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A Population Model of Chaparral Vegetation Response to Frequent Wildfires

Timothy A. Lucas · Garrett Johns · Wancen Jiang · Lucie Yang

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Abstract The recent increase in wildfire frequency in the Santa Monica Mountains (SMM) may substantially impact plant community structure. Species of Chaparral shrubs represent the dominant vegetation type in the SMM. These species can be divided into three life history types according to their response to wildfires. Nonsprouting species are completely killed by fire and reproduce by seeds that germinate in response to a fire cue, obligate sprouting species survive by resprouting from dormant buds in a root crown because their seeds are destroyed by fire, and facultative sprouting species recover after fire both by seeds and resprouts. Based on these assumptions, we developed a set of nonlinear difference equations to model each life history type. These models can be used to predict species survivorship under varying fire return intervals. For example, frequent fires can lead to localized extinction of nonsprouting species such as *Ceanothus megacarpus* while several facultative sprouting species such as *Ceanothus spinosus* and *Malosma (Rhus) laurina* will persist as documented by a longitudinal study in a biological preserve in the SMM. We estimated appropriate parameter values for several chaparral species using 25 years of data and explored parameter relationships that lead to equilibrium populations. We conclude by looking at the survival strategies of these three species of chaparral shrubs under varying fire return intervals and predict changes in plant community structure under fire intervals of short return. In particular, our model predicts that an

T.A. Lucas (✉) · G. Johns · W. Jiang · L. Yang
Mathematics Department, Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263, USA
e-mail: timothy.lucas@pepperdine.edu

G. Johns
e-mail: garrett.johns@pepperdine.edu

W. Jiang
e-mail: wancen.jiang@pepperdine.edu

L. Yang
e-mail: yuezhao.yang9922@yahoo.com

average fire return interval of greater than 12 years is required for 50 % of the initial *Ceanothus megacarpus* population and 25 % of the initial *Ceanothus spinosus* population to survive. In contrast, we predict that the *Malosma laurina* population will have 90 % survivorship for an average fire return interval of at least 6 years.

Keywords Chaparral · Wildfire · Population ecology

1 Introduction

The Santa Monica Mountains (SMM) of southern California are a member of the Transverse Mountain Ranges and home to many species of chaparral shrubs that are threatened by recent anthropogenic increases in fire frequency (Keeley et al. 1999). These plants can be divided into three categories according to their response to wildfires as described in Keeley (1986) and Pratt et al. (2008). Nonsprouters (NS) are completely killed by fire and reproduce by seeds that are promoted to germinate by fire cues and grow in direct sunlight away from existing shrubs. Obligate sprouters (OS) are not completely destroyed by fire, but instead their roots survive fire and dormant buds in the root crown resprout. Obligate sprouters exclusively recruit seedlings in the shade of adult shrubs between wildfire events because their seeds are non-refractory and are thus destroyed by fire. Facultative sprouters (FS) both resprout and reestablish by seeds that are promoted to germinate by fire cue. Facultative sprouter seedlings have highest survival in the partial shade of resprouts. Within these three life history types, each individual species varies in seedling survival and resprout success. Figure 1 gives a visual comparison of the three plant types a few months before and a few months after a fire event.

A mathematical model of this system is particularly relevant given that the increase in fire frequency in the Santa Monica Mountains has the potential to render some of the species locally extinct. A reduction in species numbers leads to change in plant community structure, increasing the likelihood of invasion by exotic species. Often such invasions in California are by exotic grasses that increase flammability and exacerbate fire frequency (Keeley and Brennan 2012; Keeley et al. 1999; Witter et al. 2007). From 1925–2001, the average fire return interval for the entire Santa Monica Mountains was 32 years (Witter et al. 2007). We will focus on a study site in a biological preserve on the Malibu campus at Pepperdine University where the average fire return interval from 1985–2012 has been just over 6 years. After premature fires in 1993 and 1996, *Ceanothus megacarpus*, a nonsprouter, was eliminated from our study site. The extinction of selected species of chaparral plants can alter community structure and species diversity. A reduction in vegetation cover could lead to a decrease in slope stability with increases in soil erosion and mudslides (Ainsworth and Doss 1995; Radtke 1983). The development of models that predict the ecological impact of frequent wildfires is of great importance given the costs associated with fighting wildfires, loss of structures, erosion deterrence, and clean up of mud and rock slides.

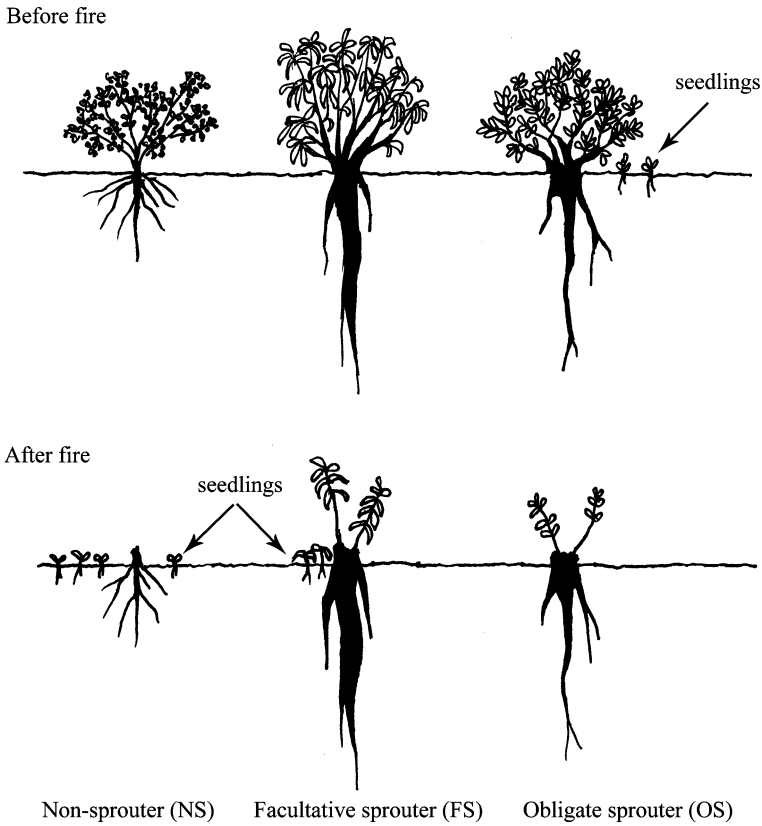

Fig. 1 A visual comparison of the resprout and seedling recruitment strategies of Nonsprouting, Facultative sprouting and Obligate sprouting species a few months before fire and a few months after fire. Note that OS seedlings before fire are killed by the fire event with no emergence of new seedlings 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)

1.1 Empirical Data

The mathematical models in this paper are inspired by a longitudinal study of several chaparral species at a biological preserve on the Malibu campus of Pepperdine University as described in Davis (1989), Thomas and Davis (1989), and Witter et al. (2007). The study began after the Piuma Fire of October 14, 1985, near Malibu, CA, and has continued through subsequent fires, the Malibu Fire in 1993, the Calabasas Fire in 1996, and the Canyon Fire in 2007. After the 1985 fire, 100 burned stumps were tagged for two different species of facultative sprouters in order to track resprout emergence and resprout establishment. At the same time, seedlings of the same species of facultative sprouter and one species of nonsprouter were monitored at 21 permanent quadrats. Figure 2 shows the survivorship of seedlings and resprouts for each species. *Malosma (Rhus) laurina*, a facultative sprouter, had an initial 100 % resprout emergence post-fire with 99 % survival through year 7, while seedling survival was less than 1 %. This species dominates the landscape of the study site.

