Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland

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Abstract. A current focus of ecology is the investigation of spatial effects on population and community dynamics; however, spatiotemporal theory remains largely untested by empirical observations or experimental studies. For example, the segregation hypothesis predicts that intraspecific aggregation should increase the importance of intraspecific competition relative to interspecific competition, thereby enhancing local coexistence in plant communities. We applied recent methods of point pattern analysis to analyze a unique long-term data set on fully mapped seedling emergence and subsequent survival in a Mediterranean gorse shrubland after experimental fires and simulated torrential rainfall events. Our overall aim was to test if the observed spatial patterns were consistent with the segregation hypothesis during the entire community dynamics from early seedling emergence to the establishment of a mature community, i.e., we explored if the observed initial segregation did indeed prevent interspecific competition from becoming dominant. We used random labeling as the null model and specific test statistics to evaluate different biological effects of the spatial interactions that determine mortality.

We found that mortality was clearly not random. Comparison of the probability of mortality in dependence on the distance to conspecific and to heterospecific plants showed that mortality was controlled almost entirely by intraspecific interactions, which is consistent with the segregation hypothesis. Dead plants were aggregated and segregated from surviving plants, indicating two-sided scramble competition. Spatial interactions were density dependent and changed their sign over the course of time from positive to negative when plants grew to maturity. The simulated torrential rainfall events and subsequent erosion caused nonspecific mortality of seedlings but did not reduce the prevalence of intraspecific competition. Our results provide support for the hypothesis that the spatial distribution of plants may profoundly affect competition and can be an important determinant in the coexistence of species and biodiversity.

Key words: facilitation; fire; Mediterranean shrubland; pair correlation function; random mortality hypothesis; scramble and contest competition; spatial point pattern analysis.

INTRODUCTION

A current focus of ecology is the investigation of the effect of spatial interactions on population and community dynamics (Murrell et al. 2001). Spatial structures and interactions are expected to be especially important for plants which cannot move (except via births and deaths) and are therefore likely to respond directly to their immediate neighborhood (Purves and Law 2002, Wiegand et al. 2006, Miriti 2007, Das et al. 2008). The interest of ecologists in spatial structures of plant communities is twofold. First, theory shows that spatial structures may play an important role in coexistence processes (e.g., Hurtt and Pacala 1995, Tilman and

Kareiva 1997, Bolker and Pacala 1999, Chesson 2000, Hubbell 2001, Schupp et al. 2002). For example, the spatial segregation hypothesis (Pacala 1997, Pacala and Levin 1997) is based on the idea that intraspecific aggregation increases the importance of intraspecific competition relative to interspecific competition, thereby enhancing local coexistence in plant communities (e.g., Pacala and Levin 1997, Murrell et al. 2001, Stoll and Prati 2001).

The second reason for the growing interest in spatial structures is that spatial processes are expected to create identifiable spatial patterns, and that analysis of the spatial patterns may help to identify the underlying processes (e.g., Levin 1992, Wiegand et al. 2003, 2007*a*, 2009, Wiegand and Moloney 2004, McIntire and Fajardo 2009). One example of this is competition (Kenkel 1988): under scramble competition (i.e., a limited resource is partitioned equally among contes-

tants so that no competitor obtains the amount it needs), dense clumps of conspecifics may die, thereby causing segregation of surviving and dead individuals. On the other hand, contest competition (i.e., unequal partitioning so that some competitors obtain the amount they need and others less) will lead to attraction of the suppressed dead individuals by the surviving superior rivals.

More generally, we can expect that different spatial patterns mirror differences in species abilities to overcome intra and interspecific competition during community dynamics (Getzin et al. 2006). Analyzing the changes in spatial patterns over time should therefore reveal, for example, the effects of density-dependent mortality (Plotkin et al. 2002). However, observation of attractive or clustered spatial patterns may also suggest facilitation effects, or, at least tolerance (Callaway and Walker 1997). In fact, the balance between positive and negative interactions may change in intensity and sign through time and space (Miriti 2006), depending on factors such as availability of resources, plant life history and stage, abiotic stress, and predation pressure (Bertness and Callaway 1994, Callaway 1998, Armas and Pugnaire 2005, Riginos et al. 2005).

Spatial patterns may thus carry information on processes shaping community dynamics and promoting coexistence (Murrell et al. 2001, Wiegand and Moloney 2004, Wiegand et al. 2007a, 2009, McIntire and Fajardo 2009). A considerable challenge in plant ecology is therefore to understand how the temporal and spatial dimension of plant–plant interactions, such as competition or facilitation, shapes the spatial distribution of plants (Getzin et al. 2006, Miriti 2007, Das et al. 2008). Surprisingly, the spatial dimension of plant interactions has received relatively little attention (Dieckmann et al. 2000). This is in part a consequence of a lack of data sets on spatiotemporal patterns of community dynamics that would allow observation on how density- and scale-dependent spatial interactions change in time (but see Maestre et al. 2003a, b, Miriti 2007, Das et al. 2008, De la Cruz et al. 2008, Felinks and Wiegand 2008). However, such studies are of prime importance in the better understanding of the contribution of spatial processes and mechanisms to coexistence in plant communities (Maestre et al. 2003a).

