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Original article

A resprouter herb reduces negative density-dependent effects among neighboring seeders after fire

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ABSTRACT

Plant communities are often composed of species belonging to different functional groups, but relatively few studies to date have explicitly linked their spatial structure to the outcome of the interaction among them. We investigated if mortality of seeder species during their establishment after fire is influenced by the proximity of the resprouter herb *Brachypodium retusum*. The study was conducted in a Mediterranean shrubland (00°39' W; 38°43' N), 40 km northwest of Alicante (Spain) with *Ulex parviflorus*, *Cistus albidus*, *Helianthemum marifolium*, and *Ononis fruticosa* as dominant obligate seeder species and a herbaceous layer is dominated by the resprouter *B. retusum*. We followed the fate of mapped seedlings and the biomass of *B. retusum* one, two, three and nine years after an experimental fire. We used point pattern analyses to evaluate the spatial pattern of mortality of seeder species at these years in relation to the biomass of *B. retusum*. We hypothesize that *B. retusum* may initially have a positive impact on seeder survival. We implemented this hypothesis as a point process model that maintains the overall number of dead seeder plants, but seeder survival varied proportionally to the biomass of *B. retusum* in its neighborhood. We then contrasted this hypothesis with a previous analysis based on a random mortality hypothesis. Our data were consistent with the hypothesis that proximity of *B. retusum* reduced the mortality of seeder plants at their establishment phase (i.e., 2 yrs after fire). However, we found no evidence that *B. retusum* influenced seeder mortality when plants grow to maturity. We also found that, under the more stressful conditions (fire + erosion scenario), *B. retusum* had a lower impact on the performance of seeder species. Our results suggest that *B. retusum* may reduce negative density-dependent effects among neighboring seeder plants during the first years after fire.

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1. Introduction

The analysis of spatial patterns has a long tradition in evaluating plant–plant interactions (Fowler, 1986; Callaway, 2007). This is not surprising because such analysis can provide important insights on the outcome of these interactions and about the underlying mechanisms (e.g., Mertens and Lambin, 1997; Barot et al., 1999; Maestre et al., 2005; Wiegand et al., 2009). Plant communities are often composed of species belonging to different functional groups, but relatively few studies to date have explicitly linked their spatial structure to the outcome of the interaction among them

(e.g. Schurr et al., 2004; Tirado and Pugnaire, 2005; Kikvidze et al., 2005; Perry et al., 2009). A substantial part of the literature on interactions between different plant functional groups (reviewed by Callaway, 2007) has used either manipulative experiments or observations, but not spatial analyses. Furthermore, most of the empirical studies on how the spatial structure of communities influences the outcome of plant–plant interactions have focused on those occurring between species belonging to the same functional group (e.g., Rees et al., 1996; Stoll and Prati, 2001; Idjadi and Karlson, 2007; De la Cruz et al., 2008; Raventós et al., 2010; but see Biganzoli et al., 2009 and Perry et al., 2009 for recent exceptions).

Fire is a common element influencing the structure, composition and function of Mediterranean ecosystems (Naveh, 1974). In these environments, two main regenerative strategies to stand-replacement fires can be found: the resprouting capacity and the ability to retain a persistent seed bank (propagule-persistence

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capacity; Bond and van Wilgen, 1996; Pausas and Verdu, 2005). In the Mediterranean basin, most individuals from species with propagule-persistence capacity are readily killed by fire, and stands are re-established by massive seedling recruitment from a pre-existing, soil-, or canopy-stored seed bank (De Luis et al., 2008a). Such “seeder” species produce numerous seeds, allocating fewer resources per unit (Lamont and Wiens, 2003). On the other hand, “resprouter” species exhibit low seed production and germination rates in inter-fire periods, but resprouting allows space to be occupied rapidly, often before seeder species have germinated (Oechel, 1990). However, not all resprouter species behave the same way after disturbance. This fact needs to be considered when modeling the vegetation dynamics (see Pausas, 1999 for a review). As a consequence, interactions between resprouters and seeders may occur at different spatio-temporal scales after a fire, and are likely to play an important role in the long-term post-fire dynamics of these ecosystems (Maestre et al., 2004; Biganzoli et al., 2009; Perry et al., 2009). Despite their potential importance, such interactions have been poorly assessed in Mediterranean environments, particularly at different temporal stages after a fire (Pausas, 1999).