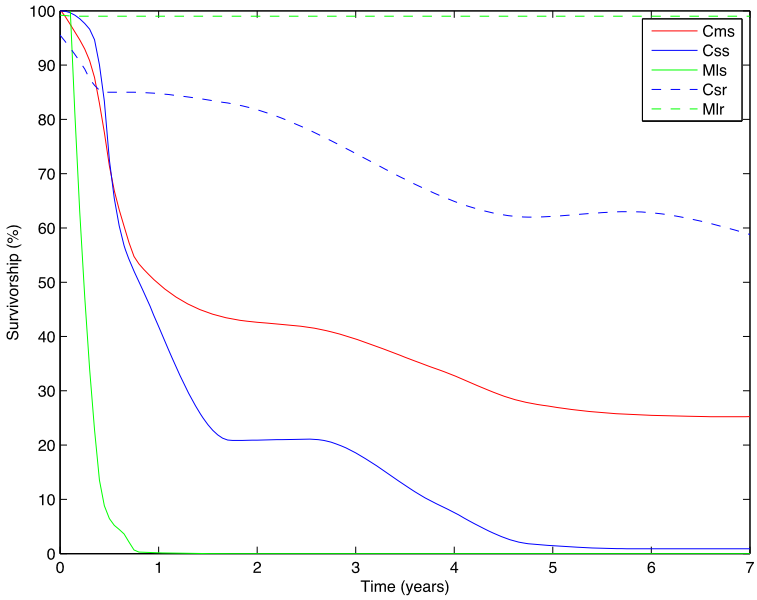

Fig. 2 Survivorship of three species of chaparral resprouts and seedlings between wildfires in 1985 and 1993 as seen in Thomas and Davis (1989) and Witter et al. (2007). After 7 years, 99 % of *Malosma (Rhus) laurina* resprouts (Mlr) survived and less than 1 % of seedlings (Mls) survived. Over that same time period 62 % of *Ceanothus spinosus* resprouts (Csr) and 1 % of seedlings (Css) survived. In contrast to Mls and Css, 25 % of *Ceanothus megacarpus* seedlings (Cms) survived, whereas no adults were observed to resprout after fire. Thus survivorship for *Ceanothus megacarpus* resprouts is 0 %

Another facultative sprouter, *Ceanothus spinosus* had an 83 % resprout emergence with 62 % survival over 7 years. Initially seedlings of *Ceanothus spinosus* had an 18 % survival rate which declined to about 1 % by year 7. This species still persists through resprouts, but all seedlings were destroyed by the fires in 1993 and 1996. As discussed in Frazer and Davis (1988), the wildfire survival strategy of *Ceanothus megacarpus*, a nonsprouter, is in direct contrast to the *Malosma laurina*. *Ceanothus megacarpus* has the highest seedling survivorship over 7 years at 25 %, but does not resprout. There was not sufficient time between the 1985 and 1993 fires for significant numbers of *Ceanothus megacarpus* seedlings to reach reproductive maturity and release seeds to the soil. This resulted in localized extinction of the nonsprouting species at this study site.

2 Nonsprouters

2.1 Nonsprouter Population Model

Nonsprouter (NS) plant types are decimated by wildfire and are sustained solely by the germination of fire-stimulated seeds (Pratt et al. 2008). (In earlier literature, e.g., Keeley (1986), nonsprouting species were referred to as obligate seeders.) We model the NS population by considering transitions between three phases

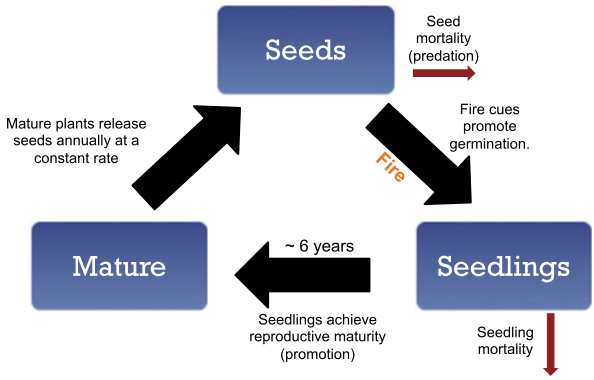

Fig. 3 The three phases of the nonsprouter (NS) population cycle

of a plant's life, seed, seedling, and mature shrub, as depicted in Fig. 3. A mature plant drops seeds annually in the spring and in the absence of fire can persist for at least 100 years (Keeley 1975). Approximately 90 % of the seeds in the ground are eaten by predators (VanElderen et al. 1988). The remaining seeds lie dormant in the ground until stimulated to germinate by the intense heat of a wildfire or the chemicals from burned wood or smoke (Keeley 1991, 1997; Keeley and Fotheringham 1997; Schlesinger et al. 1982). These wildfires generally occur during the late summer and early fall. Seedlings of nonsprouters preferentially establish in direct sunlight (Pratt et al. 2008). The first summer dry season after germination causes high seedling mortality due to water stress (Pratt et al. 2008; Saruwatari and Davis 1989; Thomas and Davis 1989). Mortality continues in subsequent years due to competition (Schlesinger et al. 1982; Tyler 1996), herbivory (Mills 1986) and continued summer drought. Seedlings fully mature after approximately six years and begin to drop seeds annually (Zammit and Zedler 1993). Given that the subsistence of the NS plant type is dependent upon the presence of seeds in the soil, a rapid succession of fires may result in the localized extinction of NS plant types as seedlings are deprived of the time needed to mature and release seeds. The annual cycle of events for nonsprouters is depicted in Fig. 4.

From these assumptions, we construct a model for the seedlings or young plants, Y_t, mature plants, M_t, and seeds, S_t where events occur on an annual basis. For consistency with the data, Y_t and M_t represent the population in early February when the first seedlings emerge post-fire. S_t represents the seedbank population after predation in the spring from which a percentage of seeds will germinate if a fire occurs the following year. A nonlinear system of difference equations for these populations is given by

$$\begin{aligned} Y_t &= F_{t-1} g S_{t-1} + (1 - F_{t-1})(1 - P_{t-1}) f_Y(Y_{t-1}; K_t, \alpha_Y), \\ M_t &= (1 - F_{t-1})\big(M_{t-1} + P_{t-1} f_Y(Y_{t-1}; K_t, \alpha_Y)\big), \\ S_t &= \big[(1 - F_{t-1}) S_{t-1} + r M_t\big](1 - \rho). \end{aligned} \tag{1}$$

The seed release rate, seed predation rate, and seed germination rates are r, ρ, and g, respectively. The model assumes that more seedlings are produced than will eventually mature and therefore seedlings decline at a rate α_Y to a carrying capacity K_t

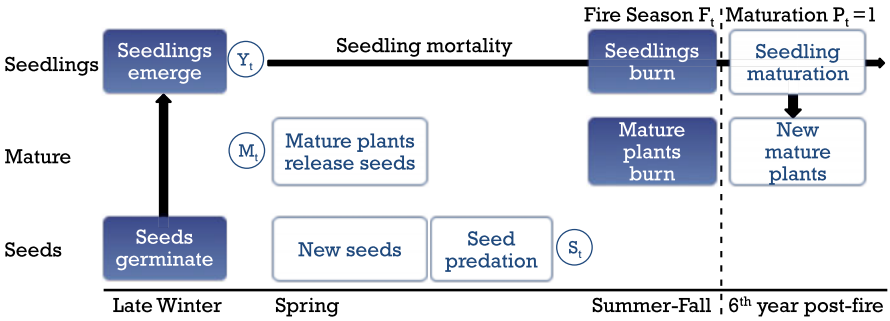

Fig. 4 Annual cycle of events for nonsprouter (NS) simulation. Events in *filled boxes* only occur in the year that directly follows a wildfire. The circles Y_t and M_t indicate that the seedling and mature populations are updated in early February after seedlings emerge post-fire. The circle S_t indicates that the seedbank is updated after predation in the spring. Seedling mortality occurs throughout the year. Seedling maturation only occurs in the sixth year post-fire

via a nonlinear function of the seedling population f_Y. Both F_t and P_t are indicator functions with value 1 whenever fire or seedling maturation occur, respectively. Note that if a fire occurs in the previous year, all mature plants and seedlings are destroyed and seeds germinate to create new seedlings. In the absence of fire, seedlings decline and mature plants persist and release seeds. We will consider both deterministic models where fires occur at regular intervals and seedling promotion occurs 6 years after each fire as well as stochastic models where the fire return interval is sampled from a Poisson distribution with a mean of 6 years and seedling promotion occurs on average 6 years after each fire.

In the Appendix, we compare several functions f_Y that can be used to model seedling decline. Ultimately, we chose the discrete logistic equation

$$f_Y(Y_{t-1}; K_t, \alpha_Y) = Y_{t-1} + \alpha_Y Y_{t-1}\left(1 - \frac{Y_{t-1}}{K_t}\right) \tag{2}$$

which minimizes the sum of the squares of the error between the data in Fig. 2 and the model. The parameter K_t represents the seedling survivorship, which depends on factors such as water stress as discussed in Davis (1989). We model seedling survivorship as a fraction k_Y of the number of seedlings that germinate post-fire. The seedling survivorship remains constant in the fire-free interval and is only updated after wildfire to reflect the newly germinated seeds in response to the fire, i.e.,

$$K_t = (1 - F_{t-1})K_{t-1} + F_{t-1} g S_{t-1} k_Y. \tag{3}$$

Using the *Ceanothus megacarpus* seedling survival data, we estimated the seedling decay rate α_Y to be 0.0993 and the seedling survival percentage k_Y to be 0.1693.