We use a unique data set on fully mapped seedling emergence and subsequent nine year monitoring in a Mediterranean gorse shrubland after experimental fires and simulated torrential rainfall events. The experimental fires allowed us to "reconstruct" this ecosystem from almost zero because they killed all individuals and restarted the system though the germination processes. The torrential rainfall events that were applied two months after fire had no effect on seedling emergence (De Luis et al. 2005a), but significantly affected the temporal seedling survival (De Luis et al. 2005b) and seedling growth (De Luis et al. 2001). This experimental treatment allows us to compare the spatial dynamics of

an "overstocked" community (i.e., without experimental rainfall event) and a community which was "thinned" at an early developing stage by a mortality event. Comparison of the two treatments will also show if our results are robust.

In a previous analysis, dealing only with the initial spatial pattern analysis of recruitment, we found that all species showed an aggregated intraspecific spatial pattern and that the clusters of individual species were spatially segregated (De Luis et al. 2008a). Theoretical models predict that this spatial pattern will promote species coexistence (i.e., the segregation hypothesis; Pacala 1997, Pacala and Levin 1997). In this study, we use our long-term data set to conduct a detailed spatiotemporal pattern analysis of mortality to test if the segregation hypothesis holds during the entire community dynamics from early seedling emergence to the establishment of a mature community, i.e., we explore if the observed initial segregation did prevent interspecific competition from becoming dominant (Murrell et al. 2001, Chesson and Neuhauser 2002). To guide our analyses, we addressed the following specific hypothesis motivated by general theory.

H1: Because of the observed intraspecific clustering and interspecific segregation of seedlings in the emergence process (De Luis et al. 2008a), we expect intraspecific interactions to be critical and more important for long-term community dynamics than interspecific interactions.

H2: We expect that competition should be of the two-sided scramble type because we did not observe stark differences in plant size that could give rise to one-sided competition as, for example, observed in forest ecosystems (e.g., Kenkel 1988).

H3: Positive density dependent effects (facilitation) should dominate during the earlier stage of seedling establishment, but negative effects (competition) will dominate in later years when plants grow to maturity.

H4: We expect that the simulated torrential rainfall event and subsequent erosion will cause non-specific mortality of seedlings and thus reduce the prevalence of intraspecific competition.

Methods

Study site

The study was carried out in three 33×33 m plots located in the Sierra de Onil (00°39′ W; 38°43′ N; 800 m above sea level), 40 km northwest of Alicante (Spain). Plots were located on slopes facing south, northeast, and north with slope angles ranging between 21° and 27°. 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. The three plots studied consist of a stage in the degradation of a former Aleppo pine (*Pinus halepensis*) forest burned in 1994, which afterward formed a Mediterranean gorse shrubland dominated by *Ulex parviflorus* (Fabaceae).

Experimental design and seedling monitoring

In October 1996, after the first autumn rains and on windless days, we burned the three plots (fire scenario; F). Plots were previously delimited by a 5 m wide firebreak in which the vegetation was eliminated by mechanical brushing. The fires were ignited in the upper part of each plot with the fire fronts being made in a continuous line downhill. Two months after fire, we applied in each of the three plots a torrential rainfall simulation treatment in two of the four 2×0.5 m subplots (fire + rainfall scenario; F + R). Rainfall intensity applied was 2.6 mm/minute for 105 minutes and produced soil losses between 60 and 800 g/m^2, representing soil losses between 0.2 and 1 mm (De Luis et al. 2003). An evolutionary response to these two scenarios is discussed on De Luis et al. 2008b.

Immediately after fire and for the next three years, we monitored the seedling survival of all species present in four 2×0.5 m subplots within each experimental site. All individuals were identified and located using *x*- and *y*-coordinates. At the end of the first, second, and third years, we recorded the state of each individual as live or dead. An additional sampling was made in autumn of 2005 (nine years after fire). We focused our analyses on the four most common species *Cistus albidus* with a total of 931 seedlings, *Helianthemum marifolium* (578 seedlings), *Ulex parviflorus* (327 seedlings), and *Ononis fruticosa* (282 seedlings; see Appendix H). Seedlings of 11 other species were too infrequent for our purpose; they added up to a total of 360 seedlings

Spatial pattern analysis

We used recent techniques of spatial point pattern analysis to analyze the spatial component of plant mortality. To describe the spatial patterns we used test statistics based on univariate and bivariate pair-correlation functions, $g(r)$ and $g_{12}(r)$, respectively. Pair correlation functions are (intensity normalized) distance-dependent neighborhood density functions applicable to completely mapped point patterns (Stoyan and Stoyan 1994, Wiegand and Moloney 2004, Illian et al. 2008). We used a numerical estimator of the bivariate pair correlation function $\hat{g}_{12}(r) = \hat{O}_{12}(r)/\hat{\lambda}_2$ based on the O-ring statistic $O_{12}(r)$ (Wiegand and Moloney 2004):

$$\hat{O}_{12}^{w}(r) = \frac{\dfrac{1}{n_1}\displaystyle\sum_{i=1}^{n_1}\text{Points}_2\left[R_{1,i}^{w}(r)\right]}{\dfrac{1}{n_1}\displaystyle\sum_{i=1}^{n_1}\text{Area}\left[R_{1,i}^{w}(r)\right]} \qquad (1)$$

where $\hat{\lambda}_2$ is an estimator of the intensity λ_2 (i.e., the number of plants of pattern 2 divided by the area of the study plot), n_1 is the number of plants of pattern 1, $R_{1,i}^{w}(r)$ is a ring with radius r and width w centered in the *i*th plant of pattern 1, Points$_2[X]$ counts the plants of pattern 2 in a region X, and the operator Area$[X]$ determines the area of the region X. Thus, the $O_{12}(r)$

determines the average density of plants of pattern 2 at distance r from plants of pattern 1 and the pair correlation function is the corresponding intensity normalized function. The univariate estimator of $O(r)$ is calculated analogously by setting pattern 1 equal to pattern 2. In this case, the focal points of the rings are not counted.