In recent decades, the spread of *Ulex parviflorus* shrublands has posed a severe problem for fire prevention in the western Mediterranean Basin (Baeza and Roy, 2008). These fire-prone shrublands represent the pioneer stage of burned former *Pinus halepensis* forests and may eventually be replaced by a shrub community of the Rosmarino-Ericion alliance (De la Torre and Alías, 1996). In western Mediterranean areas, the presence of woody resprouters is scarce due to historical agricultural land uses (Abad et al., 1996). As a consequence, post-fire regeneration of plant cover is primarily driven by obligate seeder species, but it relies in the short term on presence of the resprouter herb *Brachypodium retusum* (De Luis et al., 2004b). This species is the only resprouter existing in the vegetation community, and plays a particularly important role in protecting the soil from erosion after forest fires (De Luis et al., 2004b). In particular, its presence may promote the establishment of seeder species by avoiding the loss of sediments, nutrients and seeds typically observed in bare areas (De Luis et al., 2003). Given that seeder and resprouter species coexist after fire, and that their interactions are likely to play an important role in the long-term post-fire vegetation dynamics, *U. parviflorus* shrublands provide an excellent system for studying the interactions between these functional groups using spatial pattern analyses.

Here we use a unique data set on seedling emergence after experimental fire in Mediterranean *U. parviflorus* shrublands (Raventós et al., 2010) to explore the role of *B. retusum* on the spatial patterns of mortality of plants of the four dominant seeder species (*Cistus albidus*, *Ulex parviflorus*, *Helianthemum marifolium*, and *Ononis fruticosa*) which are all woody shrubs. Our data set comprises the fate of mapped seedlings of these seeder species and the density of the dominant herbaceous resprouter species *B. retusum* one, two, three and nine years after experimental fire. Since fire and erosion represent two potential filters constraining the temporal window of seedling establishment in Mediterranean shrublands, we considered two experimental post-fire scenarios (fire and fire + erosion) on three different times elapsed since last fire (two, three and nine years after the experimental fires).

The two functional groups show differential architecture and morphology. *Brachypodium retusum* is a perennial grass with an extensive below-ground rhizome that forms a dense root network at 5–10 cm depth (Caturla et al., 2000), which remains within the low herbaceous layer whereas seeder individuals occupy higher vertical strata. The two functional groups show also different responses to fire. As a consequence of their higher survival and faster growth rate, herbaceous perennials usually dominate the first stages of post-fire recovery in Mediterranean systems (Caturla

et al., 2000; De Luis et al., 2005). Indeed, *B. retusum* accounted for 90% of plant biomass and cover after one year whereas seeder species yielded less than 5% cover (De Luis et al., 2004b). The presence of *B. retusum* may thus prevent small-scale nutrient loss immediately after fire and facilitate the subsequent growth of seeder plants by providing more benign micro sites for seedlings. In this context, we tested the following hypotheses:

H1: During the first year after fire, mortality of seeders species will be lower in the neighborhood of *B. retusum* (the resprouter species).

H2: When seeder plants grow to maturity and occupy the higher vertical strata the positive effect of *B. retusum* will disappear.

H3: Since the influence of *B. retusum* on seedling survival is expected to be mediated by the size of seedlings, this species will have a lower impact on the performance of seeder species in the fire + erosion treatment, where surviving plants are bigger (De Luis et al., 2001), than in the fire-only scenario.

2. Material and methods

2.1. Study site

This study was carried out in three sites located in the Serra de Onil (00° 39' Lat.; 38° 43' Long.), 40 km NW of Alacant (E Spain). They were separated by ca 300 m, and have 21°–26° slopes facing S, NE and N. Altitude is 800 m. a.s.l., and climate is dry-subhumid Mediterranean. According to the nearest weather station, Banyeres (00° 39' Lat.; 38° 42' Long.), mean monthly temperature and precipitation are 13.8 °C and 466 mm, respectively. Soils are loamy Typic Calcixeroll (De la Torre and Alías, 1996), developed from Miocenic marls.

The community studied encompasses shrubland formations of the Rosmarino-Ericion alliance (De la Torre and Alías, 1996). The three sites represent a degraded stage of a previous *Pinus halepensis* community that burned in 1985. Before the experimental fires in October 1996, the vegetation height was approximately 1.3 m with 99% cover, and the shrubland was dominated by *U. parviflorus*. Subdominant shrubs include other obligate seeders such as *C. albidus* and *Rosmarinus officinalis* (De Luis et al., 2004a). Few woody resprouters are present, and the sparse herbaceous layer is dominated by *B. retusum*. Due to the high accumulation of necromass of species such as *U. parviflorus*, and social and climatic factors, Mediterranean shrublands such as studied are frequently affected by wildfires (Baeza et al., 2002; Pausas, 2004).