The other important parameters in the model are the seed release rate r ($r \geq 0$), predation rate ρ ($0 \leq \rho < 1$) and germination rate g ($0 \leq g \leq 1$). In the absence of fire, the number of seeds per mature plant s_t is given by

$$s_t = (1 - \rho)(s_{t-1} + r). \tag{4}$$

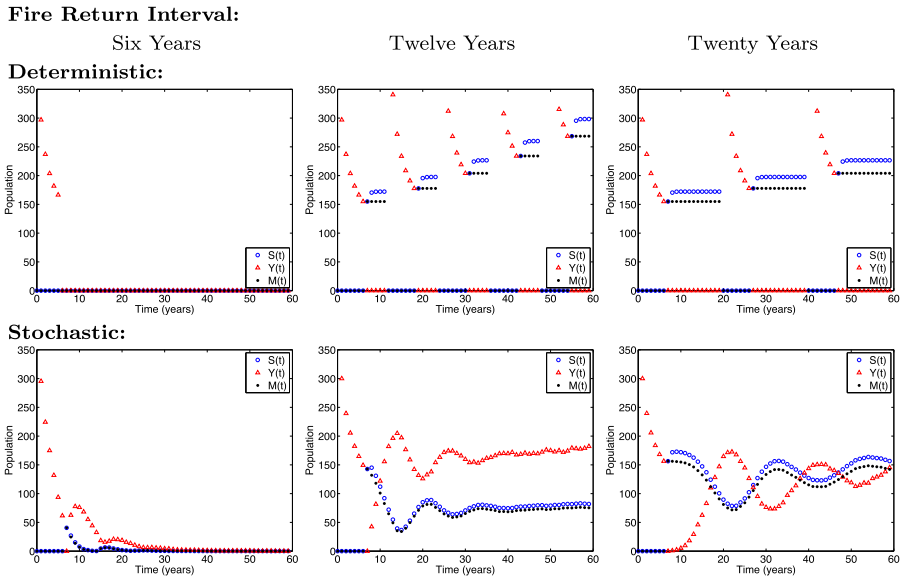

Fig. 5 Simulation of *Ceanothus megacarpus* population numbers with fixed (*top*) and average (*bottom*) fire return intervals of 6 (*left*), 12 (*center*), and 20 (*right*) years and a maturation rate of 6 years post-fire. Germination rate $g = 0.0195$, seed release rate $r = 2000$, seed predation rate $\rho = 0.9$, seedling decay rate $\alpha = 0.0993$, and seedling survival percentage $k = 0.1693$. The initial seedlings germinate after a fire at $t = 0$ from a seedbank of 30,000 seeds. The seed population is scaled by one tenth of the seed release rate

As t gets large, $s_t \to r(1-\rho)\rho^{-1}$. Given a sufficiently large fire return interval, the average number of seedlings per mature plant is

$$\bar{y} = gr\frac{1-\rho}{\rho}. \tag{5}$$

For our study site, the number of *Ceanothus megacarpus* seedlings that emerge post-fire per mature prefire shrub was estimated to be 4.3 (Thomas and Davis 1989). As stated previously, the seed predation rate for that same study site was estimated to be $\rho = 0.9$. The seed release rate fluctuates based on factors such as the size of the plant and the amount of rainfall, e.g., Keeley (1991), Zammit and Zedler (1993, 1994). In order to match the number of seedlings per mature *Ceanothus megacarpus* shrub, we will use $r = 2000$ and $g = 0.0195$.

2.2 *Ceanothus Megacarpus* Simulations

Given our parameter estimates from the previous section, we can use the nonsprouter model (1) to simulate a *Ceanothus megacarpus* population under varying fire return intervals. Figure 5 shows sample *Ceanothus megacarpus* populations with fixed and average fire return intervals of 6, 12, and 20 years and a maturation rate of 6 years. The simulations show that if the fire return interval is fixed at 6 years, the seedlings do not have sufficient time to achieve reproductive maturity and drop seeds, rendering the nonsprouter population locally extinct after the second fire. In the same way, if the

fire return intervals are sampled from a Poisson distribution with a mean of 6 years, on average the nonsprouter population becomes locally extinct within 25 years. As the fire return interval increases to 12 and 20 years, the seedlings mature and begin building a seedbank that sustains the nonsprouter population. We note that if the average time between fires is 12 or 20 years, there is still a probability that two fires will occur close enough together to completely eliminate the nonsprouter population. This accounts for the lower number of mature plants in the stochastic fire frequency versus that deterministic fire frequency. These simulations suggest that the success of the nonsprouter is heavily dependent on the fire return interval and that one short fire return interval can have a long term impact. This behavior is also reflected in the data in Fig. 2 where a short gap between fires in 1985 and 1993 extirpated *Ceanothus megacarpus* from the Malibu study site.

2.3 Nonsprouter Parameter Study

We now consider parameter relationships in (1) with logistic decay (2) that lead to a steady-state population of mature shrubs $\bar{M}$ after each fire. We will assume that there is sufficient time between fires for the seedbank to reach a limiting value $\bar{S}$. We will also assume that during each fire-free interval there is sufficient time for the seedling population to reach the equilibrium $\bar{Y} = \bar{K}$ where $\bar{K} = gk_Y\bar{S}$ is defined by (3). After promotion, the subsequent mature population is $\bar{M} = \bar{K} = gk_Y\bar{S}$. Substituting $M_t = \bar{M}$ and $S_t = \bar{S}$ into the seedbank equation from (1) leads to

$$\begin{aligned} \bar{S} &= (\bar{S} + grk_Y\bar{S})(1-\rho), \\ 1 &= (1 + grk_Y)(1-\rho), \\ 1 &= grk_Y\left(\frac{1-\rho}{\rho}\right) = \bar{y}k_Y. \end{aligned} \tag{6}$$

This relationship between the parameters is also exhibited in Fig. 6, which displays combinations of the germination rate g, seed release rate r, seed predation rate ρ, seedling decay rate α_Y, and seedling survival percentage k_Y that lead to steady-state mature populations in the simulations. For each value of ρ, the log–log plot of r versus g has approximate slope of -1 which is consistent with the fact that r and g are inversely proportional. Under the assumption that the seedling population reaches the carrying capacity before promotion, (6) does not depend on the seedling decay rate α_Y. The log–log plot of g versus k_Y in Fig. 6 gives evidence to support this claim for α_Y sufficiently large.

We define

$$\phi = grk_Y\left(\frac{1-\rho}{\rho}\right) = \bar{y}k_Y, \tag{7}$$

which can be interpreted as the average number of post-fire mature shrubs produced by a single prefire mature shrub. For $\phi > 1$, we expect the mature population to increase after each successive fire and for $\phi < 1$ we expect the mature population to decline after each successive fire. This is similar to the concept of a basic reproductive rate in epidemiology as described in Anderson and May (1992). Figure 7

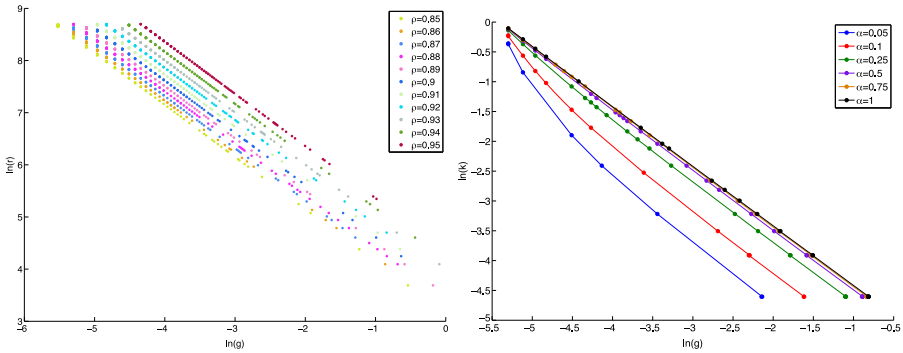

Fig. 6 (*Left*) A log–log plot of seed release rate r versus germination rate g for varying predation rate ρ. A log–log plot of the seedling survival percentage k_Y versus germination rate g for varying seedling decay rate α

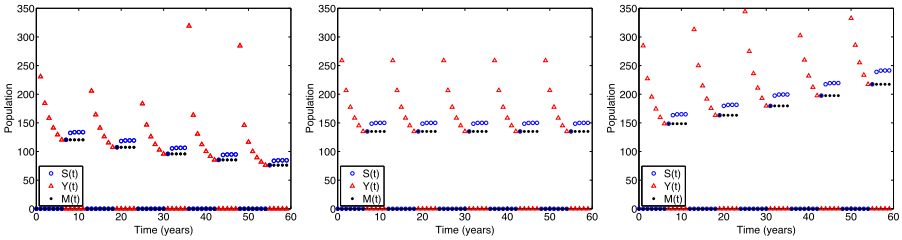

Fig. 7 Simulation of a generic nonsprouter population with a fixed fire return interval of 12 years where $\phi < 1$ (*left*), $\phi = 1$ (*center*) and $\phi > 1$ (*right*). The initial seedlings germinate after a fire at $t = 0$ from a seedbank of 30,000 seeds. The seed population is scaled by one-tenth of the seed release rate

provides examples where the nonsprouter population grows without bound ($\phi > 1$), the nonsprouter population approaches a steady-state ($\phi = 1$), and the nonsprouter population declines to zero ($\phi < 1$). We also observe that the rate of growth or decline is dependent on the fire frequency and that a short fire return interval can extirpate an otherwise successful population.

