



Fire-mediated interactions between shrubs in a South American temperate savannah

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We examined spatial patterns of fire-caused mortality and after-fire establishment of two dominant shrub species, *Baccharis dracunculifolia* and *Eupatorium buniifolium* in a humid temperate South American savannah. Our objective was to determine whether fires mediate in interactions between these two species. After a natural fire burned a large tract of savannah, we established two plots (respectively 550 and 500 m²) within which we mapped all surviving and dead shrubs as well as all individuals of shrub species that recruited in the following year. We used techniques of point-pattern analysis to test specific null hypotheses about spatial associations in the distribution, mortality, and establishment of shrubs. Results support the notions that fire mediates interactions between these two species. Fire-caused death of *E. buniifolium* tended to occur selectively in the vicinities of *Baccharis* individuals, and recruitment of *B. dracunculifolia* tended to be concentrated in the places of dead shrubs. These responses, however, were contingent on local abundances of shrubs which depend in part from the recent fire history. Anthropogenic perturbation of the natural fire regime would have therefore distorted the role of fire mediated interactions as drivers of the dynamics of the vegetation of this temperate savannah.

Fires influence the structure and dynamics of savannah vegetation by differentially affecting the mortality and regeneration of component plant species (Walker and Noy-Meir 1982, Motzkin et al. 1993, Bond and van Wilgen 1996, Menges and Kimmich 1996, Lesica 1999, Platt 1999, Quintana-Ascencio and Menges 2000). Depending on fire characteristics such as season, intensity, or duration, different plant species exhibit different rates of survival to fire as well as different rates of post-fire recruitment via vegetative reproduction or seedling establishment (Platt et al. 1988, Sparks and Oechel 1993, Hodgkinson 1998, Hoffmann 1998, Núñez and Calvo 2000, Cirne and Scarano 2001, Menges and Deyrup 2001, Danthu et al. 2003).

In relation to these responses, shrubs from fire-prone savannahs may be grouped in two contrasting patterns of population dynamics in the presence of fire: sprouters and seeders (Keeley 1986, Pate et al. 1991, Bond and van Wilgen 1996). Sprouters survive fire in substantial proportions and regenerate mostly from vegetative tissues (Hodgkinson 1998, Vesik and Westoby 2004). In contrast, seeders are killed by fire and regenerate exclusively from seed (Moreno and Oechel 1992, Clemente et al. 2007). As a result of these differences, the abundances of sprouter and seeder shrub

species in fire-prone savannahs are driven by survival to fire and by post-fire recruitment, respectively.

Effects of fire on each shrub population may be influenced by other plant species present in the community. For example, sprouter shrub species with high survival to fire and rapid growth after fire may pre-empt space limiting the establishment of seedlings (Bond and Midgley 2001, Keith et al. 2007). In this case, seeder populations may develop a fugitive strategy, persisting and growing as a result from rapid seedling colonization of the spaces emptied by fire (Platt 1975, Tyler 1995, Eshel et al. 2000). Alternatively, seeders might locally affect fire characteristics in ways that increase the mortality of neighbour plants, and as a consequence, increase the amount of space open for seedling establishment (a killer strategy sensu Bond and Midgley 1995). Some species favoured by fire might even have characteristics that increase the probability of fire and consequently increase the mortality of their competing neighbours (pyrogenic species, Mutch 1970, Williamson and Black 1981, Platt et al. 1991, Bond and Midgley 1995, Kerr et al. 1999, Schwilk and Kerr 2002, Ojeda et al. 2005).

Fire-mediated interactions between species differentially favoured by fire are expected to determine specific spatial patterns of mortality and regeneration (Silver and Di Paolo 2006). First, if fire-caused mortality of sprouters were increased by shrubs of seeder species, it should be higher in areas where the density of seeders at the time of the fire is high. Second, if establishment of seeders after the fire were

limited by space pre-emption by sprouters, the density of seedlings of seeder species should be higher in emptied spaces and lower in the vicinities of resprouting shrubs (Bond and Midgley 1995, Kerr et al. 1999, Schwilk and Kerr 2002, Ojeda et al. 2005). Detailed analysis of spatial patterns of shrub mortality and regeneration should have the potential to pinpoint existing interactions between shrub species (Barot et al. 1999, de la Cruz et al. 2008).

In this study we examine spatial patterns of distribution, fire-caused mortality, and subsequent establishment of shrubs in a humid temperate palm-savannah site in Argentina. We search for evidence of fire-mediated interactions between the two dominant species in the shrub layer: *Baccharis dracunculifolia* and *Eupatorium buniifolium*. The first is a species of short-lived, single-stemmed shrubs that are readily killed by fire but establish abundantly from seed in recently burnt sites; the second is a species of long-lived, multi-stemmed shrubs with ability to survive and resprout vigorously after fires (Galíndez et al. 2009). Based on these general species traits, we hypothesized that space pre-emption by individuals of *E. buniifolium* resprouting after a fire might limit the seedling establishment of *B. dracunculifolia*, and that therefore *B. dracunculifolia* might benefit from locally increasing the mortality of *E. buniifolium* (Bond and Midgley 1995). After a natural fire burned a sizable track of savannah at El Palmar National Park in 2000, we set up two plots and mapped all dead and surviving shrubs as well as all new shrubs that recruited over the subsequent year. Based on these maps, we conducted detailed statistical tests aimed at establishing whether the spatial patterns of shrubs, fire-caused mortality, and post-fire establishment were consistent with our notion of fire-mediated interactions between the target species. To conduct our statistical tests, we constructed appropriate null models to be contrasted by means of simulation and resampling techniques (Barot et al. 1999, Wiegand and Moloney 2004, Getzin et al. 2006).

Methods

Study area

The study was conducted in the upland savannahs of the El Palmar National Park, Argentina (31°51–55'S, 58°13–18'W; 40–50 m a.s.l., Fig. 1). The climate in the park is temperate, with cool winters (mean temperature of the coldest month is 12°C) and warm summers (mean temperature of the warmest month is 26°C). Mean annual rainfall is about 1300 mm and water deficit occurs frequently in the summertime (Goveto 2005). The landscape of the park is occupied by a mosaic of vegetation types, including forests along rivers and streams, tall grasslands on humid alluvial plains, xeric steppes on sandy outcrops, and shrublands and palm savannahs dominated by *Butia yatay* on the uplands (Movia and Menville 1994).

The shrublands we studied occur on upland clayey soil with a characteristic surface undulation named gilgai (Corbett 1969, van der Sluijs 1971, Bertolini 1995). This microrelief is formed by micro-ridges and micro-valleys about 5 m wide with a difference in elevation of about 35 cm which are likely to affect the moisture regimes (Corbett 1969). Vegetation is dominated by shrubs of the genera *Baccharis*, *Eupatorium* and *Vernonia* and a diverse mixture of grasses (e.g. *Panicum prionitis*, *Paspalum quadrifarium*, *Andropogon lateralis*, *Axonopus suffultus*) whose biomass is higher in patches with low shrub cover.