2.2. Fire and rainfall simulation

In October 1997, we experimentally set fire to a 33 × 33 m plot in each of the study sites. Within 4 weeks after the experimental fires, we carried out a 240 mm rainfall simulation lasting c. 2 h. The rainfall simulation produced an erosion effect similar to a torrential rainfall event. We carried out the simulation in one 2 × 2 m plot in each of the previously burnt areas, while another plot of the same size was also selected in each area as a control (fire without rainfall simulation). Further details on the experimental design, the experimental fires and the rainfall simulations can be found in De Luis et al. (2003). The torrential rainfall event caused the removal of ash, litter, and topsoil, generating substantial loss of sediment and changes in micro-soil levels, leading to exposure of the fine surface roots of the perennial resprouter grass *B. retusum* and causing a reduction in the rate and amount of vegetation recovery (De Luis et al., 2004b). Additionally, the torrential rainfall event caused a significant increase in mortality of seedlings

(De Luis et al., 2005) with substantial changes in vegetation structure (De Luis et al., 2001).

Immediately after the experimental fire, and for the next three years, seedling emergence and survival of all species present in four 2 m × 0.5 m subplots within each of the 2 × 2 m experimental plots was monitored. All individuals were identified and located using X and Y coordinates. At the end of the first, second and third years, the state of each individual was recorded as alive or dead. An additional sampling was made in the autumn of 2005 (9 years after fire). The analyses focused on the four most common species, with a total seedling emergence (i.e., pooled across all plots) per species as follows: *C. albidus* (931), *H. marifolium* (578), *U. parviflorus* (327), and *O. fruticosa* (281). Seedlings of all other species ($n = 11$) were too infrequent for the purposes of this study (360).

Brachypodium retusum was the only resprouter species present in the experimental plots. To monitor its development after the experimental treatments, all 10 × 10 cm quadrants were visually classified within the 2 × 2 m plots in 10 cover classes (from 0–10% to 90–100%). Measurements were taken annually for three years. We estimated above-ground biomass for *B. retusum* from cover with the allometric functions described in De Luis et al. (2004b).

Seeder species with shallow fibrous root systems can produce either large or small seeds and tend to grow first vertically and then spread the upper part, producing umbrella-shaped plants (Bell et al., 1993, 1996). In contrast, *B. retusum* is a perennial grass with stems growing 15–20 cm, leaves are up to 10 cm × 2–4 mm in size, becoming convolute when dry, and has an extensive below-ground rhizome that forms a dense root network at 5–10 cm depth (Caturla et al., 2000).

2.3. Spatial analyses: marked point patterns

Our data follow the fate of mapped seedlings over a nine year period, thus for each year of analysis (i.e., year 1, 2, 3, and 9) we know if a given seeder plant was alive or dead. However, following hypothesis H1 we expect an influence of the first year *B. retusum* biomass on survival of the seeder plants to year 2. Therefore, we cannot use the first year survival data set of seeders for our analysis. The information on survival status is a “mark” (or label) that characterizes the pattern of seeder plants. Therefore, the analysis of marked point patterns requires the framework of “marked point patterns” (Stoyan and Stoyan, 1994; Goreaud and Pelissier, 2003). In a previous study, Raventós et al. (2010) found evidence that mortality of seeder plants did not follow the random mortality hypothesis. Due to the strong intraspecific clustering and inter-specific segregation between seedlings (De Luis et al., 2008b), mortality was controlled almost entirely by intraspecific interactions among seeders. However, interactions with other plant functional groups were not considered in the analysis, which leaves the possibility that the observed departures from random mortality were mediated by presence of plants from other functional groups.

In this study, we investigate the potential role of the resprouter herb *B. retusum* on the observed non-random mortality of the seeder species. On a spatial basis, we hypothesize that survival of seeder plants should be higher in places with higher biomass of *B. retusum* and lower in places with lower biomass. Thus, the effect of *B. retusum* has the potential to interact with competitive interactions among seeder individuals in a way that competition (and thus mortality) is more intense in areas without *B. retusum* and that the effect of negative density dependence is reduced in areas with *B. retusum*.

We implemented this hypothesis in a non-parametric way (analogously to a non-parametric approach to simulate heterogeneous Poisson processes; e.g., Wiegand et al., 2007) by modifying the random mortality null model used in Raventós et al. (2010).

Under random mortality (Kenkel, 1988), the observed mark “dead” is randomly shuffled among all seeder plants in a given plot. In this case each seeder plant has the same probability of mortality (i.e., the number of dead seeder plants in the plot divided by the number of dead and surviving seeder plants). However, in our modified point process model (hereafter called “*B. retusum* model”) we assumed that the probability of mortality of a seeder plant was proportional to the biomass of *B. retusum* in its neighborhood. A given simulation of this model assigns the mark “dead” stochastically to the seeder plants in such a way that (1) the same number of seeder plants is assigned to be dead as observed in the plot, and (2) the probability of survival is proportional to the biomass of *B. retusum* in the neighborhood of the plant. Given these two assumptions, the *B. retusum* model has no free parameter to be fitted and therefore the same level of complexity as the random mortality null model. However, since the relationship between mortality and biomass could potentially be any monotonous function of biomass, the *B. retusum* model represents a specific parameterization of a more general relationship between mortality and biomass. If our hypothesis is wrong (e.g., if *B. retusum* would in reality have a negative impact on seeder survival) the *B. retusum* model would fit the observations equally well or even worse than the random mortality null model.

