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ORIGINAL PAPER

An individual-based model of chaparral vegetation response to frequent wildfires

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Abstract The Santa Monica Mountains are home to many species of chaparral shrubs that provide vegetative cover and whose deep roots contribute to the stability of the steep slopes. Recently, native chaparral have been threatened by an unprecedented drought and frequent wildfires in Southern California. Besides the damage from the wildfires themselves, there is the potential for subsequent structural losses due to erosion and landslides. In this paper, we develop a mathematical model that predicts the impact of drought and frequent wildfires on chaparral plant community structure. We begin by classifying chaparral into two life history types based on their response to wildfires. Nonsprouters are completely killed by a fire, but their seeds germinate in response to fire cues. Facultative sprouters survive by resprouting but also rely on seed germination for post-fire recovery. The individual-based model presented here simulates the growth, seed dispersal, and resprouting behavior of individual shrubs across two life history types as they compete for space and resources in a rectangular domain. The model also incorporates varying annual rainfall and fire frequency as well as the competition between plants for scarce resources. The parameters were fit using seedling and resprout survivorship data as well as point quarter sampling data from 1986 to 2014 at a biological preserve within the natural landscape of the Malibu campus of Pepperdine University. The simulations from our model reproduce the change in plant community structure at our study site which includes the local extinction of the nonsprouter *Ceanothus megacarpus* due to shortened fire return intervals. Our simulations predict that a combination of extreme drought and frequent wildfires will drastically reduce the overall density of chaparral, increasing the likelihood of invasion by highly flammable exotic grasses. The simulations further predict that the majority of surviving shrubs will be facultative sprouting species such as *Malosma laurina*.

Keywords Chaparral · Wildfire frequency · Population ecology · Life history type

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Introduction

From 2012 to 2015, California experienced not only the worst drought in the past century according to temperature and precipitation data (Diffenbaugh et al. 2015), but possibly the worst drought in the last 1200 years according to tree ring data from Griffin and Anchukaitis (2014). Several recent models (Cook et al. 2015; Diffenbaugh et al. 2015; Underwood 2015; Swain et al. 2016) predict that the risk of future sustained periods of extreme drought in California has increased due to climate change. They predict that the current trajectory will continue for at least a century and not return to previous conditions. Drought is a large contributor to higher wildfire frequency (Keeley and Zedler 2009; Pausas and Fernández-Muñoz 2012; Pausas et al. 2016) in addition to invasive grasses and urbanization (Pausas and Keeley 2014a). The Santa Monica Mountains, a member of the Transverse Mountain Ranges in Southern California, have an average time between fires of 32 years, but some locations such as Malibu Canyon have an 8 year average fire return interval (Witter et al. 2007). In these areas, the anthropogenic increases in fire frequency have threatened vegetation type conversion of chaparral to a degraded landscape of exotic weeds and coastal sage shrub (Keeley et al. 1999).

Chaparral represent the dominant vegetation type in the Santa Monica Mountains and the shrubs are responsible for maintaining the stability of the steep slopes (Hanes 1971). The roots of chaparral can range from depths of 2 m for *Ceanothus megacarpus* to greater than 13 m for *Malosma laurina* (DeSouza et al. 1986; Davis 1989; Thomas and Davis 1989). Although chaparral persist in a fire-adapted ecosystem, individual species differ in their recovery mechanisms with some species (e.g., *C. megacarpus*) solely recovering through post-fire seed germination, while other species (e.g., *M. laurina*) primarily recover through post-fire resprouting from a root crown. Therefore, some nonsprouting species of chaparral such as *C. megacarpus* suffer from what Zedler (1995) describes as an "immaturity risk" because a short time between wildfires does not allow enough time for seedlings to reach reproductive maturity and build a sufficient seedbank to successfully recover post-fire. The localized extinction of such species due to short fire return intervals (Lucas et al. 2013) opens space for the invasion by exotic grasses that increase flammability and exacerbate fire frequency (Keeley and Brennan 2012; Keeley et al. 1999; Witter et al. 2007). Without sufficient deep-rooted vegetation, slope stability will likely decrease, leading to greater landslides and slope failure (Ainsworth and Doss 1995; Radtke 1983; Cammeraat et al. 2005).

Given the importance of chaparral to the local structures of the Santa Monica Mountains and the costs associated with disturbances such as wildfires, extreme soil erosion and landslides, there are well-defined benefits to developing mathematical models that predict the impact of drought and frequent wildfires on chaparral plant community structure. Previously, Lucas et al. (2013) used discrete population models of individual species to predict that chaparral community structure is threatened by average fire-return intervals of less than 12 years. Although these models were fit using chaparral survivorship data from a period of severe drought, they do not incorporate variable rainfall and do not account for the spatial organization of the chaparral within the landscape. Zedler and Seiger (2000) and Keeley and Zedler (2009) have developed such models, but in order to describe larger portions of the landscape, they were forced to assume individual stands were exclusively composed of a single dominant species in that area. In contrast, we will consider a model that describes the growth, seed dispersal, and resprouting behavior of individual shrubs from several interacting species that compete for space and resources. This model is intended to capture the realistic population dynamics of several species in a mixed chaparral community and predict the changes to the vegetative landscape that occur in response to current trends of enhanced drought and frequent wildfires.

Chaparral life history types

Chaparral species can be divided into three life history types relative to their individualized response to wildfire. These broad categories are described in Lucas et al. (2013), Pratt et al. (2008), and Witter et al. (2007) and are pictured in Fig. 1. Post-fire nonsprouters (sometimes referred to as obligate seeders) are completely killed by fire, leaving unoccupied soil for fire-promoted seed germination and an open canopy for seedling establishment in direct sunlight. In contrast, obligate sprouters survive after fire exclusively through vegetative resprouting because seeds are killed by fire and seedlings emerge only under deep shade of closed canopies during fire-free intervals. Facultative sprouters rely on a combination of both vegetative resprouting and seed germination for post-fire recovery. Seedlings of facultative sprouters typically recruit under the partial shade of post-fire resprouts. Within these three life history types, each individual species varies in seedling survival and resprout success (Frazer and Davis 1988; Thomas and Davis 1989; Pratt et al. 2012).

Empirical data

The individual-based model described in this paper draws from a longitudinal study of the survivorship of the nonsprouter *C. megacarpus* (Cm) and facultative sprouters

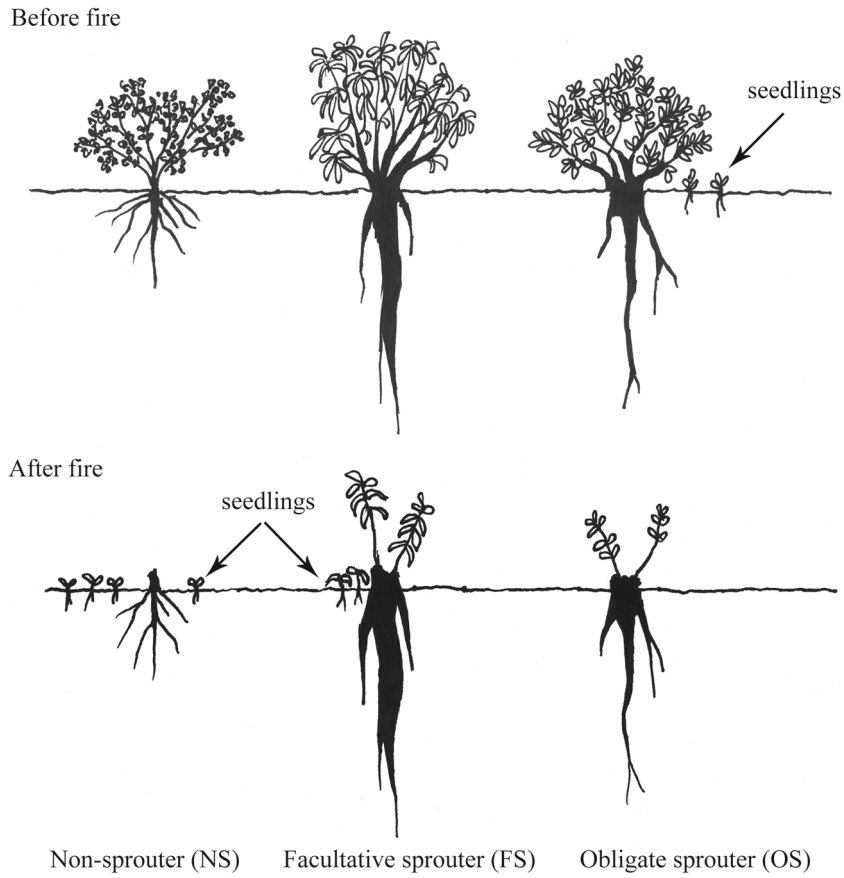

Fig. 1 A visual comparison of the resprout and seedling recruitment strategies of nonsprouting, facultative sprouting, and obligate sprouting species a few months before fire and a few months after fire. Note that OS seedlings before fire are killed by the fire event with no emergence of new seedlings after fire. In contrast, NS and FS seedlings only emerge after fire because seeds require a fire cue to germinate. Adapted from the first figure in Pratt et al. (2008)

Ceanothus spinosus (Cs), *Malosma (Rhus) laurina* (Ml), and *Rhus ovata* (Ro) at a biological preserve in the natural landscape of the Malibu campus of Pepperdine University. The study began after the Piuma Fire of October 14, 1985 near Malibu, CA, and the first results are described in Frazer and Davis (1988), Thomas and Davis (1989), and Saruwatari and Davis (1989). Data collection has continued through 2014 and includes the Malibu Fire in 1993, the Calabasas Fire in 1996, and the Canyon Fire in 2007 each of which burned the entire study site and were classified as stand replacement fires. The collected data include post-fire resprout success, seedling emergence, and seedling establishment as well as point-quarter sampling of chaparral community structure during post-fire succession. Although the study site contains two species of obligate sprouters, *Heteromeles arbutifolia* and *Rhamnus ilicofia*, there are very few individuals present. For this reason, we chose to focus our model on nonsprouters and facultative sprouters.