The upland vegetation of El Palmar National Park has been historically subjected to natural fires. These fires occurred predominantly in the summertime affecting substantial areas within the park about once per decade. Since effective European settlement in the eighteen hundreds, however, the natural fire regime has been perturbed by cattle farming and, more recently, by conservation management (Goveto 2005).

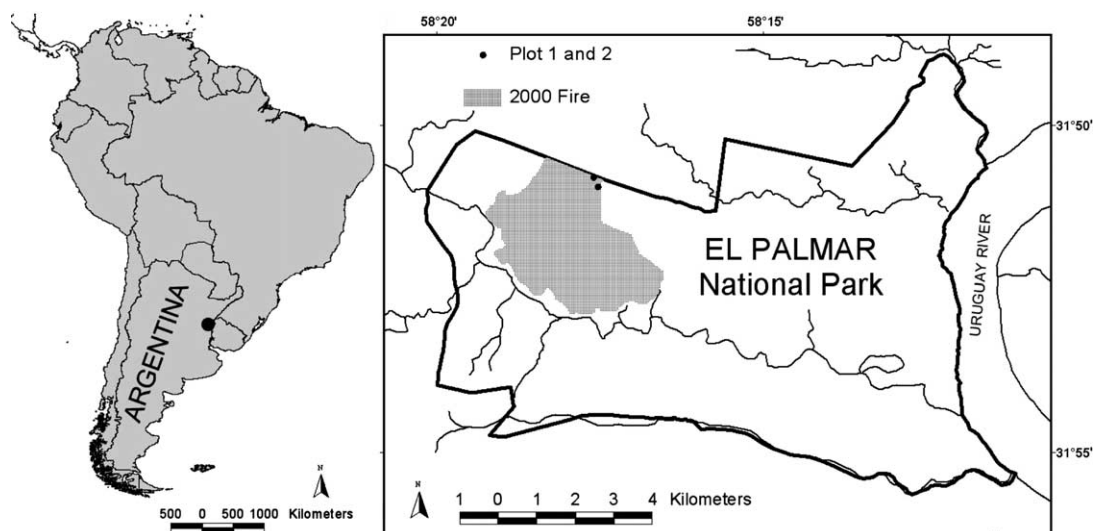


Figure 1. Geographic location of El Palmar National Park and detail of the 2000 fire and plots location.

Study species

Baccharis dracunculifolia and *Eupatorium buniifolium* are two species of Asteraceae shrubs widely distributed in Paraguay, Uruguay, southern Bolivia and Brazil, and north and central Argentina (Cabrera 1974). *Baccharis dracunculifolia* (hereafter *Baccharis*) are tall dioic shrubs (1.5–5 m) with a single main stem and superficial roots. These shrubs have a short life span, rarely exceeding seven years, and do not survive fire; *Baccharis* is a seeder, with reproductive and growth traits of an early successional species (Gomes and Fernandes 2002). *Eupatorium buniifolium* (hereafter *Eupatorium*) are medium-tall shrubs (0.8–3 m) usually with many stems and with deep roots. These shrubs may survive fire and sprout from a subterranean woody xylopod. Both *Baccharis* and *Eupatorium* bloom and disperse seeds in the fall. Dispersal units are free floating achenes.

Study plots

In January 2000, a natural fire spread over 1100 ha of shrublands and palm savannahs at El Palmar National Park. The fire occurred prior to the dispersal of seeds of the two shrub species we studied; as a consequence, these species did not produce seeds on that year within the area affected by the fire. For both species, seed banks remaining after the fire

contributed 70% of total seedling emergence, and newly dispersed seeds from not burned neighbouring sites contributed the remaining 30% (Galíndez 2008). A month after the fire, we established two plots in sites characterized as typical of the open palm savannah by a previous vegetation survey (Goveto 2005). Plot 1 (550 m²) was placed at a site affected by fire eight years before, and plot 2 (500 m²) at a site not affected by fire for at least 30 years. Both plots were located at upland positions within the landscape and had similar gently rolling microrelief.

Admittedly, the two plots examined in this study are not statistical replicates of the savannah sites from the El Palmar National Park. For this reason, data from these plots was not used to make statistical inference about the prevalence of the observed spatial patterns, or about their response to vegetation differences, across the landscape. Instead we tested spatial patterns within each plot to examine a priori hypotheses about interactions between shrubs.

Data recording

Within each plot, we identified and mapped all live and dead shrubs (Fig. 2a). Recognition of dead-shrub species was easy based on bark characteristics. We took the spatial arrangements of all living and dead individuals together as an estimate of the pre-fire arrangement (Kenkel 1988,

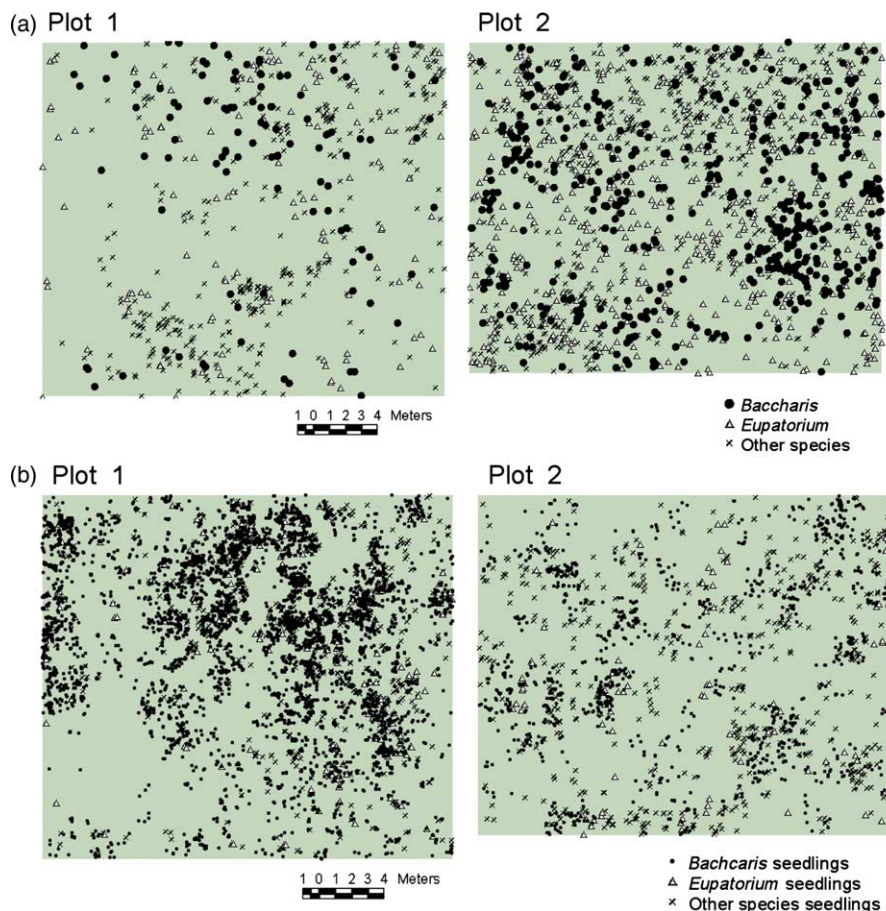


Figure 2. (a) General appearance of shrub spatial distribution in plot 1 and 2 before fire, drawn from live and dead shrub individuals, and (b) newly established individuals 1 year after fire.

