Habitat fragmentation and altered fire regime create trade-offs for an obligate seeding shrub

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Abstract. Habitat loss is widely considered the greatest threat to biodiversity. However, habitat loss brings with it myriad other threats that exacerbate impacts to biodiversity. For instance, altered fire regime is associated with habitat loss and fragmentation with unknown consequences to biodiversity. Plant functional groups that rely on fire to complete their life cycle may be adversely affected by disruptions to the natural fire regime, particularly when coupled with population declines due to habitat loss. We used a spatially explicit stochastic population model linked with fire hazard functions to investigate the cumulative effects of habitat loss, fragmentation, and altered fire regime on the expected minimum abundance of a long-lived obligate-seeding shrub, *Ceanothus greggii* var. *perplexans*. This species is endemic to the California Floristic Province, a biodiversity hotspot, and is representative of a functional group of plants found in many fire-prone ecosystems. We tested the impact of a range of different fire frequencies under three different combinations of fuel accumulation and weather. The best average fire return interval for population abundance was consistently in the range of 30–50 years. However, observed average fire return intervals in highly fragmented areas can be approximately 20 years or less, and model results show this to be detrimental to *C. greggii* populations. Results also show that if fires are uncorrelated across habitat fragments then the impact of altered fire regime on populations is worse than the impact of habitat fragmentation because of spatial and temporal decoupling of fire events across the landscape. However, the negative impacts of altered fire regime are outweighed by habitat loss as fragmentation increases. Our results show that large unplanned fires, operating under an altered fire regime, are ultimately detrimental to perennial obligate-seeding shrubs in fragmented landscapes.

Key words: California, USA; Ceanothus greggii var. perplexans; chaparral; disturbance; fire; habitat fragmentation; habitat loss; obligate-seeding shrub; population dynamics; population model.

INTRODUCTION

As threats to biodiversity increase in number and magnitude there is a growing need to understand the consequences of interactions between multiple stressors. Habitat loss and fragmentation are widely considered to be the greatest threats to global biodiversity (Dobson et al. 1997, Czech et al. 2000); however, they also promote myriad other threats that exacerbate impacts to biodiversity. Synergies between threats are predicted to intensify as biodiversity is confronted with increased anthropogenic reliance on natural resources; increased natural disturbances such as adverse weather and fire events (Westerling et al. 2006); increased invasive species encroachment (Simberloff and von Holle 1999); and the direct and indirect effects of climate change (Rosenzweig et al. 2008). To plan for the future of biodiversity it is essential to establish a better understanding of the dependencies between threats and how they influence species' risks of decline or extinction (Myers 1996).

In this paper we investigate the cumulative effects of habitat fragmentation and altered fire regime on a fire-dependent shrub, *Ceanothus greggii* var. *perplexans*, in the southern California, USA, chaparral. This species is representative of an important functional group of plants found in all fire-prone ecosystems: obligate seeders (Pausas et al. 2004). Here we focus on obligate seeders whose germination is strongly fire dependent, sometimes referred to as "fire recruiters" (Keeley 1992). In this case, habitat loss and fragmentation due to urbanization reduce population sizes by removing available habitat and indirectly altering the fire regime, which in turn alters the timing of recruitment events. The consequences of these combined threats are currently unknown for this plant functional group.

Fire is considered to be one of the most important factors affecting community structure and the dynamics of natural populations in mediterranean climates including southern California, Western Australia, Chile, the Cape region of South Africa, and the Mediterranean basin (Dell et al. 1986, Moreno and Oechel 1994). Obligate seeders are a key component of the exceptional plant diversity of some mediterranean-type ecosystems (Cowling and Lombard 2002, Lamont and Wiens 2003).

While crown fire kills all established plants, it is also necessary to stimulate seed germination in many species from this functional group (Schlesinger and Gill 1980, Pausas 2004). Human population density, urban growth, and agriculture have increased in mediterranean-climate regions, leading to habitat loss and fragmentation (Underwood et al. 2009). Fragmentation can decrease fire frequency in isolated habitat fragments within developed areas but also increase fire frequency due to human-caused ignitions and land use change at the expanding wildland–urban interface (Soulé et al. 1992, Moreno et al. 1998, Keeley et al. 1999, Syphard et al. 2006). If the fire frequency is shorter than the time it takes an obligate seeder to build a sufficient seed bank then the species could be extirpated after two subsequent fires (Zedler et al. 1983). On the other hand, for long fire return intervals, the seed bank may become unviable and the adult population could reach senescence, leading to extirpation (Zedler et al. 1983). The frequency of fires in fire-prone ecosystems may also increase with global climate change, including in mediterranean-type and other fire-prone ecosystems (Piñol et al. 1998, Williams et al. 2001, Lenihan et al. 2003, Fried et al. 2004, Pausas 2004, Westerling et al. 2006). Since fire plays an important role in the ecology and evolution of many plant species and fire-prone mediterranean-type ecosystems support much of the world's plant biodiversity, changes to the fire regime are likely to have significant effects on biodiversity (Cowling and Lamont 1987, Pausas 1999, Russell-Smith et al. 2002). Synergies between urbanization or other forms of land use intensification and fire are profoundly affecting mediterranean-type and other ecosystems worldwide (Uhl and Kauffman 1990, Gill and Williams 1996, Richardson et al. 1996, Radeloff et al. 2005, Syphard et al. 2007, Theobald and Romme 2007).