The original biomass data on *B. retusum* were obtained from a 10 cm × 10 cm grid. These data were then converted to the 1 cm × 1 cm resolution of our point pattern analyses using a moving window with a Epanechnikov kernel of band width $R = 10$ cm to obtain smooth biomass values (Stoyan and Stoyan, 1994). As a result of this procedure, we obtained a map with a grid of 1 cm × 1 cm cells with values that represents the *B. retusum* biomass within a 10 cm neighborhood of a given cell. To analyze the effect of *B. retusum* on the survival of the individuals of the seeder species, we used the map representing *B. retusum* biomass of the first year when analyzing the survival of seeder species to the second-year; and the second- and third-year densities of *B. retusum* were used when analyzing the third- and nine-year survival of seeder species, respectively.

2.4. Test statistics

Because potential departures from randomness in mortality can be manifold, three different test statistics were used to characterize the spatial structure of the mortality process, and to quantify departures of the observed patterns from the random mortality null model and the specific point process model where seeder survival was lower in areas of higher biomass of *B. retusum*. In the following, the subscript “1” refers to dead plants and the subscript “2” to surviving plants.

The test statistic $g_{11}(r)$ is especially tailored to detect clustering of dead individuals (Wiegand and Moloney, 2004; Raventós et al., 2010; Jacquemyn et al., 2010). In this case, according to our hypothesis 1 (mortality is higher in areas without *B. retusum*), we expect that, for small scales of r , the values of the test statistic $g_{11}(r)$ under the *B. retusum* model will “move up” the $g_{11}(r)$ simulation envelopes relative to that of the random mortality null model used in Raventós et al. (2010). The second test statistic, $g_{12}(r)$, is tailored to detect segregation between dead and live plants (Goreaud and Pelissier, 2003). In this case, since our hypothesis 2 is that plants are more likely to die and survive in areas of low and high biomass of *B. retusum*, respectively, we expect, for small scales of r , that the *B. retusum* model will “move down” the $g_{12}(r)$ simulation envelopes compared to that of the random mortality null model. Finally, we used a third test statistic, $g_{1,1+2}(r) - g_{2,1+2}(r)$, specifically tailored to detect density dependent effects in mortality (Yu et al., 2009; Raventós et al., 2010; Jacquemyn et al., 2010). It compares the

density of dead and surviving plants (i.e., 1 + 2) around dead plants (i.e., pattern 1) with that found around surviving plants (i.e., pattern 2). A high biomass of *B. retusum* will cause higher seeder survival in the *B. retusum* model thereby creating the appearance of a positive density dependent mortality. Thus, the *B. retusum* model will “move up” the simulation envelopes for the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ compared to that of the random mortality null model.

2.5. Simulation conditions

For each plot, year, and treatment, 999 Monte Carlo simulations of the random mortality null model and the *B. retusum* model were performed to generate approximately 95% simulation envelopes. For each test statistic, the 25th-lowest and 25th-highest value at a given scale r were used as simulation envelopes. However, the simulation envelopes cannot be interpreted as confidence intervals (Loosmore and Ford, 2006). To assess the overall fit of a null model for a given test statistic, a GoF test with a Cramer von Mises test statistic was used. If the rank was larger than 950, the data showed a significant departure from the null model with an error rate $\alpha = 0.05$ (Loosmore and Ford, 2006).

Spatial patterns up to 25 cm, half the width of the plots, were analyzed in all cases using a ring width $w = 2$ cm and a spatial resolution of $1 \text{ cm} \times 1 \text{ cm}$. This resolution is fine enough to answer the questions posed, and close to the mapping error of the data. For the analyses of each treatment, year and null model, the data of all four seeder species (*C. albidus*, *U. parviflorus*, *O. fruticosa*, and

H. marifolium) were pooled. The results of the analyses of the six replicate plots were then combined using aggregation methods (see details in appendix A of Raventós et al., 2010). This means that, in biological terms, focus was on the average spatial mortality patterns, i.e., the broad picture of what was of primary interest in the study, but less on the potential variability among individual subplots. All the spatial analyses were done with the Programita software (Wiegand and Moloney, 2004). Estimators of the second-order statistics and the edge correction used in Programita are detailed in Wiegand and Moloney (2004).