Our data follow the fate of mapped seedlings over nine years, thus we know for each year (i.e., year 1, 2, 3, and 9) if a given plant was alive or dead. Analysis of such data requires using the framework of "marked point patterns" (Stoyan and Stoyan 1994, Illian et al. 2008) where each plant at a given year can have the marks "dead" (in the following indicated by subscript 1) or "alive" (subscript 2). The fundamental question is to find out if the process that distributed the marks was a random process (i.e., random labeling implying random mortality) and to characterize and interpret potential departures from random mortality (Kenkel 1988, Goreaud and Pelissier 2003). If random mortality is rejected or if biological knowledge strongly suggests that truly random effects are unlikely to be a significant driver, later steps of modeling may involve testing more specific point process models such as size-dependent or density-dependent mortality.

To describe precisely the nature of potential departure from random mortality (which is required to test our hypotheses and interpret our results) and minimize the risk that departures from random mortality may go undetected, we used five test statistics simultaneously. Note that each test statistic captures a somewhat different biological effect: (1) the univariate $g_{11}(r)$ function is especially suitable to detect clustering of dead individuals, (2) the $g_{12}(r)$ function reveals attraction vs. segregation among dead (subscript 1) and surviving plants (subscript 2), (3) the $g_{1,1+2} - g_{2,1+2}$ function tests directly for density dependent mortality (Yu et al. 2009), and (4) two mark-connection functions (Getzin et al. 2008, Illian et al. 2008) describes the probability of mortality of plants of a focal species in dependence on the distance to conspecific plants (i.e., $p_{1+2,1}$) and to heterospecific plants h (i.e., the plants of the other three species; $p_{h,1}$). To test our four guiding hypotheses we used random labeling as null model and the five test statistics presented above. Additional information on the test statistics can be found in Appendix A: Table A1. Random labeling analyses were done at four different time steps: 1, 2, 3, and 9 years after germination and under the two treatments, fire (F plots) and fire + rainfall (F + R plots).

Tests of hypotheses

Hypothesis H1: intra- vs. interspecific interactions.—To test the impact of intraspecific interactions on mortality, we performed a conventional random labeling analysis for each species. The null model of random labeling is implemented in a way that the label "dead" is randomly assigned to the locations of the combined set

of surviving and dead plants (Goreaud and Pelissier 2003). To quantify departures from the random mortality hypothesis we used the three test statistics $g_{11}(r)$, $g_{12}(r)$, and $g_{1,1+2} - g_{2,1+2}$. Note that each test statistic evaluates a different biological effect of the spatial interactions that determine mortality (see Appendix A). In this way, we gain a comprehensive understanding of the spatial aspects of intraspecific interactions in our study system and reduce the risk that a departure from random mortality may go undetected.

To test the impact of interspecific vs. intraspecific interactions on mortality of a given focal species, we ask if the probability of mortality of plants of the focal species depends on the distance from heterospecific plants and on the distance from conspecific plants, respectively. The appropriate approach for this question is trivariate random labeling (Biganzoli et al. 2009, Xu et al. 2009), i.e., we test if the presence of plants of a given pattern (i.e., heterospecific or conspecific plants) influenced the probability of mortality of plants of the focal species. Note that the same approach has also been called "independent labeling" (De la Cruz et al. 2008). In practice, conventional random labeling was executed between the two patterns of surviving (subscript 2) and dead plants (subscript 1) of the focal species, but test statistics were used that estimate the probability of mortality of plants in the focal species depending on the distance r from heterospecific plants (subscript h) or conspecific plants (subscript 1+2). To obtain a test statistic with the interpretation of a probability of mortality, we divided the bivariate neighborhood density $\lambda_1 g_{h,1}(r)$ that describes the neighborhood density of dead plants of the focal species (subscript 1) around heterospecific plants (subscript h) by the neighborhood density of focal plants (i.e., dead and surviving: 1+2) around heterospecific plants (h), i.e., $(\lambda_1 + \lambda_2)g_{h,1+2}(r)$:

$$p_{h,1}(r) = \frac{\lambda_1}{(\lambda_1 + \lambda_2)} \times \frac{g_{h,1}(r)}{g_{h,1+2}(r)} \qquad (2)$$

where the $(\lambda_1 + \lambda_2)$ and λ_1 are the intensities of plants of the focal species and of the dead plants of the focal species, respectively. The analogous test statistic for testing the influence of conspecific plants on mortality yields

$$p_{1+2,1}(r) = \frac{\lambda_1}{(\lambda_1 + \lambda_2)} \times \frac{g_{1+2,1}(r)}{g_{1+2,1+2}(r)}. \qquad (3)$$

Note that these test statistics are formally analogous to mark-connection functions (Getzin et al. 2008, Illian et al. 2008). The expectation of the test statistics under random labeling is the overall probability of mortality, i.e., number of dead plants divided by number of plants. With negative interactions exerted from hetero- or conspecific plants at distance r (i.e., competition), we expect a higher probability of mortality, e.g., $p_{h,1}(r) > \lambda_1/(\lambda_1 + \lambda_2)$, whereas positive interactions would be indicated by a lower probability of mortality in the proximity of heterospecific or conspecific plants, e.g.,

$p_{h,1}(r) < \lambda_1/(\lambda_1 + \lambda_2)$. Following hypothesis H1 we expect significant effects in the intraspecific test statistic $p_{1+2,1}(r)$ but no significant effects in the heterospecific test statistic $p_{h,1}(r)$.