Various studies have investigated the separate effects of altered fire frequencies or fragmentation and found both to have significant consequences for the survival of endemic species (Soulé et al. 1992, Richardson et al. 1996, Cunningham 2000, Regan et al. 2003). Using a landscape-modeling approach, Syphard et al. (2007) found that an obligate-seeding Ceanothus species was more vulnerable to fire than to urbanization. However, to our knowledge, no study has systematically investigated the cumulative effect of these two threats on the population dynamics of this plant functional type. We use spatially explicit stochastic population models appropriate for the life history characteristics of obligate seeders, coupled with fire hazard functions, to investigate the population-level responses of C. greggii to a range of habitat fragmentation levels and fire frequencies. We identify the optimal fire frequency for C. greggii and determine the conditions under which altered fire regime has a greater impact on population abundance than does habitat fragmentation. Finally, we postulate the long-term impacts of frequent fires and ongoing

habitat fragmentation to obligate seeders in fire-prone ecosystems.

METHODS

Study species

Ceanothus greggii A. Gray var. perplexans (Trel.) Jepson (hereafter referred to as C. greggii) is an evergreen shrub found within the southwestern portion of the California Floristic Province spanned by the San Bernardino Mountains and the Peninsular Ranges of Baja and southern California (Hickman 1993). Its core habitat is chaparral dominated by chamise (Adenostoma fasciculatum) occurring in elevations of ~1200–1900 m (Kelly and Goulden 2008). Chaparral is an evergreen sclerophyllous shrubland, a vegetation formation typical of mediterranean-type ecosystems. C. greggii is a classic fire-recruiting obligate seeding shrub, typical of mediterranean-type ecosystems. All standing plants expire in a fire event. Fire, in turn, stimulates germination from a soil-stored seed bank. Therefore, populations grow as even-aged cohorts, with germination events rarely occurring in the absence of fire (Keeley 1992). C. greggii has highly restricted dispersal, making recolonization of extirpated patches extremely rare (Holl et al. 2000). The maximum life span of plants is uncertain but is thought to range from 85 to 155 years (Zammit and Zedler 1993). It is fairly common and locally abundant within its range and was selected for study because, as an important component of the chaparral community, it has been the subject of a number of population, community, and ecosystem studies, hence sufficient data on demographic rates and postfire responses exist in the published literature with which to parameterize a population model. Since our aim is to gain insights into the impacts of threats to a plant functional type, we used composite data from obligate-seeding species within the genus Ceanothus occurring in southern California when data for C. greggii were lacking.

Survival rates

We chose an age-based matrix model because most of the available data were reported in terms of stand age. Background survival rates (i.e., in the absence of fire) for the first 15 years were parameterized with stem ring data from C. megacarpus (Schlesinger and Gill 1978). C. greggii reaches its maximum size between 15 and 20 years, after which mortality is reduced significantly (Schlesinger and Gill 1980). The survivorship function from Zammit and Zedler (1993), $L_x = 1.087 - 0.01x$, was used to calculate survival rates of shrubs older than 15 years, where L_x is the survivorship of plants of age x. Background survival rates for ages greater than 15 years were compared with an independent data set from Keeley (1977) as well and were found to lie within a plausible range of variability. The survival rate of germinant seedlings is reported to be 95% (Schlesinger and Gill 1978), with a coefficient of variation of 3% (based on the variability in germinant survival found in

Schlesinger and Gill [1978] and Keeley [1977]). Coefficients of variation for the remaining survival rates ranged from 1% to 8% based on variations across slope aspect (Zammit and Zedler 1993), across stands (Schlesinger and Gill 1980), and across studies. Low year-to-year variability in survival rates of established plants is typical for long-lived species. Environmental variation in survival rates was represented via a lognormal distribution with these means and standard deviations.

