

# Assessing the impact of fire on the spatial distribution of *Larrea tridentata* in the Sonoran Desert, USA

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**Abstract** In southwestern American deserts, fire has been historically uncommon because of insufficient continuity of fuel for spreading. However, deserts have been invaded by exotic species that now connect the empty space between shrubs to carry fire. We hypothesized that fire would change the spatial distribution of surviving *Larrea tridentata* shrubs. We established two study plots, one each in a burned and unburned area, and recorded location and living status of all shrubs. We performed univariate and bivariate point pattern analyses to characterize the impact of fire on the overall distribution of shrubs. Additionally, we used a simple wildfire model to determine how close we could come to reconstructing the observed spatial pattern of living and dead shrubs. We found a hyper-dispersed pattern of shrubs at finer scales and a random pattern at broader scales for both the unburned plot and for the living and dead shrubs combined in the burned plot, the latter providing an approximation of the pre-burn distribution of shrubs. After fire, living shrubs showed a clustered pattern at scales >2.5 m, whereas dead shrubs were randomly distributed, indicating that fire caused a change in the spatial pattern of the surviving shrubs. The fire model was able to

partially reconstruct the spatial pattern of *Larrea*, but created a more clustered distribution for both living and dead shrubs. Our study reinforces the key role of fire in altering landscapes that had not been habituated to fire, and suggests the existence of potential cascading effects across the entire plant community.

**Keywords** Spatial pattern · Desert shrublands · Pair correlation function (PCF) · Point pattern analysis · Ecological fire effects

## Introduction

Fire is an important disturbance in many ecosystems worldwide. It can alter vegetation structure, soil properties, and other ecosystem functions (Sugihara et al. 2006; Whelan 1995). To date, a great deal of the literature has focused on explaining how fire regimes are changing around the globe due to climate change (see Grissino-Mayer and Swetnam 2000; Cary 2002; Bowman et al. 2009) and historical fire suppression. In North American hot deserts, however, fires have been historically uncommon (MacMahon 1999), in part because of the relatively low abundance of perennial plant cover (e.g., shrubs) and the wide spacing among plants, resulting in insufficient continuity of fuel to carry fire (Brown and Minnich 1986). However, the risk of fire in these systems has increased over the last several decades, due to increased human activities over time, resulting in extensive invasions by annual grasses and forbs (D'Antonio and Vitousek 1992). Invasive species (mostly winter annual grasses such as *Bromus* sp. and *Schismus* sp.) can increase fire risk by providing connections between the perennial shrubs through the production of more fine fuel (e.g., dry biomass) in the previously unvegetated space.

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As a result, wildfires in deserts have become more common and more severe (i.e., hotter fires) over the past several decades (Brooks et al. 2004; McDonald and McPherson 2013), impacting the biological, chemical, and physical properties of desert soils, as well as landscape structure and population dynamics of the plant community (Allen et al. 2011). Hence, an increase in fire frequency and severity may have negative consequences for an entire community that has generally been considered to be poorly adapted to fire (Allen et al. 2011; Brown and Minnich 1986; O’Leary and Minnich 1981). This may, in turn, act to reduce the abundance of the less fire-tolerant, native species (Burquez-Montijo et al. 2002).

In summer 2005, a wildfire outbreak occurred in the Sonoran Desert, burning large extents of lowlands (Brooks and Matchett 2006; Esque et al. 2013), which are generally dominated by creosote bush [*Larrea tridentata* (DC.) Cov., hereafter referred to as *Larrea*]. *Larrea* is a perennial shrub that plays a key role in structuring soil features, as well as annual plant diversity (Mudrak et al. 2014; Schafer et al. 2012; Schlesinger et al. 1996). Historically unprecedented fires in creosote bush shrublands of the Sonoran Desert started in the mid-1970s. Since then, large portions of native vegetation in burned areas have been replaced by exotic grasses (especially from the genera *Bromus*, *Schismus*, and *Pennisetum*; Burgess et al. 1991; Rutman and Dickson 2002). Usually, wildfires in the *Larrea* shrublands spread during periods of high temperature (35–40 °C on average), low relative humidity (10–20 %), and high wind speeds, ranging from 35 to 70 km/h, especially when the preceding rainy season had a significantly above-normal precipitation rate, resulting in denser and more widespread annual grass litter between shrubs (Brown and Minnich 1986). These were the conditions that likely fueled the wildfires in 2005 (Brooks and Matchett 2006; Esque et al. 2013).

A major impact of fire upon the desert landscape is the removal of many of the *Larrea* shrubs from the system. In Sonoran lowlands, *Larrea* has been found to be hyper-dispersed at spatial scales less than approximately 2.0 m, but is randomly distributed at greater scales (Yeaton et al. 1977). However, a shift in the fire regime has the potential to change *Larrea*’s spatial pattern by modifying the proportion and spatial arrangement of living and dead shrubs, leading to more openness in the landscape. This can cause impacts on the entire plant community, both directly (e.g., modifying soil nutrient availability) and indirectly (e.g., providing more open space to be colonized by exotic species), which is particularly important since *Larrea* has a low post-fire establishment rate, due to limited resprouting (3–30 %) and low reproductive success (Abella 2009). Thus, wildfires may directly affect long-term community structure. Indirectly, fire can potentially alter plant community dynamics by having negative impacts on both soil nutrients and soil

microorganisms in the mid- and long-term. Furthermore, removal of shrubs by fire could be advantageous for exotic plant species, which might be successful in colonizing and establishing in the “empty spaces”, with high levels of nutrients left by *Larrea* after fire. *Larrea* plays a key role in maintaining diversity and function of Sonoran shrublands. Understanding how the spatial structure of *Larrea* shrublands might be changed by fire can provide useful insights for both conservation purposes and fire risk management.