3 Obligate Sprouters

In contrast to nonsprouters, obligate sprouting shrubs (OS) do not persist by way of post-fire seed germination. Instead, OS plant types endure solely by means of vegetative resprouting (Pratt et al. 2008). Resprouts grow out of the burned root crowns of both pre-fire mature plants and prefire resprouts (Keeley and Zedler 1978). Similar to nonsprouter seedlings, we model resprout decline using a nonlinear logistic decay $f_R(R_{t-1}; L_t, \alpha_R)$ where L_t is the resprout survivorship and α_R is the resprout decay rate. In contrast to seedlings, resprouts are able to drop a small number of seeds the first year after a fire and the seed dispersal rate grows until the resprout regains its

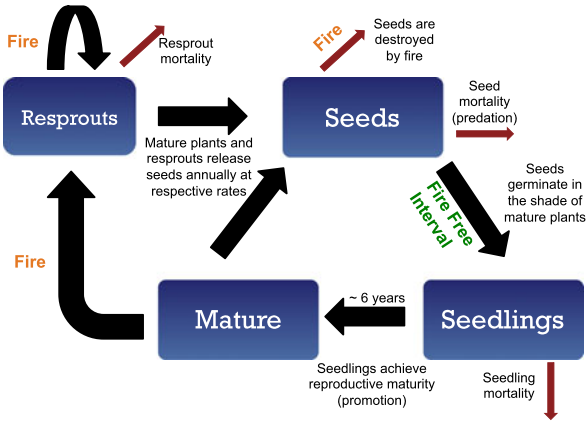

Fig. 8 The four phases of the obligate sprouter (OS) population cycle

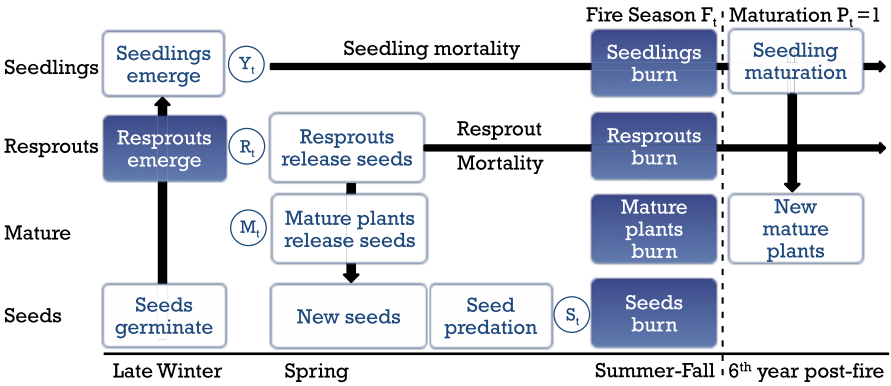

Fig. 9 Annual cycle of events for the obligate sprouter (OS) simulation. Events in *filled boxes* only occur in the year that directly follows a wildfire. The circles Y_t, R_t, and M_t indicate that the seedling, resprout, and mature populations are updated in early February after seedlings emerge post-fire. The circle S_t indicates that the seedbank is updated after predation in the spring. Seedling and resprout mortality occur throughout the year. Seedling maturation only occurs in the sixth year post-fire

prefire canopy area. In our model, resprouts do not transition to mature plants because of the difference in how we model the annual release of seeds. As with nonsprouters, we assume that it takes approximately 6 years for seedlings of obligate sprouters to become mature plants that release seeds annually. Obligate sprouters recruit seedlings in the shade of larger plants during fire free intervals, but their seeds are completely destroyed by fire (Keeley 1992). Seeds only germinate during fire free intervals. The population cycle of the OS plant type is depicted in Fig. 8 and the annual cycle of events is outlined in Fig. 9.

From these assumptions, we construct a model of the obligate sprouter where R_t represents the resprout population in early February when the first resprouts emerge post-fire. The resulting difference equations are

$$\begin{aligned}
Y_t &= gS_{t-1} + (1-P_{t-1})(1-F_{t-1})f_Y(Y_{t-1};K_t,\alpha_Y),\\
R_t &= F_{t-1}h(M_{t-1}+R_{t-1}) + (1-P_{t-1})(1-F_{t-1})f_R(R_{t-1},R_t;L_t,\alpha_R),\\
M_t &= (1-F_{t-1})\big(M_{t-1}+P_{t-1}f_Y(Y_{t-1};K_t,\alpha_Y)\big),\\
S_t &= \big[(1-F_{t-1})(1-g)S_{t-1} + rM_t + r_tR_t\big](1-\rho)
\end{aligned} \tag{8}$$

where h is the post-fire resprout rate and

$$r_t = r\big(1-e^{-\gamma t}\big) \tag{9}$$

is the resprout seed release rate. The seedling survivorship K_t is given by (3) and likewise the resprout survivorship is updated after each fire via

$$L_t = (1-F_{t-1})L_{t-1} + F_{t-1}h(M_{t-1}+R_{t-1})k_R \tag{10}$$

where k_R is the resprout survival percentage.

If the fire return intervals are too short, localized extinction for obligate sprouters is inevitable as they will be unable to establish mature plants or an adequate number of resprouts to reestablish the required seedbank. Two species of obligate sprouters, *Heteromeles arbutifolia* and *Rhamnus ilicofia*, are rare at the Malibu study site. Since there are very few obligate sprouters at the study site, we cannot estimate reasonable parameters for the simulations. We instead use the obligate sprouter model to help us understand the facultative sprouter model, which incorporates assumptions from both the nonsprouter and obligate sprouter models.

4 Facultative Sprouters

4.1 Facultative Sprouter Population Model

Facultative sprouters survive wildfire through a combination of post-fire seed germination and vegetative resprouting. The population cycle of the FS plant type is depicted in Fig. 10. Like nonsprouters, seeds are stimulated to germinate by fire, but preferentially establish as seedlings under partial shade (Frazer and Davis 1988; Pratt et al. 2008; Thomas and Davis 1989). Again seedlings will achieve reproductive maturity after roughly six years (Zammit and Zedler 1993). Like obligate sprouters, facultative sprouters are able to persist after wildfires through resprouts which release seeds at a rate similar to obligate sprouters. The annual cycle of events for facultative sprouters is depicted in Fig. 11. Given these assumptions, our FS model is

$$\begin{aligned}
Y_t &= F_{t-1}gS_{t-1} + (1-P_{t-1})(1-F_{t-1})f_Y(Y_{t-1};K_t,\alpha_Y),\\
R_t &= F_{t-1}h(R_{t-1}+M_{t-1}) + (1-P_{t-1})(1-F_{t-1})f_R(R_{t-1},R_t;L_t,\alpha_R),\\
M_t &= (1-F_{t-1})\big(M_{t-1}+P_{t-1}f_Y(Y_{t-1};K_t,\alpha_Y)\big),\\
S_t &= \big[(1-F_{t-1})S_{t-1} + rM_t + r_tR_t\big](1-\rho),
\end{aligned} \tag{11}$$