Fecundity and seed survival

The number of seeds produced per plant, $f_s(x)$, is a function of stand age, with maximum seed production achieved within two decades of establishment (Zammit and Zedler 1993), $f_s(x) = 848.33 + 10.12x - 0.44(x - 38)^2$, where $x > 3$ yr is the age of mature plants in the stand. Only 50% of seeds produced by C. greggii shrubs in each year are viable (Keeley 1977). Sources reporting predation rates differed dramatically (91% in Davey [1982] and 34% in Zammit and Zedler [1993]), so a weighted mean (weighted by sample size) was used to estimate a predation rate of 74.8%. Variation in fecundity was estimated using the mean coefficient of variation (CV) across the five stands sampled in Zammit and Zedler (1993) to give CV = 0.5612, which was then multiplied by the mean fecundity (adjusted for seed mortality) for each age class to calculate standard deviations. The number of seeds entering the seed bank per year was drawn from a lognormal distribution with these calculated means and standard deviations.

Quick and Quick (1961) germinated seeds stored in the laboratory aged 10–25 years and found a mean germination rate of 99% ± 0.01%, indicating that under ideal conditions the seeds remain viable for long periods. However, loss of viability is not the only source of seed bank mortality. The seed bank is subject to annual pulses and losses due to soil erosion and subsequent predation, resulting in minimal net accumulation of seeds with time (Quinn 1994).

Quinn (1994) and Davey (1982) reported numbers of weathered seeds (indicating previous establishment in the seed bank) and new seeds incorporated into the seed bank, counted almost immediately after seed fall. To obtain a survival rate of seeds within the seed bank, the new seed numbers reported were reduced by predation and viability, and the number of weathered seeds was divided by the updated total number of seeds to give 85.75% ± 14.38%. Since net accumulation of seeds is minimal, this number is assumed to represent the annual percentage of seeds surviving in the seed bank. With this rate of annual seed survival the seed bank would be reduced to 5% of its original value in 20 years with no additional seed input. This was assumed to be a plausible estimate for annual seed survival; it is consistent with Quick and Quick's (1961) viability estimate and what is known about other sources of seed mortality.

Postfire recruitment

During a fire event 90% of seeds in the seed bank are killed (Quinn 1994). Additional predation of exposed seeds by rodents and birds reduces seed densities by a further 67%, leaving ~45 viable seeds/m^2 in the seed bank (Quinn 1994). Seedling densities at the beginning of the postfire growing season are 43.8 ± 7.84 germinants/m^2; however, 90% of these die by December, leaving 4.4 germinants/m^2 (Kummerrow et al. 1985). Our model is structured around a prefire season census, so this seedling death is included in our germination rate (i.e., 4.4 seedlings/45 seeds surviving to the end of the first year). When fire mortality, predation, and first-year survival are accounted for, germination of the seed bank occurs at a rate of 0.0032.

Carrying capacity and self-thinning

To ensure that simulated C. greggii population densities remained within biologically realistic bounds, ceiling carrying capacities based on stand age were calculated for the first 20 years using maximum recorded densities. For germinants, the upper bound on the 95% confidence interval for population densities (592 000 seedlings/ha) from Kummerow et al. (1985) was used. Maximum recorded values for ages 3, 12, and 21 years (from Schlesinger and Gill 1980; D. M. Lawson, personal observation) were used to plot the function $K(x) = 0.0056x^2 - 0.6944x + 15.033$, where $K(x)$ is the carrying capacity per hectare of plants of age $2 < x < 21$. Ceiling densities for 21-year-old plants were applied to older stands because the survival rates and size of C. greggii shrubs remain fairly constant after plants reach 21 years of age (Schlesinger and Gill 1980). While this might underestimate the actual ceiling possible (e.g., for years 12 and 21 maximum mean values were used because maximum observed values were not available), it provides a consistent upper bound that can be used across all scenarios for ranking and comparison of outcomes.