Lucas et al. (2013) analyzed the survivorship data for *C. megacarpus*, *C. spinosus*, *M. (Rhus) laurina* from 1986 to 1993 that are displayed in Fig. 2. As part of the longitudinal study, seedlings of each species were monitored at 21 permanent quadrats after the Piuma Fire in 1985. The seedling survivorship for the nonsprouter *C. megacarpus* was the highest at 42% after 2 years and 25% after 7 years. For the facultative sprouter, *C. spinosus* the initial survivorship was 18% after 2 years, but dropped to 1% after

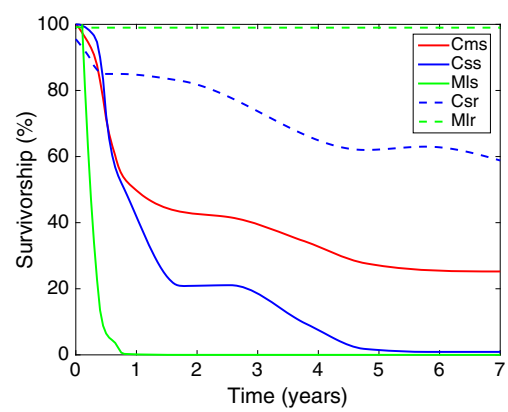

Fig. 2 Survivorship of three species of chaparral resprouts and seedlings between wildfires in 1985 and 1993 as seen in Lucas et al. (2013), Thomas and Davis (1989), and Witter et al. (2007). *C. megacarpus* seedlings (Cms) had the highest seedling survivorship with 25% while 1% of *C. spinosus* (Css) and 0% *M. laurina* seedlings (Mls) survived 7 years. In contrast, 99% of *M. (Rhus) laurina* resprouts (Mlr) and 62% of *C. spinosus* resprouts (Csr) survived 7 years while no *C. megacarpus* adults survived

7 years presumably due to protracted drought. Less than 1% of *M. laurina* seedlings survived the first year. Longitudinal resprout success and resprout survival were determined by permanently tagging 100 burnt stumps of *C. spinosus* and *M. laurina* immediately after the wildfire of 1985. Initially, *C. spinosus* had 83% resprout success with 62% survival over 7 years while *M. laurina* had 100% resprout success with 99% survival over 7 years. As expected, there were no *C. megacarpus* resprouts. The short fire-return interval between 1985 and 1993, in combination with protracted drought, did not allow significant numbers of *C. megacarpus* seedlings to become reproductively mature and release seeds, resulting in localized extinction of the nonsprouter in 1993. *C. spinosus* and *M. laurina* survived the fires in 1993 and 1996 through repeated resprouting, but no seedlings emerged after the fire in 1996, presumably due to the lack of time to accumulate a significant seed bank.

The study site was fully characterized using the method of point quarter sampling which is described in Mitchell and Colleges (2007). The site contains a four by eight grid of permanent rebar poles that are spaced 10 m apart for a total rectangular survey area of 3200 m^2. The space surrounding the point at which each pole is inserted into the ground was divided into four quadrants along north-south and east-west axes. In each quadrant, the distance to the closest chaparral shrub or seedling was measured and the species, height, crown diameter, and basal diameter were recorded. This method produces a statistical sampling of 128 shrubs over a 3200 m^2 area that served as a description of the plant community structure. Table 1 shows that from 1985 to 2014, the relative density of the highly successful resprouters *M. laurina* and *R. ovata* increased while the less successful sprouter *C. spinosus* decreased. The decrease in *C. spinosus* resprout success after fire during the 1985 to 2014 sampling period is consistent with other reports in the literature (Pratt et al. 2014). These data also confirm the localized extinction of *C. megacarpus* after the Malibu Fire in 1993.

Table 1 A comparison of the relative densities of four species of chaparral at the Malibu study site in 1985 and 2014

Species	Relative density 1985 (%)	Relative density 2014 (%)	Change in relative density 1985–2014 (%)
Cm	17.9	0.0	−17.9
Cs	26.0	22.4	−3.6
Ml	37.4	52.8	15.4
Ro	18.7	24.8	6.1

The chaparral species are the nonsprouter *Ceanothus megacarpus* (Cm) and the facultative sprouters *Ceanothus spinosus* (Cs), *Malosma laurina* (Ml), and *Rhus ovata* (Ro)

Life history models

Lucas et al. (2013) provide conceptual models of the nonsprouter and facultative sprouter that will serve as a basis for our individual-based model. These diagrams are similar to those for annual plants found in Weiner and Conte (1981) and contain similar ideas to those for chaparral in Zedler (1995) and Pausas and Keeley (2014b). From these diagrams, we are able to construct an annual sequence of events that describe how to update the status of each model plant during the seed, seedling, and adult life stages.

Nonsprouters

Prefire adults of nonsprouting species are killed by fire and persist only by post-fire germination of seeds (Lucas et al. 2013). Figure 3 depicts the transitions between three life phases of a nonsprouting chaparral plant: seed, seedling, and reproductively mature shrub. Each spring the reproductively mature plants drop seeds, but predators will consume approximately 90% of the seeds in the soil (VanElderen et al. 1988). Surviving seeds will not germinate until they receive a fire cue (smoke, chemicals released from charred wood, or heat) (Schlesinger et al. 1982; Keeley 1991, 1997; Keeley and Fotheringham 1997). Nonsprouter seedlings preferentially germinate in open canopy regions previously occupied by their parents. They survive best in direct sunlight and typically experience moderate mortality due to depletion of soil moisture by shallow roots during the first dry summer after wildfire (Pratt et al. 2008; Saruwatari and Davis 1989; Thomas and Davis 1989). Additional contributions to seedling mortality include competition (Schlesinger et al. 1982; Tyler 1996) and herbivory (Mills 1986). Seedlings become reproductively mature after approximately 6 years (Zammit and Zedler 1993). Mature plants can live for over 100 years in the absence of fire (Keeley 1975).

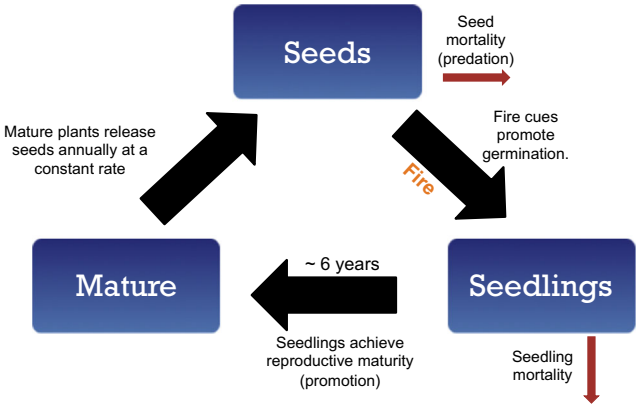

Fig. 3 The three phases of the nonsprouter (NS) population cycle

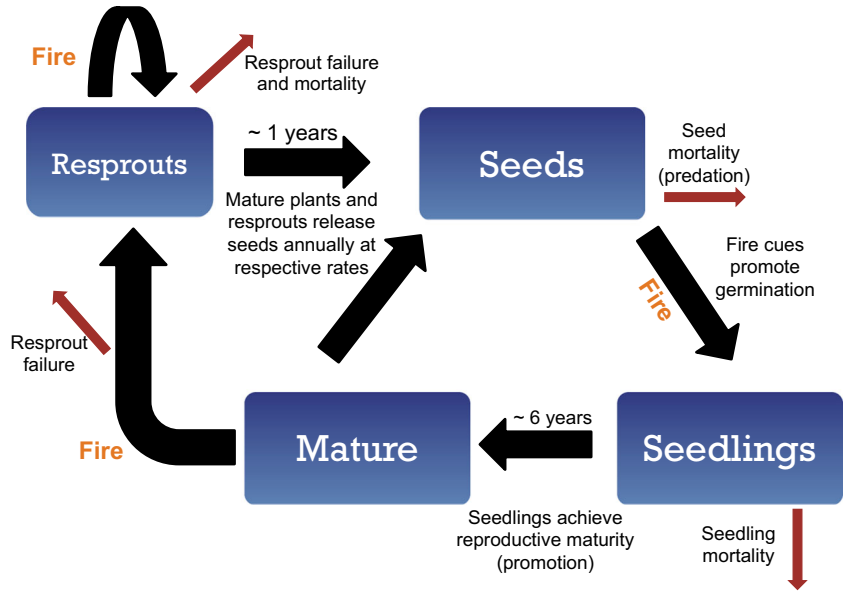

Fig. 4 The four phases of the facultative sprouter (FS) population cycle

Facultative sprouters

Facultative sprouters have a dual response to wildfires with seeds that germinate in response to fire cues and vegetative resprouting from a root crown (Lucas et al. 2013). Figure 4 is similar to the nonsprouter life cycle, but includes a fourth category of resprouts that emerge from the burned root crowns of prefire resprouts and mature shrubs (Keeley and Zedler 1978). As seen previously in Fig. 2, resprout success and mortality rates vary amongst facultative sprouting species. Successful resprouts are able to release a small number of seeds during the first year post-fire and that number grows annually until the shrub recovers its prefire size. Like nonsprouters, the seeds of facultative sprouters only germinate in response to fire cues and seedlings become reproductively mature after approximately 6 years (Zammit and Zedler 1993). As previously stated in the discussion of Fig. 2, seedlings of facultative sprouters experience higher mortality than nonsprouting species (Frazer and Davis 1988; Thomas and Davis 1989; Pratt et al. 2008).