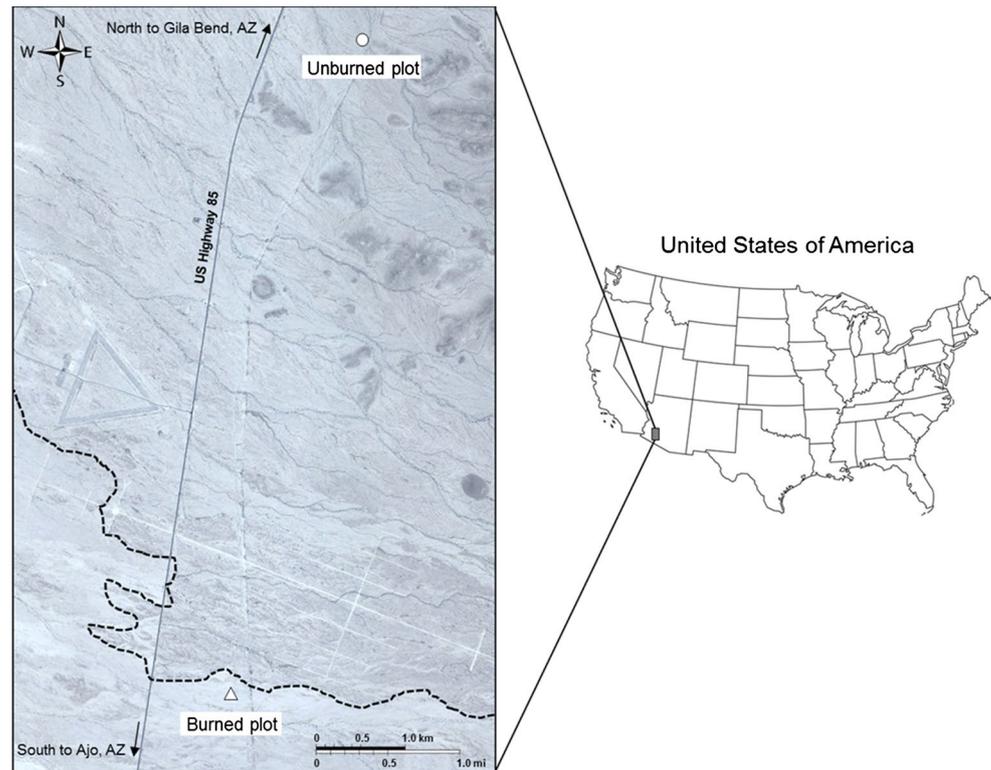
Spatial analysis and fire modeling provide useful tools for exploring the impact of disturbances (i.e., wildfire) on a given natural population, and may provide valuable insights for management of novel fire prone systems. In desert ecosystems, spatial data analysis has been used to investigate plant interactions and vegetation associations, reproductive success and dispersion patterns (Tirado and Pugnaire 2003; Miriti 2007; Rayburn et al. 2011), but little is known about how fire changes the spatial pattern of *Larrea*. In this study, we primarily focused on the potential for change in the post-fire spatial distribution of surviving shrubs in the Sonoran Desert. We hypothesize that fire may mediate a change in the spatial pattern of *Larrea* shrubs in a non-random way, leading to a fundamentally different relationship among the remaining living individuals that escaped the fire (e.g., clustered into patches). We then developed a spatially explicit model aimed at reconstructing the pattern observed in the field for living and dead *Larrea* shrubs, using a simple, completely spatially random (CSR) fire-spread algorithm. The goals of this research were to: (1) determine the spatial distribution of the remaining living *Larrea* shrubs within burned areas, relative to the pattern of adjacent unburned areas; (2) determine the spatial distribution of dead shrubs (i.e., plants not showing any sign of resprouting after fire), relative to survivors, as an indicator of the pattern of fire movement through the landscape; and (3) develop a simple initial fire model as a practical example aimed at reproducing the spatial pattern shrubs observed in the field and gaining insights into the potential initialization of fire within our study area.

## Materials and methods

### Study area and sampling plots

The study was conducted within *Larrea* (creosote bush)-dominated shrubland sites in the Sonoran Desert, in a system characterized by scattered perennial shrubs, cacti, forbs, and grasses, with interspaces consisting of sparsely vegetated soils (Abella 2010). The primary study site was located at an elevation of 320 m within the eastern section of the Barry M. Goldwater Range (US Air Force Range), 35 km south of Gila Bend, AZ. The mean annual temperature is 23.4 °C and

**Fig. 1** The study area within the Sonoran Desert in Arizona, USA that depicts the boundary of the wildfire occurred in 2005. The location of the unburned and burned plots is indicated with a *circle* and *triangle*, respectively. Note that the aerial image in not scaled to the *dashed box* in the larger map. Image taken from Maricopa County Historical Aerial Photography database, URL <http://gis.maricopa.gov/Index.html>



mean annual precipitation is 135 mm (Western Regional Climate Center, Gila Bend weather station), with wet seasons occurring in summer and winter. There is no evidence that the site has been impacted by fire in recent history. The second site considered in the study (located at an elevation of 360 m) was affected by a wildfire that covered approximately 28,000 ha in 2005. The wildfires occurred after above-normal rainfall rates in the preceding wet season, resulting in an abundance of fine fuels. The cumulative rainfall prior to the fire from July 2004 to April 2005 was 246 mm and the mean maximum temperature for June and July was 47.2 °C (Western Regional Climate Center, Gila Bend weather station). This rainfall was unusual, representing about 3.5 times the average. Above average rainfall in these water-limited areas results in above-normal plant production, especially exotic annual grasses from the genera *Bromus* and *Schismus*, and represents a key factor for the spread of fire in desert environments (Brooks et al. 2004).

In 2010, 5 years after the fire in the burned site, we established two plots: one was located in the wildfire site, and the other was located within the unburned area (see Fig. 1). The two plots were 83 × 130 m, and were approximately 11 km apart (32°37'46"N, 112°51'18"W for the burned plot and 32°41'49"N, 112°50'22"W for the unburned plot). The burned plot was chosen as the closest fire-affected site to our primary, unburned study site, that had been established for a more extensive study (cf., Mudrak et al. 2014; Schafer et al. 2012). The two plots were oriented so that the

longer side ran north–south. We used a GPS to locate the corners of each plot and stakes were placed to delineate the boundaries in the field. The two study plots we worked in are located near to an active military training area, which produces an increased risk of ignition due to the active use of explosives and firearms.

We acknowledge that this work was conducted in a system impacted by natural (uncontrolled) conditions. Also, we are only comparing one burned with one unburned site. However, much can be learned in “natural experiments”, especially in systems where controlled experiments mimicking natural processes are essentially impossible to conduct (cf., Sagarin and Pauchard 2012). Additionally, since replication in point pattern analysis is at the level of the individual object, each object represents a response to the process being explored (Wiegand and Moloney 2014). Greater generality would be gained by studying more sites, but the approach taken here provides very useful insights into the movement of fire through *Larrea*-dominated systems.

#### Shrub measurements

Within each of the sampling plots, we geo-referenced all *Larrea* individuals using a sub-meter Trimble Geo-XT 2003 GPS unit. We defined a “living shrub” as the collection of stems and green branches, with overlapping canopies, located on a single soil mound. The average canopy

area of a living shrub ranged from 2 to 4 m<sup>2</sup> (Mudrak et al. 2014). Similarly, a “dead shrub” was defined to be the burned stump or dried collection of branches and stems on a single soil mound. The living status of each shrub was visually assessed in the field. We recorded two attributes per shrub: location ( $x$ ,  $y$  coordinates) and status (living or dead, assuming that living shrubs survived the fire and dead shrubs were killed by the fire). Differential correction for the location and elevation data was applied by using the nearest base provider to obtain a spatial accuracy of 30–50 cm [CORS, MCDOT Buckeye (AZBK), AZ, National Geodetic Survey, NOAA 1997]. Before analysis, all UTM coordinates were transformed so that the origin was located at the SW corner of the each plot.

### Data analysis and null models

With the aim of investigating how *Larrea* shrubs were distributed across the landscape in each of the study plots prior to and post-fire, we conducted univariate and bivariate spatial analyses. Univariate analyses were used to examine the spatial patterns of a single category of point (i.e., living, dead or living + dead shrubs), whereas bivariate analyses were used to characterize the spatial relationships between living and dead shrubs within the burned plot.

#### Univariate analyses

We used  $g(r)$ , the pair correlation function (PCF), for the univariate analyses (Stoyan and Stoyan 1996; Wiegand and Moloney 2014). Although Ripley’s  $K$  function (Ripley 1981) is more familiar to ecologists, the PCF is generally more useful, since it characterizes spatial relationships as a function of distance, rather than as a function of neighborhood point density. This avoids the problem of “virtual aggregation” produced by Ripley’s  $K$ , which makes it difficult to interpret point pattern analyses correctly (Wiegand and Moloney 2014).