Fire events

There are three different processes thought to govern fire frequency, intensity, and distribution in southern California: fuel accumulation (Minnich and Chou 1997), weather conditions (Keeley and Fotheringham 2001), and a combination of both (Moritz 2003). We investigated the impacts of eight different mean fire return intervals (10, 20, . . . , 80 years) and three time–risk curves (fire hazard functions) generated by these processes on abundances of C. greggii. We used hazard functions based on the Wiebull distribution to specify the probability of an unplanned fire, $\lambda(t) = ct^{c-1}/b^c$, where $\lambda(t)$ is the probability of a fire, t is the time since last fire, c is a shape parameter describing the change in fire probability through time, and b is a scale parameter that defines the fire recurrence interval that will be exceeded 36.8% of the time (Polakow et al. 1999, Moritz 2003). Hazard functions with low-valued shape param-
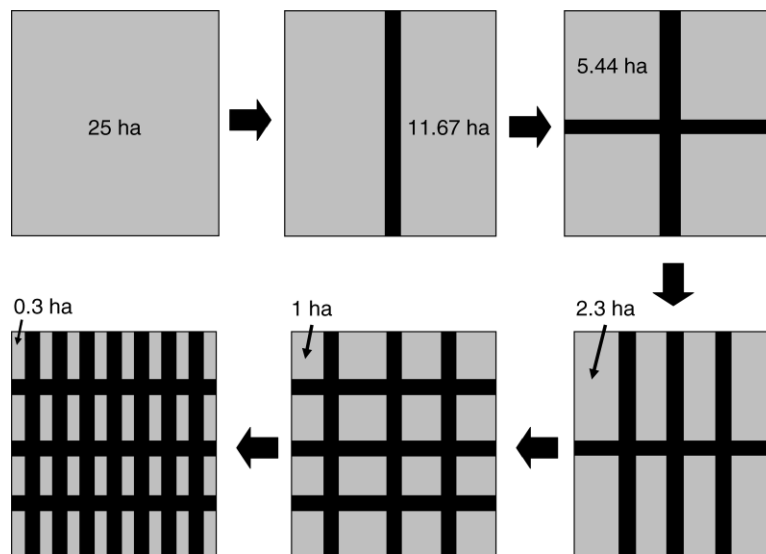
Fɪɢ. 1.   Schematic of fragmentation with habitat loss for the fire-dependent shrub *Ceanothus greggii* var. *perplexans* that was linked to the spatially explicit population model. Simulated habitat fragmentation was incorporated by sequentially dividing a continuous large patch (arbitrarily selected at 25 ha) into smaller patches, with and without habitat loss, resulting in 1, 2, 4, 8, 16, and 32 patches. The amount of habitat loss in each fragmentation scenario ranges from 1.66 ha in the two-patch scenario to 15.4 ha in the 32-patch scenario. Gray areas indicate suitable habitat; black indicate areas of unsuitable matrix. This shrub is endemic to the fire-prone California floristic province, USA.

eters represent fires exhibiting a minimal degree of vegetation age dependency, indicating fires influenced by weather. Conversely, high-valued shape parameters represent fires with a high degree of vegetation age dependency, indicating fuels play more of a role in fire frequency. Hence, fuel accumulation and weather conditions are implicit in the choice of shape parameter in the fire hazard function. We chose a value of $c = 3$ to represent the fuel accumulation scenario (i.e., the probability of fire increases with time since fire), $c = 1$ to represent the weather-driven scenario (i.e., the probability of a fire is constant with respect to time), and $c = 1.42$ is the maximum likelihood estimate for mixed chaparral in which fire risk is believed to be driven by a combination of weather and fuel accumulation (Polakow et al. 1999, Moritz 2003).

For $c = 1$ (i.e., weather-driven fires) the probability of a fire is simply 1/(mean fire return interval), i.e., the probability of a fire occurring in a given year is independent of the number of prior years without fire. For $c = 3$ and $c = 1.42$ the scale parameter b was assigned such that the desired mean fire frequency coincided with the mode of the probability density function for the fire interval distribution (Moritz 2003). The same b values arose for functions using $c = 3$ and $c = 1.42$ (Appendix A). The resulting probabilities $\lambda(t)$ were then verified through simulation that they produced the expected mean fire return intervals (which they did).

Fixed fire intervals (i.e., fires occurring exactly every n years with no unplanned fires) were also implemented. This assumes complete control over fire frequencies, which, while unrealistic, removes variation caused by

unplanned fires and allows exploration of the effects of temporal variability in fire events on populations. Each time a fire occurred, the fire function was reset to $\lambda(0)$. We implemented all fire functions and all fire frequencies on a single 1-ha patch to investigate the effects of different fire regimes in the absence of habitat fragmentation.

Habitat fragmentation

Simulated habitat fragmentation was incorporated by sequentially dividing a continuous large patch (arbitrarily selected at 25 ha) into smaller patches, with and without habitat loss, resulting in 1, 2, 4, 8, 16, and 32 patches (Fig. 1). For fragmentation scenarios with habitat loss, habitat was removed incrementally as the number of patches increased, up to ~62% habitat loss for the 32-patch scenario (Fig. 1).