An individual-based model

Our model consists of individual plants that are located on a 40 m by 80 m domain that simulates the Malibu study site. The individual plants are implemented as classes in MATLAB that are stored in a virtual study site. Each shrub is specified by a location, species, age, crown radius, and height. These plants are updated on an annual basis according to the sequence of events described in Fig. 5. After a wildfire, which generally occurs during the late summer or early fall, resprouts emerge, and a proportion of seeds are promoted to germinate and become new seedlings. The resprouting behavior differs based on the species of each shrub. Seedlings and mature shrubs grow each year based on annual precipitation as described in "Shrub growth" section, but that growth (canopy expansion and height) can be inhibited by canopy overlap with nearby plants. Resprouts and mature plants release seeds in the spring as described in "Seed dispersal and germination" section, but approximately 90% of these seeds are eaten by

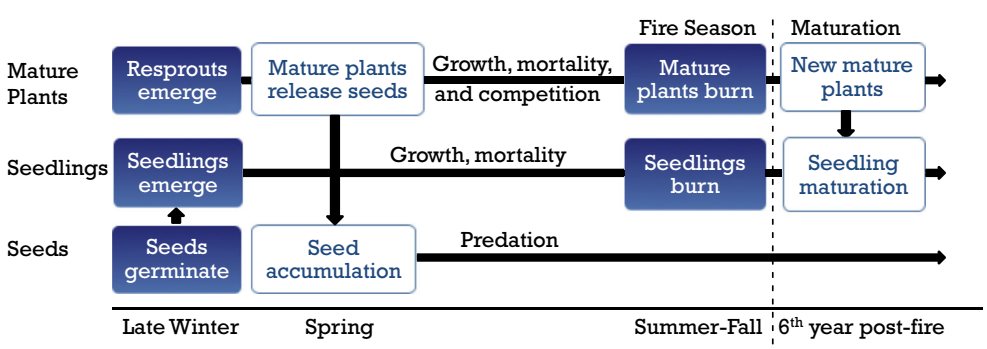

Fig. 5 Annual cycle of events for chaparral. Events in *filled boxes* only occur in the year that directly follows a wildfire. The seedlings and mature populations are updated in early February after seedlings emerge post-fire. Seedling and resprout mortality occur throughout the year. Seedling maturation only occurs in the sixth year post-fire

predators (VanElderen et al. 1988). Each year, a proportion of resprouts and seedlings die due to water stress and competition for light, space, and limited resources as described in "Survivorship and local competition" section. The annual cycle repeats and seedlings become reproductively mature saplings after a 6-year fire-free interval. A wildfire will burn all plants and the cycle is restarted in the following winter.

The simulations are initialized with a field of plants whose locations are uniformly distributed throughout the domain so that there is minimal crown overlap between individual shrubs. The species, initial heights, and crown radii are sampled from a distribution that closely matches the chaparral population statistics just before a wildfire. The initial seedbank is populated with the long-term distribution of seeds that arises from the annual release of seeds by the individual shrubs and 90% removal by predators.

External factors

The two external factors that we vary in our model are annual precipitation and fire return intervals. The annual precipitation will influence plant growth and survivorship as outlined in the following sections. Since we are modeling a small section of the biological preserve, we assume that a wildfire will burn all of the existing plants in our field study site. Each fire event begins a new cycle of resprouting and seed germination.

Lucas et al. (2013) sampled the fire return interval from a Poisson distribution for several different means. As proposed in Johnson and Gutsell (1994), we chose to use the Weibull distribution,

$$f(x;\beta,\lambda) = \frac{\beta}{\lambda}\left(\frac{x}{\lambda}\right)^{\beta-1} e^{(-x/\lambda)^{\beta}}, \quad x \geq 0, \tag{1}$$

to simulate fire return intervals in the individual-based simulation. This distribution incorporates an aging effect that increases the likelihood of a wildfire over time. This reflects the behavior of our system where soon after a wildfire, a repeat fire is unlikely, but over time plants increase fuel load to support the next wildfire. The four recent fires that burned our study site are not sufficient to estimate the shape, β, and scale, λ, parameters. To match the fire frequency of our study site, we set $\beta = 2.5$ and $\lambda = 8.45$ which correspond to a mean time between fires of 7.5 years, but make it very unlikely that a simulated fire would occur within 3 years. To investigate the effect of varying fire-return intervals on species survivorship and vegetation cover at our study site, we vary λ from 1 to 34 which corresponds to an average fire return interval of 1 to 30 years.

The most complete historical database of annual precipitation near our study site is from Los Angeles International Airport (Western Regional Climate Center 2015). Figure 6 displays annual precipitation with the best-fit parameters for several distributions and the corresponding Akaike information criterion (AIC). The distribution that best fits the annual precipitation from 1945 to 2015 is a log-normal distribution,

$$f(x) = \frac{1}{x\sigma\sqrt{2\pi}} e^{-\frac{(\ln x-\mu)^2}{2\sigma^2}}, \quad x > 0,$$

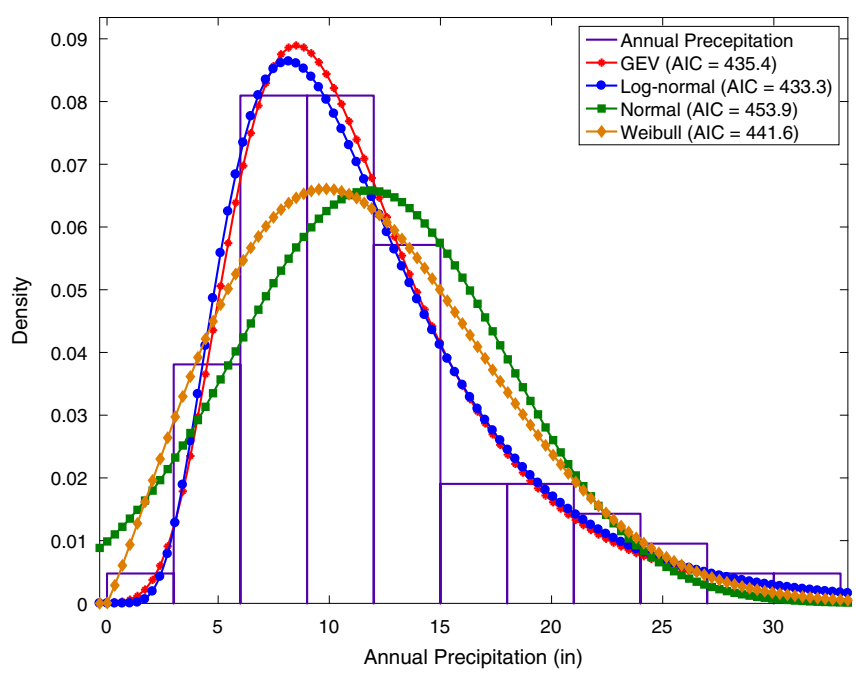

Fig. 6 Histogram of annual precipitation at Los Angeles International Airport from 1945 to 2015 (Western Regional Climate Center 2015) with the best-fit generalized extreme value, normal, log-normal, and Weibull distributions and corresponding AIC

with $\mu = 2.35$ and $\sigma = 0.50$, which corresponds to an average annual precipitation of 11.88 in. To investigate the effect of annual precipitation on shrub growth and survivorship, we vary μ from 2.178 to 2.514 which corresponds to means of 10 and 14 in.

Shrub growth

To model the growth of resprouts and seedlings, we utilized the point-quarter sampling data collected at our study site. The longest fire-free intervals in our data set are 1986–1993 and 1996–2006. Since all four species are present from 1986 to 1993, we used these data to estimate parameters for several growth models and select the best fit. There were fewer observations from 1996 to 2006 and therefore we chose to use the data from this interval to validate our choice of model.