For the unburned plot, which we considered to be the control pattern, we calculated the PCF for all *Larrea* individuals. We also computed the PCF for the living and dead shrubs combined within the burned plot, hypothesizing that this pattern should represent pre-burn conditions, and be similar to the pattern in the unburned plot, if the spatial structure was essentially the same prior to the fire. We followed up with two additional univariate analyses, complementing the information provided by the PCF analysis:  $G(r)$ , the nearest neighbor distribution function, and  $H(r)$ , the spherical contact distribution.  $G(r)$  is a summary statistic of the cumulative distribution of the distance from the points of a pattern (e.g., shrubs) to their nearest neighbors. This provides information about the variability of the point pattern that is being investigated, especially if the pattern comprises areas of low

density (e.g., areas with isolated points). It is also useful in detecting subtle details of local clustering (Wiegand et al. 2013).  $H(r)$  is related to  $G(r)$ , but instead measures the distribution of the distances from test locations to the nearest points in the pattern (see Diggle 2003). This function is useful for characterizing the “holes” in a pattern, as it measures the size of the gaps. We computed these two functions for the shrubs in the unburned plot, as well as for the living and dead shrubs combined in the burned plot. For these three univariate analyses [i.e., PCF,  $G(r)$ , and  $H(r)$ ], we used complete spatial randomness (CSR) as the null model for detecting aggregation or inhibition among the shrubs. CSR is the simplest and most commonly used null model, and assumes no interaction between events in a given pattern (e.g., random distribution). For a completely random point process,  $g(r) = 1$  for all values of  $r$ . Values of  $g(r) > 1$  indicate aggregation (clustering) at distance  $r$ , whereas values  $< 1$  indicate regularity or segregation. Significance tests were calculated by conducting 199 Monte Carlo simulations to create 95 % CSR confidence envelopes. Values of the PCF falling outside of the envelopes are considered to be statistically different from random. We apply a conservative approach to interpreting significance and do not consider slight departures from the significance envelopes to be significant (Baddeley et al. 2014). We also consider patterns exhibiting a series of adjacent values lying outside the envelopes as being of greater significance than isolated values. We also have not applied goodness-of-fit tests in the current study since our analyses are exploratory in nature, we do not have a priori expectations of the critical scales of interaction, and we are not making claims of significance for small departures from the Monte Carlo simulations envelopes (cf., Baddeley et al. 2014 vs. Loosmore and Ford 2006).

We used the *pcf* command in the *spatstat* R package to compute the PCF values, with  $r = 20$  and a precision of 0.1 (Baddeley and Turner 2005). Confidence envelopes for  $G(r)$  and  $H(r)$  were created using the same protocol as in the PCF analysis. Values of  $G(r)$  below the theoretical expectation suggest an inhibitory pattern of over-dispersion, whereas values above suggest clustering at scale  $r$ . Similarly, values of  $H(r)$  below the theoretical expectation indicate a clustered pattern, whereas values above suggest an over-dispersed pattern. We used the commands *Gest* and *Hest* within the *spatstat* R package to calculate  $G(r)$  and  $H(r)$ , respectively (Baddeley and Turner 2005).

In a second set of analyses, we calculated the PCFs,  $G(r)$ , and  $H(r)$  separately for the living and dead shrubs within the burned plot to characterize the impact of the fire on the spatial structure of the system. For this, we used random labeling (RL) as the null model. RL assumes random assignment of labels (e.g., living or dead) to the fixed locations of the shrubs, holding the proportion of each type of label equal to that of the observed pattern. Under RL,

the locations of the objects in the pattern arise from a univariate spatial point process, and the marks (e.g., living or dead) are determined a posteriori by some phenomenon (e.g., wildfire) (Goreaud and Pelissier 2003). This form of analysis investigates whether or not the shrub class (“living” or “dead”) was randomly distributed within the given spatial structure of the living and dead shrub combined (Wiegand and Moloney 2004). Confidence envelopes were created using the same protocol described above, but specifying RL as the null model.

### Bivariate analyses

We conducted bivariate analyses to characterize the spatial relationship between living and dead shrubs within the burned plot. For this, we used random labeling (RL) as the null model. We used a multi-type PCF approach [which is essentially a crossed  $g(r)$  analysis] to investigate at which (if any) spatial scales the two classes of shrub were aggregated or segregated. Values of cross  $g(r)$  above the confidence envelopes indicate aggregation and below indicate segregation among shrubs of the different classes. The 95 % confidence envelopes were created by running 199 Monte Carlo simulations of RL (*pcfross* command in the *spatstat* R package; Baddeley and Turner 2005). We also calculated two additional bivariate functions to complement the cross PCF: the cross  $G(r)$  and the mark connection function  $\rho(r)$ . The cross  $G(r)$  function (*gcross* command in the *spatstat* R package) characterizes the nearest neighbor distance between the two shrub classes, with the results dependent upon which class is treated as the focal class and which is the neighbor class. When living shrubs are used as the focal class, we determine the nearest neighbor distances to the dead shrubs and vice versa. The  $\rho(r)$  function qualitatively analyzes the process (i.e., wildfire) that distributes the marks “living” versus “dead” over the univariate pattern. In this context, for a marked point pattern with living and dead individuals at distance  $r$ ,  $\rho_{li-de}(r)$  is defined as the probability that the first point is of type living, and the second of type dead, and  $\rho_{de-li}(r)$  is defined as the probability that the first point is of type dead, and the second of type living (*markconnect* command from the *spatstat* R package; Baddeley and Turner 2005). Confidence envelopes for cross  $G(r)$  and  $\rho(r)$  were created using the same protocol as in the cross PCF analysis.

### Fire modeling approach

We used NetLogo, a multi-agent-based modeling environment (Wilensky 1999), to develop a fire model based only on the spatial data of *Larrea* shrubs in the Sonoran Desert ( $n = 640$ ). No other information was included in the model. We set the locations of shrubs in the model to be identical

to the pre-fire pattern observed in the burn plot (i.e., living and dead shrubs combined). Fires were initiated using a single shrub selected at a random location. The probability that additional shrubs would ignite  $P(r)$  was determined as a function of the distance  $r$  from the original ignition point or from another burning shrub.  $P(r)$  varied within a radial distance of 10 m, following a negative exponential decay curve defined as:

$$P(r) = \begin{cases} a * e^{-b*r} & r < 10 \text{ m} \\ 0 & r \geq 10 \text{ m} \end{cases}$$