Rebertus et al. 1989, Little 2002). All recorded individuals were considered as adults, as we assumed that any juveniles present before the fire were likely to be completely consumed by fire. For *Eupatorium*, we registered xylopod perimeter as a measure of pre-fire shrub size. One year later, we identified and mapped all newly established individuals of shrub species in the plots (Fig. 2b). In addition, we surveyed the topography of each plot by measuring the elevations on 2 × 1 m grids with a LEICA TCR 1105 Total Station. Based on our field observations, we deemed the 2 × 1 m grid appropriate to characterize the gentle undulation we observed. We used these measurements to interpolate an elevation value for the location of each mapped shrub (ArcView GIS 3.3-ESRI Inc. 2002).

Analysis

First order spatial patterns

To characterize the context in which we searched for evidence of fire mediated interactions between shrub species, we first examined coarse-scale associations between microrelief and shrub distributions and fire-caused mortality. We described the spatial associations between shrub locations and elevation by comparing densities of shrubs between the parts of the plots with elevation higher and lower than the median. Approximate 95% confidence limits for mean densities were calculated based on the Poisson distribution.

To examine the association between topography and mortality of shrubs, we classified the shrubs of each of two elevation classes using the median elevation as class limit, and then we constructed 95% binomial confidence intervals for the mortality rates in each class (Steel and Torrie 1980, p. 479). In addition, we plotted the cumulative frequency distributions of the observed elevations of dead and surviving *Eupatorium* shrubs, and we compared them with 95% envelopes for the frequencies expected under the hypothesis that mortality was equal at all locations in each

plot. To this end, we performed 1000 simulations in which we randomly labelled the shrubs as dead or alive with probability equal to the observed fire mortality. From these simulations, we produced 1000 cumulative frequency distributions of the elevations of dead and of surviving shrubs respectively, and obtained the 95% envelopes by eliminating the 2.5% higher and lower frequency values corresponding to each elevation. By maintaining the locations of the shrubs fixed in the simulations, we evaluated the association between shrub mortality and topography, avoiding spurious association due to density differences among portions of the plots with different elevations. In addition, we used a χ^2 -test to compare mortality rates between plots (Steel and Torrie 1980, p. 483).

Second order spatial patterns

We performed a series of spatial point-pattern analyses (Ripley 1981, Stoyan and Stoyan 1994, Diggle 2003) tailored to answer seven specific questions about spatial associations in the distribution, mortality, and establishment of shrubs in our mapped plots (Table 1). Questions 1 to 3 relate to the pre-fire patterns of shrub distribution, the scenarios for any fire-mediated interactions that might occur; questions 4 to 6 provide for the description of *Eupatorium* survival and mortality patterns which was necessary to infer about the notion that *Baccharis* may increase the proportion of *Eupatorium* killed by fire; and question 7 organizes the analysis of shrub recruitment pattern necessary to assess the possible influence of resprouting shrubs on seedling recruitment.

The analyses were based on the O-ring statistic $O(r)$, which measures the expected density of neighbouring points located at a distance r from an arbitrary point of a configuration under study (Getis and Franklin 1987, Penttinen et al. 1992, Condit et al. 2000, Wiegand and Moloney 2004). To examine the spatial association between

Table 1. Hypotheses tested to identify shrub interactions in response to fire disturbance.

	Null hypothesis	Null model	
<u>Pre-fire patterns</u>			
1	Were shrubs of each species and life stage aggregated or segregated in space?	No interactions among shrubs at small scales <5 m	Heterogeneous Poisson processes with 5 m moving window to estimate intensity
2	Were adult <i>Eupatorium</i> , <i>Baccharis</i> or other shrubs associated or segregated among them?	Independence between patterns	Toroidal shift null model
3	Were small <i>Eupatorium</i> individuals associated with <i>Baccharis</i> shrubs?	Random disposition of small <i>Eupatorium</i> individuals relative to <i>Baccharis</i>	Trivariate random labeling using novel test statistic
<u>Post-fire patterns</u>			
4	Did mortality and/or survival of <i>Eupatorium</i> occur in clumps?	Random mortality of <i>Eupatorium</i>	Univariate random labeling, univariate test statistic $g_{11}(r)$
5	Were dead and surviving <i>Eupatorium</i> associated or segregated from each other?	Random mortality of <i>Eupatorium</i>	Random labeling, bivariate test statistic $g_{12}(r)$
6	Did <i>Baccharis</i> (or other shrub species) increase <i>Eupatorium</i> mortality due to fire?	Random mortality of <i>Eupatorium</i>	Trivariate random labeling using novel test statistic
7	Were seedlings of <i>Eupatorium</i> or <i>Baccharis</i> that established one year after fire influenced by the patterns of adult shrubs?	Independence between seedling and adult patterns	Antecedent condition (shrub pattern fixed) and heterogeneous Poisson processes for seedling patterns

points of two classes 1 and 2, an O-ring statistic $O_{12}(r)$ measuring the density of points of class 2 located at distance r from an arbitrary point of class 1 is estimated as:

$$\hat{O}_{12}^w(r) = \frac{\sum_{i=1}^{n_1} \text{points}_2[R_i^w(r)]}{\sum_{i=1}^{n_1} \text{area}[R_i^w(r)]} \quad (1)$$

where $\text{points}_2[\]$ is an operator that counts the observed number of points of class 2 in a ring, $R_i^w(r)$, with radius r and width w centered in the i th point of class 1, $\text{area}[\]$ is an operator that counts the area of the same ring $R_i^w(r)$, and n_1 is the total number of class 1 points in the plot (Wiegand and Moloney 2004). For analyzing a univariate pattern, class 2 is the same as class 1. Note that the O-ring statistic is closely related to the intensity-normalized pair-correlation function $g_{ij}(r)$ (Stoyan and Stoyan 1994) which satisfies

$$O_{12}(r) = \lambda_2 g_{12}(r) \quad (2)$$

where λ_2 is the average density of points of class 2.

O-ring statistics and pair-correlation functions were computed for appropriate selections of points in our maps (i.e. surviving and dead individuals of the two species and seedlings) required to respond to our questions. Departures of the observed $\hat{O}(r)$ from expectations under the null models underlying our hypotheses were tested by means of Monte Carlo simulations performed to generate specific probability distributions of the corresponding $O(r)$ under each null hypothesis. Observed $\hat{O}(r)$ below the percentile 2.5 of the corresponding null distribution were interpreted as significant segregation between the corresponding point classes at distance r , while observed $\hat{O}(r)$ above the percentile 97.5 of the null distribution were interpreted as significant aggregation between the corresponding point classes at distance r . The selected percentiles do not provide an accurate measure of the significance level of the tests because type I error inflation may occur due to simultaneous inference (Loosmore and Ford 2006).