Hypothesis H2: contest vs. scramble competition.—To test for scramble competition, we used the two test statistics g_{11} and g_{12}. Under scramble competition, we expect aggregation of dead plants (which is tested by g_{11}) and non-attraction of dead and surviving plants (which is tested by g_{12}). However, under contest competition we expect attraction of dead plants around surviving plants (which is tested by g_{12}).

Hypothesis H3: temporal changes in the balance of negative and positive interactions.—We compared the results of the analyses obtained for years 1, 2, 3, and 9 by using the third test statistic (i.e., $g_{1,1+2} - g_{2,1+2}$). This test statistic directly reveals departures from random mortality due to density dependent effects.

Hypothesis H4: torrential rainfall reduces prevalence of intraspecific competition.—To test this hypothesis we compared the results of the two treatments.

Simulation conditions

We analyzed spatial patterns up to 25 cm, which is half of the width of our subplots using a spatial resolution of 1×1 cm for all analyses. This resolution is fine enough to respond to our questions and close to the mapping error of our data. For each subplot and year, we performed 999 Monte Carlo simulations of the random labeling null model. For each test statistic, we generated approximately 95% simulation envelopes by using the 25th-lowest and 25th-highest value at a given scale r. This allowed us to approximately assess scale effects and to illustrate the strength and direction of significant effects. However, to avoid problems due to simultaneous inference (e.g., Diggle 2003), we evaluated the overall ability of the random labeling null model to describe the data by means of a goodness-of-fit test (Diggle 2003, Loosmore and Ford 2006). This test reduces the scale-dependent information contained in the different test statistics into a single test statistic u_i which represents the total squared deviation between the observed and the expected patterns across the distances of interest.

For each treatment, we collected data at six replicate subplots. To use the full statistical power of our data and to present our results in a succinct way, we used a specific method that combines the results of the individual analyses of each single subplot and of individual species into one overall test statistic (Riginos et al. 2005, De Luis et al. 2008a, Illian et al. 2008; for technical details, see Appendix A). This means that, biologically, we focus on the average spatial mortality patterns, i.e., the broad picture which is of primary interest in our study, but less on the potential variability among individual subplots and species. However, we present the results obtained for individual species in appendices B–G. All spatial analyses were done with 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).

RESULTS

Intra- and interspecific effects on mortality

Our analysis using the method of (trivariate) random labeling (De la Cruz et al. 2008, Biganzoli et al. 2009, Xu et al. 2009) showed that the proximity of heterospecifics at best showed very weak effects on the probability of mortality (Fig. 1A–H). At the overstocked F plots, mortality was lower within the proximity of hetero-specifics, pointing to a facilitative effect (Fig. 1A), whereas mortality was slightly higher than expected at the plots given torrential rainfall treatment (Fig. 1B).

However, we found that the probability of mortality depended significantly on the distance to conspecific plants. Initially, plants at the F plots had a lower risk of mortality when located closer to conspecifics (Fig. 1I) but in subsequent years the positive effect disappeared and was replaced by a negative interaction (Fig. 1K, O) which was strongest at the last year of observation. Note that Fig. 1M does not follow the expected trend of increasingly powerful intraspecific competition over time. The same trend is also shown in Fig. 2S, U, W. This suggests that some alternative process may have been operating during this period. It is noteworthy that approximately 31% of the initial seedlings died from year 0 to 1 and from year 1 to 2, but only 7% from year 2 to 4 and 15% from year 3 to 9. Thus, the year 3 is probably a transition year where the dominance of mortality processes changed.

The torrential rainfall treatment showed similar results than plots of the other treatment, but no positive effect occurred at the first year (Fig. 1J). The results of the first year for plot without torrential rainfall treatment (Fig. 1A, I) suggest that both, nearby conspecific and nearby heterospecific plants had a positive effect on survival.

Thus, application of the two test statistics $p_{h,1}(r)$ and $p_{1+2,1}(r)$ provided support for our first hypothesis, indicating that intraspecific interactions were more important for long-term community dynamics than interspecific interactions.

Dead plants are aggregated (univariate g_{11} function)

The analyses of the spatial patterns of surviving seedlings using the test statistics g_{11} indicated, in all cases, significant aggregation of dead individuals at scales up to 2–3 cm. This was true for all years and the two treatments (Fig. 2A–H). However, when analyzing the data for each of the four species separately, we found some differences between families and treatments (see Appendices B and C).

Dead and surviving plants are segregated (bivariate g_{12} function)

The analyses using the $g_{12}(r)$ test statistic revealed strong and significant segregation on small scales up to

at least 3 cm for all years and treatments (Fig. 2I–P). The predominant aggregation pattern of dead plants, together with the segregation of surviving and dead plants, suggests that intraspecific scramble competition was the dominant interaction in this community, thus providing support for hypothesis H2. Again, at the family level, we found some differences (see Appendices D and E).