3. Results

3.1. Test statistic g_{11}

A significant departure from the random mortality null model was observed in all the studied years for both treatments (Figs. 1A–C and 2A–C). In all cases, dead seeder plants were more aggregated than expected by random mortality. In the fire treatment and two years after fire, the *B. retusum* model approximated the observed g_{11} more precisely than the random mortality null model (cf. Fig. 1A and D); it yielded a decrease in the rank of the GoF test from 1000 ($P < 0.001$) for the random mortality null model (Fig. 1A) to 987 ($P = 0.022$) for the *B. retusum* model (Fig. 1D). Thus, low neighborhood biomass of *B. retusum* can explain some of the aggregation of dead individuals of seeder species. However, other effects such as direct interactions among seeder individuals may still contribute to the observed remaining aggregation of dead

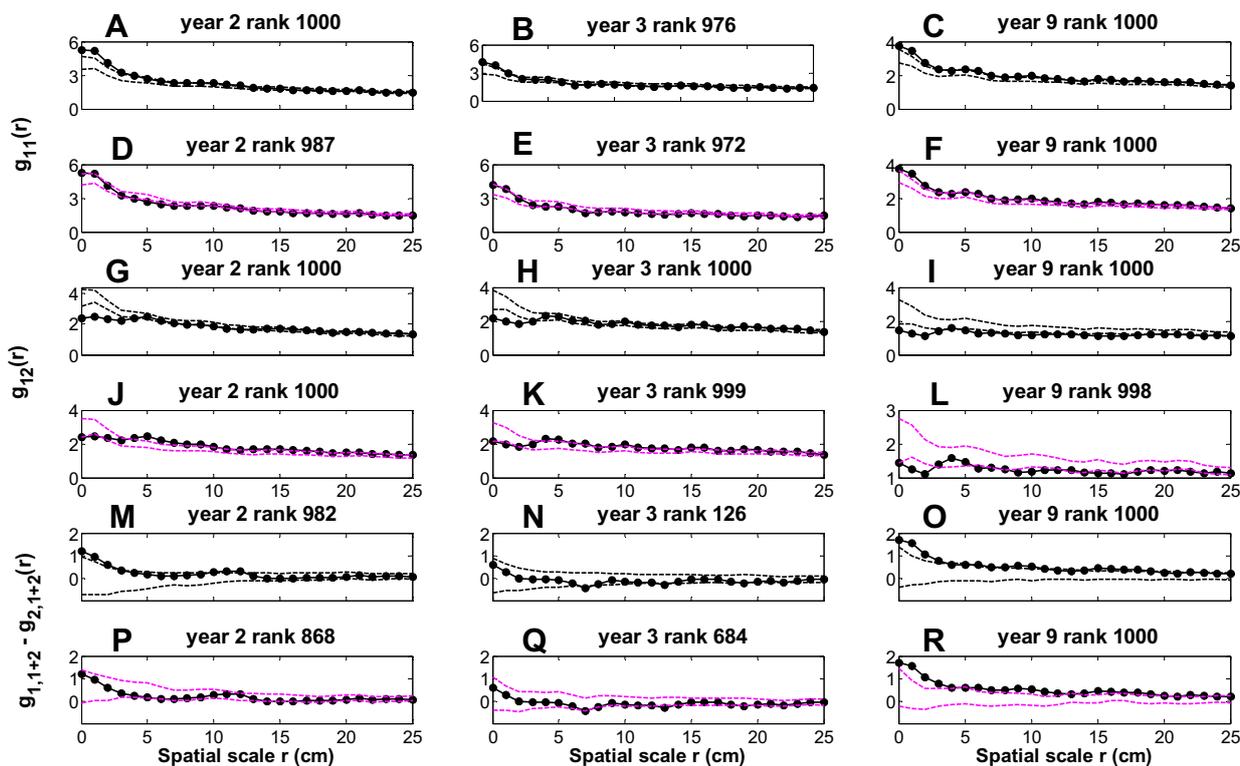


Fig. 1. Results of the spatial analyses in the fire treatment. The black simulation envelopes are that of the random mortality null model (already presented in Raventós et al., 2010) and the pink envelopes are those of the *B. retusum* model that assumes higher survival of seeder plants in the neighborhood of *B. retusum*. The univariate test statistic $g_{11}(r)$ is tailored to detect clustering of dead individuals [i.e., $g_{11}(r)$ above simulation envelopes]; the $g_{12}(r)$ can detect segregation between dead and live individuals [i.e., $g_{12}(r)$ below simulation envelopes], and the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ tests for density dependent effects in mortality. If the later test statistic is below or above the