To remove first order patterns (i.e. density trends across the plots or very large clumps) which could obscure the effects of interactions among shrubs (Wiegand and Moloney 2004), the $O(r)$ were simulated under null models based on heterogeneous Poisson processes maintaining the intensity of the patterns at larger scales but removing spatial structures at smaller scales (Wiegand and Moloney 2004, Wiegand et al. 2007a, 2007b). To this end, the heterogeneous Poisson process was applied randomizing the points based on their density in a circular moving window with radius $R = 5$ m rather than on the mean density in the whole plot, as done for the homogeneous Poisson process (Wiegand and Moloney 2004, Getzin et al. 2006). This restricts our second-order pattern interpretations to interactions between shrubs occurring at distances 5 m or less (Wiegand and Moloney 2004). The 5 m radius was subjectively adopted based on the lengths of the plots (20 to 25 m) and the scale at which shrub density patterns within them appeared to be heterogeneous (Wiegand and Moloney 2004). However, because neither *Baccharis* nor *Eupatorium* have widely spread lateral roots (Biganzoli unpubl.), direct shrub-to-shrub interactions between in-

dividuals of these species separated more than 5 m would rarely be important.

Calculations were done with the software Programita (<www.thorsten-wiegand.de/towi_programita.html>, Wiegand and Moloney 2004). This software uses of a grid-based approach to estimate the O-ring statistic for the observed and simulated patterns and corrects edge effects by weighting the proportion of the ring area lying inside the plot. We used a grid of 0.25×0.25 m cells and rings 0.25 m wide.

Each of the questions in which we organized the study of second order patterns was addressed with a specific analysis defined by a selection of points from the maps and a null model corresponding to a particular hypothesis of no interaction (Barot et al. 1999, Goreaud and Pélissier 2003, Wiegand and Moloney 2004).

Analysis 1. Were shrubs of each species and life stage aggregated or segregated in space?

To answer this question, we analyzed the univariate spatial patterns of shrub distribution. We used a heterogeneous Poisson process as the null model accounting for density differences within the plot to reveal spatial interactions between shrubs of the same type.

Analysis 2. Were adult shrubs of different species (*Eupatorium*, *Baccharis* or other species) associated to each other, segregated from each other or independently distributed?

We analyzed the bivariate spatial patterns of shrub distribution using the toroidal shift null model (Dixon 2002, Wiegand and Moloney 2004) to test for independence between the patterns of two different species. In this null model, the spatial relationship among points is preserved within each species, but the pattern of one of them moves randomly relative to the other in any simulation under the null model.

Analysis 3. Were small *Eupatorium* individuals associated with *Baccharis* shrubs?

To answer this question, we developed a new test statistic to analyse three patterns. The first pattern was the spatial pattern of *Baccharis* shrubs (i.e. an 'antecedent pattern'), and the other two patterns corresponded to the marked pattern of *Eupatorium* (i.e. 1: small, 2: not small). The procedure to test whether the mark 'small' on *Eupatorium* shrubs was associated to the presence of neighboring *Baccharis* shrubs was the following: We visited all *Baccharis* shrubs i and determined the number of small *Eupatorium* located at distance r from each one [$=n_{i,1}(r)$] as well as the number of cells located at distance r which hosted *Eupatorium* shrubs [$=a_i(r)$]. With these counts we calculated the following statistic,

$$p_{a,1}(r) = \frac{\sum_i n_{i,1}(r)}{\sum_i a_i(r)} \quad (3)$$

In our case, the cell size was small enough not to contain more than one *Eupatorium* shrub and, therefore, this statistic is a mark-connection function (Illian et al. 2008). The mark-connection function $p_{a,1}(r)$ describes

the conditional probability that a randomly chosen *Eupatorium* shrub located at distance r from a *Baccharis* shrub is small. The test was based on the null model produced by labeling at random all *Eupatorium* shrubs with either the 'small' mark or the 'not small' mark keeping the original proportions of small and not small. de la Cruz et al. (2008) developed a similar test statistic for this null model.

Analysis 4. Were the mortality of *Eupatorium* caused by fire and/or the survival of *Eupatorium* to fire clumped?

We approached this question within the framework of marked point processes (Stoyan and Stoyan 1994). Here the mark of the pattern of *Eupatorium* is the property 'dead' and the essential question is whether or not the process which assigned the label dead to the shrubs acted randomly over the shrub pattern (i.e. random mortality; Kenkel 1988). Dead *Eupatorium* shrubs were labelled as class 1 and surviving shrubs the class 2. We used the random labelling null model (Dixon 2002, Goreaud and Pélissier 2003, Wiegand and Moloney 2004) which randomly assigns the label dead to *Eupatorium* shrubs, maintaining the observed number of dead individuals. We calculated both, the pair-correlation function of dead *Eupatorium* shrubs (g_{11}) and that of surviving shrubs (g_{22}) as test statistics to find out if dead or surviving shrubs, respectively, were aggregated conditionally on the pre-fire pattern of *Eupatorium*.

Analysis 5. Were dead and surviving *Eupatorium* associated or segregated from each other?

To answer this question we used, as in Analysis 4, the random labelling null model but we computed the bivariate pair-correlation functions g_{12} and g_{21} as the test statistics (Goreaud and Pélissier 2003).

Analysis 6. Was the mortality of *Eupatorium* caused by fire higher in the vicinity of *Baccharis* shrubs (or of other shrub species)?

To answer this question, we used the new test statistic for the examination of three patterns described for Analysis 3. In this case, the first pattern is the spatial pattern of *Baccharis* shrubs (i.e. an 'antecedent pattern') and the other two patterns are given by the marked pattern of *Eupatorium* (i.e. 1: dead, 2: surviving). We tested if the mark 'dead' of

Eupatorium shrubs was associated to the presence of neighboring *Baccharis* shrubs. The null model was again random labeling of the mark 'dead', distributed over the observed locations of the *Eupatorium* shrubs.

Analysis 7. Were seedlings of *Eupatorium* or *Baccharis* that established one year after fire influenced by the patterns of adult shrubs?

In these cases, we test if seedling establishment showed a positive or negative association to adult shrub locations. We test this with an antecedent condition null model, which retains the locations of the adult shrubs fixed and randomize the locations of the seedlings as a heterogeneous Poisson process.

Results

Pre-fire scenarios plot 1

Before the January 2000 fire, total density of shrubs in plot 1 was 1.12 ind m^{-2} . *Eupatorium* accounted for 19% of the shrubs (0.21 ind m^{-2}), *Baccharis* accounted for 18% of the shrubs (0.20 ind m^{-2}), and other shrub species (mostly *Vernonia nitidula*) accounted for the remaining 63% (Table 2).

The shrubs were distributed over the entire plot (Fig. 3a). Individuals of each species exhibited some significant first-order patterns of distribution associated with microrelief. On the relatively elevated portions of the plot, the density of *Eupatorium* was slightly higher and the density of *Baccharis* was substantially higher than on the relatively depressed portions (Fig. 3b–c). Among other shrub species, the density of *Vernonia nitidula* was substantially higher on the lower portions of the microrelief, whereas the collective density of the remaining species was similar on the elevated and depressed portions (Fig. 3d).