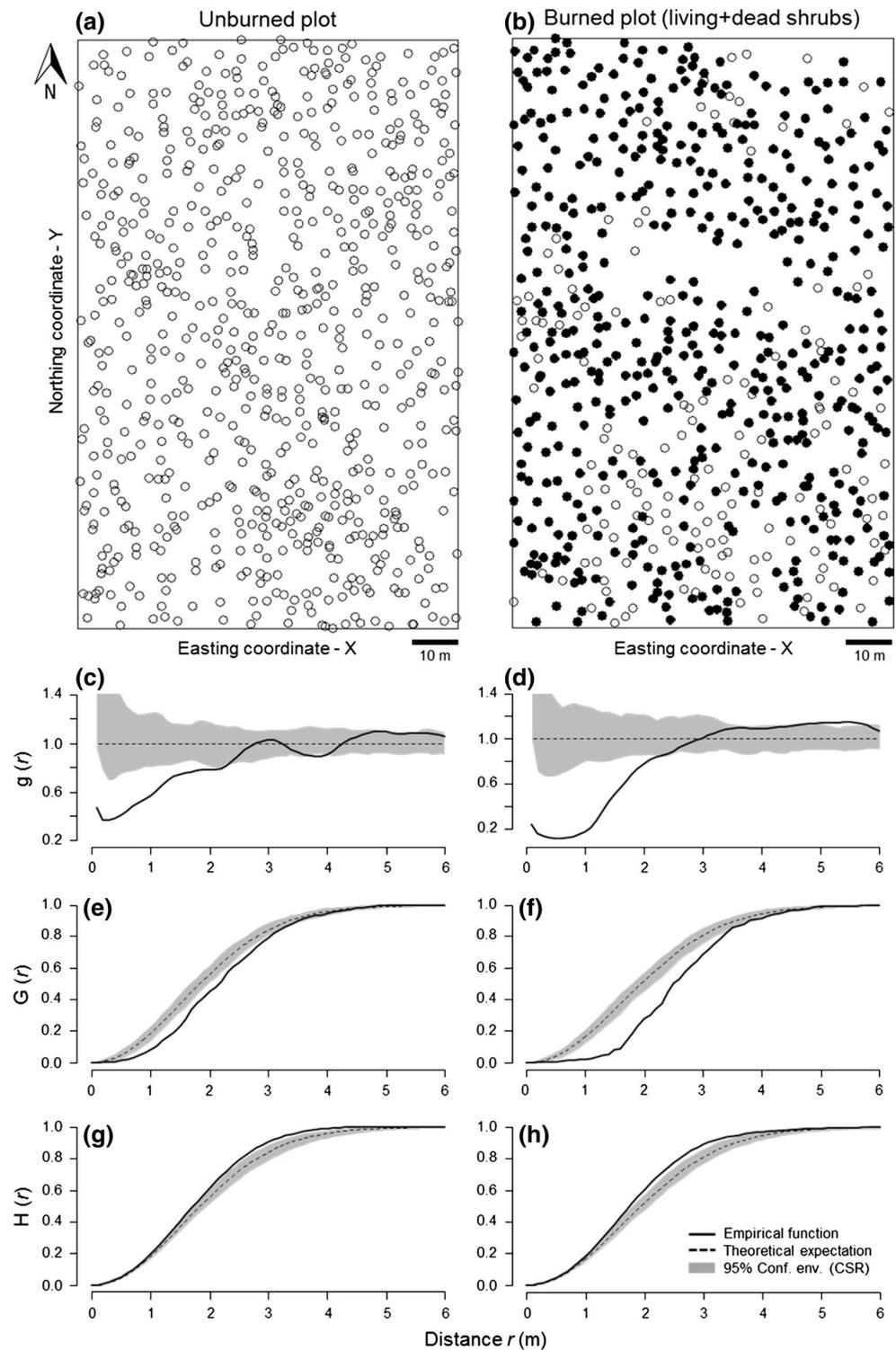
where  $a = 1$  (the probability of being burned at distance 0 from an already-burning shrub) and  $b$  is the decay rate of the probability curve. The cutoff distance of 10 m was determined from the results of the bivariate analyses as being a reasonable distance beyond which there would be little, if any, fire spread. The result of each model simulation was a set of shrubs at the observed field locations with a mark of living or dead. We performed 2,000 simulations for 16 values of parameter  $b$  (i.e., from 0.045 to 0.12 with 0.005 increments) to determine which one resulted in a mean number of dead shrubs within 10 % of the observed number in the field (i.e.,  $495 \pm 50$  dead shrubs). We provided the standard error (SE) associated to each mean, for each  $b$  value as measure of precision of the mean estimate. Of the successful parameter  $b$  values, we took the 0.025 and 0.975 percentiles of the simulated PCF distribution to create the 95 % confidence envelopes and compared it with the observed PCF for living and dead shrubs.

We also investigated the impact of the choice of initial ignition points on fire spread within our burned plot to explore how variable the resulting effects were due to the spatial configuration of shrubs occurring in the plot, and to obtain a general idea of where the fire front might have originated. We ran simulations using a value for parameter  $b$  that met our criterion above (i.e.,  $b = 0.08$  as described in “Results”), and allowed each shrub to act as the initial ignition point for 30 simulations. We then calculated the average percentage of burned shrubs for each initially ignited shrub and plotted these averages in a spatially explicit way, representing a “fire severity map” given the location of the starting ignition point. This analysis provides insights into the variability of predicted fire patterns for the simulation model based on initial conditions of ignition.

## Results

There were 713 *Larrea* shrubs within the unburned Sonoran plot (with no dead shrubs) and 640 living and dead shrubs within the burned plot, the latter comprising 145 living *Larrea* shrubs and 495 dead shrubs (Fig. 2a, b).

**Fig. 2** Observed spatial pattern of *Larrea tridentata* within an **a** unburned ( $n = 713$ ) and **b** burned ( $n = 640$ ) area. **b** Closed circles indicate dead shrubs ( $n = 495$ ) and open circles indicate living shrubs ( $n = 145$ ). Spatial summary characteristics of shrubs distribution. In the unburned plot **c**  $g(r)$ , **e**  $G(r)$ , and **g**  $H(r)$  and within the unburned plot (**d**, **f**, **h**, respectively) the pre-burn spatial pattern. **c–h** The gray-shaded areas represent the 95 % confidence envelopes. Solid lines are the observed value of the function and dashed lines correspond to the theoretical expectation under CSR



### Spatial patterns

Within the unburned plot (control pattern), the PCF analysis indicated that *Larrea* individuals were hyper-dispersed at distances  $<2.0$  m, but were randomly distributed at broader spatial scales (Fig. 2c). Similarly, for the combined pattern

of living and dead shrubs in the burned plot, the PCF showed a hyper-dispersed distribution at distances  $<2.0$  m, but a random spatial distribution at broader distances (Fig. 2d). The nearest neighbor distribution function  $G(r)$  also provides evidence of a hyper-dispersed pattern at short distances for *Larrea* individuals in the unburned plot and

for the combined pattern of living and dead shrubs in the burned plot, as there were fewer neighboring shrubs than expected by chance (Fig. 2e, f).  $H(r)$  was also consistent with the PCF results, as it confirmed the inhibitory pattern at short distances for the *Larrea* shrubs in the unburned plot, as well as for the living and dead shrub combined in the burned plot, by exhibiting larger void sizes than expected by chance (Fig. 2g, h). This hyper-dispersed pattern observed within the burned and unburned plot likely represents the natural spacing between *Larrea* shrubs, and it is closely related to the average area of an individual shrub canopy, ranging from 2 to 4 m<sup>2</sup>.

In the burned plot, the *Larrea* shrubs that survived the fire exhibited evidence of a clustered distribution at distances >2.5 m (Fig. 3a, c). The distributional pattern of the dead shrubs was similar to the pattern observed in the unburned plot and for the living and dead shrubs considered together in the burned plot (Fig. 3b, d). The PCF functions calculated separately for living and dead shrubs were consistent with  $G(r)$  for living individuals and with  $G(r)$  for dead shrubs. The  $G(r)$  for living individuals alone showed that there were more shrubs at distances >2.5 m in the surrounding neighborhood than expected by chance (Fig. 3e), and the  $G(r)$  for dead shrubs showed a random pattern (Fig. 3f). Also,  $H(r)$  showed a slower rate of increase than the expectation at intermediate scales, which indicates that there are fewer voids with radii between 5 and 15 m than expected, suggesting a clustered pattern at intermediate scales for living shrubs (Fig. 3g). For dead shrubs,  $H(r)$  indicated a random distribution (Fig. 3h).

Regarding the spatial relationship between living and dead shrubs within the burned plot (bivariate analyses), the cross PCF suggested segregation at intermediate scales (~5 m) from living to dead shrubs and vice versa (Fig. 4a, b). The cross  $G(r)$  showed that both classes of shrubs (living and dead) tended to be surrounded by dead shrubs, since from living to dead we observed a non-significant trend, whereas the pattern from dead shrubs to living was statistically significant (Fig. 4c, d). The mark connection function  $\rho(r)$  suggests that the probability for a dead shrub to be surrounded by a living shrub is significantly lower than expected under RL within ca. 10 m (Fig. 4e, f). This result suggests that the highest likelihood for an unburned shrub of catching fire is within 10 m of a burned shrub.