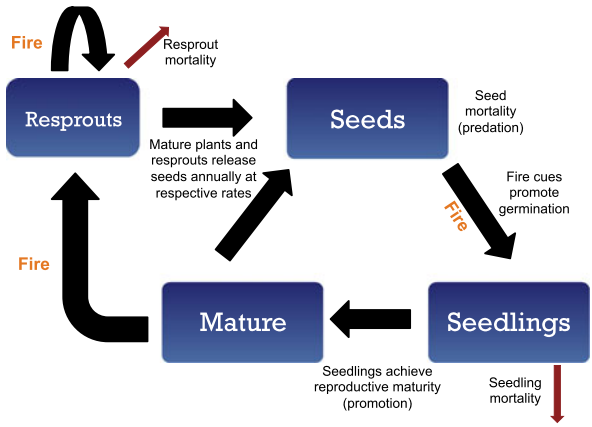

Fig. 10 The four phases of the facultative sprouter (FS) population cycle

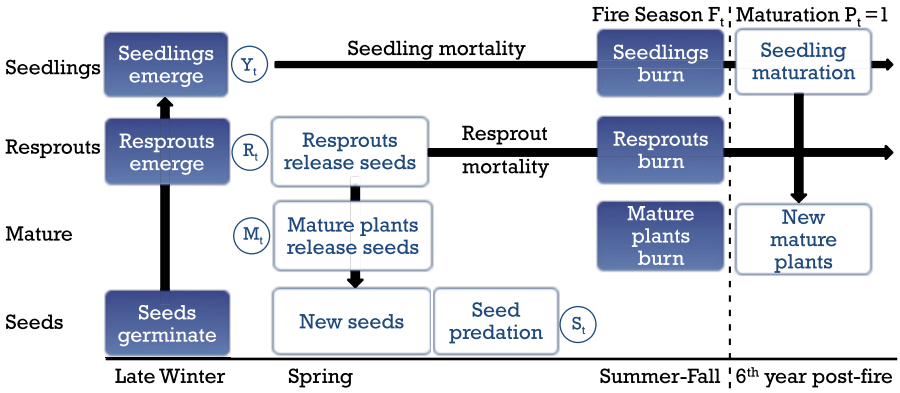

Fig. 11 Annual cycle of events for the facultative sprouter (FS) simulation. Events in filled boxes only occur in the year that directly follows a wildfire. The circles Y_t, R_t, and M_t indicate that the seedling, resprout and mature populations are updated in early February after seedlings emerge post-fire. The circle S_t indicates that the seedbank is updated after predation in the spring. Seedling and resprout mortality occur throughout the year. Seedling maturation only occurs in the sixth year post-fire

where the resprout seed release rate is given by (9), the resprout survivorship is given by (10) and all other parameters are defined in Sects. 2 and 3.

As evidenced in Fig. 2, the seedling survival rate of facultative sprouters is significantly lower than the nonsprouting species. Similar to the nonsprouter seedlings, we fit several models to observed population declines in *Ceanothus spinosus* and *Malosma laurina* seedlings from 1985–1993. The Gompertz model

$$f_Y(Y_{t-1}; K_t, \alpha_Y) = Y_{t-1}\left(\frac{Y_{t-1}}{K_t}\right)^{-\alpha_Y} \tag{12}$$

is the best fit for both species. In Appendix, we compare several models of resprout decline to observed *Ceanothus spinosus* resprout data from 1985–1993. We con-

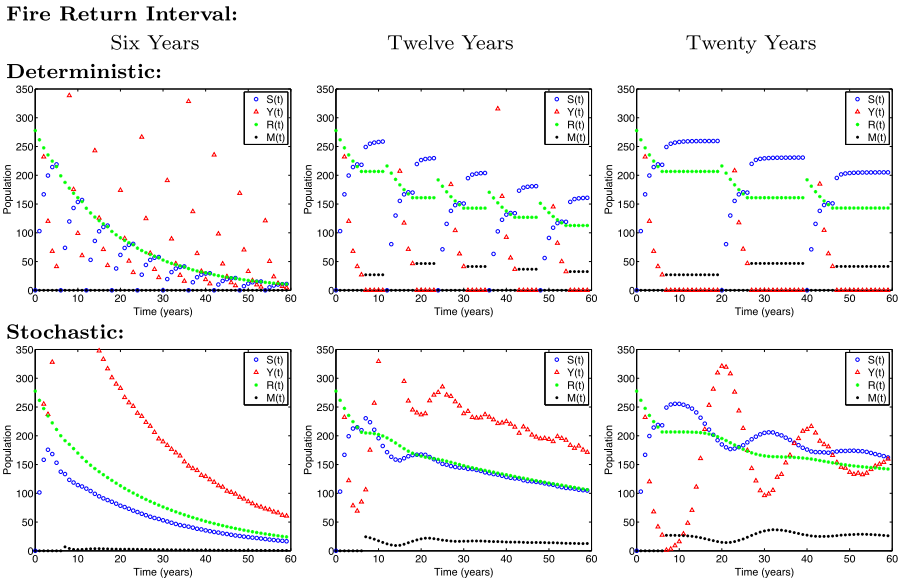

Fig. 12 Simulation of *Ceanothus spinosus* population numbers with fixed (*top*) and average (*bottom*) fire return intervals of 6 (*left*), 12 (*center*), and 20 (*right*) years and a maturation rate of 6 years post-fire. Germination rate $g = 0.0396$, seed release rate $r = 2000$, seed predation rate $\rho = 0.9$, seedling decay rate $\alpha_Y = 0.1328$, seedling survival percentage $k_Y = 0.0014$, post-fire resprout rate $h = 0.9254$, resprout decay rate $\alpha_R = 0.1589$, and resprout survival percentage $k_R = 0.4933$. After a fire at $t = 0$, seedlings germinate from a seedbank of 30,000 seeds and plants resprout from a prefire mature population of 300. The seed population is scaled by one tenth of the seed release rate

cluded that the best fit for resprout decline is the semi-implicit Gompertz model

$$f_R(R_{t-1}, R_t; L_t, \alpha_R) = R_{t-1}\left(\frac{R_t}{K_Y}\right)^{-\alpha_R}. \tag{13}$$

4.2 *Ceanothus Spinosus* Simulations

We now use the facultative sprouter model to simulate a *Ceanothus spinosus* (Cs) population under varying fire frequencies. Using the Cs seedling and resprout survival data from 1985–1993, we used the procedures outlined in Appendix to estimate the seedling and resprout decay rates, α_Y and α_R, as well as the seedling and resprout survival percentages, k_Y and k_R. The seed parameters $\rho = 0.9$, $r = 2000$, and $g = 0.0396$ yield 8.8 seedlings per mature adult as estimated in Thomas and Davis (1989).

Figure 12 shows sample Cs populations with fixed and average fire frequencies of 6, 12, and 20 years and a maturation rate of 6 years. The simulations show that if the fire return interval is fixed at 6 years, the seedlings do not have sufficient time to mature and drop seeds, but there are resprouts which drop seeds during those first few years. Every 6 years a new group of seedlings germinates, but these are destroyed by fire before they have the opportunity to mature. With a resprout survival rate of 66.8 %, the Cs population is almost completely eliminated within 60 years. If the fire return intervals are drawn from a Poisson distribution with a 6-year mean, there are

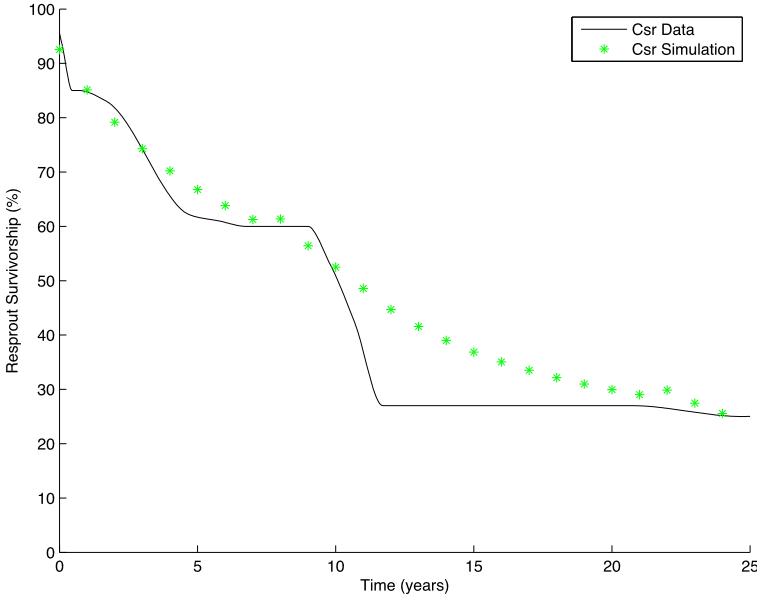

Fig. 13 A comparison of a simulation of Cs resprouts versus the field data from Fig. 2. In both, the simulation and the field data, fires occurred 8, 11, and 22 years after the initial fire in 1985. The post-fire resprout rate was $h = 0.9254$, the resprout decline rate was $\alpha_R = 0.1589$, and the resprout survival percentage was $k_R = 0.4933$

simulations where the seedlings have enough time between fires to mature and drop seeds, but again the Cs population is almost completely eliminated within 60 years. If fire return intervals are increased to 12 or 20 years, the seedlings have enough time to mature and we see a consistent mature population. These simulations indicate that *Ceanothus spinosus* has a higher survival rate than *Ceanothus megacarpus* under shorter fire return intervals, but the Cs population can still be destroyed by extremely short fire return intervals.

