processes and mechanisms which produce species coexistence and explain diversity.

One method of advancing our understanding on this complex issue is to use sophisticated techniques of exploratory spatial pattern analysis (Stoyan and Stoyan 1994, Diggle 2003, Illian et al. 2008) to describe the temporal and spatial patterns of seedling emergence as accurately as possible. To this end, specific hypotheses prior to pattern analyses may be set up (Schurr et al. 2004), which are then translated into specific null models, and departures from the observed patterns in these

“benchmark” hypotheses are explored. When these are taken together with knowledge of the study system, hypotheses can be derived to explain the observed spatial patterns which, however, have to be confirmed in subsequent field studies (Wiegand et al. 2007a).

Mediterranean gorse shrublands, which are transitionally fire-prone, but persistently species-rich, communities provide an excellent system for studying temporal and spatial patterns of seedling emergence. In these systems a large number of closely related species (i.e. morphologically, and functionally similar species) coexist in an environment with only subtle resource gradients (De Luis et al. 2006). We used a unique data set on seedling emergence in Mediterranean gorse shrublands after experimental fire to simultaneously investigate spatial and temporal patterns of seedling emergence across a number of species, at an appropriately fine level of resolution.

To guide our analyses, we addressed the following specific hypotheses which are based on the idea of temporal and spatial niches. We expected that a) temporal germination patterns would be species-specific (temporal niche differentiation); b) the dominant species involved in vegetation regeneration after fire would show intraspecific spatial aggregation, but interspecific spatial segregation (spatial niche differentiation); and c), different cohorts of each species would show small-scale differentiation in their spatial patterns.

## Methods

### Study area

The study was carried out in the Sierra de Onil, 40 km northwest of Alicante (east Spain) on three 21–27° sites facing S, NE and N (see Supplementary material, Appendix 1 for picture of site 1). According to the nearest weather station (Bañeres, 7 km away), the climate is dry-Mediterranean (mean annual precipitation is 466 mm) and the mean monthly temperature is 13.8°C. Soils are loamy Typic Calcixeroll developed on Miocenic marls (De la Torre and Alías 1996) with a high carbonate content (pH = 7.7) (García-Cano et al. 2000).

We selected three nearby 33 × 33 m sites (38.60°N, 0.66°W; 800 m a.s.l.) separated by ca 300 m with similar characteristics to serve as statistical replicates. They are representative of a stage in the degradation of a former Aleppo pine *Pinus halepensis* forest that was burned in 1984 and thereafter replaced by a new shrub community of the Rosmarino-Ericion alliance (De la Torre and Alías 1996). The vegetation is a Mediterranean gorse shrubland dominated by *Ulex parviflorus* (Fabaceae). Very few woody sprouters are present and subdominant shrubs include other obligate seeders such as *Cistus albidus* (Cistaceae) and *Rosmarinus officinalis* (Labiatae) (for details see De Luis et al. 2004, 2005).

In October, 1996, after the first autumn rains and on windless days, we burned the three selected sites. They had been previously delimited by a 5 m wide fire-break in which the vegetation was eliminated by mechanical brushing. The fires were ignited in the upper parts with the fire fronts burning in a continuous line downhill (De Luis et al. 2004).

Vegetation characteristics and fire behaviour observed in each site are reported in Table 1.

Immediately after fire and for the next three years, we monitored the seedling recruitment of all species present in four 2 × 0.5 m plots within each experimental site. All individuals were identified and located using X and Y coordinates (see Supplementary material, Appendix 2 for maps). Seedlings were tagged monthly at first, then once every two months and then each season. For the spatio-temporal analysis, the seedlings of a given species were divided into three cohorts, cohort 1 (ch1): all seedlings that emerged during the two months after the fire (i.e. October–December 1996), cohort 2 (ch2): all seedlings that emerged in the period from two months after the fire to the first summer (January 1997–June 1997), and cohort 3 (ch3): all seedlings that emerged between the first summer (July 1997) and the first autumn (October 1997).

### Statistical analysis

#### Temporal patterns

The Kaplan-Meier method (Kaplan and Meier 1958) was used to calculate cumulative germination curves of each species. Differences in the shape of curves among species were tested by the log-rank test (Pyke and Thompson 1986).

#### Spatial patterns

The spatial component of seedling emergence was analyzed using univariate and bivariate O-ring statistics (Wiegand et al. 1999, Wiegand and Moloney 2004). The O-ring statistic is closely related to Ripley’s K-function (Ripley 1981) and the pair-correlation function, g (Stoyan and Stoyan 1994, Illian et al. 2008). In essence, the O-ring statistic is a point-pattern statistic that calculates the mean density of neighbours in a ring of radius r and ring-width of

Table 1. Site, soil and vegetation characteristics in three Mediterranean gorse shrubland sites. Fire behavior in the three experimental sites.