#### Fire model

We found one value of parameter  $b$  (i.e.,  $b = 0.08$ ) that yielded a mean of 473 burned shrubs and a SE = 3.91 (see Table 1 in bold type; Fig. 5a). Using  $b = 0.08$  in simulations, model-simulated data for living shrubs exhibited a more clustered pattern (higher PCF values) at finer scales (i.e., <10 m), compared to the observed PCF distribution.

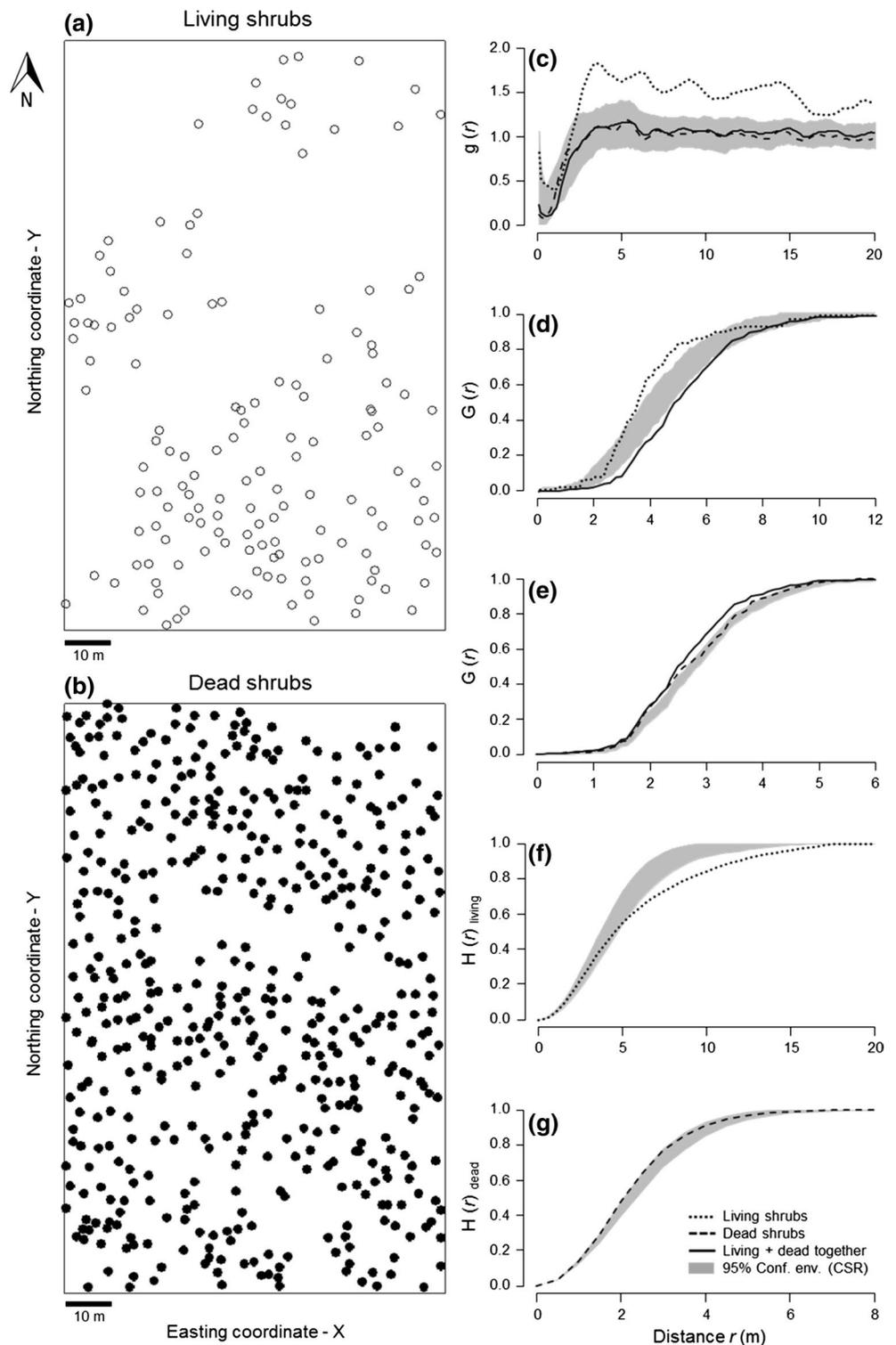
However, at broader scales (i.e., >10 m), the values of the observed PCF fell within the 95 % confidence envelopes created by the PCF of the simulated data (Fig. 5b). This indicates that the fire model did not reproduce the observed pattern of living shrubs at short distances accurately, but it did at greater distances. For model-simulated dead shrubs, we found that the PCF differed from the observed pattern across all spatial scales, creating a more clustered pattern along the entire range of scales, compared to the observed distribution in the field (Fig. 5c).

The initial location of the ignition source affected the relative number of living and dead shrubs produced across the entire plot. Thus, if a fire starts in areas where shrubs were very close to each other, the fire-spread risk (i.e., high number of burned shrubs within the plot) is higher, relative to those areas where shrubs were spaced farther apart from each other. This suggests that the wildfire front may have hit the area from the lower half of our study plot. We found that the likelihood of fire spread from shrubs in the lower half of the plot (Fig. 6) was high (relative to the upper half), burning about 75 % of the shrubs, which was the actual proportion of burned shrubs in the field. It is interesting to also note that the large void in the center of the plot tended to act as a fire barrier in the model, creating a different burn pattern for fires initiated in the upper half of the plot (i.e., relatively low fire spread) compared to the lower half (see Fig. 6).

#### Discussion

We found a consistent spatial pattern comparing the unburned plot with the pattern of living and dead shrubs considered jointly in the burned plot, indicating that the sites had similar spatial patterns before fire. *Larrea* shrubs were randomly distributed at broader scales, but hyper-dispersed at finer scales (i.e., <2.0 m). This hyper-dispersed pattern likely represents the natural spacing between the shrubs, given the average size of an individual shrub, ranging from 2 to 4 m<sup>2</sup> (Mudrak et al. 2014). This pattern is also commonly found when there is competition for resources (e.g., water and nutrients), and with other species (Yeaton et al. 1977; Fonteyn and Mahall 1978; McDonough 1963). In this area, *Larrea* competes with *Ambrosia* sp. (another common perennial shrub; Fonteyn and Mahall 1978, 1981), leading to spatial segregation between the two species, which in turn results in a random distribution for *Larrea* (Schenk et al. 2003). *Larrea* is a keystone species that predominantly determines community structure in SW deserts, and it can be viewed as a better competitor compared to other perennial shrubs (Mahall and Callaway 1992; Schenk et al. 2003). Another possible explanation of the hyper-dispersed pattern of *Larrea* at finer scales might

**Fig. 3** Observed spatial pattern of **a** living and **b** dead *Larrea* shrubs within the burned site. **c** Pair correlation function  $g(r)$  for living shrubs (dotted line), dead shrubs (dashed line), and living and dead combined (solid line).  $G(r)$  for **d** living (dotted line) and **e** dead (dashed line) shrubs contrasted with living and dead shrubs combined together (solid lines).  $H(r)$  for **f** living shrubs and **g** dead shrubs (solid lines). **c–g** The gray-shaded areas represent the 95 % confidence envelopes created from RL