Figure 7 shows the annual precipitation from 1986 to 1993 as well as the corresponding average height and crown diameter of the three species of facultative sprouters. These data suggest that growth was reduced during drought and enhanced during an abundance of rain. We hypothesized that annual growth in height and crown diameter are proportional to precipitation, but that growth decays over time. Therefore we considered models of the form

$$\Delta h(w,t) = awe^{-bt}, \quad \Delta h(w,t) = \frac{aw}{t}, \quad \text{and} \quad \Delta h(w,t) = \frac{aw}{t^b}$$

where Δh is the change in height, w is the annual precipitation, t is the time since the last wildfire in years, and a, b are constants. Using the average heights from 1986 to 1993, we estimated the growth parameters with the curve fitting tools in MATLAB for the facultative sprouters, *C. spinosus*, *M. laurina,* and *R. ovata* for each of the three models. The results are displayed in Fig. 8 with the corresponding best-fit parameters, residual sum of squares (RSS) and Akaike information criterion (AIC). We then used these parameters to predict the average increase in height for resprouts from 1996 to 2006 and the results are displayed in Fig. 9. Although the third model has a lower RSS, we chose the second model,

$$\Delta h(w,t) = a_h \frac{w}{t}, \tag{2}$$

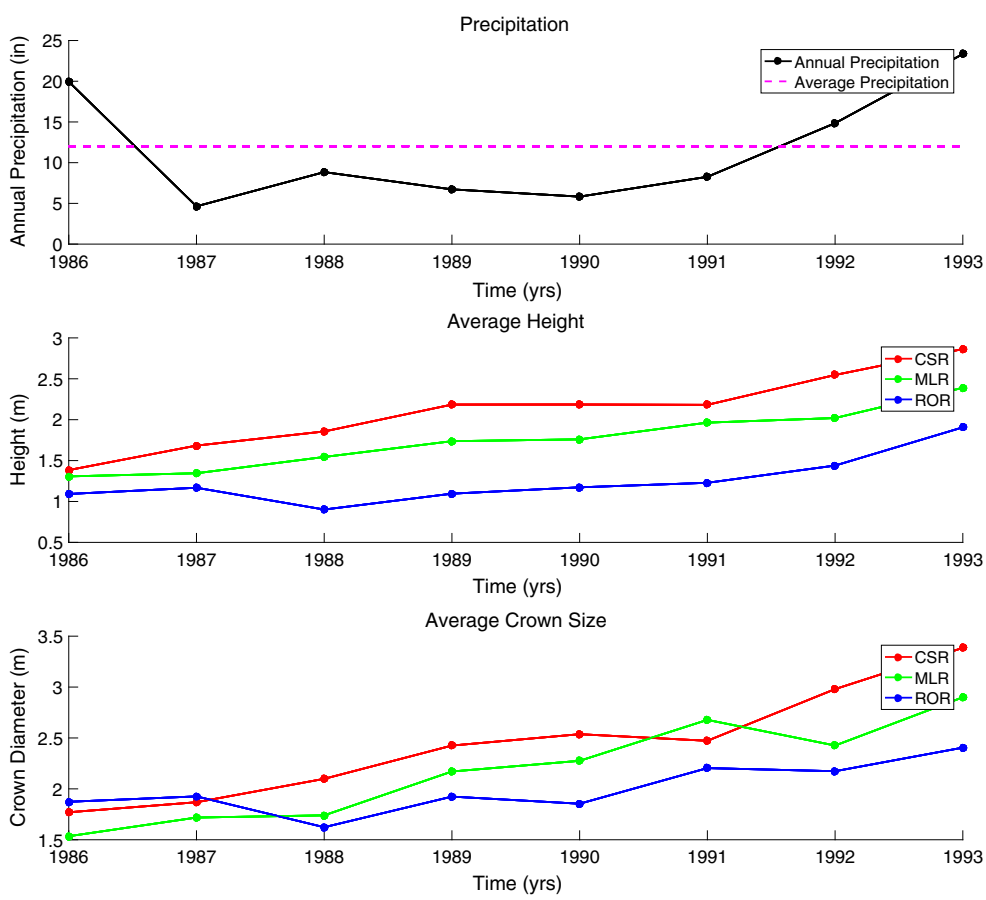

Fig. 7 Annual precipitation at Los Angeles International Airport from 1986 to 1993 with an average precipitation of 11.88 in (Western Regional Climate Center 2015). The corresponding average height and average crown diameter of *C. spinosus*, *M. laurina* and *R. ovata* from 1986 to 1993

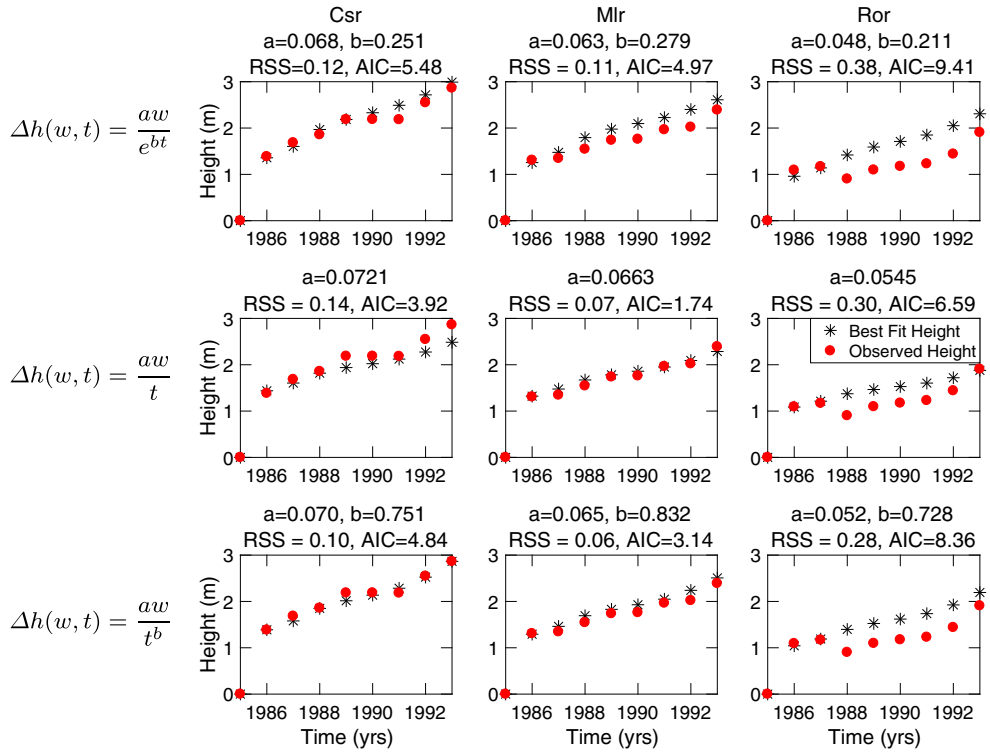

Fig. 8 Best fits versus average observed heights of *C. spinosus* (Csr), *M. laurina* (Mlr), and *R. ovata* (Ror) resprouts from 1985 to 1993 with the corresponding growth parameters, RSS and AIC

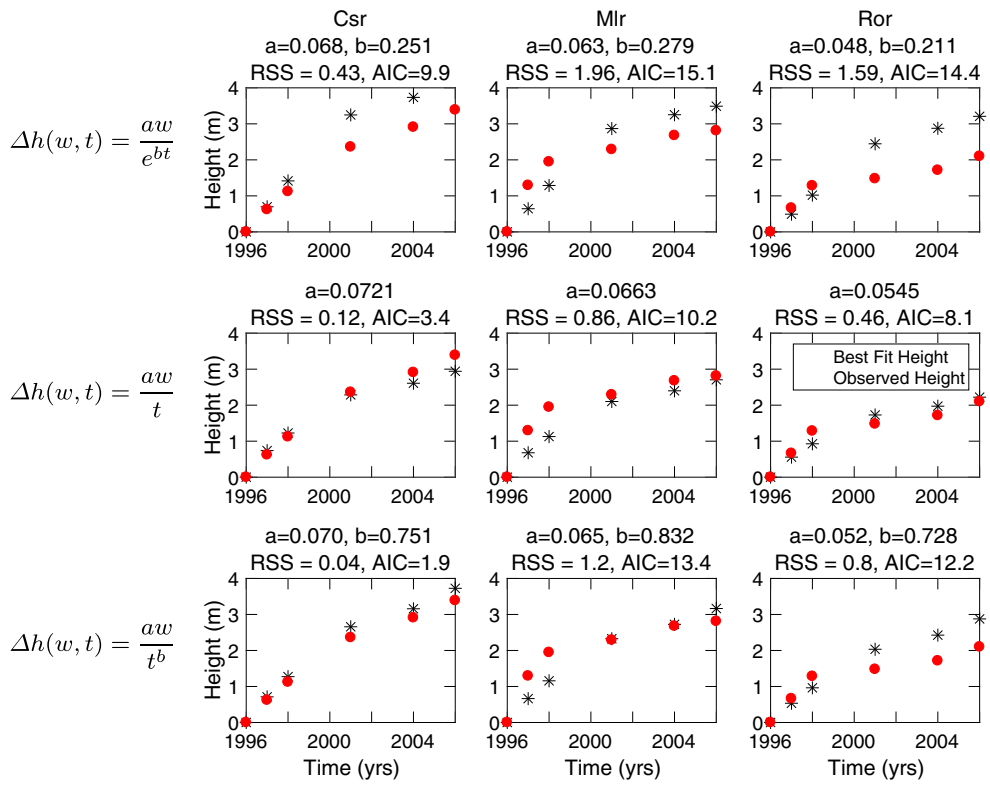

Fig. 9 Projected heights of *C. spinosus* (Csr), *M. laurina* (Mlr), and *R. ovata* (Ror) resprouts versus average observed heights from 1996 to 2006 with the corresponding growth parameters, RSS and AIC