In order to validate our resprout model, we consider a Cs simulation with fires occurring in 1985, 1993, 1996, and 2007 and compare to our Cs resprout data over that time period. As seen in Fig. 13, the simulation does not capture the dramatic decrease in resprouts between the fires in 1993 and 1996, but the model does accurately predict the resprout survivorship after 25 years. Unfortunately, we do not have sufficient data to make the same comparison for Cs seedlings.

4.3 *Malosma Laurina* Simulations

The *Malosma laurina* (Ml) population presents an interesting case because of the extremely low seedling survival rate and extremely high resprout survival rate as seen in Fig. 2. These shrubs have a 99 % resprout rate due in part to large tap roots that can extend 5 meters below the surface (Davis 1989). Using the *Malosma laurina* seedling and resprout survival data from 1985–1993, we used the procedures outlined in Appendix to estimate the seedling and resprout decay rates, α_Y and α_R,

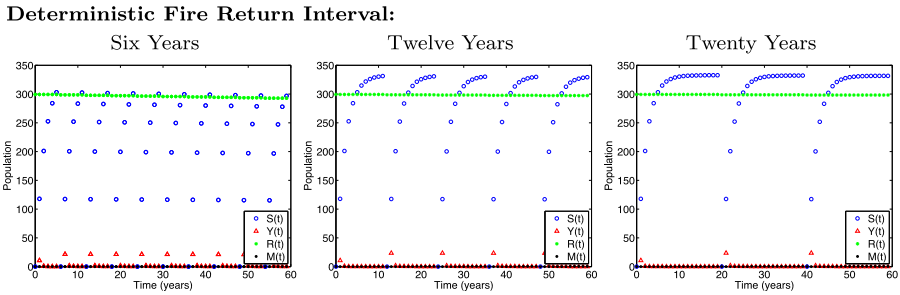

Fig. 14 Simulation of *Malosma laurina* population numbers for fixed fire return intervals of 6 (*left*), 12 (*center*), and 20 (*right*) years and a maturation rate of 6 years post-fire. Germination rate $g = 0.18$, seed release rate $r = 2000$, seed predation rate $\rho = 0.9$, seedling decay rate $\alpha_Y = 0.5782$, seedling survival percentage $k_Y = 2.0965 \times 10^{-5}$, post-fire resprout rate $h = 1.00$, resprout decay rate $\alpha_R = 0.1745$, and resprout survival percentage $k_R = 0.9974$. After a fire at $t = 0$, seedlings germinate from a seedbank of 30,000 seeds and plants resprout from a prefire mature population of 300. The seed population is scaled by one-tenth of the seed release rate

as well as the seedling and resprout survival percentages, k_Y and k_R. The seed parameters $\rho = 0.9$, $r = 2000$, and $g = 0.18$ yield 40.1 seedlings per mature adult as estimated in Thomas and Davis (1989). Figure 14 shows sample Ml populations with fixed fire return intervals of 6, 12, and 20 years and a maturation rate of 6 years. In each simulation, we see that the *Malosma laurina* population continues to thrive due to a 99 % resprout survival rate. Given the low seedling survival rate, there are very few new mature plants with fire return intervals of 12 and 20 years. Most of the existing plants survive by resprouting, but very few new plants are introduced into the population after each fire. There are no qualitative differences between the deterministic and stochastic models.

4.4 Facultative Sprouter Parameter Study

We now consider parameter relationships in (11) with seedling decay (12) and resprout decay (13) that lead to a steady-state population of mature shrubs $\bar{M}$ and resprouts $\bar{R}$. We again assume that during each fire free interval that seedlings reach the carrying capacity K_Y before promotion, i.e., $\bar{Y} = K_Y = gk_Y\bar{S}$. After promotion, the subsequent mature population is $\bar{M} = K_Y = gk_Y\bar{S}$. Likewise, we assume that the resprouts reach the carrying capacity K_R during each fire-free interval. It follows from (10) that $\bar{R} = K_R = h(\bar{M} + \bar{R})k_R$. Solving for $\bar{R}$,

$$\bar{R} = \frac{hk_R}{1 - hk_R}\bar{M} = gk_Y\frac{hk_R}{1 - hk_R}\bar{S}. \tag{14}$$

Substituting $M_t = \bar{M}$, $R_t = \bar{R}$, and $S_t = \bar{S}$ into the steady-state seedbank equation from (11) leads to

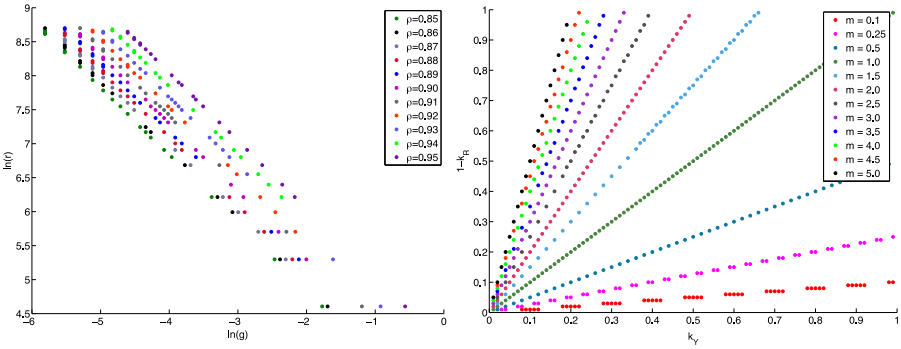

Fig. 15 (*Left*) A log–log plot of seed release rate r versus germination rate g for varying predation rate ρ and fire-frequency f. A plot of resprout mortality $1 - hk_R$ versus seedling survival percentage k_Y for varying $m = gr(1-\rho)\rho^{-1}$

$$\begin{aligned}
\bar{S} &= \left(\bar{S} + grk_Y\bar{S} + grk_Y\frac{hk_R}{1-hk_R}\bar{S}\right)(1-\rho),\\
1 &= \left(1 + gr\frac{k_Y}{1-hk_R}\right)(1-\rho),\\
1 &= gr\frac{k_Y}{1-hk_R}\frac{1-\rho}{\rho}.
\end{aligned} \tag{15}$$

This relationship is also exhibited in Fig. 15, which displays combinations of the germination rate g, seed release rate r, seed predation rate ρ, and survival percentages for seedlings and resprouts, k_Y and k_R, that lead to steady-state solutions. Again, the log–log plot of r versus g for varying ρ confirms that r and g are inversely proportional. The plot of resprout mortality $1 - hk_R$ versus seedling survival percentage k_Y for steady-state solutions is consistent with the assertion in (15) that the two parameters are directly proportional with slope $m = gr(1-\rho)\rho^{-1}$.

Similar to (7), we define

$$\psi = \frac{grk_Y}{1-hk_R}\left(\frac{1-\rho}{\rho}\right). \tag{16}$$

As with the nonsprouter model, for $\psi > 1$ we expect that eventually the resprout and mature populations will increase after each successive fire. Alternatively, for $\psi < 1$, we expect that eventually the resprout and mature populations will decline after each successive fire. Figure 16 provides examples where the mature and resprout populations grow without bound ($\psi > 1$), the mature and resprout populations approach a steady-state ($\psi = 1$), and the mature and resprout populations decline to zero ($\psi < 1$). We can also observe that the rate of growth or decay is dependent on the fire return interval and that an extremely short fire return interval can eliminate an otherwise successful population.

