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Population and community-level impacts of increased fire frequency in serpentine chaparral

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ABSTRACT

Wildfires are natural processes that revitalize the native biodiversity of many habitats by clearing landscapes and creating sunlight rich areas with low competition. This process occurs in the serpentine chaparral of California, which is home to a variety of fire obligate seeders, including whiteleaf manzanita (*Arctostaphylos viscida*) and MacNab cypress (*Cupressus macnabiana*), as well as fire facultative seeders such as chamise (*Adenostoma fasciculatum).* In our study, we surveyed serpentine chaparral habitats in sites with different burn histories to investigate the effect of fire frequency on the abundance of MacNab cypress, manzanita, and chamise populations in sites that burned 1, 6, and 21 years ago. We also constructed life tables to assess MacNab cypress population growth rate in these different burn sites. Our results indicate that the reproductive success of MacNab cypress decreases four-fold with increasing fire frequency and that increasing fire frequencies may favor fire facultative seeders over fire obligate seeders. This study provides updated research on the effects of increasing fire frequency on plant communities in serpentine chaparral.

Keywords: MacNab cypress, fire obligate seeders, fire facultative seeders, fire succession, serpentine chaparral

INTRODUCTION

Wildfires are natural processes that revitalize the native biodiversity of many habitats by clearing landscapes and creating sunlight rich areas with low competition. (Keeley et al. 2003). By removing vegetation, fires promote new stages of succession. Some plants have evolved to take advantage of the effects of fire. Fire obligate seeders reproduce when induced by the heat from fires, allowing their seeds to germinate in areas with less competition for nutrients, water, and sunlight (Kozlowski and Ahlgren 2012). Fire facultative plants increase their populations by germinating after fires, but they also have the ability to resprout from their living roots.

The serpentine chaparral of California is home to a variety of fire obligate seeders, including whiteleaf manzanita (*Arctostaphylos viscida,* hereafter referred to as manzanita), and MacNab cypress (*Cupressus macnabiana*). In addition, it has fire facultative seeders such as chamise

(*Adenostoma fasciculatum*), which releases its seeds post fire, but can also resprout. All three of these species require combustion to effectively reproduce, but the MacNab cypress is the only one with fire-induced ovulate cones that persist on the tree until triggered to release their seeds by fire (Esser 1994). The seedlings find the most success in direct sunlight and in soil with minimal detritus–conditions that are common post-burn (Esser 1994).

After germination, MacNab cypress recruits require 16 years to reach reproductive maturity (Esser 1994). A study on the Tecate cypress (*Cupressus forbesii*), another California cypress with fire-induced ovulate cones, found that the average time between wildfires in its habitat was 25 years; this gives the saplings the required time to reach reproductive maturity (Esser 1994). A previous study found that 90% of MacNab cypress populations have had at least 40 years between burns up until 2009. (Mallek 2009). Since these studies, the time between fires has changed. Due to anthropogenic global warming and fire suppression, the window for regrowth between fires is shorter than in previous decades (Keeley 2003).

Given the connection between fire and the reproductive success of fire obligate plants, we explored how increasing fire frequency impacts these communities. We surveyed serpentine chaparral habitats that have burned within the last 25 years to investigate the effect of fire frequency on shrub community structure and MacNab cypress population growth rate. We hypothesized that the sites with a history of higher fire frequency would have a lower abundance of fire obligate plants. We also predicted that the population growth rate of MacNab cypress would decline with increased fire frequency because the saplings would have burned before reaching reproductive maturity. The dependence of serpentine endemic vegetation on fire necessitates investigating new conservation strategies in response to changing fire regimes.

METHODS

This study took place at burn sites around the Donald and Sylvia McLaughlin Natural Reserve from February 23rd-28th, 2021. McLaughlin Reserve consists of oak woodland, serpentine grasslands, and serpentine chaparral habitats. Serpentine soil is a unique habitat that has a low calcium to magnesium ratio, making it inhospitable for many plants. MacNab cypress, manzanita, and chamise are some of the few species that are tolerant to these areas with manzanita and MacNab cypress growing exclusively in serpentine habitats. Within the last two decades, the LNU Lightning Fire Complex of 2020, the Jerusalem Fire of 2015, and the Sixteen Fire of 1999 have burned parts of the reserve with some areas burning in both 2015 and 2020 fires.

We measured the abundance of the MacNab cypress, whiteleaf manzanita, and chamise populations in the 1999, 2015, and 2015/2020 overlap burn sites. We chose one location with MacNab cypress populations to survey in each of our burn sites by cross referencing a vegetation map and various burn maps. At each location, we laid three 52-meter transects, each 30 meters apart. Starting at the beginning of the transect, we measured a 10 x 2 meter plot perpendicular to our transect starting at the 0-meter mark. We repeated this on alternating sides of the transect every 10 meters, totaling 6 plots per transect. We counted the number of living saplings, dead saplings, living adults, and dead adults of each study species within the plot.