Table 2 A comparison of the estimated resprout growth parameters for *C. spinosus* (Cs), *M. laurina* (Ml), and *R. ovata* (Ro)

Species	Height mean growth $\bar{a}_h$	Std Dev s_h	Crown mean growth $\bar{a}_r$	Std Dev s_r
Csr	0.0721	0.0240	0.0907	0.0350
Mlr	0.0663	0.0210	0.0774	0.0290
Ror	0.0545	0.0170	0.0884	0.0310

which only depends on one parameter and therefore has a lower AIC. The results for crown radius growth Δr were similar and best modeled by

$$\Delta r(w,t) = a_r \frac{w}{t}. \tag{3}$$

The growth parameters that best fit the 1985–1993 data for each resprout species are given in Table 2. The curve fitting tools in MATLAB also provide confidence intervals from which we calculated the standard deviations for the growth parameters and those are also recorded in Table 3.

We chose to model the annual growth of seedlings as proportional to the current height

$$\Delta h(t) = \alpha_h h(t) \tag{4}$$

or current crown radius

$$\Delta r(t) = \alpha_r r(t). \tag{5}$$

Figure 10 shows the best fit for *C. megacarpus* and *C. spinosus* seedling height and crown growth. Nearly all of the seedlings for *M. laurina* and *R. ovata* die within the first year, so there is not enough data to estimate growth parameters. Due to the short fire return interval between 1993 and 1996, there were no *C. megacarpus* or *C. spinosus* seedlings in our study site from 1996 to 2006 and therefore we could not validate the model in the same way as we did for the resprouts. The growth parameters that best fit the 1985–1993 data each seedling species including standard deviation are given in Table 3.

Table 3 A comparison of the estimated seedling growth parameters for the nonsprouter *C. megacarpus* (Cm) and the facultative sprouter *C. spinosus* (Cs)

Species	Height mean growth $\bar{\alpha}_h$	Std Dev s_h	Crown mean growth $\bar{\alpha}_r$	Std Dev s_r
Cms	0.2658	0.0684	0.3525	0.0865
Css	0.2595	0.0937	0.3392	0.1409

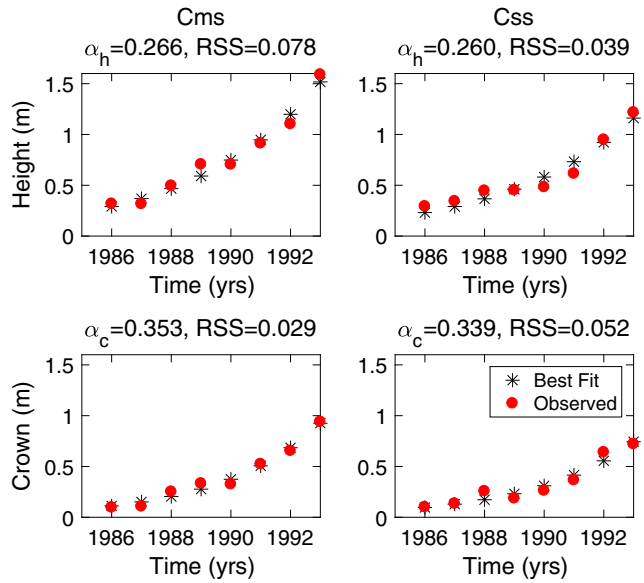

Fig. 10 (*Left*) Best fits of *C. megacarpus* (Cms) and *C. spinosus* (Css) seedling heights from 1985 to 1993 with the corresponding growth parameters and RSS. (*Right*) Best fits of Cms and Css crown widths from 1985 to 1993

Table 2 gives the mean growth parameter $\bar{a}$ and corresponding standard deviation s for each species of seedling and resprout. After a wildfire, each resprout is assigned a height growth parameter a_h and crown growth parameter a_r that are drawn from a normal distribution with mean $\bar{a}_h$ and standard deviation s_h or mean $\bar{a}_r$ and standard deviation s_r. The annual growth of each seedling is then proportional to height as in Eq. 2 or crown radius as in Eq. 3. Each new fire-germinated seedling is also assigned height and crown growth parameters in the same way and the annual growth in height and crown radius are given by Eqs. 4 and 5, respectively.

Seed dispersal and germination

The fruit of *Ceanothus* species contains three seeds, each with a thick coat. As the fruit dries, the capsule explodes and propels the seeds up to a maximum distance of 10 m (Evans et al. 1987; Keeley 1987). Based on experiments from Evans et al. (1987) with several species of *Ceanothus,* we assume that one third of seeds released by each *Ceanothus* shrub are uniformly distributed underneath the canopy. The distances of the remaining seeds are distributed exponentially with a mean of 2.35 m and the angle is distributed uniformly on $[0, 2\pi]$. A sample seed distribution for a single plant is pictured in Fig. 11. The fruit of *M. laurina* and *R. ovata* are not ballistic, and thus seeds are dropped closer to the

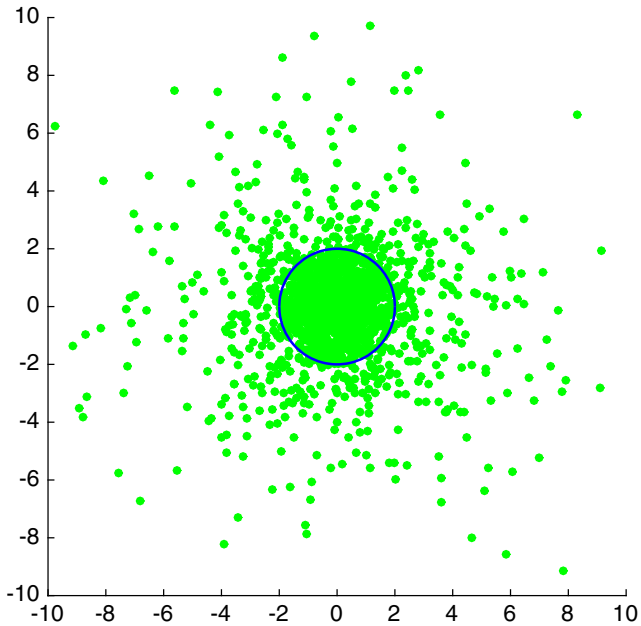

Fig. 11 A sample seed distribution from an individual plant with 2000 seeds. The *circle* represents a plant canopy of radius 2 m and the *dots* represent the seeds. One third of the seeds are distributed uniformly underneath the canopy. The distances of the remaining seeds are distributed exponentially and the angle is uniformly distributed on $[0, 2\pi]$

parent plant except when disseminated by birds or other animals. Since the mortality rate of their respective seedlings is extremely high, we assume that the seed distribution will be similar to *Ceanothus* species with a smaller mean distance.

Regardless of species, each year approximately 90% of seeds reaching the soil are eaten by predators (VanElderen et al. 1988). For computational efficiency, we only distribute the number of seeds that will germinate and become seedlings after a wildfire. As described in Davis (1989), we assume that the average number of seedlings per adult is 4.3 for the nonsprouter *C. megacarpus*, 8.8 for the facultative sprouter *C. spinosus,* and 40.1 for the facultative sprouter *M. laurina*. Since we do not have similar data for *R. ovata,* we assume that the number of seedlings per adult is comparable to *M. laurina*.

Survivorship and local competition

Lucas et al. (2013) observed that the survivorship of seedlings and resprouts displayed in Fig. 2 could be modeled by a logistic or Gompertz curve. These first chaparral population models assumed that more seedlings and resprouts appear after a wildfire than will eventually survive and therefore decline to a carrying capacity. For the individual-based model, we consider a model of competition with neighboring plants proposed in Weiner (1982). The probability of survival S_p for an individual plant p incorporates the survival probability based solely on the amount of resources available R and the local competition K_p,

$$S_p = \frac{R_p}{1 + K_p}.$$

Furthermore, our model utilizes size-asymmetric competition in which larger individuals have a disproportionately larger competition effect on smaller plants and are not as affected by the smaller plants in their growth. As in Thomas and Weiner (1989), the competition factor K_p for each shrub p is based on the size $V_p = \pi r_p^2 h_p$, where r_p is the crown radius and h_p is the height, and the distance from neighboring plants d_{np},

$$K_p = \sum_n \frac{c_p}{d_{np}^2} \frac{V_n}{V_p}. \tag{6}$$

The neighboring plants n in Eq. 6 are defined as those within a 5-m radius of the shrub p. This corresponds to half the distance between two poles in the point quarter samples of our study site. The competition weights c_p were fit by minimizing the residual sum of squares (RSS) of simulated survivorship versus the survivorship data from 1986 to 1993 in Fig. 2 and are displayed in Table 4.