Analysis of the second-order spatial patterns revealed that, within portions with relatively homogeneous density, shrubs of each species tended to form clusters. *Eupatorium* shrubs were aggregated in clusters about 1 m diameter, *Baccharis* shrubs in clusters about 0.5 m diameter, and shrubs of other species (mostly *Vernonia nitidula*) were aggregated in clusters about 5 m diameter (Table 1 question 1; Table 3 lines 1, 2 and 3). However, we did not find evidence for association

Table 2. Absolute and relative number of mapped shrubs before and after the fire in January 2000 at El Palmar National Park.

	Before fire		After fire				
			Dead	Resprouted	Seedlings		
Plot 1 (550 m ²)							
<i>Eupatorium buniifolium</i>	118	19.1%	15	12.7%	103	274	4.9%
<i>Baccharis dracunculifolia</i>	112	18.1%	112	100%	0	4669	83.3%
Other shrub species ¹	388	62.8%	10	2.6%	378	661	11.8%
Total	618		137	22.2%	481	5604	
Plot 2 (500 m ²)							
<i>Eupatorium buniifolium</i>	537	32.1%	202	37.6%	335	92	4.8%
<i>Baccharis dracunculifolia</i>	554	33.1%	554	100%	0	1129	58.4%
Other shrub species ¹	583	34.8%	148	25.4%	435	712	36.8%
Total	1674		904	54%	770	1933	

¹*Baccharis articulata*, *B. medulosa*, *B. pingraea*, *B. spicata*, *B. trimera*, *Heimia salicifolia*, *Vernonia nitidula*.

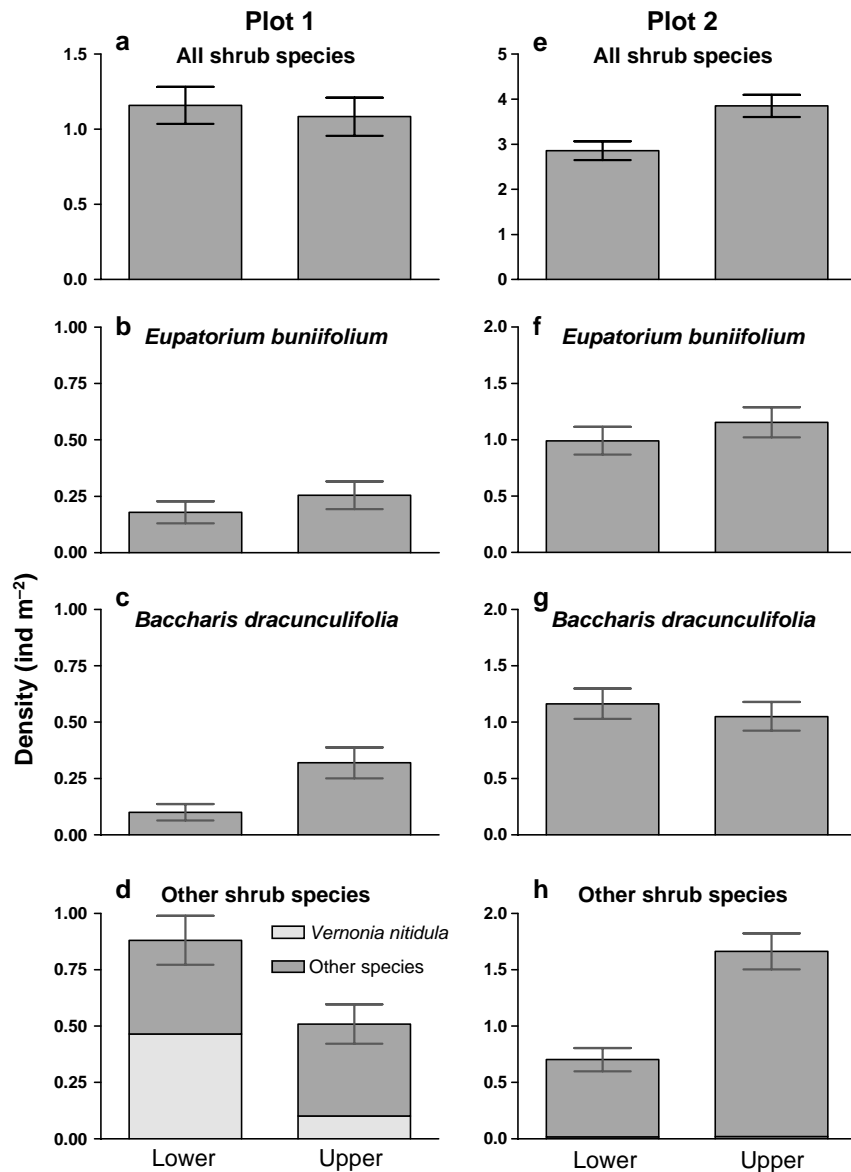


Figure 3. Shrub species density distribution on relative lower and upper portions of the plots. Bars represent 95% confidence intervals assuming Poisson distribution for density. Note differences in density axes among plots.

(either aggregation or segregation) between shrubs of different species (Table 1 question 2; Table 3 lines 4, 5 and 6). When analyzing smaller individuals of *Eupatorium* (crown diameter <10 cm) we found that they had no spatial association with *Baccharis* shrubs (Table 1 question 3; Table 3 line 7).

Pre-fire scenarios plot 2

Before the fire of January 2000, total density of shrubs in plot 2 was 3.35 ind m^{-2} . *Eupatorium* accounted for 32% of all shrubs (1.07 ind m^{-2}), *Baccharis* accounted for 33% (1.11 ind m^{-2}), and other shrub species accounted for the remaining 35% (Table 2).

In this higher density plot the shrubs were distributed over the entire plot with higher density on the relatively elevated portions (Fig. 3e). As in plot 1, the density of *Eupatorium* was

slightly higher on the relatively upper portions (Fig. 3f). In contrast, in this plot the density of *Baccharis* did not differ significantly between elevated and depressed portions of the microrelief (Fig. 3g). Density of other shrub species (mostly *Baccharis medullosa* and *B. trimera*) tended to be concentrated on the upper portions of the plot (Fig. 3h).

Analysis of the second-order spatial pattern revealed that individuals of each shrub species tended to form clusters. *Eupatorium* shrubs were aggregated in clusters about 1 m diameter, *Baccharis* shrubs in clusters about 4 m diameter, and shrubs of other species were aggregated in clusters about 8 m diameter (Table 1 question 1; Table 3 lines 1, 2 and 3). As in plot 1, our analysis revealed no patterns of association (either aggregation or segregation) between shrubs of different species (Table 1 question 2; Table 3 lines 4, 5 and 6). Particular focus on smaller individuals of *Eupatorium* (crown diameter <10 cm) shows that they had

Table 3. Results of the analysis of spatial pattern of *Baccharis dracunculifolia* (BD) and *Eupatorium buniifolium* (EB) before and after the fire. n = number of adult shrub individuals or seedlings in each analysis. Null models: HP: univariate heterogeneous Poisson process; HP2: heterogeneous Poisson for pattern 2 and pattern 1 fixed; RL: random labelling. Univariate patterns: a aggregated pattern, r: regular pattern, -: no second order effects; bivariate patterns: A: association between patterns, S: segregation between patterns, -: no second-order effects.