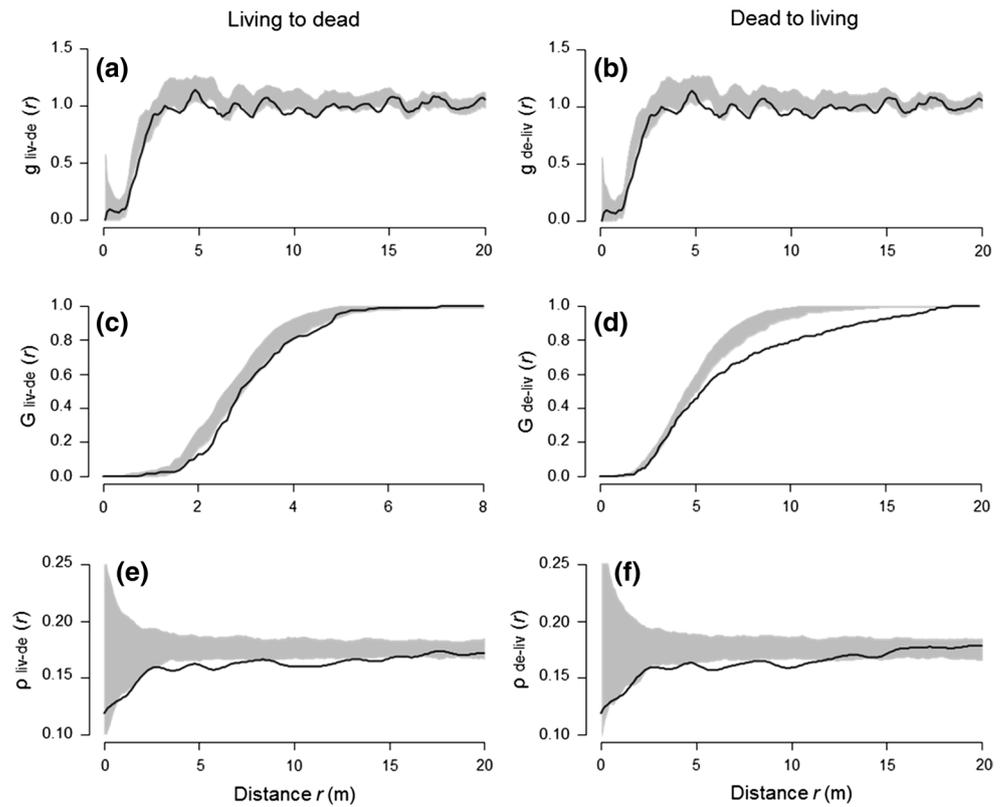


be due to the spatial distribution at seedling emergence: clumped at short distances ( $<2$  m), but randomly distributed at greater distances (Bowers et al. 2004), suggesting that competition within seedling clumps would lead to hyper-dispersion. Similar results have been shown for other shrub species in Mediterranean shrublands in Spain, where

seedlings of *Ulex parviflorus* (gorse) were aggregated in the early stages, but segregated when plants grew to maturity (Raventós et al. 2010).

In the burned plot, we found that the 145 living shrubs were clustered at distances  $>2.0$  m, whereas the 495 dead shrubs followed a hyper-dispersed pattern at finer scales

**Fig. 4** Bivariate analyses showing transitions from living to dead shrubs (*left side*) for **a**  $g(r)$ , **c**  $G(r)$ , and **e**  $\rho(r)$ , and from dead to living shrubs (*right side*), for **b**  $g(r)$ , **d**  $G(r)$ , and **f**  $\rho(r)$  within the burned area. For all panels, the gray-shaded areas represent the 95 % confidence envelopes created from RL



**Table 1** Parameter  $b$  values (decay rate) used in the fire model to examine the relationship between the observed number of burned shrubs in the field and the model

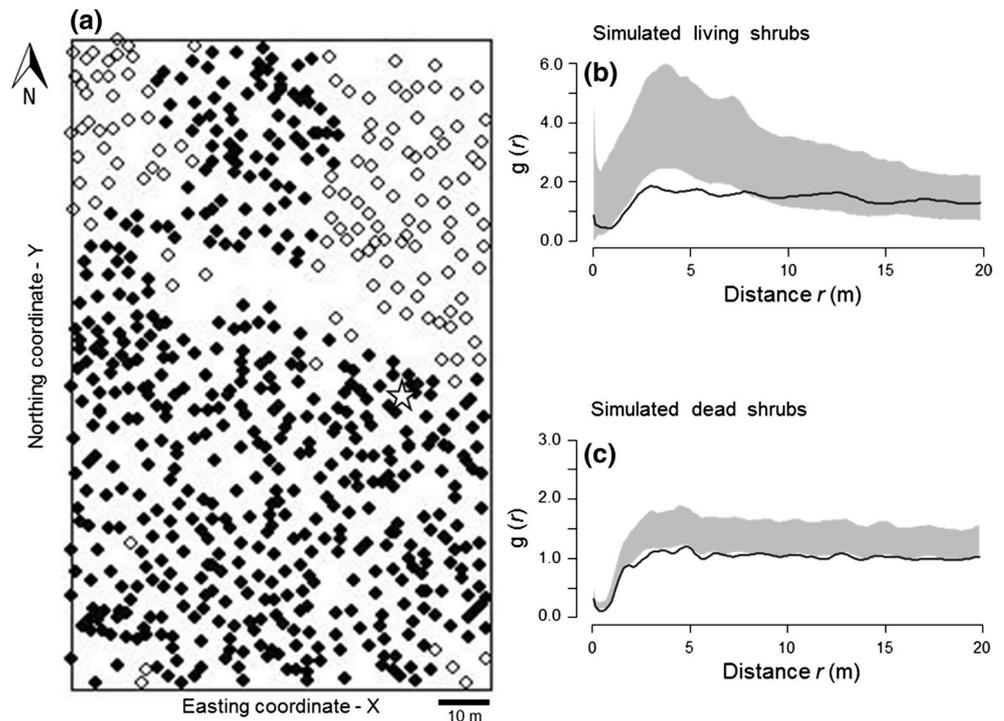
Parameter $b$	Mean no. of burned shrubs	SE
0.045	637.4	0.32
0.050	635.5	0.55
0.055	631.8	0.90
0.060	627.4	1.01
0.065	617.2	1.42
0.070	592.3	2.30
0.075	550.5	2.98
<b>0.080</b>	<b>472.5</b>	<b>3.91</b>
0.085	380.8	4.18
0.090	286.1	4.00
0.095	205.7	3.51
0.100	130.2	2.75
0.105	73.3	1.82
0.110	40.1	1.05
0.115	25.3	0.67
0.120	16.5	0.46

The  $b$  value (0.080, in bold type) met the criterion of yielding a mean number of burned shrubs encompassing the actual number of burned shrubs  $\pm 10\%$  in the field. The standard error (SE) indicates the precision of the mean estimate for each parameter  $b$  value

and were randomly distributed at broader scales (similar to the unburned plot). These findings may give us a proxy of the burning pattern of the fire itself, suggesting that fire acted as a mediator for the change of the spatial pattern. Thus, fire burned *Larrea* shrubs in an overall random way, killing a large proportion of shrubs, while leaving a small number of living individuals behind that were scattered among several small clusters (see Fig. 6). The fact that the pattern of the dead shrubs was similar to the pre-fire pattern (dead + living shrubs), and the pattern of the living shrubs was not, is most likely due to small clusters of shrubs escaping fire. The removal of a small number of points (living shrubs) might have left the pattern of dead shrubs indistinguishable from the pre-fire pattern. However, the observed distribution of the living *Larrea* shrubs after fire may represent a short-term phase, which will potentially change to a more regular distribution over time because of competition with their surrounding neighbors (see Kenkel 1988).