	Site 1	Site 2	Site 3
Site characteristics			
Slope (°)	26	26	27
Elevation (m)	800	800	800
Aspect	S	NE	N
Soil characteristics (0–10 cm)			
Clay (%)	13.8	13.3	13.2
Fine silt (%)	15.3	14.7	16
Coarse silt (%)	31.2	24.7	26
Sand (%)	39.7	47.3	44.3
Stones (> 1 mm) (%)	7.2	5.03	7.05
Vegetation characteristics			
Total biomass (g m <sup>-2</sup> )	2844	4510	4118
Seeder species (ind. m <sup>-2</sup> )			
<i>Ulex parviflorus</i>	9.7	11.4	9.5
<i>Cistus albidus</i>	0.33	2.6	4.3
<i>Rosmarinus officinalis</i>	7.9	1	2.4
Other species	0.08	0.46	0.54
Fire behavior			
Temp. max (°C) (soil surface)	343	401	238
Post-fire woody debris (g m <sup>-2</sup> )	210	304	545
Post-fire litter debris (g m <sup>-2</sup> )	91	46	237
Post-fire ash cover (%)	44.5	63.8	30.9
Post-fire litter cover (%)	43.2	22.9	42.3

dr around an “average” individual, thus isolating specific distance classes. This makes it especially suitable for exploratory data analysis (Wiegand and Moloney 2004, Perry et al. 2006, Illian et al. 2008). The univariate O-ring statistic,  $O(r)$ , measures the density of neighbouring seedlings as a function of distance,  $r$ , from the centre of an average seedling. The bivariate variant,  $O_{12}(r)$ , measures the density of neighbouring seedlings of species 2 as a function of distance from the centre of an average seedling of species 1 (Wiegand and Moloney 2004). The pair-correlation functions are the intensity normalized versions of the neighbourhood density function, i.e.  $O(r) = \lambda g(r)$  and  $O_{12}(r) = \lambda_2 g_{12}(r)$  where  $\lambda$  and  $\lambda_2$  are the intensities of the univariate pattern and of component 2 of the bivariate pattern, respectively.

In all cases, data from all 12 replicate plots were combined into one overall mean function (Diggle et al. 1991, Illian et al. 2008). This method is a straight-forward extension of the usual analysis of single plots, but only rarely used in ecology (however, see Riginos et al. 2005). In short, the grid-based estimator of the O-ring statistic in plot  $j$  places rings with width  $dw$  and radius  $r$  around all points of pattern 1 and divides the mean number of points of pattern 2 within the rings  $[=P_2^j(r)]$  by the mean area of these rings  $[=A^j(r)]$ , counting only the points and area inside the study region:  $O_{12}(r) = P_2^j(r)/A^j(r)$ . The estimator for the O-ring statistic that joins data from the different plots  $j$  yields:

$$O_{12}(r) = \frac{\sum_j \frac{n_1^j}{N} P_2^j(r)}{\sum_j \frac{n_1^j}{N} A^j(r)}$$

where  $N$  is the total number of points of pattern 1 taken over all replicates  $j$ , and  $n_1^j$  the number of points of pattern 1 at plot  $j$ .

Biologically, grouping data from different plots means that we focus on the average emerging spatial patterns, i.e. the broad picture, and not on the potential variability among individual plots. This approach is justified if the treatment in all plots is the same and if the individual plots are representative of the community under study. This was the case in our study. This approach also increases the statistical power, as it increases the sample size considerably. Details are given in Supplementary material, Appendix 3.

We performed three groups of analyses. First, we performed univariate analyses to assess the individual spatial pattern for each species. Next we applied bivariate analyses to analyze the spatial relation between paired species and, finally, we compared the spatial relation between each pair of cohorts within each species. All these spatial analyses were done against an appropriate null hypothesis (see below).

#### **Null model for univariate spatial analysis**

For the univariate analyses we used the null model of complete spatial randomness (CSR) as a null hypothesis, because a priori all seeds produced by the seeder species present before the fire could potentially disperse throughout the plot. Thus, a potential departure from the null model may be due to interaction between seedlings, heterogeneous

micro-site conditions, or a non random seed bank. With the CSR null hypothesis, there is regularity if the data fall below the simulation envelopes (see below), and aggregation if they are above. Note that using CSR in each individual plot, but grouping the data from the 12 replicate plots together, means that, for the grouped data, we basically used a heterogeneous Poisson null model (see below), as we randomized the seedlings only within plots (i.e. keeping the number of seedlings per plot) but not among plots.

#### **Null model for bivariate spatial analysis**

With the bivariate analyses, we investigated whether co-occurring species showed interspecific spatial segregation and whether a cohort of a given species showed spatial attraction or segregation. We therefore used the null hypothesis that the two species (or cohorts) would occur within the same areas of the plot.