To assess impacts of fire frequency on plant reproductive success and population growth, we counted ovulate cones on a MacNab cypress at each plot to construct life tables for their populations. We sampled the adult MacNab cypress closest to the transect for our visual seed count and noted whether it was alive or dead. If there were no MacNab cypress adults present inside the plot, we counted the cones on the adult nearest to the plot.

To approximate the number of seeds per cone for the life table, we selected adult trees from the 1999 and the 2015 burn sites. We extracted and counted seeds from five cones from five different trees in each site to estimate the average number of seeds produced per cone and per tree.

We ran an ANOVA to investigate the effect of burn year, plant age class, and species on plant abundance. To predict the population growth rate of the MacNab cypress, we created a life table for the population that burned once in 1999 (Once Burned) and a life table for this population if it were to burn again (Twice Burned) by using the mortality data from the 2015/2020 burn overlap site. The abundance of living saplings and adults from the 1999 burn site informed our values for the variables used in the life tables (Table 1; Krebs 2009). The change in survival rates between the 2015 burn site and the 2015/2020 overlap burn site informed the new l(x) and g(x) variables in the Twice Burned life table. Using the life tables, we calculated the difference in the average number of offspring produced per MacNab cypress (R_0) between these two fire regimes.

Table 1. Life table variables. Description of variables and formulas used in MacNab cypress life table. Variable n(x) was counted in the field and b(x) was calculated by multiplying the number of adults by the average number of cones per adult by the average number of seeds per cone.

Variable	Definition	Equation
n(x)	number of living individuals at stage x	[recorded in field]
l(x)	proportion of individuals surviving to stage x	$\frac{n_x}{n_0}$
g(x)	probability of survival from stage x to stage x+1	$\frac{n_{x+1}}{n_x}$
b(x)	average number of offspring at stage x	[recorded in field]
l(x)b(x)	average recruitment at stage x	$l_x \cdot b_x$
q(x)	per capita mortality rate from stage x to stage x+1	$1 - l_x$
R_0	mean number of offspring produced by an individual over its lifetime	$\sum_0^\infty l_x b_x$

RESULTS

We surveyed 49 plots across the three burn sites. The greatest density of living plants was observed in the 1999 site, while the 2015 and 2020 overlap sites had the lowest density of living plants (Fig. 1, Table 2). MacNab cypress were most dense in the 1999 site (39.27 plants/20m^2). Manzanitas were most dense in the 2015 site (10.17 plants/20m^2) compared to MacNab cypress and chamise (6.78 plants/20m^2 and 3.81 plants/20m^2, respectively) (Fig. 2, Table 2). Every species was found at its lowest density in the twice burned site (3.96 cypress/20m^2, 0.12 manzanita/20m^2, and 0 chamise/20m^2) (Fig. 2, Table 2). The 1999 site had the greatest MacNab cypress sapling density (71.88 plants/20m^2) and MacNab cypress adult density (6.67 plants/20m^2) (Fig. 3, Table 2). The 2015 site had the greatest manzanita sapling density (20.22 plants/20m^2) and adult density (0.11 plants/20m^2) (Fig. 4, Table 2). No adult manzanitas were present in the 1999 or overlap burn sites (Fig. 4, Table 2). Chamise had the greatest sapling (2.83 plants/20m^2) and adult (7.88 plants/20m^2) populations in the 1999 site (Fig. 5, Table 2).

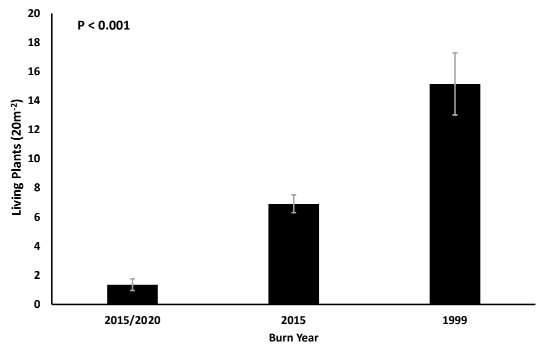

Figure 1. Effect of time since most recent fire (1 year, 6 years, 21 years) on average density of living MacNab cypress, manzanita, and chamise per 20m^2 in 1999, 2015, and 2015/2020 overlap burn sites. 1999 burn sites had the most living plants whereas the 2015/2020 burn sites had the fewest. Vertical bars represent one standard error from the mean.

Table 2. ANOVA statistics for the effects of burn year, age class, species, and their combined interactions on the abundance of whiteleaf manzanita, chamise, and MacNab cypress in serpentine chaparral. Data collected in Lake County and Napa County, California, at the Donald and Sylvia McLaughlin Natural Reserve.