Another potential scenario is that, once the fire has removed some shrubs from the system, the structure and function of the entire plant community may be permanently affected (considering the low post-fire recovery rate of *Larrea*; Abella 2009). Indeed, invasive grasses like *Bromus* sp. and *Schismus* sp. can take advantage of the removal of

**Fig. 5** Results from one run of the fire simulation model showing **a** the spatial pattern created by the fire model using parameter  $b = 0.08$ . *Closed points* indicate dead shrubs and *open points* indicate living shrubs. The *star* indicates the shrub that was initially ignited in this model run. Observed PCFs (*solid lines*) for **b** living and **c** dead shrubs plotted with the 95 % confident envelopes (*gray-shaded areas*) created from the simulated data (using 2,000 simulation for parameter  $b = 0.08$ ) for each class of shrub (i.e., living and dead)



*Larrea* and occupy the “empty spots”, which still represent islands of fertility, leading to a broader and more uniform invasion. But, more importantly, as these exotic species are the primary fuel that carries fire in SW American deserts (Brooks et al. 2004; McDonald and McPherson 2013), the chances of repeated fires are greater in burned areas than in unburned ones (D’Antonio and Vitousek 1992; Brooks and Lusk 2008). This may imply a shift of the fire regimes from rare fires (i.e., Sonoran Desert) into an increased severity and frequency of wildfires, likely reducing the abundance of less fire-tolerant species (McLaughlin and Bowers 1982; Brown and Minnich 1986; Burquez-Montijo et al. 2002).

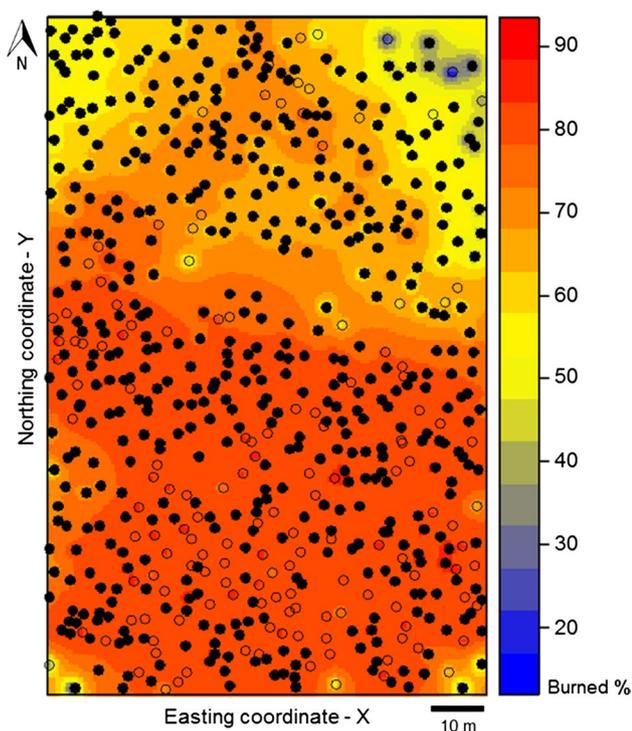
#### Fire model

We were successful in fitting a fire model based on spread as a function of the distances separating shrubs that did a reasonably good job of matching the observed number of burned and living shrubs. However, the spatial pattern of the simulated data only partially agreed with the observed PCF for both living and dead *Larrea* shrubs. The spatial data from the fire model overestimated the value of the PCF (especially at short distances), producing a more clustered pattern compared to what we observed in the field. Additionally, the fire model provided basic information regarding the potential locations where the fire front may have first arrived at our plot, discarding those locations with lower probability of fire spread (colder colors of map

in Fig. 6). Although quite simple in design, the modeling approach we used presents a first step in determining how best to model fire spread for these kinds of systems.

More complex fire models might also include other environmental factors, such as wind conditions, temperature and relative humidity, topography, and vegetation cover (Adou et al. 2010; Sunderman and Weisberg 2012), especially after an above-normal wet season (Brown and Minnich 1986). These were the conditions in 2005 when fire burned the site considered here. It is important to mention that our fire model did not include any input regarding shrub features. While information on shrub size would no doubt increase the accuracy of our model, we had no information on the size of burned shrubs before the fire. However, our research group is currently working on techniques to accurately determine shrub size and volume using aerial imagery, aiming at using images of multiple sites (i.e., higher replication) before and after wildfires, to develop much-improved models.

In summary, we found a change in the spatial pattern of *Larrea* shrubs surviving the fire that shifted to a more clustered distribution. This was consistent for the three summary statistics we used: PCF,  $G(r)$ , and  $H(r)$ . The novel post-fire spatial structure of the *Larrea* shrublands might be favorable for the establishment of exotic species (especially *Bromus* sp. and *Schismus* sp. grasses). This may, therefore, act to increase the abundance fine fuel, making the grass–fire cycle stronger (D’Antonio and Vitousek 1992; Brooks



**Fig. 6** Fire severity map for the burned plot given the locations of the first ignited shrub using parameter  $b = 0.08$ . Each shrub was ignited 30 times and the average percentage of burned shrubs for that given initially ignited shrub was recorded. *Colder colors* indicate lower potential of fire spread and *hotter* indicate higher fire spread (in percentage of burned shrubs). Note that the observed spatial distribution from the field was superimposed over the color-coded map (*closed circles* indicate dead shrubs and *open circles* indicate living shrubs from the observed pattern in the field)

et al. 2004). We think that fire modeling of *Larrea* shrublands based on proximity (radial distance) from burning shrubs is a good starting point for exploring the relationship between the burning pattern of fire and the spatial distribution of shrubs. However, with the recent development of digital image analysis and its application to ecology, using aerial photographs or high-resolution satellite images, coupled with more detailed simulation models, we may be able to develop an improved understanding of fire dynamics at broader spatial scales with better predictions.

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## References

- Abella SR (2009) Post-fire plant recovery in the Mojave and Sonoran deserts of western North America. *J Arid Environ* 73:699–707. doi:10.1016/j.jaridenv.2009.03.003
- Abella SR (2010) Disturbance and plant succession in the Mojave and Sonoran deserts of the American Southwest. *Int J Environ Res Public Health* 7:1248–1284. doi:10.3390/ijerph7041248
- Adou JK, Billaud Y, Brou DA, Clerc JP, Consalvi JL, Fuentes A, Kaiss A, Nmira F, Porterie B, Zekri L, Zekri N (2010) Simulating wildfire patterns using a small-world network model. *Ecol Model* 221:1463–1471. doi:10.1016/j.ecolmodel.2010.02.015
- Allen EB, Steers RJ, Dickens SJ (2011) Impacts of fire and invasive species on desert soil ecology. *Rangel Ecol Manag* 64:450–462. doi:10.2111/rem-d-09-00159.1
- Baddeley A, Turner R (2005) *spatstat*: An R package for analyzing spatial point patterns. *J Stat Softw* 12:1–42
- Baddeley A, Diggle PJ, Hardegen A, Lawrence T, Milne RK, Nair G (2014) On tests of spatial pattern based on simulation envelopes. *Ecol Monogr* 84:477–489
- Bowers JE, Turner RM, Burgess TL (2004) Temporal and spatial patterns in emergence and early survival of perennial plants in the Sonoran Desert. *Plant Ecol* 172:107–119. doi:10.1023/B:VEGE.0000026026.34760.1b
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Marston JB, Moritz MA, Prentice IC, Roos CI, Scott AC, Swetnam TW, Van der Werf GR, Pyne SJ (2009) Fire in the Earth system. *Science* 324:481–484. doi:10.1126/science.1163886
- Brooks ML, Lusk M (2008) Fire management and invasive plants: a handbook for land managers. United States Fish and Wildlife Service, Arlington
- Brooks ML, Matchett JR (2006) Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *J Arid Environ* 67:148–164. doi:10.1016/j.jaridenv.2006.09.027
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54:677–688. doi:10.1641/0006-3568
- Brown DE, Minnich RA (1986) Fire and changes in Creosote bush scrub of the western Sonoran desert, California. *Am Midl Nat* 116:411–422
- Burgess TL, Bowers JE, Turner RM (1991) Exotic plants at the desert laboratory, Tucson, Arizona. *Madroño* 38:96–114
- Burquez-Montijo A, Miller ME, Martinez-Yrizar A (2002) Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). In: Tellman B (ed) Invasive exotic species in the Sonoran region. University of Arizona Press and The Arizona-Sonora Desert Museum, Tucson, pp 126–146
- Cary GJ (2002) Importance of a changing climate for fire regimes in Australia. *Flammable Australia: the fire regimes and biodiversity of a continent*, chap 2. Cambridge University Press, Cambridge, pp 26–46
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Diggle PJ (2003) Statistical analysis of spatial point patterns, 2nd edn. Arnold, London
- Esque TC, Webb RH, Wallace CSA, van Riper CIII, McCreedy C, Smythe L (2013) Desert fires fueled by native annual forbs: effects of fire on communities of plants and birds in the lower Sonoran Desert of Arizona. *Southwest Nat* 58:223–233. doi:10.1894/0038-4909-58.2.223