Test of density-dependent mortality (bivariate difference $g_{1,1+2} - g_{2,1+2}$)

The third test statistic revealed substantial changes in the sign of density-dependent effects that resembled that of the test statistic $p_{1+2,1}(r)$ closely. In the first year, we found significant and positive density-dependent spatial interactions in mortality in F plots, but not in the F + R plots. This means that surviving seedlings in F plots had more pre-mortality neighbors than dead seedlings, thus pointing to facilitation effects. Significant positive effects were detected up to scales of 5 cm, and peaked at 1–2 cm (Fig. 2Q). At species level, we found significant and positive density-dependent spatial interaction only for *O. fruticosa* in the plots without experimental rainfall event (see Appendix G: Fig. G1I).

After the first year, the positive density-dependent mortality disappeared for the F plots and switched into a significant negative density-dependent mortality (Fig. 2S, W), which was maintained into the ninth year. This means that dead plants had, at later stages of vegetation dynamics, more neighbors than surviving plants, thus pointing to density-dependent effects. For the F + R treatment, strong negative density dependent effects developed for years 2, 3, and 9 (Fig. 2T, V, W). Thus, our hypothesis 3 was clearly supported for F plots and partly for F + R plots (because, here, the first year showed only a nonsignificant tendency to positive effects). Note that we analyzed "accumulative" mortality (instead of looking only at plants that died during the last year). This means that strong negative effects are required to cancel the signature of positive effects in the data.

This also means that the extreme rainfall event at the F + R plots was not able to reduce the prevalence of intraspecific interactions as expected from hypothesis H4. What happened, however, was that the seedling mortality caused by the experimental rain event reduced the prevalence of positive density dependence in mortality (Fig. 2R, first year) and reduced the degree of segregation between surviving and dead seedlings (Fig. 2J, first year). However, when looking at the temporal development, we found contrasting results in the analyses at species level (see Appendices F and G)

DISCUSSION

Ecological theory suggests a strong impact of spatial patterns on plant–plant interactions, community dy-namics, and eventually coexistence mechanisms (Pacala 1997, Bolker and Pacala 1999, Murrell et al. 2001,
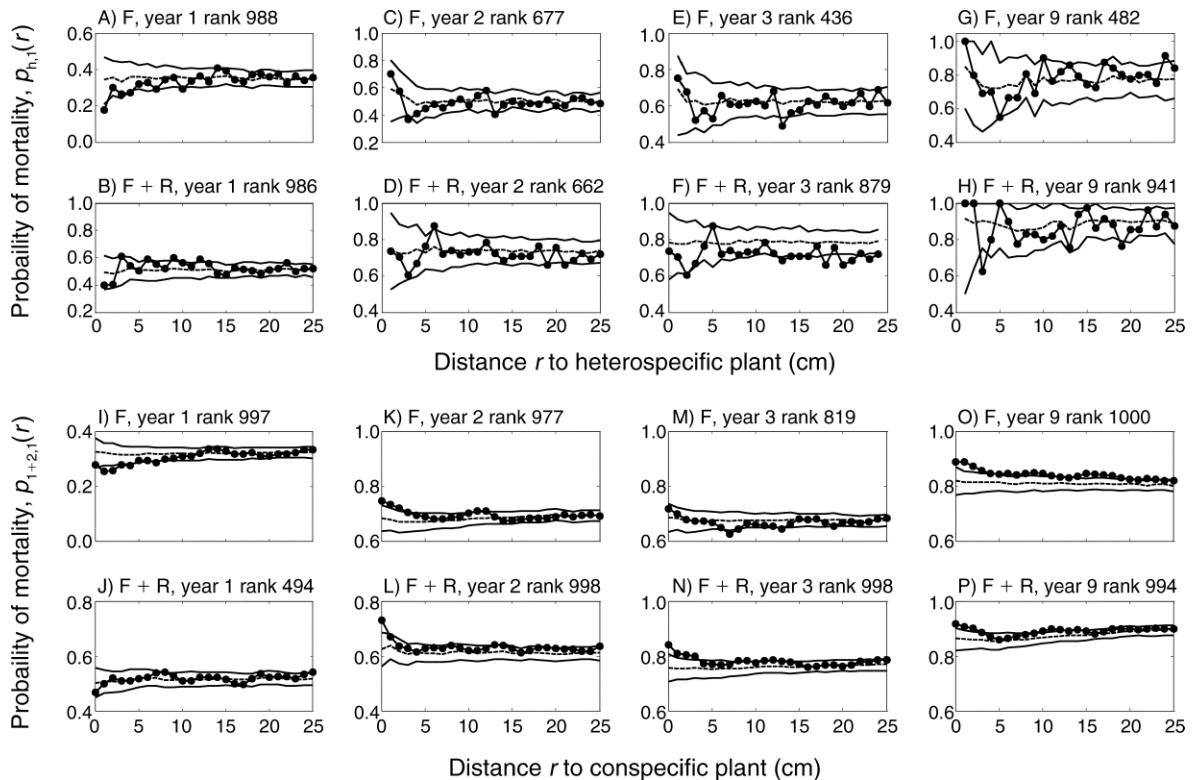
FIG. 1. Trivariate random labeling analysis to study the effect of heterospecific plants (A–H) and of conspecific plants (I–P) on mortality. The test statistics $p_{h,1}(r)$ and $p_{1+2,1}(r)$ evaluate the probability of mortality at distance r from heterospecific and conspecific plants, respectively. Solid circles are the observed test statistic; dashed lines show the expectation under the null model (average of all simulations of the null model), and solid lines without circles show simulation envelopes, being the 25th smallest and largest values of the 999 simulation of the null model. If the test statistic was below the simulation envelopes, mortality was lower than expected (i.e., facilitative effects), and if it was above the simulation envelopes, mortality was higher than expected (i.e., competitive effects). F plots were only subjected to experimental fire, while F + R plots were subjected to burning and experimental rainfall.