The parameter R_p gives the probability of seedling or resprout survival without the effects of competition. As seen in Fig. 12, the highest mortality rates for *Ceanothus* occur in the first year when competition is the highest and in years where the annual precipitation dips below 8 in. To that end, we set the survival probability R_p for *Ceanothus* species to 1.0 for annual precipitation above 8 in and estimate R_p using the survivorship data from 1986 to 1993 in Fig. 2. As discussed previously for *M. laurina* and *R. ovata*, the survivorship of resprouts is 99% and the survivorship of seedlings is less than 1%. Therefore, we set the survivorship probabilities for each resprout species at 0.99 and seedling species at 0.01 and ignore the competition factors for simplicity.

As described previously, each shrub has a specified height and crown size. The crown radius is stored as four distinct radii that define the shape of each plant as four quarter ellipses as in Fig. 13. Initially, our simulated plants are

Table 4 A comparison of the estimated drought survival R_p and competition weights c_p for *C. megacarpus* (Cm) and *C. spinosus* (Cs)

Species	Drought survival R_p	Competition weight c_p
Cms	0.80	0.002
Css	0.55	0.002
Csr	0.95	0.035

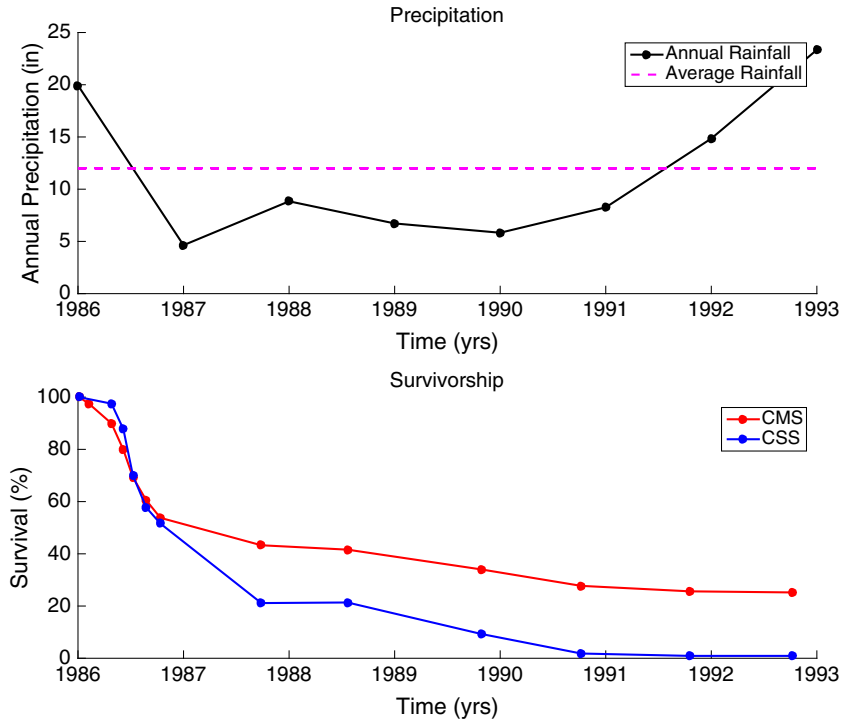

Fig. 12 Annual precipitation at Los Angeles International Airport from 1986 to 1993 with an average precipitation of 11.88 in (Western Regional Climate Center 2015). The corresponding survivorship percentage for *C. megacarpus* seedlings and *C. spinosus* seedlings and resprouts from 1986 to 1993

circular but in crowded areas a plant's growth can be inhibited by limitations of space. If two plants overlap, the growth of the overlapping radii is inhibited at a rate proportional to the overlap. Figure 13 shows three plants that have grown in close proximity and caused their shapes to deform. The simulation also allows for smaller plants to die due to larger plants overtaking their space.

Model validation

As discussed in "An individual-based model" section, the growth, competition, and survivorship parameters for each species of chaparral were fitted using point-quarter and species survivorship data collected from 1986 to 1993. This is the longest fire-free interval in which all four species exist at our study site and there is data available from almost every year. To validate the model, we simulated the Malibu study site from 1985 to 2014 using annual precipitation from Los Angeles International Airport (Western Regional Climate Center 2015) and the wildfire dates in 1985, 1993, 1996, and 2007. The initial relative densities of chaparral species in the simulations were set to closely match those of the Malibu study site in 1985. Table 5 shows that the final relative densities of each species over 1000 simulations are close to those recorded at the Malibu study site in 2014.

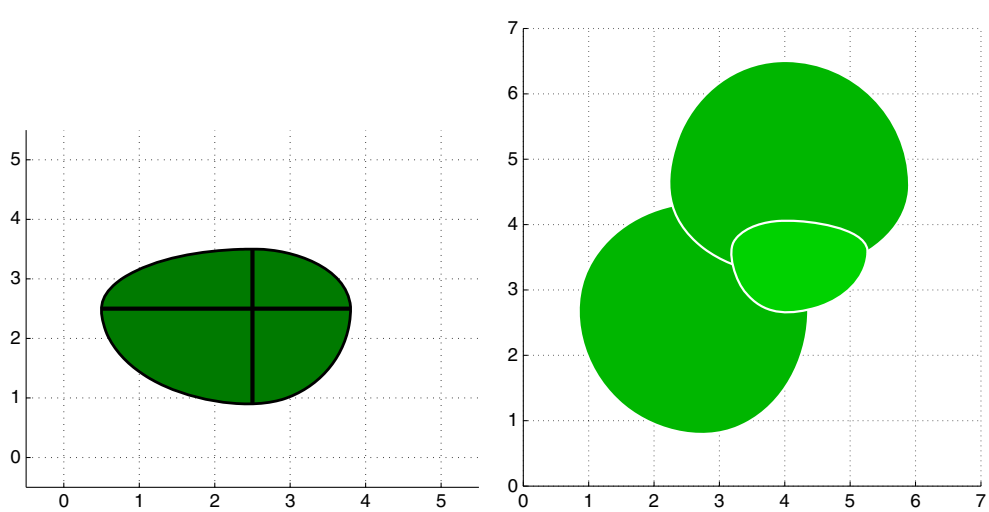

Fig. 13 (*Left*) An example of a plant with four distinct radii. (*Right*) An example of three plants that have grown in close proximity causing their shapes to deform

Table 5 A comparison of the actual and simulated relative densities of four species of chaparral at the Malibu study site in 1985 and 2014

	Relative density 1985		Relative density 2014		Change in density	
Species	Actual (%)	Simulation (%)	Actual (%)	Simulation (%)	Actual (%)	Simulation (%)
Cm	17.9	17.0	0.0	0.0	−17.9	−17.0
Cs	26.0	27.3	22.4	21.1	−3.6	−6.2
Ml	37.4	37.6	52.8	55.2	15.4	17.6
Ro	18.7	18.0	24.8	23.7	6.1	5.7

Figure 14 shows an aerial view of the Malibu study site in 2014 and the output from a simulation of the study site as described above. Using the aerial view, we determined that the chaparral canopy covers 51% of the study site. The average final canopy coverage in 2014 over 1000 simulations of the study site from 1985 to 2014 was 54.2% with a standard deviation of 1.9%. A sample simulation is also included in Fig. 14 for comparison.

We varied the parameters in Table 4 in order to determine the sensitivity of the resulting canopy coverage and relative densities from Table 5. Varying the seedling competition weight c_p by 0.001 for either *Ceanothus* species changes the final canopy coverage by 0.8% and the relative densities up to 2.0%. In contrast, varying the resprout competition weight c_p for *C. spinosus* by 0.05 changes the final canopy coverage by 0.7% and the relative densities up to 2.0%. Finally, varying the drought survival R_p of either *Ceanothus* species by 0.05 changes the final canopy coverage by 0.8% and the relative densities up to 3.0%.