- Fonteyn PJ, Mahall BE (1978) Competition among desert perennials. *Nature* 275:544–545. doi:[10.1038/275544a0](https://doi.org/10.1038/275544a0)
- Fonteyn PJ, Mahall BE (1981) An experimental-analysis of structure in a desert plant community. *J Ecol* 69:883–896. doi:[10.2307/2259643](https://doi.org/10.2307/2259643)
- Goreaud F, Pelissier R (2003) Avoiding misinterpretation of biotic interactions with the intertype K-12-function: population independence vs. random labelling hypotheses. *J Veg Sci* 14:681–692. doi:[10.1111/j.1654-1103.2003.tb02200.x](https://doi.org/10.1111/j.1654-1103.2003.tb02200.x)
- Grissino-Mayer HD, Swetnam TW (2000) Century-scale climate forcing of fire regimes in the American Southwest. *Holocene* 10:213–220. doi:[10.1191/095968300668451235](https://doi.org/10.1191/095968300668451235)
- Kenkel NC (1988) Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69:1017–1024. doi:[10.2307/1941257](https://doi.org/10.2307/1941257)
- Loosmore NB, Ford ED (2006) Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87:1925–1931
- MacMahon JA (1999) Disturbance in deserts. In: Walker LL (ed) *Ecosystems of disturbed ground*, vol 16, 1st edn. Elsevier, Amsterdam, pp 307–330
- Mahall BE, Callaway RM (1992) Root communication mechanisms and intra-community distributions of 2 Mojave Desert shrubs. *Ecology* 73:2145–2151. doi:[10.2307/1941462](https://doi.org/10.2307/1941462)
- McDonald CJ, McPherson GR (2013) Creating hotter fires in the Sonoran Desert: buffelgrass produces copious fuels and high fire temperatures. *Fire Ecol* 9:26–39. doi:[10.4996/fireecology.0902026](https://doi.org/10.4996/fireecology.0902026)
- McDonough WT (1963) Interspecific associations among desert plants. *Am Midland Nat* 70:291–299. doi:[10.2307/2423057](https://doi.org/10.2307/2423057)
- McLaughlin SP, Bowers JE (1982) Effects of wildfire on a Sonoran desert plant community. *Ecology* 63:246–248
- Miriti MN (2007) Twenty years of changes in spatial association and community structure among desert perennials. *Ecology* 88:1177–1190. doi:[10.1890/06-1006](https://doi.org/10.1890/06-1006)
- Mudrak EL, Schafer JL, Fuentes-Ramirez A, Holzapfel C, Moloney KA (2014) Predictive modeling of spatial patterns of soil nutrients related to fertility islands. *Landsc Ecol* 29:491–505. doi:[10.1007/s10980-013-9979-5](https://doi.org/10.1007/s10980-013-9979-5)
- O’Leary JF, Minnich RA (1981) Postfire recovery of creosote bush scrub vegetation in the western Colorado Desert. *Madrono* 28:61–66
- Raventós J, Wiegand T, De Luis M (2010) Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* 91:2110–2120. doi:[10.1890/09-0385.1](https://doi.org/10.1890/09-0385.1)
- Rayburn AP, Schiffers K, Schupp EW (2011) Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community. *Plant Ecol* 212:585–594. doi:[10.1007/s11258-010-9848-0](https://doi.org/10.1007/s11258-010-9848-0)
- Ripley BD (1981) *Spatial statistics*. Wiley, New York
- Rutman S, Dickson L (2002) Management of buffelgrass on Organ Pipe Cactus National Monument, Arizona. In: Tellman B (ed) *Invasive exotic species in the Sonoran region*. University of Arizona Press, Tucson, pp 311–318
- Sagarin R, Pauchard A (2012) *Observation and ecology*. Island Press, Washington, DC
- Schafer JL, Mudrak EL, Haines CE, Parag HA, Moloney KA, Holzapfel C (2012) The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran deserts. *J Arid Environ* 87:129–135. doi:[10.1016/j.jaridenv.2012.07.013](https://doi.org/10.1016/j.jaridenv.2012.07.013)
- Schenk HJ, Holzapfel C, Hamilton JG, Mahall BE (2003) Spatial ecology of a small desert shrub on adjacent geological substrates. *J Ecol* 91:383–395. doi:[10.1046/j.1365-2745.2003.00782.x](https://doi.org/10.1046/j.1365-2745.2003.00782.x)
- Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:1270. doi:[10.2307/2265595](https://doi.org/10.2307/2265595)
- Stoyan D, Stoyan H (1996) Estimating pair correlation functions of planar cluster processes. *Biom J* 38:259–271. doi:[10.1002/bimj.4710380302](https://doi.org/10.1002/bimj.4710380302)
- Sugihara NG, van Wagtenonk JW, Fites-Kaufman J (2006) Fire as an ecological process. In: Sugihara NG, Wagtenonk JW, Fites-Kaufman J, Shaffer KE, Thode AE (eds) *Fire in California’s ecosystems*. University of California Press, Berkeley, pp 58–74
- Sunderman SO, Weisberg PJ (2012) Predictive modelling of burn probability and burn severity in a desert spring ecosystem. *Int J Wildland Fire* 21:1014–1024. doi:[10.1071/wf11172](https://doi.org/10.1071/wf11172)
- Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136:296–301. doi:[10.1007/s00442-003-1264-x](https://doi.org/10.1007/s00442-003-1264-x)
- Whelan RJ (1995) *The ecology of fire*. Cambridge University Press, Cambridge
- Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209–229. doi:[10.1111/j.0030-1299.2004.12497.x](https://doi.org/10.1111/j.0030-1299.2004.12497.x)
- Wiegand T, Moloney KA (2014) *Handbook of spatial point pattern analysis in ecology*. Chapman and Hall/CRC, Boca Raton
- Wiegand T, He F, Hubbell SP (2013) A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography* 36:92–103. doi:[10.1111/j.1600-0587.2012.07361.x](https://doi.org/10.1111/j.1600-0587.2012.07361.x)
- Wilensky U (1999) *NetLogo*. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston. <http://ccl.northwestern.edu/netlogo/>
- Yeaton RI, Travis J, Gilinsky E (1977) Competition and spacing in plant communities: Arizona upland association. *J Ecol* 65:587–595. doi:[10.2307/2259503](https://doi.org/10.2307/2259503)