		Null model	Plot 1							Plot 2							
			n	Radius						n	Radius						
				0	1	2	3	4	5 m		0	1	2	3	4	5 m	
<u>Before the fire</u>																	
1	EB	HP	118	a	a	-	-	-	-	-	537	a	a	-	-	-	-
2	BD	HP	112	a	-	-	-	-	-	-	554	a	a	a	a	-	-
3	Other	HP	388	a	a	a	a	a	a	-	583	a	a	a	a	a	-
4	BD – EB	independence	112–118	-	-	-	-	-	-	-	554–537	-	-	-	-	-	-
5	BD – others	independence	112–388	-	-	-	-	-	-	-	554–583	-	-	-	-	-	-
6	EB – others	independence	118–388	-	-	-	-	-	-	-	537–583	-	-	-	-	-	-
7	EB small – BD	trivariate RL	71 (118)–112	-	-	-	-	-	-	-	391 (537)–554	-	-	-	-	-	-
<u>Immediately after the fire</u>																	
8	EB surviving (i.e. resprouted)	RL, g22	103	a	a	-	-	-	-	-	335	a	a	a	a	-	-
9	EB dead	RL, g11	15	-	-	-	-	-	-	-	202	a	a	-	-	-	-
10	EB dead – BD	trivariate RL	15 (118)–112	-	-	-	-	-	-	-	202 (537)–554	-	A	A	A	-	-
11	EB dead – surviving	RL, g12	15–103	-	-	-	-	-	-	-	202–335	S	S	S	S	-	-
12	EB dead – others	trivariate RL	15 (118)–388	-	-	-	-	-	-	-	202 (537)–583	S	S	S	S	-	-
<u>1 year after the fire</u>																	
13	BD seedlings	HP	4669	a	a	a	a	a	a	-	1129	a	a	a	a	-	-
14	BD seedlings – BD dead	HP2	4669–112	A	A	A	A	A	A	-	1129–554	-	-	-	-	-	-
15	BD seedlings – EB resprouted	HP2	4669–102	S	-	A	A	A	A	-	1129–335	-	-	-	-	-	-
16	BD seedlings – EB dead	HP2	4669–15	-	-	-	S	S	-	-	1129–202	A	A	A	A	-	-
17	BD seedlings – other resprouted	HP2	4669–353	S	S	S	S	-	-	-	1129–435	-	S	-	-	-	-
18	BD seedlings – other dead	HP2	4669–10	-	-	-	-	-	-	-	1129–148	-	-	-	-	A	A
19	EB seedlings	HP	274	a	a	a	a	a	-	-	92	a	a	a	a	-	-
20	EB seedlings – BD dead	HP2	274–112	A	A	-	-	-	-	-	92–554	-	-	-	-	-	-
21	EB seedlings – EB resprouted	HP2	274–102	-	-	-	-	-	-	-	92–335	-	-	-	-	-	-
22	EB seedlings – EB dead	HP2	274–15	-	-	-	-	-	-	-	92–202	-	A	-	-	-	-
23	EB seedlings – other resprouted	HP2	274–353	-	-	-	-	-	-	-	92–435	-	-	-	-	-	-
24	EB seedlings – other dead	HP2	274–10	-	-	-	S	S	-	-	92–148	-	-	-	-	-	-
25	BD seedlings – EB seedlings	independence	4669–274	-	-	-	-	-	-	-	1129–92	A	A	A	A	-	-

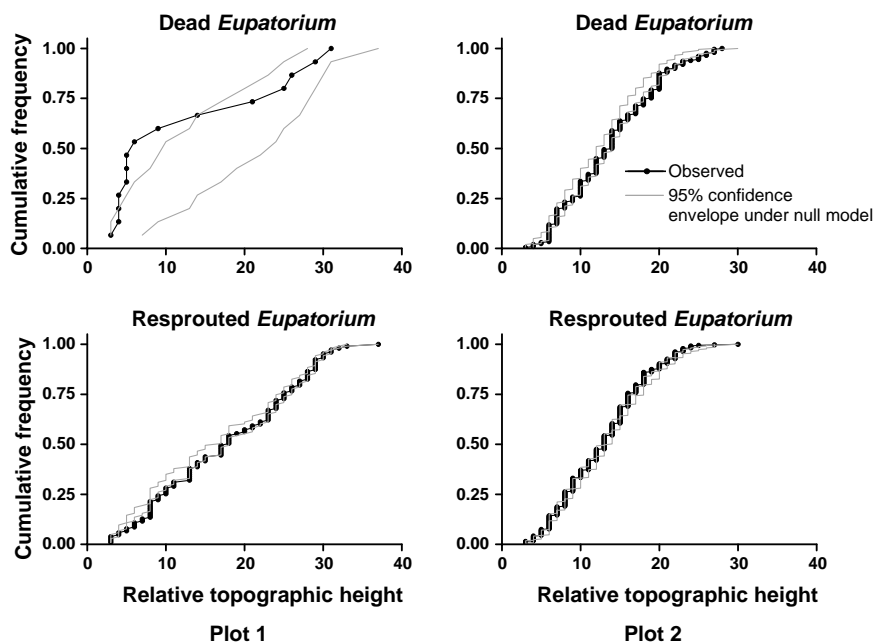


Figure 4. Relationship between *Eupatorium* mortality and microrelief. Black lines represent cumulative frequency distribution of dead or resprouted *Eupatorium* shrubs. Gray lines represent a 95% confidence envelope after 1000 random realizations of mortality events.

no spatial association with *Baccharis* shrubs (Table 1 question 3; Table 3 line 7).

Mortality patterns

Plot 1

The fire killed all *Baccharis* shrubs, 12.7% of the *Eupatorium* shrubs and 2.6% of the shrubs of other species (Table 2). The total number of dead *Eupatorium* shrubs was 15, among which 9 were located at relative elevations <10 cm. This number of dead individuals in depressed portions is significantly higher than the number expected under a random selection of 15 individuals from the population present at the time of the fire (Fig. 4).

Analysis of second-order spatial patterns of mortality revealed that the pre-fire clustering of *Eupatorium* shrubs persisted after the fire, while there was neither significant clustering nor significant segregation among the few dead *Eupatorium* (Table 1 question 4; Table 3 lines 8 and 9). In addition, no spatial association was detected between dead *Eupatorium* and dead *Baccharis*, dead and surviving *Eupatorium*, or dead *Eupatorium* and shrubs of other species (Table 1 questions 5 and 6; Table 3 lines 10, 11 and 12).

Plot 2

The fire caused 100% mortality of *Baccharis*, 37.6% mortality of *Eupatorium*, and 25.4% mortality of other shrub species (Table 2). Both the mortality of *Eupatorium* and the mortality of other species were significantly higher than in plot 1 ($\chi^2_{1\text{gl}}=27.08$, $p<0.0001$; $\chi^2_{1\text{gl}}=88.95$, $p<0.0001$). Higher mortality of *Eupatorium* in this plot resulted from substantially higher mortality of smaller individuals (Fig. 5).