To test this hypothesis, we used a null model where the spatial distribution of seedlings of species 1 remained unchanged, but where the seedlings of species 2 were randomized following a specific heterogeneous Poisson process. In this point process the occurrence of any seedling is independent of that of any other, but the seedlings are distributed in accordance with an intensity function,  $\lambda(x, y)$ , that varies with location  $(x, y)$  (Stoyan and Stoyan 1994, Wiegand and Moloney 2004). To construct the intensity function, we used the seedlings of species 1. Thus, in the null model, the seedlings of species 2 follow the intensity function of species 1 (i.e. they occur within the same areas of the plot). This null model is, therefore, especially suitable for detecting segregation (Wiegand et al. 2007b). To estimate the intensity function  $\lambda(x, y)$ , we used the circular moving window estimator with bandwidth,  $R$ , proposed by Wiegand and Moloney (2004), which conserves the larger-scale  $r > R$  (first-order structure) of the pattern of species 1, but removes any potential smaller-scale  $r < R$  (second-order) structure. We used a bandwidth of  $R = 10$  cm. Note that the heterogeneous Poisson null model conserves the overall intensity  $\lambda_2$  of seedlings of species 2 within each plot.

If the  $O_{12}(r)$  fall inside the simulation envelopes of the null model, then species 1 and 2 occupy the same space. If  $O_{12}(r)$  fall only for scales  $r < R$  outside the simulation envelopes, then both species share the same spatial niche, but show additional small-scale attraction or repulsion. If the  $O_{12}(r)$  fall outside the simulation envelopes for scales  $r > R$ , then the species use different spatial niches.

#### **Simulation envelopes**

We analyzed spatial patterns up to 25 cm, which is half of the width of our plots, with a spatial resolution of  $1 \times 1$  cm. If the scales were larger, edge effects due to the existence of neighbours not under observation outside the plots would aggravate. We performed 999 simulations of each null model and used the 25 lowest and highest value of  $O(r)$  as simulation envelopes. However, the simulation envelopes cannot be interpreted as confidence intervals. Due to simultaneous inference (i.e. we test at several spatial scales,  $r$ , simultaneously), type I error may occur if the value of  $O(r)$  is close to a simulation envelope (i.e. the null model may be rejected even if it is true; Loosmore and Ford 2006).

All spatial analyses were done with “Programita” software. Estimators of the second-order statistics and the edge correction used in Programita are detailed in Wiegand and Moloney (2004).

We focused our analyses on the four most common species: *Cistus albidus* with a total of 931 seedlings, *Helianthemum marifolium* (578), *Ulex parviflorus* (327), and *Ononis fruticosa* (281). Seedlings of all other species (n = 11) were too infrequent for our purpose (360) (De Luis et al. 2006).

## Results

### Temporal dynamic of seedling emergence

Although the experiment lasted three years, most seedling emergence for all four species was concentrated in the first year post-fire. Ninety-four percent of emergence of all species occurred during the first year and no shrub seedlings emerged after the second year after fire. However, there was differentiation among species for temporal germination patterns throughout this period (Fig. 1). Cistaceae species (*H. marifolium* and *C. albidus*) displayed a bimodal pattern of germination with an absolute maximum soon after burning. A secondary peak was observed during the following autumn (Fig. 1). The cumulative distribution of emergence showed no significant difference between these two species. However, we found that their seedling emergence patterns differ from that of the other two species (Fig. 1). The Fabaceae species (*O. fruticosa* and *U. parviflorus*) also displayed a bimodal pattern of seedling emergence; however, the absolute maximum of seedling emergence did not occur soon after burning, but in the following autumn (Fig. 1). There was no significant difference between the two Fabaceae species in their cumulative distribution; however, they did differ from the two Cistaceae species (Fig. 1). These results do not confirm

hypothesis (a) because the temporal differences were found at the family level, not at the species level.

### Spatial patterns of seedling emergence

When we analyzed spatial patterns of the seedlings of the four different species individually, we found that each of them was significantly aggregated. For example, for *H. marifolium*, *U. parviflorus*, *C. albidus*, and *O. fruticosa*, the density of conspecific seedlings 5 cm from an average seedling was 2.4, 2.0, 2.2, and 4.6 times, respectively, the expected density under a completely random pattern (Fig. 2). The range of significant aggregation was > 25 cm for *H. marifolium*, 12 cm for *U. parviflorus*, 18 cm for *C. albidus*, and 22 cm for *O. fruticosa* (Fig. 2). This result supports hypothesis (b) of non-random emergence patterns.

However, when we compared the spatial patterns of pairs of these four species, we found that they showed significant segregation at almost all distances analyzed (i.e. up to 25 cm) (Fig. 3). Since the univariate analysis indicated that all species were grouped in clusters, the bivariate analysis thus indicated an overall repulsion among clusters of different species, confirming our hypothesis (b).