simulation envelopes, positive (i.e. facilitation) or negative dependent mortality (i.e. competition) is expected to occur, respectively. If there is a positive impact of *B. retusum* on the survival of the seeder species, the simulation envelopes of the facilitation null model will “move up” (relatively to that for the random mortality null model) for test statistics g_{11} and $g_{1,1+2} - g_{2,1+2}$, and “move down” for the g_{12} statistical tests. The null model with facilitation explains the observed patterns better than the random mortality null model if the rank of the goodness-of-fit (GoF) decreases. If the rank was larger than 950, the data showed a significant departure from the null model with error rate $\alpha = 0.05$. The results of the random mortality null model are the same as those shown in Fig. 2 in Raventós et al. (2010).

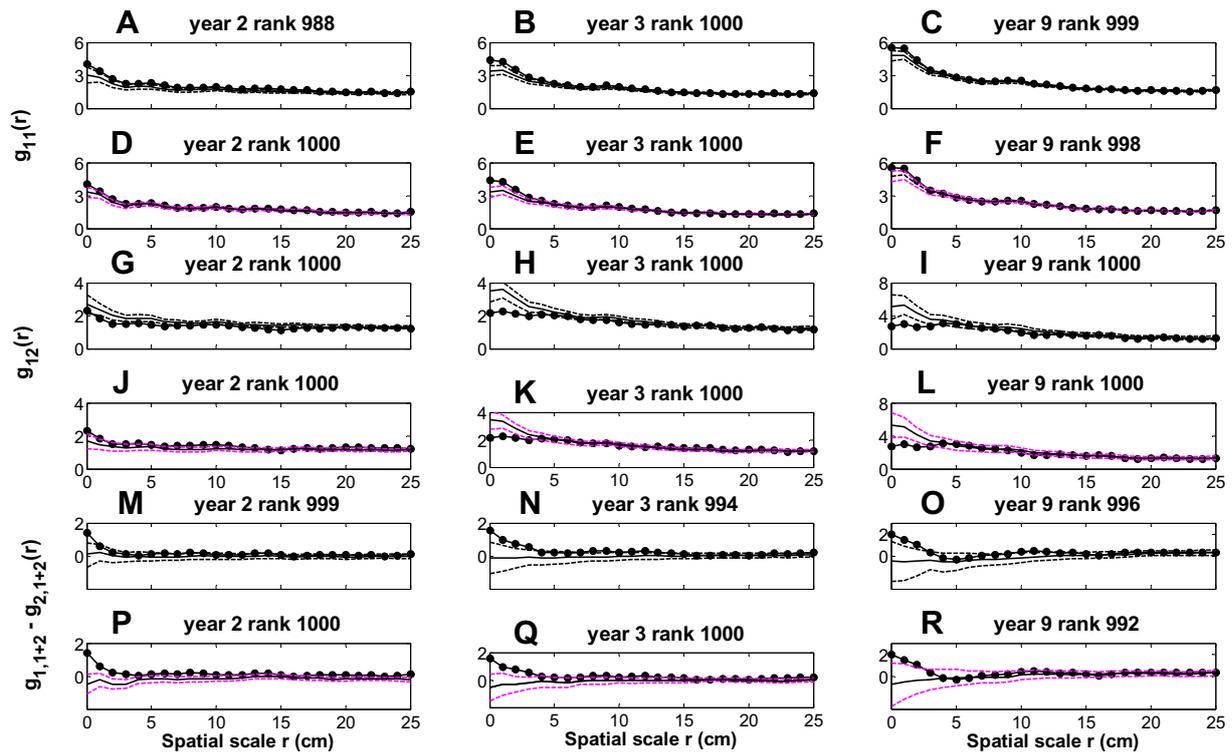


Fig. 2. Results of the spatial analyses in the fire and erosion treatment. Rest of legend as in Fig. 1.

seeders. In the fire treatment and three years after the fire, the effect of *B. retusum* on aggregation of dead seeders was still in the right direction (i.e., shifting the simulation envelopes upward) but weak since the rank of the GoF rank changed from 976 to 972 (cf. Fig. 1B and E). Finally, this effect completely disappeared nine years after the fire (cf. Fig. 1C and F). However, assuming seeder survival was proportional to the biomass of *B. retusum* (i.e., the *B. retusum* null model) did not influence the simulation envelopes associated with the $g_{11}(r)$ test statistic in the fire + erosion treatment (Fig. 2A–F) relative to that of the random mortality null model.