Fragmentation scenarios were subjected to the eight unplanned fire frequencies (10- to 80-year mean fire return intervals). For the fragmentation comparison we restricted our consideration to the fire hazard function with $c = 1.42$, the most realistic current fire function for regions where *C. greggii* occurs (Polakow et al. 1999). Fires were implemented in the model with and without spatial correlation of fire events; when fires were spatially correlated all patches burnt simultaneously and when they were uncorrelated fire events were independent across patches. Additionally, fragments were subjected to both correlated and uncorrelated environmental variation in demographic rates to determine whether synchrony of "good" and "bad" years (with respect to background survival rates and fecundi-
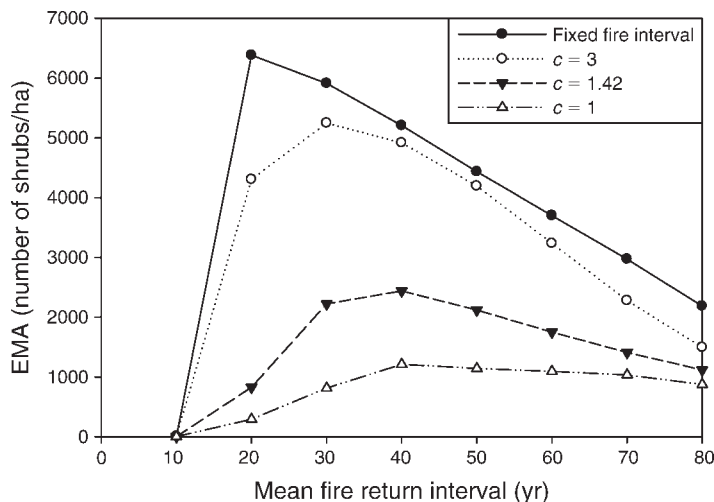
Fig. 2. Expected minimum abundances (EMAs) for four different fire functions with mean fire return intervals ranging from 10 years to 80 years in 10-year increments. Results are for a single 1-ha patch. The parameter c is the shape parameter for the Weibull hazard function: $c = 1$ indicates weather-driven fires, $c = 3$ indicates fuel-driven fires, and $c = 1.42$ is the shape parameter best describing both weather- and fuel-driven fires in southern California, USA.

ties) across patches is an important factor in the abundance of populations under threat.

Model simulation

We used RAMAS Metapop (Akçakaya and Root 2005) to link the spatial arrangement of patches, the stochastic age-based matrix population model, and the stochastic fire functions. The initial population comprised 14 350 germinants/ha. Environmental and demographic stochasticity was incorporated through Monte Carlo simulations for 1500 replications over a 200-year time period. This time period was selected so that multiple fire events could occur for long fire return intervals. The expected minimum abundance (EMA), excluding seeds, across the 1500 replications was used to compare results across all treatments (McCarthy and Thompson 2001). We performed sensitivity analyses on survival rates, fecundities, and variability in these parameters, as well as on assumptions related to seed mortality due to fire, germination in the absence of fire, and seed longevity (see Appendix B).

Results

Fixed fire interval, single patch

The set of fixed fire interval scenarios was tested exclusively on the single 1-ha patch. A 10-year interval was by far the most adverse fixed fire interval, resulting in an EMA of 0 (Fig. 2). The 20-year fire interval resulted in the highest EMA of all mean fire return intervals (Fig. 2). As the fixed fire interval length increased beyond 20 years, EMA steadily decreased. Expected minimum abundances for the fixed fire interval scenarios exceeded those for all other fire functions tested (Fig. 2).

Unplanned fuel-driven fires, single patch

When unplanned fuel-driven fires (i.e., $c = 3$) were applied to the single contiguous 1-ha patch model, C. greggii's risk of extirpation increased due to the added variability in fire frequency. The 30-year mean fire interval supported the largest populations, with an EMA of 5246 (Fig. 2). As the mean fire interval increased beyond 30 years, EMA decreased.

Unplanned weather-driven fires, single patch

For unplanned weather-driven fires (i.e., $c = 1$) applied to the single contiguous 1-ha patch model, the 40-year mean fire interval gave the highest EMA of 1210, and EMAs for longer mean fire frequencies differed from this only slightly (Fig. 2).

Weather- and fuel-driven fires, single patch

The EMAs for a single contiguous 1-ha population exposed to a fire regime defined by a hazard function with shape parameter $c = 1.42$ (weather- and fuel-driven fires) fall between those found for $c = 1$ and for $c = 3$ (Fig. 2). Thirty- to 40-year mean fire return intervals resulted in EMAs of 2222 and 2437, respectively (Fig. 2). Longer mean fire return intervals resulted in lower EMAs.