The spatial pattern of different cohorts of a given species showed significant segregation at distances < 10 cm for most species and cohorts (Fig. 4) confirming our last hypothesis. (However, cohorts 1 and 3 in *H. marifolium* and *C. albidus* do not differ from the null hypothesis.) This result indicates that different seedling cohorts of the same species tend to occupy different regions of the cluster but occupy the same large niche as found in Fig. 2.

## Discussion

Here, we present a fine-resolution analysis of the spatial and temporal pattern of seedling emergence after an experi-

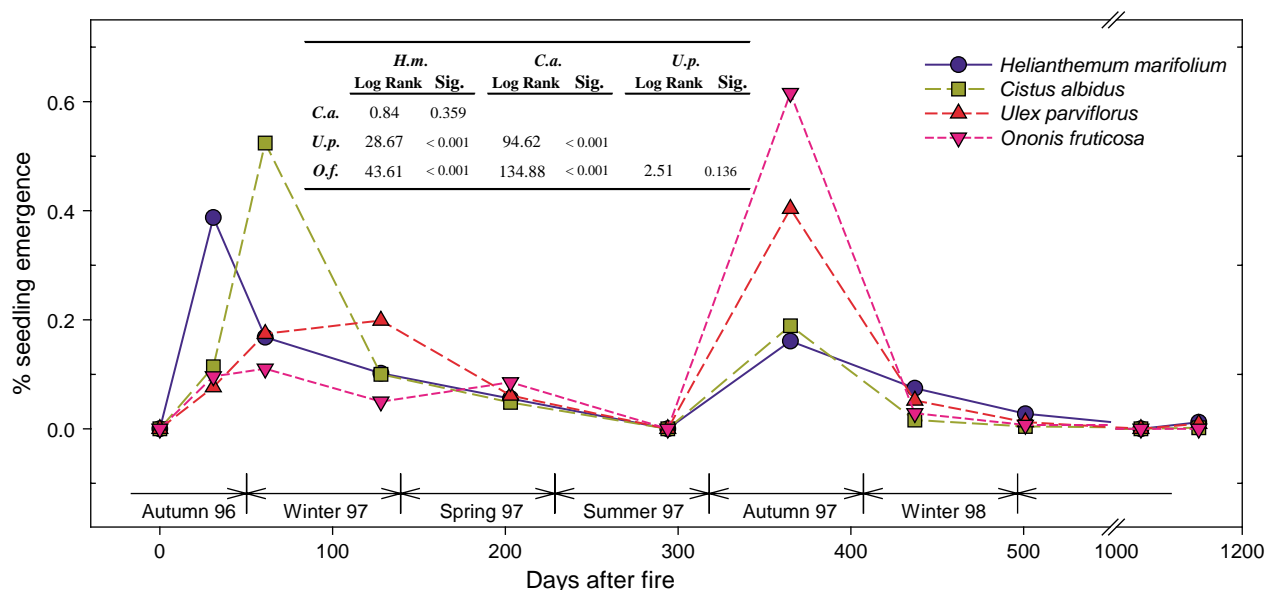


Figure 1. Differences in the time sequence of germination of various species in the 3-yr regeneration process. *C.a.*: *Cistus albidus*; *H.m.*: *Helianthemum marifolium*; *U.p.*: *Ulex parviflorus*; *O.f.*: *Ononis fruticosa*. Log Rank test statistic and significance levels are shown.

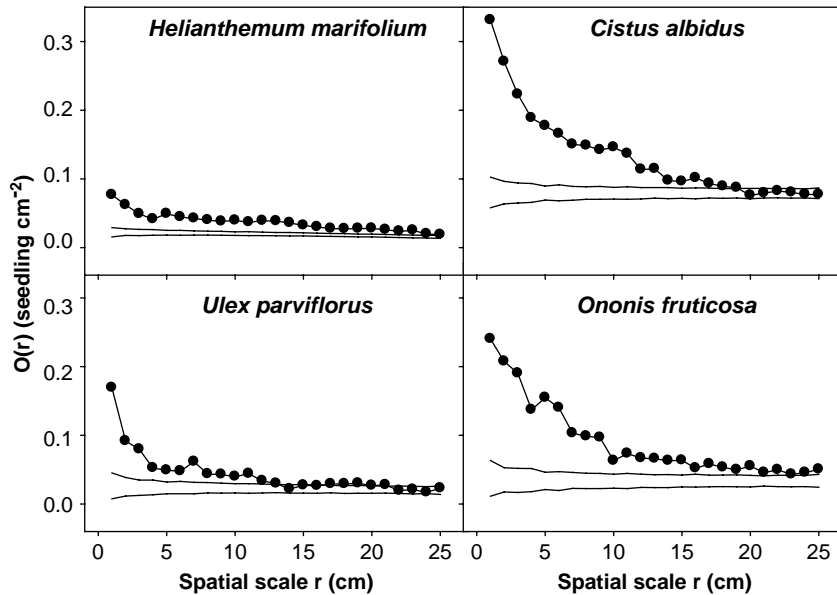


Figure 2. Univariate O-ring statistics to assess the individual spatial pattern for each species. We used the null model of complete spatial randomness (CSR) in individual plots, but grouped the results of all 12 plots together. All seedlings of a given species were grouped together.