Our results indicate that including the negative effect of *B. retusum* absence on seeder seedling survival produced agreement with the observed aggregation of dead seedlings. This is consistent with our first hypothesis. We also found that the initial impact of *B. retusum* on seeder mortality disappeared in later years, confirming our second hypothesis. Furthermore, consideration of the impact of *B. retusum* on seeder mortality did not change the simulation envelopes of the fire + erosion treatment; this result is consistent with our third hypothesis.

3.2. Test statistic g_{12}

The random mortality null model revealed significant small-scale segregation between dead and live seeder individuals, as depicted by test statistic $g_{12}(r)$, during the entire study period (Figs. 1G–I and 2G–I). However, the *B. retusum* model describing a positive impact of *B. retusum* on seeder survival approximated the observed data more closely than the random mortality model. This occurred early after the application of the fire treatment at year 2 (cf. Fig. 1G and J) where the GoF rank dropped from 1000 to 945, and at year 3 (cf. Fig. 1H and K) where the GoF rank dropped from 1000 to 947. However, no improvement was observed in the last year of study (cf. Fig. 1I and L) and in the second year of study in the fire + erosion treatment (cf. Fig. 2G and J). These results indicate

that *B. retusum* contributed to the observed segregation between dead and surviving individuals of the seeder species at shorter distances (at 0–5 cm; Fig. 1 panels G to K and Fig. 2G, J). In these cases, seeder individuals located in areas without *B. retusum* died in groups that were spatially segregated from surviving individuals, due to the presence of *B. retusum*. Our results also suggest that *B. retusum* had no effects on survivorship of nine year-old individuals in any treatment, and that its effect on these individuals was weaker with the erosion treatment, being consistent with our second and third hypotheses.

3.3. Test statistic $g_{2,1+2} - g_{2,1+2}$

The statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ is tailored specifically to test whether the observed risk of mortality is higher for seeder individuals that are surrounded by more individuals of the same functional group (Figs. 1 and 2, panels M to R). Negative density dependent mortality occurred in all years and treatments, except in year 3 of the fire treatment (Figs. 1M–O and 2M–O). The *B. retusum* model was able to account for the observed density-dependent mortality in the fire treatment plots during the second year after fire. In this case (cf. Fig. 1M and P), we observed a decrease in the rank of the GoF test from 982 for random mortality null model ($P = 0.018$) to 868 ($P = 0.132$) for the *B. retusum* model. Notably, and for small spatial scales (<4 cm), the observed test statistics was within the simulation envelopes. Thus, the observed departure from random mortality (where seeder individuals were more likely to die if they had more seeder individuals in their neighborhood) at small scales can be accounted for by the presence of *B. retusum*. In this case, seeders tended to have higher densities in areas with low *B. retusum* biomass (which may be an effect of competition for space); interactions in these high biomass patches was more intense, leading to aggregation of dead seeders and segregation from live ones. In the third year after fire there was no significant departure of this test statistic from neither the random mortality

null model nor the *B. retusum* model. Nine years after fire, the simulation envelopes of both null models were almost identical, indicating highly significant departures. Considering *retusum* in the null model did not influence the outcome of point pattern analysis for both, the fire and erosion treatment (Fig. 2M–R).

4. Discussion

Studying the interplay between facilitation and competition has been a core research topic of plant community ecology over the last two decades (see reviews in Callaway, 2007; Brooker et al., 2008; Brooker and Callaway, 2009). The analysis of the existing spatial distribution of plant species has often been successfully used to provide insights on the outcome of these interactions (e.g., Mertens and Lambin, 1997; Barot et al., 1999; Maestre et al., 2005; De Luis et al., 2008b; Raventós et al., 2010). In this direction, the spatial aggregation of plant species and individuals has often been considered as indirect evidence of positive interactions (i.e. facilitation) among these, while spatial segregation has often been interpreted as an evidence of the existence of negative interactions (i.e. competition; see Tirado and Pugnaire, 2003; Cheng et al., 2006 for a review). In Raventós et al. (2010) we observed in the fire treatment of the second year after experimental fire marked departures from random mortality: aggregation of dead seeder plants (among all seeder plants; Fig. 1A), segregation of surviving and dead seeder plants (Fig. 1G), and that dead seeder plants were neighbored by more (pre-mortality) seeder plants than surviving seeder plants (Fig. 1M). In this study we put forward a specific hypothesis to explain the observed departures from random mortality. We hypothesized that the resprouter *B. retusum*, which quickly occupies the bare soil left after the fire, had a positive effect on survival of the seeder species (conversely its absence has a negative effect on survival). We implemented a specific point process (the *B. retusum* model) that represents this hypothesis, and found that it matched for all three test statistics the observations better than the random mortality null model. Note that this ability was not granted because the *B. retusum* model has no free parameter to be fitted and represents a very specific hypothesis. As expected, the influence of the resprouter species *B. retusum* disappeared during later years of succession and the impact of *B. retusum* was weaker in the fire + erosion treatment.