Murrell and Law 2003, Wiegand et al. 2007a, b). An important spatial coexistence mechanism that has been discussed widely in the theoretical literature is intraspecific aggregation (interspecific segregation), which reduces the number of unfavorable heterospecific interactions for poorer competitors (the segregation hypothesis; Murrell et al. 2001). However, only a few empirical studies have allowed direct observation of how the spatial structure of communities influences inter- and intraspecific competition (e.g., Rees et al. 1996, Stoll and Prati 2001, Monzeglio and Stoll 2005, Idjadi and Karlson 2007, De la Cruz et al. 2008). Our study is unique in that our long-term data set allowed for a direct empirical test of the segregation hypothesis. Our analyses found results consistent with the hypothesis that intraspecific interactions should be dominant from the initial seedling emergence up to the mature community, and we provided appropriate techniques of spatial pattern analysis to quantify such effects.

Our approach follows a third avenue for analyzing the impact of spatial structure on community dynamics. Two approaches have been predominantly used to study the effects of spatial structure on community dynamics.

First, experimental studies aimed to determine whether a prescribed spatial pattern can have measurable effects on the performance of species (Murrell et al. 2001, Stoll and Prati 2001, Idjadi and Karlson 2007). A second approach is to fit models of community dynamics, which incorporate spatial interactions and dispersal, to empirical data and evaluate the significance of the spatial vs. nonspatial terms of the model (e.g., Pacala and Silander 1990, Rees et al. 1996). A third, intermediate, approach is direct statistical analysis of mortality. For example, "individual-based" statistical approaches have been used to analyze neighborhood effects and negative density dependence in mortality in fully mapped plots of tropical forests (e.g., Hubbell et al. 2001, Peters 2003, Uriarte et al. 2005, Queenborough et al. 2007). For this purpose, we used recent techniques of point pattern analysis, which are increasingly used in ecology (Wiegand and Moloney 2004). Note that our approach of using pair-correlation functions is closely linked to the moment equation approximation used in theoretical models (e.g., Bolker and Pacala 1999, Murrell and Law 2003). This makes our approach compatible with the theory of spatiotemporal dynamics and should stimulate
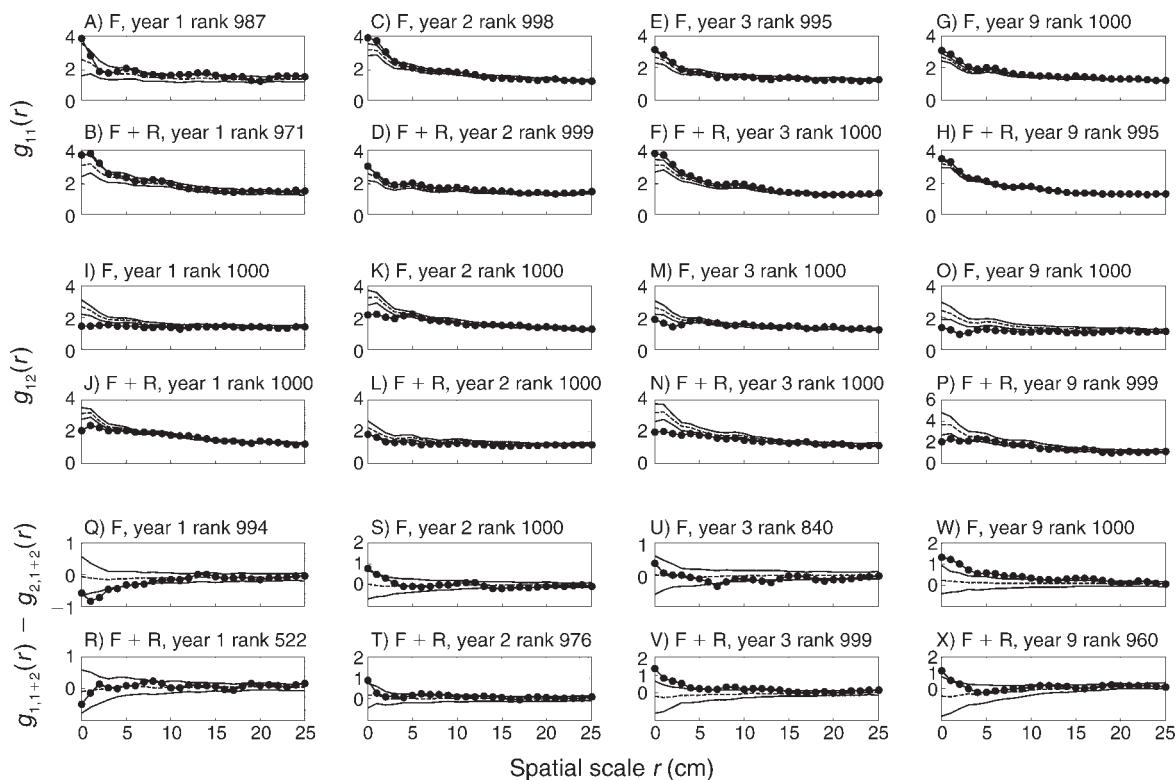
Fig. 2. Random labeling analyses using the g_{11} (A–H), g_{12} (I–P), and $g_{1,1+2} - g_{2,1+2}$ (Q–X) function as test statistic to assess the spatial pattern of dead individuals. (A–H) If the g_{11} was above the simulation envelopes, dead plants were aggregated, conditionally on the pattern of dead and surviving plants. (I–P) If the test statistic g_{12} was below the simulation envelopes, dead and surviving plants were segregated, indicating scramble competition. Conversely, attraction (g_{12} above the simulation envelopes) would indicate contest competition. (Q–X) If the test statistic $g_{1,1+2} - g_{2,1+2}$ was below the simulation envelopes, mortality was positive and density dependent (i.e., facilitation). Conversely, if the test statistic $g_{1,1+2} - g_{2,1+2}$ was above the simulation envelopes, we observed negative dependent mortality (i.e., competition). F plots were only subjected to experimental fire, while F + R plots were subjected to burning and experimental rainfall. The results are given for 1, 2, 3, and 9 years after germination. The test statistic of the data is shown as a solid line with solid circles. The expectation of the null model is indicated with a dashed line, and the simulation envelopes, being the 25th smallest and largest values of the 999 simulation of the null model, are represented by solid lines with no circles. Spatial resolution is 1×1 cm.