Fragmentation and altered fire frequency

Under all fragmentation levels, spatially correlated fires and environmental variation resulted in the lowest EMAs for all mean fire return intervals, whereas fragments simulated with spatially uncorrelated fire resulted in the largest EMAs (Fig. 3a). Fragments simulated with spatially uncorrelated fire events and correlated environmental variation in vital rates were not significantly different from patches with uncorrelated fire and environmental variation, indicating that the effects of spatial and temporal decoupling of fire events outweigh decoupling of environmental variation in survival rates and fecundities. In all five fragmentation scenarios, a 40-year mean fire return interval resulted in the largest EMA values, irrespective of whether fires were uncorrelated or not. The 10-year mean fire return interval resulted in extirpation of C. greggii populations
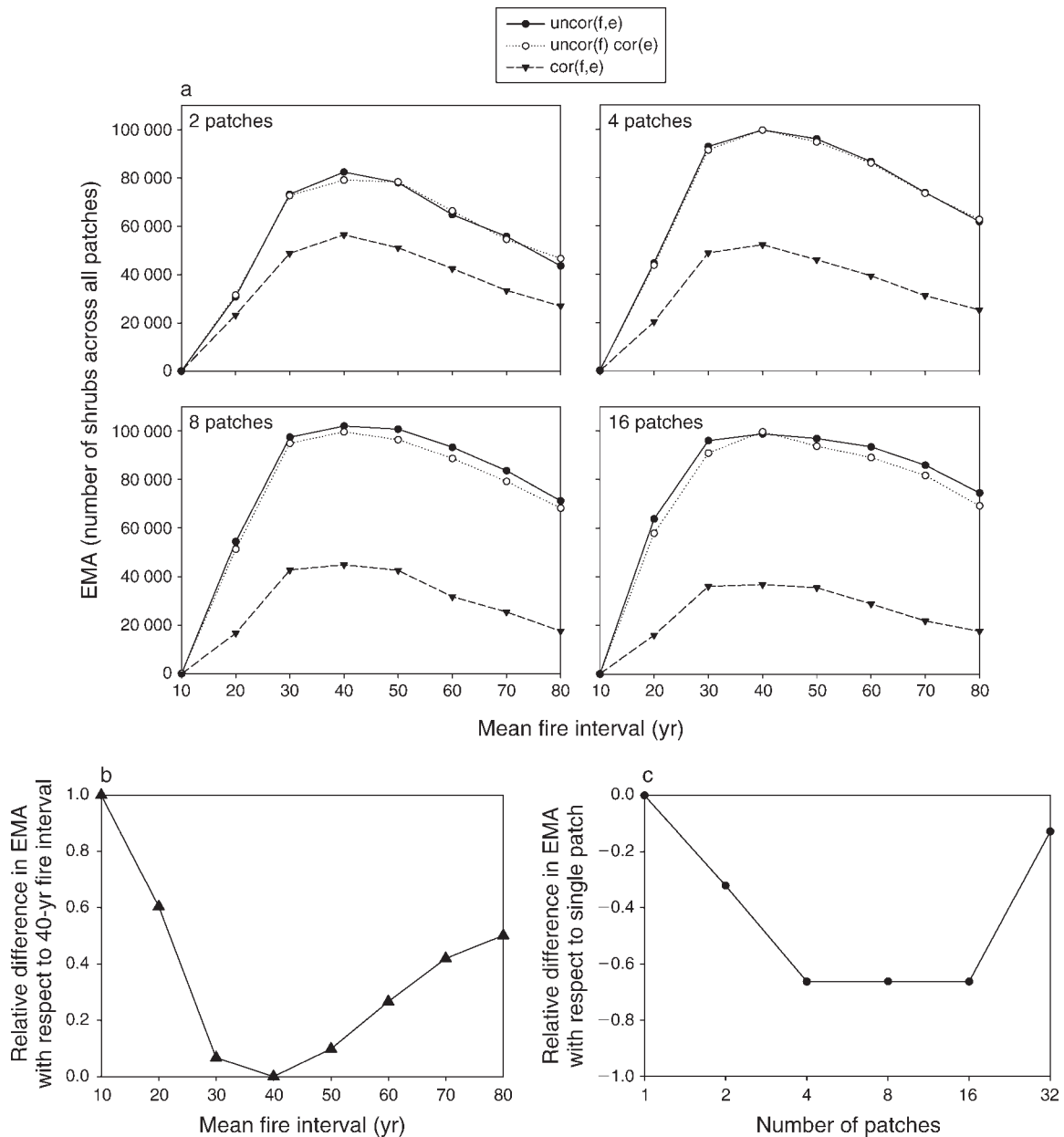
FIG. 3. (a) Expected minimum abundances (EMAs) vs. mean fire return interval for *Ceanothus greggii* under habitat fragmentation with habitat loss. EMA values are the number of shrubs across the total number of patches in each scenario. Each scenario has 25 ha, but decreasing amounts of habitat depending on the number of patches. Combined fuel- and weather-driven fires are implemented ($c = 1.42$). In panel (a), "2 patches" indicates two 11.67-ha patches; "4 patches" indicates four 5.44-ha patches; "8 patches" indicates eight 2.3-ha patches; and "16 patches" indicates 16 1-ha patches. Results for a single patch and 32 patches are not shown. Abbreviations: uncor(f,e) indicates that both fires and environmental stochasticity are spatially uncorrelated; uncor(f) cor(e) indicates that fires are spatially uncorrelated and environmental stochasticity is spatially correlated; and cor(f,e) indicates that both fires and environmental stochasticity are spatially correlated. (b) Relative difference in EMA for one patch with a 40-year mean fire return interval and alternative mean fire return intervals. (c) Relative difference in EMA for 40-year mean fire return interval in one patch and alternative numbers of patches. Fires are spatially uncorrelated, and c (the shape parameter for the Weibull hazard function) = 1.42 in all scenarios in panels (b) and (c).

across all patches for both correlated and uncorrelated fires (Fig. 3a).