mental fire in a fire-prone plant community. Our analyses take a significant step forward because, to our knowledge, this is the first time that both spatial and temporal patterns of several species have been studied together. The application of recent methods of point-pattern analysis revealed a clear picture of the spatio-temporal dynamics of seedling emergence, which is that most seedling emergence occurred

during the first year, seedlings of individual species showed a clustered spatial pattern, the clusters of individual species showed an internal structure with seedlings of different cohorts having a tendency to avoid each other, and the seedlings of different species were spatially segregated. Below, we will interpret these findings in the light of our knowledge of our study systems and current general

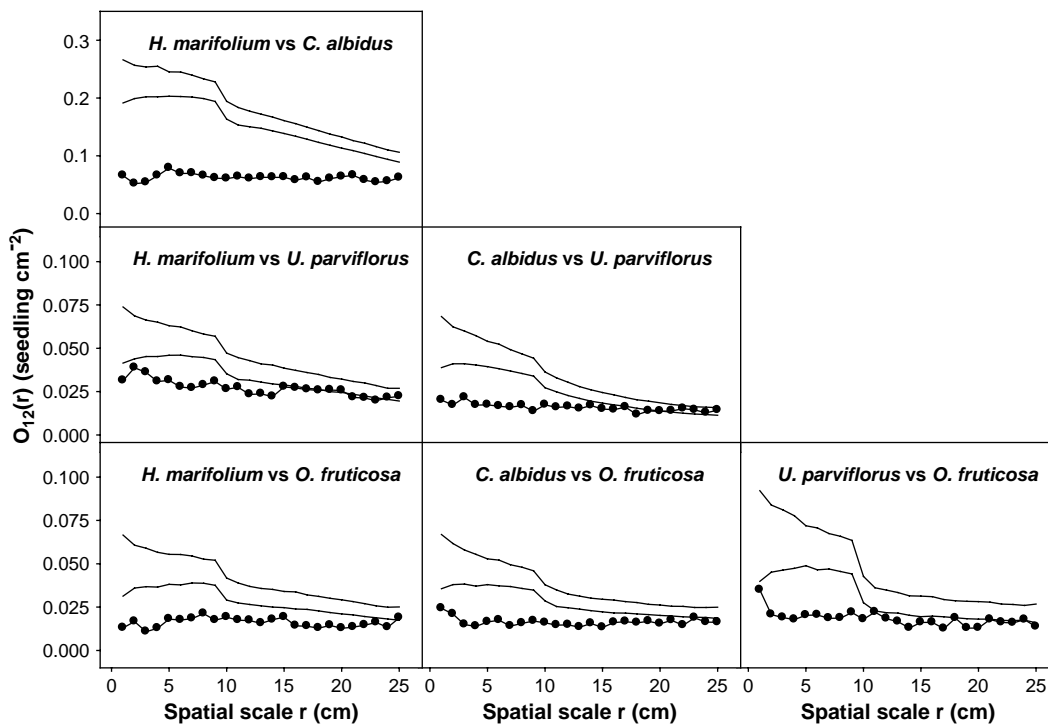


Figure 3. Bivariate O-ring statistics to analyze the spatial relation between paired species. We used a bivariate heterogeneous Poisson null model where the points of species 1 remain unchanged, but where the points of pattern 2 are randomized following a heterogeneous Poisson process. All seedlings of a given species were grouped together.