fruitful interaction between spatial pattern analysis and theoretical modeling.

Our study provides, to our knowledge, the first direct evidence that the spatial segregation hypothesis (Pacala 1997, Pacala and Levin 1997) appeared to work. Clearly, several studies have documented intraspecific spatial aggregation and interspecific segregation in plant communities (e.g., Dale and John 1999, Gratzer and Rai 2004, Wiegand et al. 2007a, b, De Luis et al. 2008a, Perry et al. 2009), however, this observation of spatial structure alone does not demonstrate that aggregation is indeed important in determining vital rates such as mortality (Rees et al. 1996). We separated the scale-dependent spatial effects of intra- and interspecific neighborhood density on mortality and found that the risk of mortality depended significantly on the distance to conspecifics, but not on the distance to heterospecifics. Thus, interspecific interactions were unable to control population dynamics as postulated by competitive exclusion (e.g., Chesson and Neuhauser 2002).

Note that none of the species initially present as seedlings became extinct in our study plots.

Our study unambiguously rejects the random mortality hypothesis for the entire nine-year observation period in favor of a model of differential mortality. We found that the dominating conspecific interactions were consistent with two-sided scramble competition, probably for soil nutrients and water. However, we found no evidence for contest competition. One reason for this may be that plants in the gorse shrubland, which are basically one cohort that was established after fire, do not show the stark differences in size required to exert strong one-sided competition by close neighbors. Alternatively, contest competition may not occur at all in this community because light may not be as limiting as, for example, for the jack pine stands studied by Kenkel (1988).

We found that positive density-dependent spatial interactions acted during the first year in the plots that were not subject to the experimental rainfall event. Later

on, the positive interactions became overpowered by negative interactions. Positive species interactions have received less attention than negative interactions, but recent studies show that they are more important than previously assumed (Miriti 2006, Brooker et al. 2008, Chu et al. 2008, Gross 2008). For example, the "stress gradient hypothesis" (SGH) predicts that the relative importance of facilitation and competition should vary inversely along gradients of abiotic stress, with facilitation increasing in importance over competition as abiotic stress increase (Holzapfel and Mahall 1999, Maestre et al. 2003a). During the first year after the experimental fire, our system would be located on the low stress end of the gradient because all seedlings were small in size, had plenty of light, and an extra input of nutrients from litter and ashes. However, in contrast to the predictions of SGH, we found significant positive density dependence in mortality where surviving seedlings had, in small neighborhoods, more neighbors and were spatially aggregated. Similar results were found by Perry et al. (2009) based on a nearest neighbor analysis of species-rich shrubland communities.

Interestingly, the positive density dependence was not found in the plots that were subject to the torrential rainfall event. This could be because of the effect of non-density-dependent mortality induced by the rainfall event. De Luis et al. (2005b) found in nonspatial analyses a significant increase in seedling mortality, both from direct impact (seedlings buried by sediment or seedlings totally or partially unearthed) and from indirect impact as result of soil and litter losses (De Luis et al. 2004). The experimental rainfall event thus apparently caused a reduction in the density of individuals, which prevented the establishment of positive density-dependent effects during the first year. Additionally, we observed at the plots without torrential rainfall event that the risk of mortality was smaller in the proximity of both hetero- and conspecific seedlings. This suggests that non species specific abiotic factors, such as local differences in soil moisture, might act during the first year. High seedling densities may reduces soil evaporation directly through shading or indirectly from reducing wind driven drought. This mechanism is consistent with the absence of positive effect of density on the "thinned" plots of the torrential rainfall event. An alternative mechanism without resource to positive interactions would be that seedlings establish preferentially in favorable microsites and suffer at these sites lower mortality risk.