Fig. 3b shows the relative difference between the EMA for a single 25-ha patch with a 40-year mean fire

return interval and the same single patch with alternative fire frequencies. Fig. 3c shows the relative difference between the EMA for a single 25-ha patch with a 40-year mean fire return interval and the same fire regime
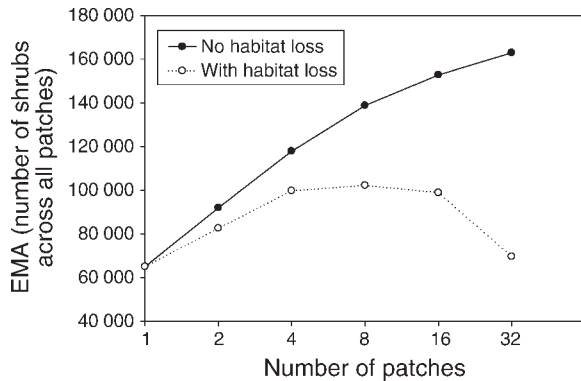
Fig. 4. Expected minimum abundance (EMA) vs. number of patches using the habitat fragmentation scenarios in Fig. 1, with and without habitat loss. EMA values are as described in Fig. 3. Fires are uncorrelated across patches. Fire function is combined fuel- and weather-driven with c (the shape parameter for the Weibull hazard function) = 1.42 and a 40-year mean fire return interval.

with alternative levels of fragmentation. Comparisons were based on 40-year mean fire intervals because these are optimal for *C. greggii* (Fig. 3a). The positive relative differences in Fig. 3b indicate that the EMA for a single patch with a 40-year fire interval is the highest of those compared, whereas the negative relative differences in Fig. 3c indicate that the EMA for fragmented populations is higher than for the single patch. The larger magnitudes of relative difference indicate a greater relative difference. Together, these results show that if fires are uncorrelated across habitat fragments then the impact of altered fire regime on populations is worse than the impact of habitat fragmentation; however, as habitat fragmentation increases, the positive effects of decoupled fires diminish.

Fig. 4 illustrates the effects of habitat loss due to fragmentation on populations experiencing uncorrelated fires. As the population is incrementally fragmented from one to eight patches, the EMA increases because fires are uncorrelated, effectively creating a population of multiple (spatially separated) age classes, thus spreading risk. In this way habitat fragmentation creates a trade-off for obligate seeders if fires are uncorrelated: as habitat loss increases (at least for low levels of fragmentation) the EMA increases. However, after eight patches, habitat loss associated with fragmentation outweighs the beneficial effects of decoupling fire events. Comparison with the scenario of fragmentation with no associated habitat loss (i.e., a decoupling of fires without habitat loss) demonstrates that while habitat loss due to fragmentation reduces expected minimum abundance, it is tempered, at least for low levels of habitat loss, by the beneficial population-level effects of uncorrelated fires.

DISCUSSION

The results of this study provide insight into generalities regarding the impacts of habitat fragmenta-

tion and altered fire regime on long-lived obligate seeders in the chaparral ecosystem and further afield. Our results show that in order to achieve higher abundances for these obligate seeders (1) fires need to occur at an optimal mean interval of 30–50 years and (2) fires need to be smaller than the species' distribution. While habitat fragmentation may facilitate small fires (relative to a species distribution) by creating fire breaks, it interacts with the fire regime by providing opportunities for increased human ignitions, reducing the mean fire return interval to 20 years or less. Our results show that as fires become more frequent (e.g., less than a mean return interval of 30 years), obligate seeders decline, irrespective of how small the fires are. This is because of the increased likelihood of fires occurring in rapid succession in the same patch as the average fire return interval decreases and the "immaturity risk" (Zedler 1995) to these populations intensifies. This is cause for concern for obligate seeders with restricted range, such as rare and endemic species occurring at the urban–wildland interface, where fires are more frequent. This also has ramifications for all fire-prone environments supporting long-lived obligate seeders experiencing increased fire risk, increased human ignitions, and higher fire frequency due to climate change. While the optimal fire frequency for obligate seeders in other ecosystems will be different from that found here, the general principle governing optimality is the same.