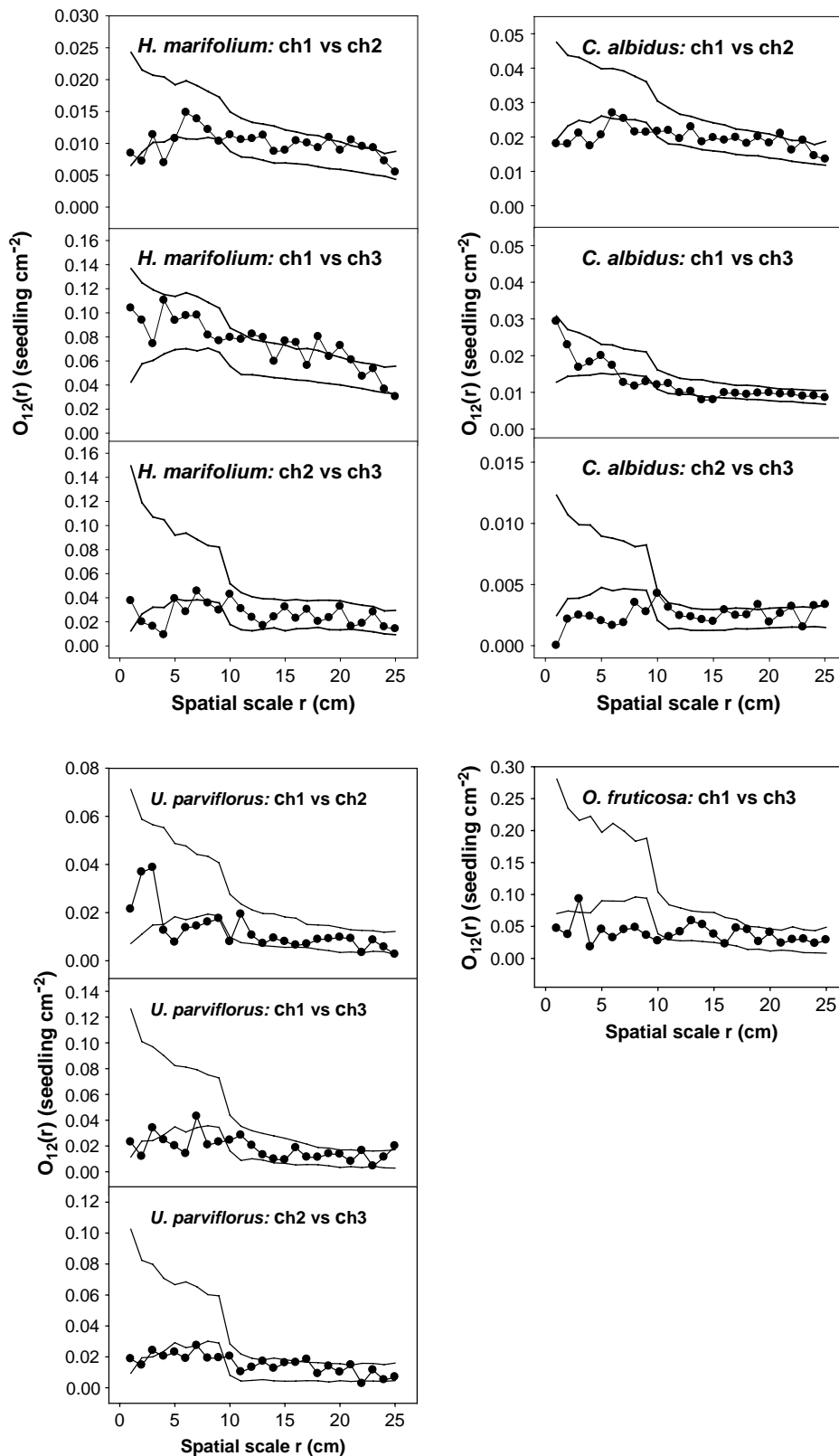


Figure 4. Bivariate O-ring statistics to analyze the spatial relation between paired cohorts of a given species. We used a bivariate heterogeneous Poisson null model where the points of cohort 1 remain unchanged, but where the points of pattern 2 are randomized following a heterogeneous Poisson process. In this analysis, the seedlings of a given species were divided into three cohorts, cohort 1 (ch1): all seedlings that emerged during the two months after the fire, cohort 2 (ch2): all seedlings that emerged in the period comprising two months after the fire to the first summer (1997), and cohort 3 (ch3): all seedlings that emerged from the first summer following the fire (1997) to the first autumn (1997) after the fire.

ecological theory, and discuss patterns, potential processes, and mechanisms favoring coexistence among species.

### Temporal pattern of emergence and coexistence

Early emergence and diversification in regeneration strategies are traditionally considered as suitable adaptations that allow plants to persist in fire-prone Mediterranean environments (Keeley and Zedler 1998, Pausas et al. 2004). Early emergence after fire may increase fitness, because it allows seedlings to be the first in occupying the resources and, therefore, to better survive, grow or reproduce (Verdú and Traveset 2005, De Luis et al. in press). However, uncertainty in the timing of suitable environmental conditions may favor a strategy of continuous emergence, instead of concentrating emergence early in the season, to better spread the risk of mortality (Mathias and Kisdi 2002). Our data revealed an interesting pattern that indicates a mixture of the two strategies. Seedlings of all four dominant species emerged immediately after fire and continued to do so into the first year. Emergence of the two Cistaceae species (*H. marifolium* and *C. albidus*) was higher earlier after fire, whereas that of the two Fabaceae species (*O. fruticosa* and *U. parviflorus*) was higher in the autumn following fire. Our four dominant species thus showed a clear diversification in time.