Mortality of *Eupatorium* occurred throughout the entire plot and not related with microrelief (Fig. 4). While surviving *Eupatorium* were aggregated in clusters about

3.5 m diameter, dead *Eupatorium* individuals appeared significantly aggregated in clusters about 1 m diameter (Table 1 question 4; Table 3 lines 8 and 9). Dead *Eupatorium* appeared significantly associated to dead *Baccharis* at distances between 0.25 and 1 m, and significantly segregated from surviving *Eupatorium* at distances up to 1.25 m and from shrubs of other species at distances up to 1 m (Table 1 questions 5 and 6; Table 3 lines 10, 11 and 12).

Summarizing, while no *Baccharis* shrub survived the fire in either plot, the fire produced higher mortality of *Eupatorium* in the high density plot 2 than in the low density plot 1 as a result of substantially increased mortality of small individuals. In the higher-density plot 2, *Eupatorium* mortality was higher in the vicinities of (killed) *Baccharis* individuals and lower in the vicinities of surviving shrubs than in other places. In the lower-density plot 1, mortality of *Eupatorium* was somehow more severe in the relatively depressed than in the upper portions of the micro-relief.

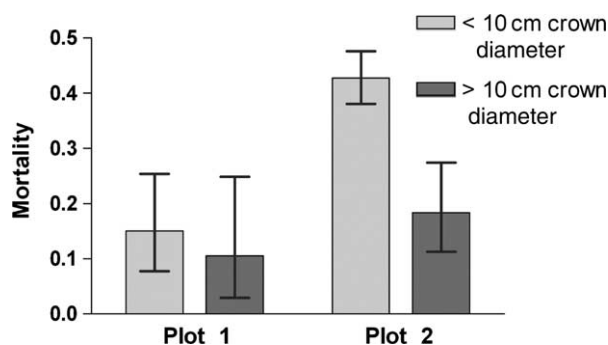


Figure 5. *Eupatorium* mortality for two size classes. Bars represent 95% binomial confidence intervals.

Establishment patterns

Plot 1

One year after the fire, we found 5604 new individuals of shrub species (10.2 ind m^{-2}) among which 83.3% were *Baccharis* seedlings and 4.9% were *Eupatorium* seedlings (Table 2). Recruits of these species established throughout the plot with higher density on the relatively elevated portions of the microrelief than on the lower ones (Fig. 6a).

Analysis of second-order patterns indicated that *Baccharis* seedlings appeared aggregated in very large clusters about 9.5 m diameter (Table 1 question 1; Table 3 line 13). These seedlings appeared significantly associated to the locations of *Baccharis* killed by the fire up to distances of 4.5 m, and significantly segregated from resprouting *Eupatorium*, up to distances of 0.25 m, and from other resprouting shrubs up to distances of 2 m (Table 1 question 7; Table 3 lines 14, 15 and 17). Seedlings of *Eupatorium* appeared aggregated in clusters about 4.5 m diameter with no significant spatial association to *Baccharis* seedlings (Table 1 question 2; Table 3 lines 19 and 25). These seedlings appeared associated with locations occupied by *Baccharis* before the fire (Table 1 question 7; Table 3 line 20).

Plot 2

Establishment observed in this plot was 2.5 times lower than in plot 1. One year after the fire, we found 1933 new individuals including 58% *Baccharis* and 5% *Eupatorium* (Table 2). Recruits of these species established throughout the plot with slightly higher density on the relatively elevated portions of the microrelief (Fig. 6b).

For both species, recruits appeared in clusters about 3 m diameter distributed with relative regularity throughout the plot (Table 1 question 1; Table 3 lines 13 and 19). *Baccharis* and *Eupatorium* seedlings appeared significantly associated at distances up to 1.5 m (Table 1 question 2; Table 3 line 25). In addition, seedlings of *Baccharis* were significantly associated to locations occupied by *Eupatorium* killed by the fire at distances up to 2.75 m (Table 1 question 7; Table 3 line 16). *Eupatorium* seedlings were not significantly associated with the locations of adult shrubs of any species (Table 1 question 7; Table 3 lines 20–24).

Summarizing, one year after the fire, establishment of shrub species was much higher in the plot that had lower shrub density prior to the fire. In both plots, observed establishment of either species occurred in clusters. *Baccharis* recruits appeared in both plots significantly associated

with areas about shrubs killed by the fire (either conspecifics or *Eupatorium*). In the plot where recruitment was more abundant, *Baccharis* seedlings appeared significantly segregated from locations of resprouting shrubs, and *Eupatorium* seedlings appeared associated with locations of *Baccharis* killed by the fire.

Discussion

According to our analysis of the pre-fire shrub spatial pattern, individuals of *Baccharis* and *Eupatorium* were exposed to a variety of neighbourhood configurations at the time of the fire. Plot 1 had low total shrub density and less than 50% *Baccharis* and *Eupatorium* shrubs, whereas plot 2 had high total shrub density and about two thirds of its shrubs from either of these two species. In the low density plot 1, *Baccharis* shrubs formed very small clusters and were associated to the gilgai micro-ridges, whereas in the high density plot 2, individuals of this species formed relatively large clusters and were not significantly associated with microrelief. *Eupatorium* individuals, in contrast, formed small clusters in the two plots and were slightly more frequent on the upper than on the lower portions of the microrelief. In none of the plots were there any detectable patterns of aggregation or segregation between *Baccharis* and *Eupatorium* or between these species and the remaining shrubs. The resulting variety of neighbourhood configurations to which different individual shrubs were exposed in our two plots was sufficient to produce second-order patterns of fire mortality and subsequent establishment of shrubs which can be interpreted as resulting from interactions between species.

Our data support the notion that *Baccharis* may increase the proportion of *Eupatorium* shrubs killed by fire (Bond and Midgley 1995). This effect was noticeable where the density of shrubs was high and, therefore, a substantial proportion of *Eupatorium* individuals occurred in close proximity to *Baccharis*. In plot 1, where the collective density of *Baccharis* and *Eupatorium* was low (\approx one individual every 2.4 m^2), the fire killed only a few *Eupatorium* shrubs which were at the lower portions of the plot at locations having no detectable association with *Baccharis* or any other shrubs. In this plot, the failure to detect spatial associations between *Eupatorium* mortality and the distribution of other shrubs may result from the small number of dead *Eupatorium* reducing the power of