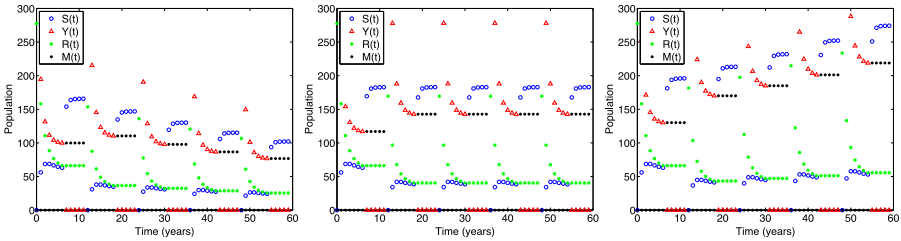

Fig. 16 FS simulations with a fixed fire return interval of 12 years where $\psi < 1$ (*left*), $\psi = 1$ (*center*) and $\psi > 1$ (*right*). After a fire at $t = 0$, seedlings germinate from a seedbank of 30,000 seeds and plants resprout from a prefire mature population of 300. The seed population is scaled by one tenth of the seed release rate

Table 1 A comparison the estimated parameters for *Ceanothus megacarpus* (Cm), *Ceanothus spinosus* (Cs), and *Malosma laurina* (Ml). *Data from Thomas and Davis (1989)

Species	Seedlings per prefire adult* $\bar{y}$	Seedling survival k_Y	Resprout survival k_R
Cm	4.3	0.1984	NA
Cs	8.8	0.001378	0.4221
Ml	40.1	0.000021	0.9976

5 Conclusions

We conclude by comparing the survival strategies of nonsprouters and facultative sprouters. First, we examine the parameters most closely related to seedling and resprout success for the three species discussed throughout this paper: *Ceanothus megacarpus* (Cm), *Ceanothus spinosus* (Cs), and *Malosma laurina* (Ml). Table 1 shows the contrast between the high seedling survival rate and nonexistent resprout rate of the Cm population and the extremely low seedling survival rate and extremely high resprout success of the Ml population. The parameters for the Cs population sit in between these two extremes, but the seedling survival rate is still much smaller than the Cm population. These observations are supported by the field data in Fig. 2.

Using the parameters from Table 1 we simulated the *Ceanothus megacarpus*, *Ceanothus spinosus* and *Malosma laurina* populations for varying fire return intervals, both fixed and stochastic. Figure 17 shows the resulting survivorship of each species which is defined as the percentage of mature plants and resprouts that survive 60 years after the initial fire. These simulations indicate that facultative sprouters with their dual survival response are best suited to persist in environments with extremely short fire return intervals. *Malosma laurina* thrives in both frequent and infrequent fires due to its high resprout success. Although *Ceanothus spinosus* is more successful for longer fire return intervals, the population still outperforms the nonsprouting *Ceanothus megacarpus* in the simulations when wildfires return within 10 years. The *Ceanothus megacarpus* simulations support the hypothesis that species survival is dependent on there being enough time between wildfires for seedlings to mature and build a seedbank, which is consistent with the field data in Fig. 2. We note that the

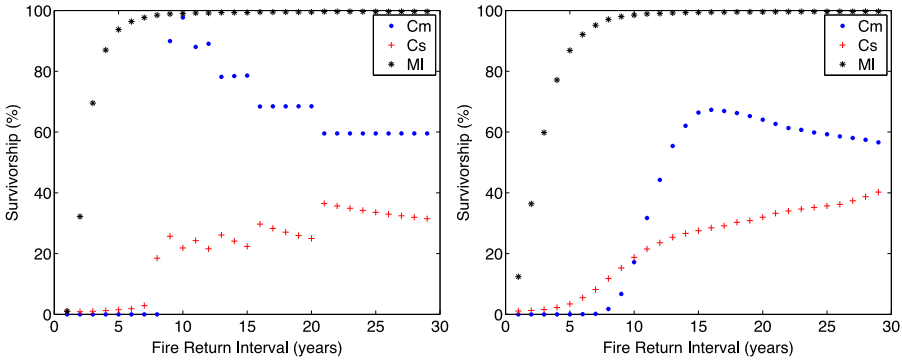

Fig. 17 Overall survivorship (mature plants and resprouts) after 60 years of *Ceanothus megacarpus* (Cm), *Ceanothus spinosus* (Cs) and *Malosma laurina* versus fixed fire frequency (*Left*) and average fire frequency (*Right*)

survivorship of Cm is lower when the time between fires is allowed to vary because a short interval between fires is capable of completely eliminating the Cm population. Given an average time between fires greater than 10 years, the Cm population has a higher survivorship than the Cs population due to a much higher seedling survival rate. We conclude from our model that if the average fire return interval is greater than 12 years, *Ceanothus spinosus* survivorship is greater than 25 % and *Ceanothus megacarpus* survivorship is greater than 50 %. In contrast, if the average fire return interval is ≥6 years, *Malosma laurina* survivorship is greater than 90 %.

The simulations in Fig. 17 suggest that the chaparral populations are threatened by the increase in incidence of wildfires. Specifically, species such as *Ceanothus megacarpus* and *Ceanothus spinosus* can be completely destroyed or significantly reduced by a rapid succession of wildfires. Differential species response to anthropogenic increases in fire events potentially causes shifts in plant community structure. This can lead to invasion by exotic species which increases flammability and further exacerbates fire return intervals.

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Appendix: Seedling and Resprout Survivorship Curves

We begin by outlining the procedure of comparing several models of seedling survivorship. The decline of seedlings in the model is based on data on *Ceanothus megacarpus* seedling survival from 1985–1993 that is displayed in Fig. 2. In Table 2, we compare several functions $f_Y(Y_{t-1}, Y_t; K_Y, \alpha_Y)$ that can be used to model seedling decline. For each model, the parameter α_Y represents the rate of seedling decline and $K_Y = gSk_Y$ represents the seedling survivorship, which is constant throughout a single fire-free interval. We rule out the exponential decay model because it

Table 2 A comparison of various models of seedling decline against the *Ceanothus megacarpus* data for seedling survival from 1985–1993 using a residual sum of squares of the error (RSS) and the Akaike information criterion (AIC). From Burnham and Anderson (2010), AIC $= n\log(\mathrm{RSS}/n) + 2p$ where n is the number of data points and p is the number of parameters

Model	$f_Y(Y_{t-1}, Y_t; K_Y, \alpha_Y)$	k_Y	α_Y	RSS	AIC
Exponential	$Y_{t-1} - \alpha_Y Y_{t-1}$		0.1988	2235.22	68.91
Logistic	$Y_{t-1} + \alpha_Y Y_{t-1}(1 - \frac{Y_{t-1}}{K_Y})$	0.1693	0.0993	292.99	44.50
Morisita	$Y_{t-1} + \alpha_Y Y_t(1 - \frac{Y_{t-1}}{K_Y})$	0.2135	0.2218	340.32	46.44
Hirota	$Y_{t-1} + \alpha_Y Y_{t-1}(1 - \frac{Y_t}{K_Y})$	0.2006	0.2486	357.98	47.10
Gompertz	$Y_{t-1}(\frac{Y_{t-1}}{K_Y})^{-\alpha_Y}$	0.2574	0.4052	453.85	50.19
New Gompertz	$Y_{t-1}(\frac{Y_t}{K_Y})^{-\alpha_Y}$	0.2432	0.6073	443.79	49.90

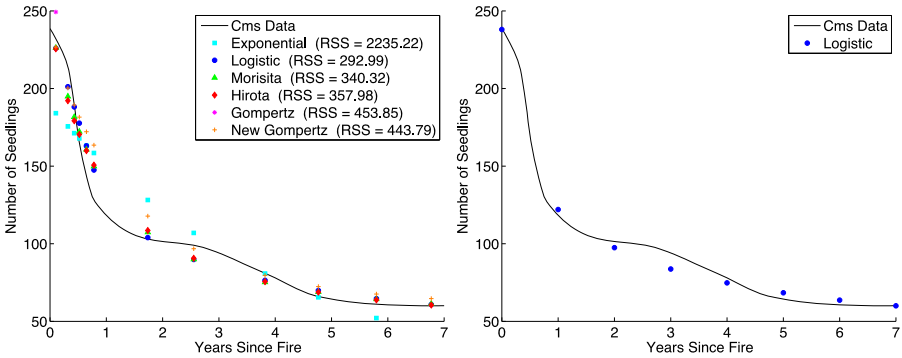

Fig. 18 (*Left*) Visual comparison of various mathematical models to fit observed seedling survival of *Ceanothus megacarpus*. Models are listed in Table 2. (*Right*) Comparison of the logistic model to the same data

assumes that the seedling population declines to zero and it is not a good fit of the data. Instead, we will consider several variations of the logistic and Gompertz models in the case where the initial population is greater than a sustainable population level. Besides the standard discrete logistic model described in Murray (2002), Morisita (1965) proposed a semi-implicit version equation and Hirota (1979) proposed a slightly different semi-implicit model. Morisita argues that his semi-implicit model is more natural when discretizing the continuous logistic equation. In contrast to the standard discrete logistic model, the Morisita and Hirota models have solutions that explicitly depend on time which are given in Satoh and Yamada (2002). We also consider a discrete version of the Gompertz model from Satoh (2000) and a semi-implicit version from Satoh (2003). As seen in Table 2, the standard discrete logistic model is the best fit of the *Ceanothus megacarpus* seedling data, but we note that all of the nonlinear models are significantly better fits than the exponential model. A visual comparison of the models from Table 2 can be found in Fig. 18. Based on the minimum residual sum of squares (RSS) and Akaike information criteria (AIC), we have chosen to use the logistic equation for nonsprouter seedling decline. We note