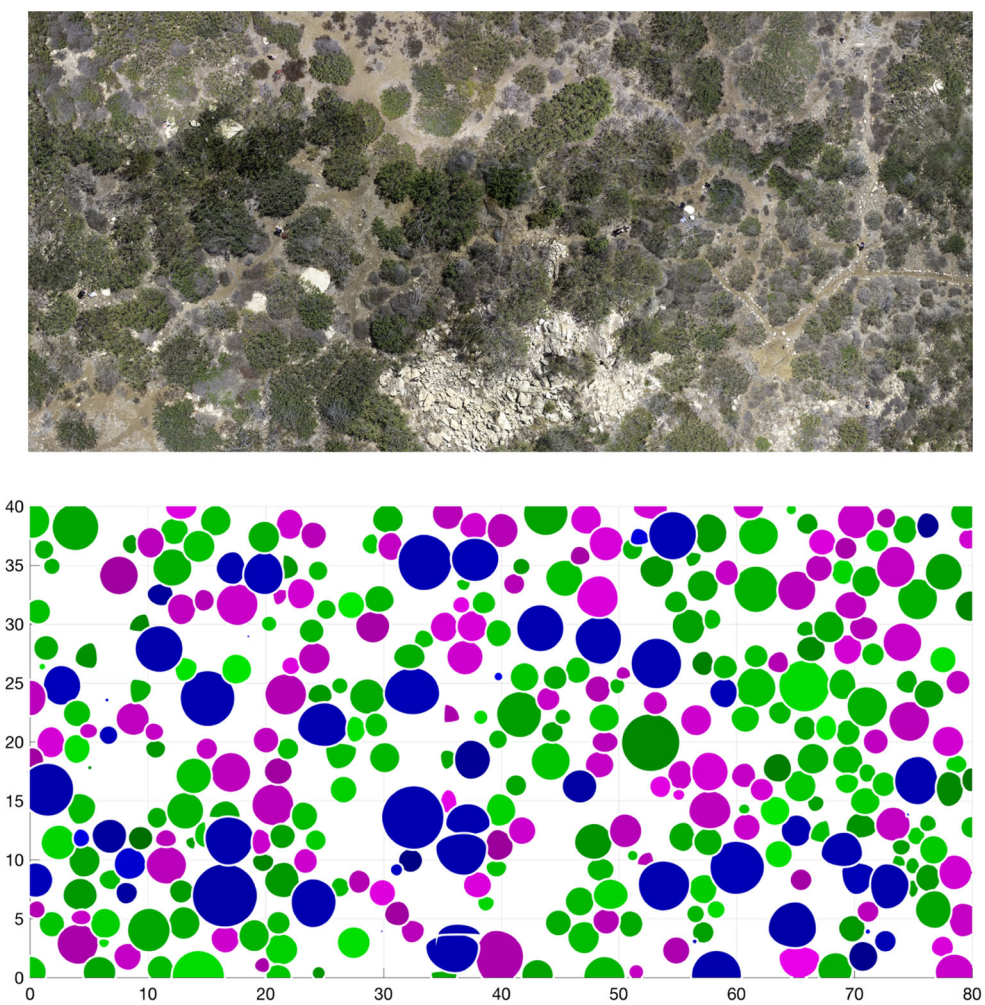

Fig. 14 (*Top*) An aerial view of the 3200 m^2 Malibu study site. The chaparral canopy covers 51% of the study site. Photo by R. Brandon Pratt. (*Bottom*) The final output from a simulation of the 3200 m^2 study site from 1985 to 2014 which includes wildfires in 1985, 1993, 1996, and 2007. The species are identified by color, including the nonsprouter *C. megacarpus* (*Red*) and facultative sprouters *C. spinosus* (*Blue*), *M. laurina* (*Green*), and *R. ovata* (*Purple*). The shade of each plant indicates the relative height with darker shades representing taller plants. The initial relative density closely matches the data from 1985 in Table 5 and the annual precipitation is taken from Los Angeles International Airport (Western Regional Climate Center 2015) and the simulation includes wildfires in 1985, 1993, 1996 and 2007. The chaparral canopy covers 56% of the simulated study site

Simulations and results

We begin by presenting several examples of simulations that demonstrate the effects of varying external parameters such as annual precipitation and fire return interval. The annual precipitation in each simulation is distributed log-normally with a mean of either 10 in (low), 12 in (normal), or 14 in (high) as described in "External factors" section. The normal annual rainfall corresponds to the average rainfall from 1945 to 2015 (11.88 in) and the low annual rainfall corresponds to the average rainfall from 2000 to 2015 (10.28 in). The fire return intervals (FRI) are sampled from a Weibull distribution as described in "External factors" section with $\beta = 2.5$ and $\lambda = 8.45$ or $\lambda = 16.9$ which corresponds to an average fire return interval of 7.5 or 15 years. Figure 15 shows the final output for several simulations of a 3200 m^2 domain for 60 years. We observe that the average plant size and overall canopy coverage increases with increases in annual precipitation. We also observe that the nonsprouter *C. megacarpus* is only present in the simulations with a 15-year average fire return interval and that the overall canopy coverage is greater for those simulations.

We now consider the impact of annual precipitation and fire return interval on the plant community structure of our model study site. For each simulation, the initial relative density of *C. megacarpus* (Cm), *C. spinosus* (Cs), *M. laurina* (Ml), and *R. ovata* (Ro) closely matches the data from 1985 in Table 5. We vary the average fire return interval (FRI) from 1 to 30 years using a Weibull distribution with $\beta = 2.5$ and $1 \leq \lambda \leq 34$. The length of each simulation is 60 years. The annual precipitation in each simulation is distributed log-normally with an average of either 10 in (low), 12 in (normal), or 14 in (high). We define the final canopy density to be the total area of the plants at the end of a simulation divided by the 3200 m^2 domain.

Figure 16a shows the average final canopy density versus average fire return interval where each data point represents an average over 500 simulations. We observe that the canopy density decreases sharply as average fire return interval decreases below 10 years. The canopy density increases slowly or remains relatively constant as fire return interval increases beyond 15 years depending on the level of precipitation. We also observe that the average final canopy density is reduced for lower annual precipitation

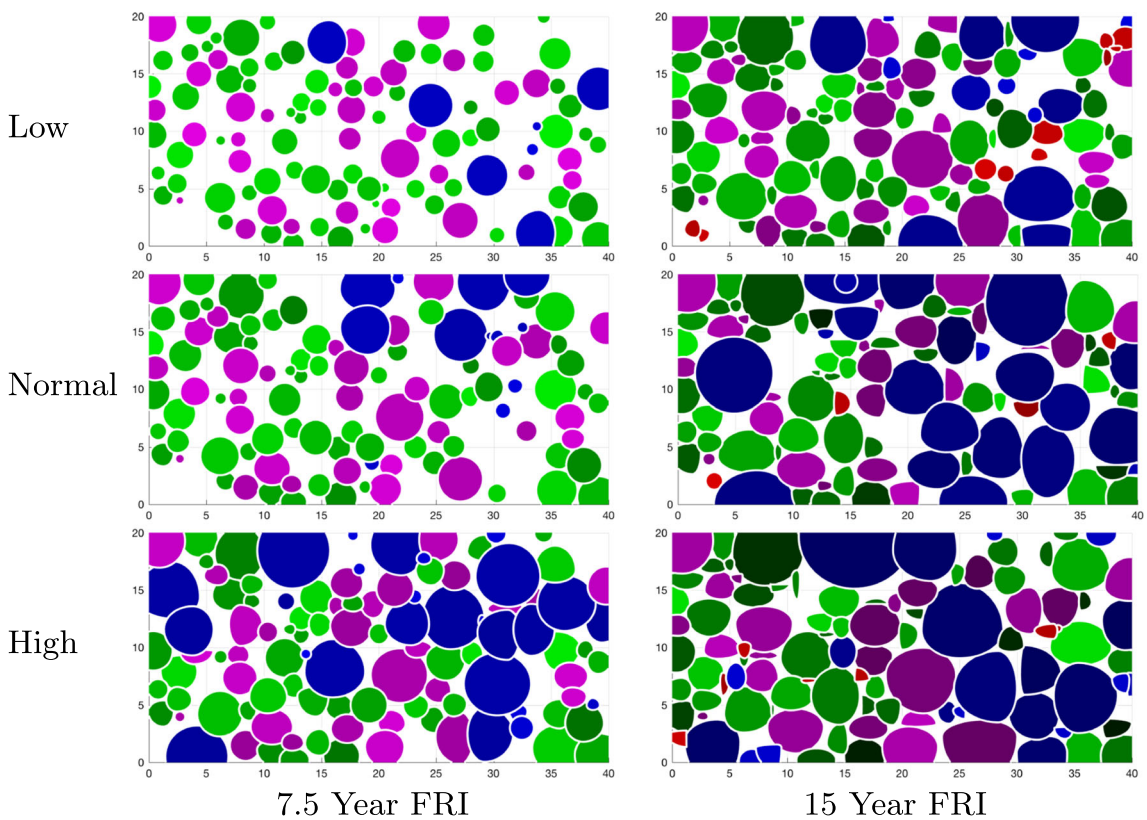

Fig. 15 Examples of simulations of a 3200 m^2 domain for 60 years with average fire return intervals of 7.5 and 15 years and mean annual precipitation levels of 10 (*low*), 12 (*normal*), and 14 (*high*) inches. The species are identified by color, including the nonsprouter *C. megacarpus* (*red*), and the facultative sprouters *C. spinosus* (*blue*), *M. laurina* (*green*), and *R. ovata* (*purple*). The shade of each plant indicates the relative height with darker shades representing taller plants