Finally, our study provides evidence that the occurrence or non-occurrence of significant effects in spatial mortality vary between species and depends on environmental factors. When looking in more detail on effects occurring at the family and species level, we found that dead individuals of the Cistaceae species (H. marifolium and C. albidus) tended to be aggregated, mainly in plots without experimental rainfall treatment, whereas the locations of dead individuals of the

Fabaceae species (U. parviflorus and O. fruticosa) did not differ from the expectation of random mortality. We also found that positive density-dependent interactions were not significant under the experimental rainfall treatment and that significant negative interactions were delayed. In line with these results, De la Cruz et al. (2008) found that specific causes of mortality, related to potentially confounding factors such as environmental heterogeneity and drought, have the potential to alter spatial effects in the balance of competition and facilitation. Getzin et al. (2008) found, in accordance with predictions by Colasanti and Hunt (1997), evidence that the same forest community showed two sided scramble competition under homogeneous conditions and to one-sided contest competition under heterogeneous conditions.

We contrasted our data to the null model of random mortality and interpreted the departures of different test statistics from the null model in terms of biological effects. Clearly, the random mortality is a somewhat unrealistic model given our expectations, but its usefulness is grounded in its function as dividing hypothesis between positive and negative effects and it reveals the significance of the observed effects against purely stochastic effects. Null models that randomize the data structure are the best starting points in point pattern analysis (Illian et al. 2008), but subsequent studies may contrast alternative models to the data and try to identify the model that receives most support from the data. This approach is common in model fitting (e.g., Burnham and Anderson 2002) but less common in point pattern analysis (see, e.g., Illian et al. 2008: Chapter 7). More specific models to test would include, e.g., modeling directly density dependent mortality, as suggested by our analyses, or size dependent mortality.

The results of our study are consistent with density dependent effects mediated by facilitation when seedlings were small (i.e., first year) and by competition in later years of population dynamics. However, we cannot exclude the possibility that mortality might be related to other density-dependent mechanisms.

In general, inferring processes and mechanisms from observed patterns is a difficult task because substantially different processes may produce the same patterns (Levin 1992, Wiegand et al. 2003, Grimm et al. 2005). For example, a pathogen might cause similar spatial patterns in mortality if it kills in patches and/or spreads better to close neighbors. Microsite heterogeneity may also cause clustered patterns of dead individuals if certain sites do not support seedlings beyond a certain size and cause them to die off in patches and be spatially segregated from survivors that are located in more favorable microsites. He and Duncan (2000) showed that environmental factors might result in outcomes that appear to support density-dependent mortality even when such mortality may not be the driving mechanism.

The effect of pathogens, especially soil pathogens, could influence the spatial patterns of seedling mortality in temperate forest (Packer and Clay 2000, Abe et al. 2008), however, is unlikely to act in Mediterranean environments where the most relevant causes of plant deaths are summer drought and herbivory (De la Cruz et al. 2008). The effect of microsite heterogeneity is difficult to quantify. Although there is no apparent heterogeneity in environmental features at our study site (see De Luis et al. 2008a: Appendix 2), the fire created a mosaic of ash and nutrient accumulations that may have caused microsite differences and influenced the initial emergence process. However, while microsite heterogeneity may explain that plants died in clumps it is somewhat unlikely that clumps of seedlings were just located in unfavorable microsites and isolated survivors in favorable microsites. Furthermore, alternative processes causing the observed density dependent effects would not affect our general messages that the initial spatial segregation structure of seedlings after fire apparently prevented dominance of intraspecific interactions into a mature community (see De Luis et al. 2008b: Figs. 5 and 6), and more generally, that spatial structures can have a long-lasting impact on plant community dynamics.

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APPENDIX A

Details on methods of spatial pattern analysis (*Ecological Archives* E091-146-A1).

APPENDIX B

Univariate g_{11} function testing the aggregation of dead plants on F (fire) and F + R (erosion) treatments for each species of Cistaceae family (*Ecological Archives* E091-146-A2).

APPENDIX C

Univariate g_{11} function testing the aggregation of dead plants on F (fire) and F + R (erosion) treatments for each species of Fabaceae family (*Ecological Archives* E091-146-A3).

APPENDIX D

Bivariate g_{12} function testing the aggregation of dead and surviving plants on F (fire) and F + R (erosion) treatments for each species of Cistaceae family (*Ecological Archives* E091-146-A4).

APPENDIX E

Bivariate g_{12} function testing the aggregation of dead and surviving plants on F (fire) and F + R (erosion) treatments for each species of Fabaceae family (*Ecological Archives* E091-146-A5).

APPENDIX F

Bivariate difference test $g_{1,1+2} - g_{2,1+2}$ testing the density-dependent mortality on F (fire) and F + R (erosion) treatments for each species of Cistaceae family (*Ecological Archives* E091-146-A6).

APPENDIX G

Bivariate difference test $g_{1,1+2} - g_{2,1+2}$ testing the density-dependent mortality on F (fire) and F + R (erosion) treatments for each species of Fabaceae family (*Ecological Archives* E091-146-A7).

APPENDIX H

Total number of seedlings observed from year 0 to 9 after fire on different subplots (*Ecological Archives* E091-146-A8).