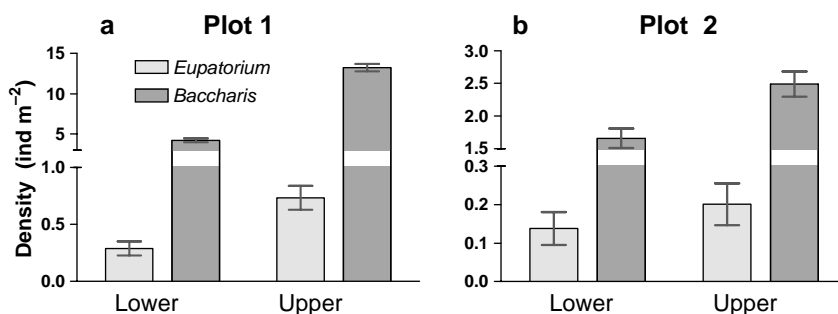


Figure 6. Seedlings density distribution on relative lower and upper portions of the plots. Bars represent 95% confidence intervals assuming Poisson distribution for density. Note differences in density axes among plots.

our test or, alternatively, from wide spacing between shrubs. In contrast, in plot 2, where there was one individual of either species every 0.5 m² (a density 4.5 times higher), the fire killed three times more *Eupatorium* shrubs than in plot 1. This increased fire mortality affected especially the small individuals (crown diameter <10 cm), and tended to occur selectively away from clumps of surviving *Eupatorium* or other species but in the vicinities of *Baccharis* individuals. Apparently, a large number of relatively small *Eupatorium* in plot 2 were 'within reach' of any effects that *Baccharis* might have had that resulted in increased mortality. The large proportion of small *Eupatorium* that were closely exposed to *Baccharis* was a simple result of high density, as small *Eupatorium* had no detectable spatial association with *Baccharis* before the fire.

The difference between plots in overall *Eupatorium* mortality was associated with differences in both *Eupatorium* population structure and fire lethality to individual shrubs. The proportion of small *Eupatorium* individuals, which sustained the largest mortality, was somewhat larger in plot 2 (73% vs 60% in plot 1). This difference, however, does not fully account for the overall mortality difference we observed; as individuals in the small size class sustained much higher mortality in the high-density plot 2 (44% vs 15% in plot 1). Spatial patterns observed in plot 2 suggest that high fire lethality was associated with high density of *Baccharis* as mortality of *Eupatorium* was higher near *Baccharis* and lower near surviving *Eupatorium* or other shrubs (Rebertus et al. 1989, Platt et al. 1991).

Local differences in *Eupatorium* mortality between patches located near *Baccharis* and patches located near surviving *Eupatorium* or other species might reflect patterns of shrub susceptibility to fire and/or patterns of fire behaviour (Grace and Platt 1995, van Mantgem and Schwartz 2004, Keeley 2006). Differential susceptibility might result from differences between patches in pathogen or parasite damage or in the competition exerted by neighbouring shrubs. These biotic interactions could affect the development of underground surviving structures of the shrubs. Increased lethality of fire might in addition result from characteristics of the fire itself related to the amount and the properties of the accumulated fuel (Thaxton and Platt 2006). In the vegetation we studied, humidity of the accumulated plant biomass after a long drought is likely to differ between patches dominated by *Eupatorium* or *Baccharis* because the roots of *Eupatorium* take water from deeper soil layers than those of *Baccharis*. This might cause the fire to be either hotter or longer persistent in the vicinities of *Baccharis* than in the vicinities of *Eupatorium* (Platt et al. 1991).

Abundances of *Baccharis* and *Eupatorium* recruitment after the fire are consistent with general responses expected from seeders and sprouters (Lamont and Wiens 2003). In our plots, post-fire seedling recruitment was at least one order of magnitude more abundant for *Baccharis* than for *Eupatorium*. Responses similar to these were observed to occur in different fire-frequented ecosystems as a result of differences in either seed set or seedling establishment rate between seeders and sprouters (Keeley and Zedler 1978, Enright and Lamont 1989, Benwell 1998). Because, in our study system, seed-set is not lower for *Eupatorium* than for *Baccharis* (Biganzoli et al. unpubl.), recruitment differences

between these shrub-species would be caused by different rates of seedling establishment.

Our analysis suggests that the establishment of shrub seedlings might have been limited by extant surviving shrubs. In plot 2, where the density of live shrubs was still relatively high after the fire (\approx one surviving shrub every 0.6 m²), post-fire establishment of shrub species was relatively infrequent (3.87 seedlings m⁻²). In contrast, in plot 1, where the density of surviving shrubs was lower (\approx one shrub every 1.1 m²), post-fire seedling recruitment was 2.6 times more abundant. Admittedly, these differences between plots might reflect differences in seed density and/or seed survival to fire in addition to any effects of space pre-emption by resprouting shrubs (Moreno and Oechel 1992, Tyler 1995). However, data on seed set indicate that total production of *Baccharis* and *Eupatorium* seeds increases with shrub density (Biganzoli et al. unpubl.). In addition, our second-order spatial pattern analyses contain suggestions that surviving shrubs interfered with seedling establishment.

For *Baccharis*, spatial patterns of seedling density one year after the fire were reasonably consistent with the notion that seedling recruitment was little affected by seed mortality produced by fire but was enhanced by the death of shrubs. In none of the plots were *Baccharis* seedlings segregated from the locations of dead shrubs, the spots where the fire might have attained higher intensity and potential for killing seeds (Tyler 1995). In contrast, in plot 1, where *Baccharis* recruitment was very abundant, seedlings were significantly concentrated in the places previously occupied by *Baccharis* shrubs and segregated from the vicinities of shrubs that resprouted after the fire (Ne'eman et al. 1992, Pausas et al. 2003). In this plot, *Baccharis* seedlings were not significantly associated with the locations of *Eupatorium* killed by the fire, most probably because there were too few of the latter for the corresponding test to attain sufficient power. In plot 2, where *Baccharis* recruitment was lower but many *Eupatorium* were killed by the fire, *Baccharis* seedlings were not significantly segregated from surviving shrubs but they were significantly concentrated in the locations of dead *Eupatorium*.

Post-fire recruitment of *Eupatorium* may also respond to some extent to space opened by the disturbance. In plot 1, *Eupatorium* seedlings established one year after the fire were significantly concentrated in the places of killed *Baccharis*. A similar pattern was found for the post-fire recruitment of *Rhus coriaria*, a resprouter species living in Mediterranean pine forests (Ne'eman et al. 1992). Other spatial associations between the recruitment of *Eupatorium* and dead or surviving shrubs did not emerge from our analysis possibly as a result of a stronger signal of dispersal patterns producing a clumped distribution of seedlings.

Conclusions

The results of our study are consistent with the notion that fire mediates in interactions between *Baccharis* and *Eupatorium*, a seeder and a sprouter species respectively. *Baccharis* increases fire-produced mortality of *Eupatorium*, provided its density is sufficient for a substantial proportion of the *Eupatorium* shrubs to occur in close contact with

Baccharis individuals (Bond and Midgley 1995). This 'killer' effect may substantially increase the amount of space available for post-fire regeneration of *Baccharis*. The effects of these interactions on vegetation dynamics are likely to depend on quite specific details of the structure of the community at the time fires occur, which result, in turn, from the matching between the fire regime and the times involved in the characteristic life cycles of these seeder and sprouter species. In the savannahs of the El Palmar National Park, fire-mediated interactions between shrubs may have lost relative importance as drivers of vegetation structure and dynamics as a result of anthropogenic perturbation of the natural fire regime.

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