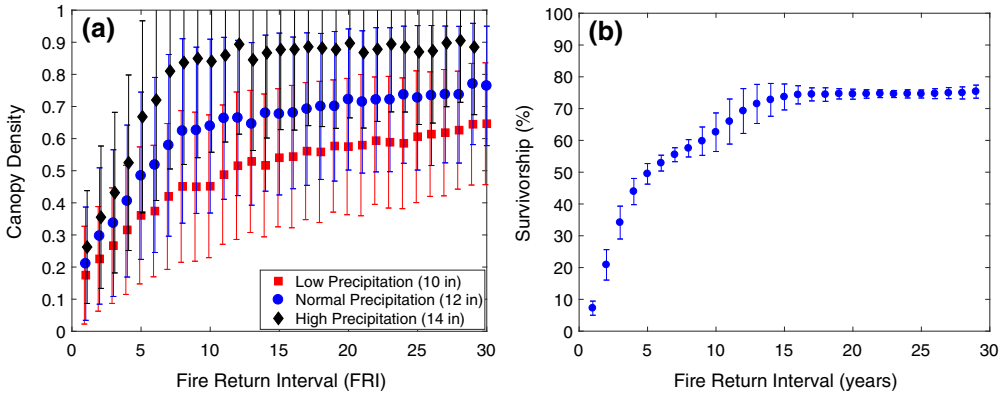

Fig. 16 **a** The average final canopy density in a 3200 m^2 domain versus average fire return interval in years. The annual precipitation in each simulation is distributed log-normally with a mean of either 10 in (*low*), 12 in (*normal*), or 14 in (*high*). The fire return intervals for each simulation are sampled from a Weibull distribution with a mean that ranges from 1 to 30 years and each data point represents an average over 500 simulations of length 60 years. The error bars represent the standard deviation for the final canopy density over 500 simulations. **b** The overall survivorship of all four species of chaparral versus average fire return interval over 1000 simulations of length 60 years using the discrete model from Lucas et al. (2013). The *error bars* represent the standard deviation for the survivorship over 1000 simulations. The initial relative density of *C. megacarpus* (Cm), *C. spinosus* (Cs), *M. laurina* (Ml), and *R. ovata* (Ro) for both types of simulations closely match the data from 1985 in Table 5

levels. We can compare these results to the discrete population models of individual species developed by Lucas et al. (2013). Figure 16b shows the survivorship of a mixed population of chaparral whose initial relative density of all four species matches the data from 1985 in Table 5. Although the discrete population simulations do not include interaction between the species, we see the same qualitative behavior where survivorship decreases rapidly with average fire return intervals below 10 years and survivorship is relatively constant for fire return intervals of greater than 15 years with increased variability during the 10–15 year transition. This transition period presumably reflects the tilting point where some but not all simulations will contain a short fire return interval that can cause the local extinction of a non-sprouting species such as *C. megacarpus*.

As seen in Fig. 16, the results of the discrete population simulations have less variability than the individual-based simulations. Although both models include variable fire return intervals, the growth and survivorship of the plants in the individual-based model depend on the annual precipitation which is varied using a log-normal distribution. This leads to more variability in the final canopy density

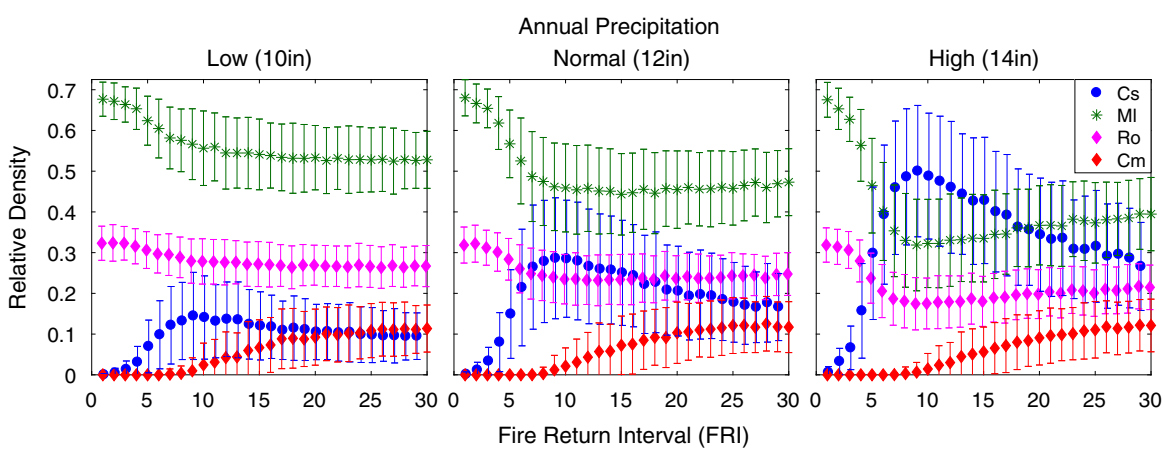

Fig. 17 The average final relative density of the nonsprouter *C. megacarpus* (Cm) and facultative sprouters *C. spinosus* (Cs), *M. laurina* (Ml), and *R. ovata* (Ro) versus average fire return interval (FRI). The annual precipitation in each simulation is distributed log-normally with a mean of 10, 12, or 14 in. The fire return intervals for each simulation are sampled from a Weibull distribution with a mean the ranges from 1 to 30 years. Each data point represents an average over 500 simulations of length 60 years and the *error bars* represent the corresponding standard deviation. The initial relative density of all four species closely match the data from 1985 in Table 5

in the individual-based simulations as opposed to the discrete models from Lucas et al. (2013) that do not incorporate annual precipitation.

Figure 17 shows the relative density of all four species of chaparral versus average fire return interval for low, medium, and high levels of annual precipitation. We observe that the nonsprouter population, *C. megacarpus*, becomes extinct or nearly extinct for average fire return intervals of less than 10 years, but that the nonsprouter population persists if the average fire return interval is greater than 15 years. These predictions are similar to the results from the discrete population models in Fig. 16b and Lucas et al. (2013). The *C. spinosus* population is threatened by average fire return intervals of 5 years or less, but otherwise persists through vegetative resprouting. The relative density of *C. spinosus* is higher for higher levels of annual precipitation due to enhanced seedling recruitment and survivorship of resprouts. The *M. laurina* and *R. ovata* populations persist regardless of the average length of fire return interval due to their high resprout success and survival rates as well as minor dependence on seedling recruitment. Overall, these simulations predict that short fire return intervals have the potential to shift plant community structure from a healthy mix of chaparral species to a landscape dominated by *M. laurina* and *R. ovata*.

Conclusions

In "An individual-based model" section, we presented an individual-based model of chaparral shrubs that grow, compete for resources, and resprout or recruit seedlings after wildfires. The parameters for each species were estimated and validated using data collected from the Malibu study site from 1985 to 2014. Simulations that incorporate local annual precipitation and instances of wildfire from that same time period capture the dynamics of the chaparral at our study site. The individual-based simulations also agree with the results of discrete population models from Lucas et al. (2013). The advantage of the individual-based model is that it incorporates the influence of annual precipitation levels and predicts the changes in the relative density of each chaparral species as a result of decreased precipitation levels and increased fire frequency.

The simulations in Figs. 16 and 17 predict that short fire return intervals have the potential to eliminate both *Ceanothus* species and change the plant community structure in the Santa Monica Mountains. Although the simulations predict that *M. laurina* and *R. ovata* will survive frequent wildfires, the overall canopy density declines as the average time between wildfires becomes shorter. These changes in plant community structure are further exacerbated by drought which leads to reduced canopy coverage. This is especially significant given the current unprecedented drought in Southern California which the simulations predict will intensify the effects of high fire frequency. Our model predicts that if the current conditions of drought and increased fire frequency continue, there will be a reduction in vegetative cover and a loss of chaparral species diversity leading to vegetation-type conversion. The open spaces that were once occupied by chaparral are susceptible to invasion by exotic weeds and coastal sage shrub which will only further increase flammability, decrease fire return intervals and decrease slope stability.

Besides the life history types and species we have discussed, this model can be expanded to include other species of chaparral with different seedling recruitment and resprouting strategies. For example, obligate sprouters recruit seedlings under the shade of the adult canopy during fire-free intervals. Their seeds are killed by wildfire, but the adults survive through post-fire vegetative resprouting. We chose not to include obligate sprouting species because they represent less than one percent of the relative density of chaparral at our study site. Obligate sprouters are abundant in regions with dense chaparral canopies and fire return intervals that are greater than 30 years such as the islands off the coast of Southern California. The rarity of obligate sprouters at our study site is not surprising given the time between fires is too short to disseminate refractory seeds and establish slow growing seedlings under shade. Our model predicts that the combination of extreme drought and frequent wildfires will create open spaces in the canopy that are inhospitable for seedling recruitment of obligate sprouters. The lack of obligate sprouters at our study site also suggests that the resprout success and survival rates would be lower than the facultative sprouters *M. laurina* and *R. ovata*. We expect our model would predict that similar to the *Ceanothus* species, the obligate sprouting species would be severely threatened by short fire return intervals and drought.

In addition to the current drought from 2012 to 2016, recent forecasts (Cook et al. 2015; Diffenbaugh et al. 2015; Underwood 2015; Swain et al. 2016) predict a progressive lengthening of drought events in Southern California over the next century. Therefore, our future models will consider the cumulative effects of long-term drought beyond seedling mortality to include mortality of chaparral resprouts and adults as documented in the Santa Monica Mountains by Pratt et al. (2014) and Venturas et al. (2016), respectively. In addition to the dieback of *C. spinosus* in these publications, we have recently observed disease induced mortality of *M. laurina* in locations near our study site. Our individual-based model can be expanded to include factors such as disease in order to capture the mortality of mature chaparral during long periods of drought.

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