“Hardseededness” and heat-stimulated germination are characteristic of the five taxa of the Cistaceae family (*Cistus*, *Fumana*, *Halimium*, *Helianthemum* and *Tuberaria*) (Thanos et al. 1992) and can also be found in the majority of Fabaceae, including our two target species (Doussi and Thanos 1994, Arianoutsou and Thanos 1996). In vegetation communities dominated by species of these families, germination takes place during the first couple of years (Naveh 1974, Roy and Sonié 1992). Our findings are in line with these general findings. As soil seed banks are usually a heterogeneous collection of seeds of different ages in different states of dormancy, intraspecific diversifications in germination behaviour have also been reported (Thanos et al. 1992, Herranz et al. 1998). In our case, there is an important trade-off between seed size and the number of seeds produced that may have important consequences in defining specific-species germination requirements and explain the differences observed between the Cistaceae and Fabaceae species. Seed production in our target Fabaceae species is considerably lower, but seeds are substantially bigger than those of our target Cistaceae species (Thanos et al. 1992, Hanley and Fenner 1998, Baeza and Vallejo 2006). Successful emergence of epicotyls is dependent on endosperm carbohydrate reserves, and the maximum depth from which emergence can occur has been related to seed size (Bond and van Wilgen 1996). Tiny seeds of Cistaceae have been described as being unable to emerge from depths >2–3 cm (Odion and Davis 2000), whereas Fabaceae seeds are capable of emerging from much deeper in the soil (Ne’eman et al. 1992, Westoby et al. 1992, Baeza et al. 2002). As a consequence, emergence of Cistaceae species is more directly related to fire stimuli (earlier response), while maximum seedling emergence for Fabaceae species was observed during the autumn following fire.

### Spatial patterns and community coexistence

It is commonly accepted that intraspecific aggregation may promote the coexistence of species in plant communities by altering competitive interaction (Pacala and Levin 1997, Stoll and Prati 2001, Murrell and Law 2003), and by reducing the occurrence of interspecific interaction relative to random patterns (Murrell et al. 2001, Wiegand et al. 2007b). If interspecific competition occurs over shorter distances than intraspecific competition (heteromyopia), spatial segregation may become strong enough to promote coexistence (Murrell and Law 2003). Enright et al. (2007) suggested that spatially structured seed bank distributions may reduce competition between species of post-fire recruits, facilitating coexistence and the maintenance of high species-richness in fire-prone shrublands of south-western Australia. A spatial analysis of >2000 pairs of common species in a species-rich tropical forest revealed that the majority of all pairs of species showed partial overlap or spatial segregation (Wiegand et al. 2007b). The general argument is that, because individuals experience only a local neighbourhood, a given individual in a clumped community will have, on average, more neighbours of the same species than neighbours of other species. On the other hand, if species with strong competitive abilities aggregate, they may leave gaps that can be exploited by weaker competitors with better colonization ability (Levins and Culver 1971, Holmes and Wilson 1998). Our study is thus an exciting documentation of the spatial patterns one would expect to emerge from the theoretical mechanism of intraspecific aggregation and interspecific segregation. However, there remain the questions as to how important the spatial patterns of seedlings are relative to non-spatial and subsequent processes for final community persistence (Chesson and Neuhauser 2002), and which specific mechanisms may have created the observed patterns.

### Potential processes and mechanisms explaining the observed spatial patterns

Inferring processes and mechanisms from observed patterns is, in general, a difficult task because substantially different processes may produce the same patterns (Levin 1992, Wiegand et al. 2003, Grimm et al. 2005). Additionally, several studies have emphasized that species coexistence may often result from combinations of processes rather than a single mechanism (Chesson 1994, Lavorel and Chesson 1995). In our study system, there are several mechanisms and processes which may have shaped the observed seedling patterns. The most important ones include the pre-fire adult distribution, fuel distribution patterns and related heat patterns, seed dispersal kernels, seed bank characteristics and seed burial depth, variability in seed temperature response among species, and small-scale habitat heterogeneity. Seed predation, competition among seedlings, or competition between seedlings and resprouting adults are probably less important in our study system. The latter processes, however, could play an important role in shaping the temporal and spatial survival patterns. This issue will be addressed in a future study.