Our results also show that while a small amount of habitat fragmentation is beneficial to *C. greggii* if it spatially and temporally decouples fire events, it is ultimately outweighed by the negative effects of habitat loss as fragmentation increases. This highlights an important aspect of spatial heterogeneity for obligate seeders and a critical difference between patchiness and habitat fragmentation. Natural patchiness in populations is beneficial because it spreads risk. If the species distribution is sufficiently wide that fires are patchy across the species' entire range, then the species will have heterogeneous stand ages irrespective of whether populations occur as spatially separated patches. Our results show that this beneficial aspect of fire patchiness can be achieved with habitat fragmentation but only up to a point and only if it induces a decoupling of fire events without increasing fire frequency. However, habitat fragmentation is associated with increased fire frequency and most real populations have already surpassed beneficial levels of fragmentation. Anthropogenic habitat fragmentation is ultimately detrimental because of accompanying habitat loss, edge effects, and the potential for demographic stochasticity to extirpate small populations (Fahrig 1997). Furthermore, wind is capable of driving fires to very large sizes, and in those cases many fuel treatments, and even roads, can be completely ineffective at curbing the spread (Keeley et al. 2004).

For species that are widespread and locally abundant within their ranges, such as *C. greggii*, populations are

buffered from the risks of all but the very largest fires. However, recent very large and overlapping fires occurring at short intervals in southern California (Keeley et al. 2009) raise the concern that even widespread obligate seeders occurring in large patches may be at risk of decline due to short intervals between fires. Further, many perennial obligate seeders have more restricted ranges and smaller subpopulations than *C. greggii*, and the smaller a patch, the more likely it will burn entirely when a fire occurs. In this way habitat loss and fragmentation indirectly promote more frequent fires burning an entire patch.

We compared fire regimes representing contrasting scenarios of no dependence and complete dependence of fire risk on the time since last fire and a combination of both. A robust conclusion from our results is that, even if the degree to which fire risk is fuel or weather driven and the magnitude of habitat fragmentation are uncertain or unknown, a 30- to 50-year mean fire return interval gave the highest expected minimum population size for *C. greggii* for all fire functions and all fragmentation levels. This demonstrates an inherent link between optimal fire frequency and plant traits irrespective of the mechanism governing fire occurrence. Furthermore, the range of optimal fire frequencies resulting from our analyses support those found through other empirical-based studies (Polakow et al. 1999).

We wish to express caution in interpreting the results obtained across the suite of fire functions used in this study. Comparing results within fire regime (i.e., within fire functions arising from a given value of the shape parameter c in the fire hazard function) is more meaningful than comparisons between fire functions. The differences in EMA across fixed fire intervals, fuel-driven fires, weather-driven fires, and a combination of fuel- and weather-driven fires for a given mean fire interval length is due to the extent of variability in each function (see Appendix A). Fire functions exhibiting greater variability will produce shorter fire intervals, leading to lower EMAs and greater risks of extirpation. The apparent higher EMAs under the fuel-driven fire regime occur because fires rarely occur at very short intervals under this fire function due to lower variation in fire interval length. However, this should not be interpreted as a better fire regime for obligate seeders. In real landscapes fire will always have some degree of unpredictable spatial and temporal stochasticity (van Wilgen et al. 2004). By modeling the full range of scenarios, including fixed fire interval, we demonstrate that the effect of mean fire interval length was equal to or greater than the effect of fire function (i.e., degree of fuel dependence of fire risk) on population size.

Our results provide initial insights into potential population-level effects of climate change on obligate seeders. First, climate change may lead to habitat contractions and fragmentation (Thuiller et al. 2005). Our results show that this is detrimental to population viability once a threshold level of habitat reduction and fragmentation is reached (Fig. 4). Distribution shifts induced by climate change, as recently observed for *C. greggii* (Kelly and Goulden 2008), may ultimately result in habitat reduction or fragmentation for populations abutting urbanized areas or shifting to higher elevations. Second, climate change is likely to increase fire risk in mediterranean-type ecosystems (Williams et al. 2001, Mouillot et al. 2002, Pausas 2004). Our results indicate that increased fire frequency can be even more detrimental to obligate seeders than habitat contractions, depending on the level of associated habitat fragmentation and whether it decouples fire events (Fig. 3). This is supported by Keith et al. (2008), who showed that increased fire frequency in South African fynbos is likely to induce larger declines in obligate seeder populations than habitat contractions due to climate change.

Long-lived perennial obligate seeders are defining elements of the biota in most mediterranean-type and other fire-prone ecosystems and are sensitive to changes in fire frequency. Hence obligate seeders are good indicators of likely consequences to plant communities under altered fire regimes resulting from direct human impacts (ignitions, suppression) or indirect effects (land use change, climate change). The application of a single-species population model to a functional type proved valuable in identifying species traits associated with vulnerability to altered fire regime, habitat loss, and fragmentation because gleaning these from communities on a species-by-species basis is intractable. Studies such as this one can help identify the likely community-level effects of multiple, interacting threats by focusing on important functional types that comprise a plant community.

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APPENDIX A

Fire hazard function parameters (*Ecological Archives* E091-079-A1).

APPENDIX B

Sensitivity analyses of age-specific survival rates, fecundities, germination rates, seed bank survival, and standard deviations (*Ecological Archives* E091-079-A2).