Table 3 A comparison of various models of resprout decay against the *Ceanothus spinosus* data for resprout survival from 1985–1993 using a residual sum of squares of the error (RSS) and the Akaike information criterion (AIC). From Burnham and Anderson (2010), AIC $= n\log(\mathrm{RSS}/n) + 2p$ where n is the number of data points and p is the number of parameters

Decay	$f_R(R_{t-1}, R_t; K_R)$	k_R	α_R	RSS	AIC
Exponential	$R_{t-1} - \alpha_R R_{t-1}$		0.0643	46.35	16.75
Logistic	$R_{t-1} + \alpha_R R_{t-1}(1 - \frac{R_{t-1}}{K_R})$	0.3509	0.0490	38.54	17.09
Morisita	$R_{t-1} + \alpha_R R_t(1 - \frac{R_{t-1}}{K_R})$	0.3931	0.0652	37.09	16.75
Hirota	$R_{t-1} + \alpha_R R_{t-1}(1 - \frac{R_t}{K_R})$	0.4221	0.0818	36.11	16.50
Gompertz	$R_{t-1}(\frac{R_{t-1}}{K_R})^{-\alpha_R}$	0.4784	0.1283	37.31	16.80
New Gompertz	$R_{t-1}(\frac{R_t}{K_R})^{-\alpha_R}$	0.4933	0.1589	35.41	16.32

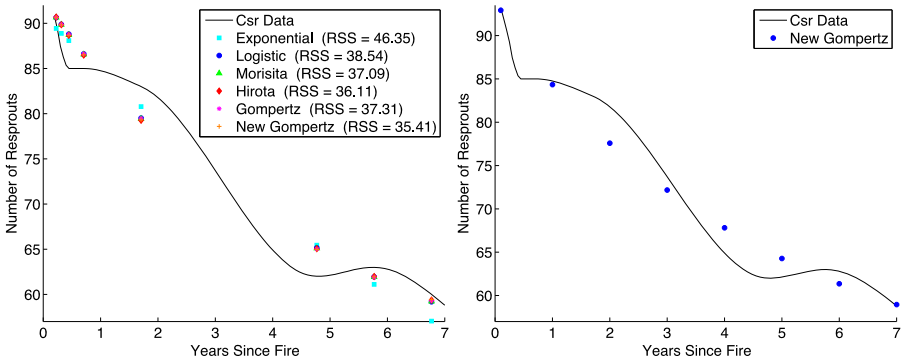

Fig. 19 (*Left*) Visual comparison of the models from Table 3 to the population declines of *Ceanothus spinosus* resprouts (Csr). (*Right*) A comparison of a simulation using the semi-implicit Gompertz model to the same data

that the Morisita equation or Hirota equation could be substituted for the logistic equation with qualitatively similar results.

We follow a similar procedure for comparing models of resprout survivorship. In Table 3 and Fig. 19, we compare several resprout decline models in a similar manner to nonsprouter seedling decline. We note that all of the models produce qualitatively similar fits. Although the exponential decay model has one less parameter and a similar AIC score to the other models, this model does not allow for a nonzero sustainable resprout population. Based on the minimum residual sum of squares and Akaike information criteria, we have chosen to use the semi-implicit Gompertz equation for resprout decline. We estimated the resprout decay α_R to be 0.1589 and the resprout survival percentage k_R to be 0.4933 which produces the fit in Fig. 19.

References

Ainsworth, J., & Doss, T. A. (1995). *Natural history of fire & flood cycles*. California Coastal Commission.

Anderson, R. M., & May, R. M. (1992). *Infectious diseases of humans dynamics and control*. London: Oxford University Press.

Burnham, K., & Anderson, D. (2010). *Model selection and multi-model inference: a practical information-theoretic approach* (2nd ed.). Berlin: Springer.

Davis, S. D. (1989). Patterns in mixed chaparral stands: differential water status and seedling survival during drought. In S. Keeley (Ed.), *Science series*: *Vol. 34*. *The California chaparral: paradigms reexamined* (pp. 97–105). Natural History Museum of Los Angeles County.

Frazer, J. M., & Davis, S. D. (1988). Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia*, *76*, 215–221.

Hirota, R. (1979). Nonlinear partial difference equations. V. Nonlinear equations reducible to linear equations. *J. Phys. Soc. Jpn.*, *46*(1), 312–319.

Keeley, J. E. (1975). Longevity of nonsprouting ceanothus. *Am. Midl. Nat.*, *93*(2), 504–507.

Keeley, J. E. (1986). Resilience of Mediterranean shrub communities to fires. In B. Dell, A. Hopkins, & B. Lamont (Eds.), *Resilience in Mediterranean-type ecosystems* (pp. 95–112). New York: Springer. Chap. 7.

Keeley, J. E. (1991). Seed germination and life history syndromes in the California chaparral. *Bot. Rev.*, *57*(2), 81–116.

Keeley, J. E. (1992). Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology*, *73*(4), 1194–1208.

Keeley, J. E. (1997). Seed longevity of non-fire-recruiting chaparral shrubs. *Four Seas.*, *10*(3), 37–42.

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, *169*, 1043–1052.

Keeley, J. E., & Fotheringham, C. J. (1997). Trace gas emissions and smoke-induced seed germination. *Science*, *276*(5316), 1248–1250.

Keeley, J. E., & Zedler, P. H. (1978). Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *Am. Midl. Nat.*, *99*(1), 142–161.

Keeley, J. E., Fotheringham, C. J., & Morais, M. (1999). Reexamining fire suppression impacts on brushland fire regimes. *Science*, *284*(5421), 1829–1832.

Mills, J. N. (1986). Herbivores and early postfire succession in Southern California chaparral. *Ecology*, *67*(6), 1637–1649.

Morisita, M. (1965). The fitting of the logistic equation to the rate of increase of population density. *Res. Popul. Ecol.*, *7*(1), 52–55.

Murray, J. D. (2002). *Interdisciplinary applied mathematics: Vol. 17*. *Mathematical biology. I* (3rd ed.). New York: Springer.

Pratt, R. B., Jacobsen, A. L., Mohla, R., Ewers, F. W., & Davis, S. D. (2008). Linkage between water stress tolerance and life history in seedlings of nine chaparral species (rhamnaceae). *J. Ecol.*, *96*, 1252–1265.

Radtke, K. W. H. (1983). *Living more safely in the chaparral-urban interface* (Tech. rep.). United States Department of Agriculture.

Saruwatari, M. W., & Davis, S. D. (1989). Tissue water relations of three chaparral shrub species after wildfire. *Oecologia*, *80*, 303–308.

Satoh, D. (2000). A discrete Gompertz equation and a software reliability growth model. *IEICE Trans.*, *E53-D*(7), 1508–1513.

Satoh, D. (2003). *A measure to distinguish between a logistic curve model and a Gompertz curve model*. Fast Abstract ISSRE.

Satoh, D., & Yamada, S. (2002). Parameter estimation of discrete logistic curve models for software reliability assessment. *Jpn. J. Ind. Appl. Math.*, *19*, 39–53.

Schlesinger, W. H., Gray, J. T., Gill, D. S., & Mahall, B. E. (1982). *Ceanothus megacarpus* chaparral: a synthesis of ecosystem processes during development and annual growth. *Bot. Rev.*, *48*(1), 71–117.

Thomas, C., & Davis, S. (1989). Recovery patterns of three chaparral shrub species after wildfire. *Oecologia*, *80*(3), 309–320.

Tyler, C. M. (1996). Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology*, *77*(7), 2182–2195.

VanElderen, E., Brown, S. L., & Davis, S. D. (1988). Chaparral seed production and loss in *Ceanothus megacarpus*, *Ceanothus spinosus*, and *Rhus laurina* after wildfire. Poster presented at thirteenth annual West Coast undergraduate research conference in the biological sciences, Los Angeles, CA.

Witter, M., Taylor, R., & Davis, S. (2007). Vegetation response to wildfire and fire history in the Santa Monica Mountains, California. In *Flora and ecology of the Santa Monica mountains* (pp. 173–194).

Zammit, C. A., & Zedler, P. H. (1993). Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *J. Ecol.*, *81*(3), 499–511.

Zammit, C., & Zedler, P. H. (1994). Organisation of the soil seed bank in mixed chaparral. *Vegetatio*, *111*(1), 1–16.