Short dispersal distances are a common characteristic of Cistaceae and Fabaceae species (Bastida and Talavera 2002, Baeza and Vallejo 2006). In a previous analysis of the experiment analyzed here, De Luis et al. (2005) found that seedlings of *C. albidus* (a species with many small seeds and a ballistic dispersion mechanism) and *U. parviflorus* (a species with one to four larger seeds that are dispersed by explosive dehiscence) were found mainly on microhabitats previously occupied by these species. López-Vila and García-Fayos (2005) found two peaks in an analysis of seed dispersal kernels of *U. parviflorus*, one under the plant, and a second peak at 130 cm. Seeds were not primarily dispersed further than 180 cm from the mother plant; however, the seeds carry elaiosome, much sought-after by ants, which removed >60% of the seeds on the ground (López-Vila and García-Fayos 2005). After removing the elaiosome, the seeds were placed by the ants in refuse piles where they germinated even in the absence of fire or scarification. Both localized dispersal and seed transportation to ant nests are mechanisms that can create the observed clustering of *C. albidus* and *U. parviflorus* seedlings. However, other mechanisms were acting for the other two study species *H. marifolium* and *O. fruticosa*. De Luis et al. (2005) found a large number of *O. fruticosa* and *H. marifolium* seedlings in plots where these species had been absent from the pre-fire vegetation. Germination of these seedlings probably relates to the existence of permanent seed banks generated after the natural fire that occurred 12 yr prior to the experimental fires (De Luis et al. 2005). However, unless populations are substantially seed limited, it has been suggested that dispersal kernels are less important than other factors to the abundance, distribution, and diversity of species (Levine and Murrell 2003). Moreover, seed dispersal in our study species occurs over larger scales than the observed patterns in seedling emergence. In this situation, alternative or complementary processes may act, leading to the observed patterns.

Plants in fire-prone communities are not only affected by fire; when they act as fuel, they, in turn, influence the nature of this disturbance (Odion and Davis 2000, De Luis et al. 2005). In fire-prone ecosystems, many plants possess traits that enhance their relative flammability and ecologists have suggested that increased flammability could result from natural selection (Schwilk and Ackerly 2001, Schwilk and Kerr 2002). Traits such as the retention of dead branches, fine branching patterns that influence the air/fuel mix, and the presence of volatile oils are potential flammability-enhancing traits (Schwilk and Ackerly 2001). In Mediterranean gorse shrublands, the Fabaceae species, mainly *U. parviflorus*, are species with a high biomass, but also have a high proportion of fine dead branches with a low moisture content that make up ca 50% of the total phytomass (De Luis et al. 2004, Baeza et al. 2006). This aerial structure favours severe fires under the canopy (De Luis et al. 2005). By contrast, the fuel load of Cistaceae individuals are considerably lower and their structure is mainly composed of green fractions with higher moisture levels favouring local conditions where fire severity is considerably lower.

Given these well-known characteristics of our study species, a complex combination of mechanisms may produce the observed emergence patterns. Below, we

summarize this into a general hypothesis. Due to localized dispersal, the seed bank under Cistaceae canopies will contain a huge quantity of tiny Cistaceae seeds, but only a few of the bigger Fabaceae seeds. Due to the low aerial biomass of Cistaceae canopies, the severity of fire will be low and stimulate mainly germination of seeds near the soil surface, thus favoring seedling emergence and establishment of Cistaceae species over Fabaceae species. Conversely, local dispersal will favor concentration of the larger Fabaceae seeds near parental plants. Due to the high fuel load and flammability of the aerial structure of Fabaceae canopies, the severity of fire will be greater and destroy a large portion of shallow Cistaceae seeds. Germination will mainly occur from seeds located on deeper soil profiles, thus favoring Fabaceae seeds that are capable of emerging from deeper in the soil over Cistaceae species.

As a summary, we hypothesize that the short-range dispersal characteristic of target species, differences in fire behavior under the canopies of different species, also the trade-off between seed size and the number of seeds could combine to explain the observed spatial segregation between different species in Mediterranean gorse ecosystems. The varying sensitivity of different seeds to fire temperatures and the stratification of seeds at different soil profiles could explain the segregation patterns we found among cohorts of the same species. Our hypothesis, however, needs to be tested in specifically designed field experiments.

Our results highlight decisive differences in regeneration strategies of closely related species of the same functional-type. If these differences were to be confirmed by field studies, they would clarify limitations of the functional-type approach that currently dominates fire ecological modeling.

## Conclusion

Our detailed analysis of spatial and temporal maps of seedling emergence in Mediterranean gorse shrublands revealed, for all four dominant species, intraspecific aggregation, interspecific segregation at species levels, segregation at the cohort level, and temporal intraspecific segregation. These are very clear patterns which have been postulated to promote species coexistence. The importance of our study is in documenting such a pattern for an entire community. While the emerging patterns are relatively simple, understanding the processes that may have contributed to the emergence of these patterns is challenging. Based on the characteristics of our study system and previous studies, we identified a number of mechanisms and factors which all have the potential to contribute to the pattern formation. However, the potential interaction among these mechanisms is complex and not easy to predict.

When taking a broader perspective, we argue that persistence in our study system relies on the presence of various mechanisms that are all potentially able to create these marked spatial patterns. This is because the efficiency of the mechanisms may depend in complex way on the specific characteristics of a given fire and having several available guarantees that the patterns are generated under a broad range of fires and environmental conditions. Clearly, more theoretical and empirical studies need to be conducted

to investigate the joint impact of these factors on the spatial pattern formation of seedling emergence and, ultimately, coexistence in fire-prone plant communities.

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