Thus, our analysis provides evidence that the presence of the resprouter species *B. retusum* had a positive effect on survival of the seeder species two year after fire. However, our hypothesis did not fully explain the observed patterns; for test statistic g_{11} there was still a weakly significant departure from our specific point process model, and for the text statistic g_{12} our hypothesis moved the simulation envelopes in the right direction (c.f., Fig. 1G and J) but at distances of 4–6 cm the g_{12} was still outside the simulation envelopes. The relatively simple techniques used here were sufficient to provide an understanding on the potential role of *B. retusum* in the early phase of recolonization after fire, and to generate a hypothesis that could be tested with specific field investigations. However, adopting a more parametric framework would be an alternative to our approach that allows fitting more flexible point processes to the data. For example, Illian et al. (2009) used a Markov pairwise interaction model to evaluate the relationship between seeders and resprouters in Western Australia. Parametric approaches allow estimating approximate likelihoods for competing models that could be combined with information-theoretic model selection approaches to find out if more complex parametric models would be justified by a better fit. Given the space-time nature of our data, the use of space-time point process analyses (e.g., Diggle et al., 1995; Rathbun and Cressie, 1994) may also be a promising avenue to explore our data.

Overall, our results confirm those from previous analysis (Raventós et al., 2010), suggesting that intraspecific competition between individual seeder species may be the key interaction controlling population dynamics after fire. Intraspecific interactions were dominant because the four species showed strong clustering and intraspecific segregation (De Luis et al., 2008b). However, our analysis further suggests that interspecific interactions between resprouter and seeder species explain a large part of the observed departures from random mortality at the initial stage of succession. A possible mechanism to explain the observed positive effect of *B. retusum* on seeder survival is that this species prevents erosion (and related small-scale nutrient loss) immediately after fire (De Luis et al., 2004b), thereby releasing intraspecific competition between the individuals of the seeder species. Cerdà and Doerr (2005) provide evidence for this hypothesis. They investigated long-term changes in soil hydrological properties and erodibility during the regrowth of different types and densities of vegetation following a severe wildfire in the eastern Mediterranean. Cerdà and Doerr (2005) found considerable variation in the erosion rate and overland flow under the different vegetation types. Plots initially dominated by *B. retusum* showed considerably faster vegetation recovery and lower erosion rate and overland flow than plots initially dominated by dwarf shrubs (such as *U. parviflorus* and *C. albidus*).

As plant-plant interactions occur at shorter neighboring distances (Harper, 1977; Stoll and Weiner, 2000), facilitative effects of *B. retusum* on seeder species only occurred at short distances (Callaway, 2007) This facilitation effect could be mediated by two combined factors: the faster regrowth of *B. retusum* after fire, which prevents the soil erosion and the physiognomy of *B. retusum*, which create a low herbaceous layer that could improve the water retention capacity of the soil and in turn decrease the evapotranspiration losses on seeder species. Maestre et al. (2003) present some evidence for this process in grass–shrub interaction in Mediterranean semiarid grasslands. As seeder seedlings grow, we found three years after fire no effect of *B. retusum* on the spatial pattern of seeder mortality. One possible explanation for this finding is that *B. retusum* plants remain through time within the low herbaceous layer, whereas seeder individuals occupy later on higher vertical strata. The presence of *B. retusum* prevented soil erosion and provided more benign conditions for seeder establishment, however, when seeder plants reach the higher vertical strata they compete intensely with each other leading to the negative density dependent mortality observed in Raventós et al. (2010). A similar changes in the sign of density dependent interaction in time was found by Greenle and Callaway (1996).

We also observed that the influence of *B. retusum* on seeder species were minimized in the fire + erosion treatment, as suggested in our third hypothesis. In the fire + erosion treatment, seedling mortality is higher (De Luis et al., 2005) but surviving plants are bigger than surviving plants in the fire treatment (De Luis et al., 2001). As a consequence, our results suggest that the intensity of the influence of *B. retusum* on seedling survival is mediated by the size of seedlings, being this influence more intense on smaller plants (like those existing on fire + erosion conditions).

Inferring processes and mechanisms from observed plant spatial patterns is a difficult task because substantially different processes may produce the same patterns (Wiegand et al., 2003). In this study we followed the approach advocated by Wiegand et al. (2009), in which a close description of the characteristics of the observed spatial patterns may allow for deriving hypotheses and inference about the underlying processes. However, additional data on species properties are necessary to correctly interpret the patterns in terms of the processes, and the specific hypothesis that results from the spatial analysis should be tested in specific field experiments.

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