P < 0.05 = * | P < 0.01 = ** | P < 0.0001 = ***

Effect	N	F
Plant Abundance		
Burn Year	294	8.67 **
Age Class	294	15.32 ***
Species	294	10.52 ***
Burn Year * Age Class	294	3.96 *
Burn Year * Species	294	10.01 ***
Age Class * Species	294	10.77 ***
Burn Year * Age Class * Species	294	7.62 ***
Cypress Abundance		
Burn Year * Age Class	98	7.17 **
Manzanita Abundance		
Burn Year * Age Class	98	11.84 ***
Chamise Abundance		
Burn Year * Age Class	98	2.39

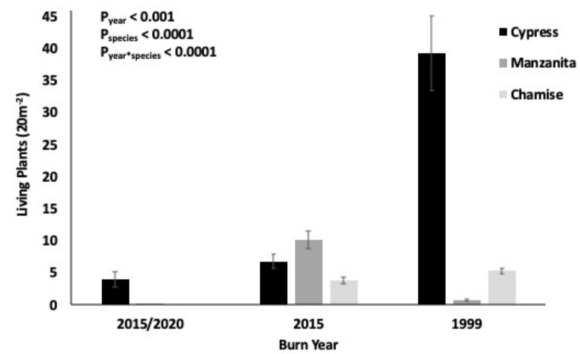

Figure 2. Effect of time since most recent fire (1 year, 6 years, 21 years) on average density of three species (cypress, manzanita, and chamise) per 20m^2 in 1999, 2015, and 2015/2020 overlap burn sites. 1999 burn sites had the most living cypress plants. 2015/2020 overlap burn sites had 0.12 manzanita per 20m^2 and no chamise plants. Vertical bars represent one standard error from the mean.

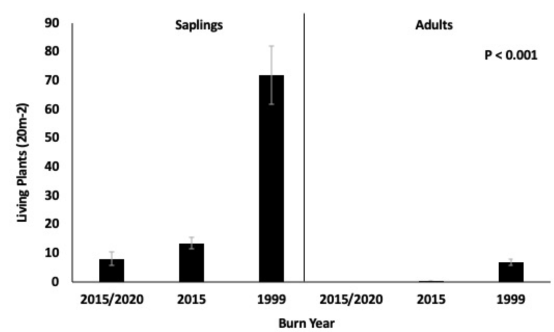

Figure 3. Effect of time since most recent fire (1 year, 6 years, 21 years) on average density of cypress saplings and adults per 20m^2 in 1999, 2015, and 2015/2020 overlap burn sites. 1999 burn sites had the most cypress saplings and adults. 2015 and 2015/2020 overlap burn sites only had 0.17 adults and zero adults, respectively. Vertical bars represent one standard error from the mean.

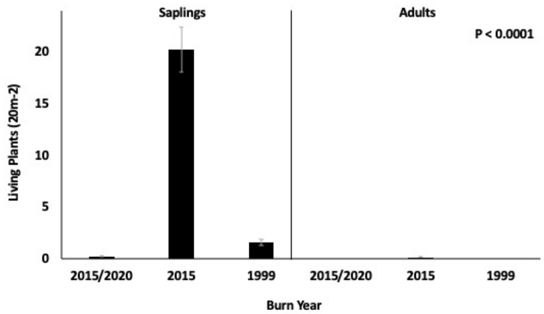

Figure 4. Effect of time since most recent fire (1 year, 6 years, 21 years) on average density of manzanita saplings and adults per 20m^2 in 1999, 2015, and 2015/2020 overlap burn sites. 2015 burn sites had the most manzanita saplings. 1999 and 2015/2020 overlap burn sites had no manzanita adults, and 2015 burn sites only had 0.11 manzanita adults. Vertical bars represent one standard error from the mean.

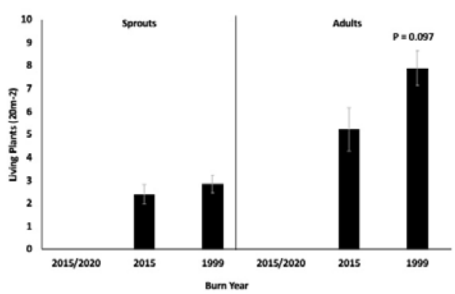

Figure 5. Effect of time since most recent fire (1 year, 6 years, 21 years) on average density of chamise sprouts and adults per 20m^2 in 1999, 2015, and 2015/2020 overlap burn sites. 1999 burn sites had the most chamise adults. 2015/2020 overlap burn sites had no chamise saplings or adults. Vertical bars represent one standard error from the mean.

We created two life tables to calculate how the population growth rate of MacNab cypress is affected by different fire intervals. In the population that burned 20 years ago, the calculated R_0 value was 27.33 (Table 3). In the life table for this population after a second burn, the new R_0 value was 6.95 (Table 3).

Table 3. MacNab cypress life tables. Comparison of life tables for MacNab cypress in regions that have burned once versus regions that have burned twice within five years. Variables in Once Burned table were calculated using data from 1999 burn regions. The changed values for l(x) and g(x) in the Twice Burned table were calculated using the difference in survival rates in 2015 burn regions versus 2015/2020 burn regions. In regions that burned twice in five years, the net reproductive rate (R_0) decreases from 27.33 to 6.95.

Stage	n(x)	l(x)	g(x)	b(x)	l(x)b(x)	q(x)	R_0
Once Burned							
Seed (0)	1244.10	1.00	0.06	0	0	0.94	
Sapling (1)	75.42	0.06	0.09	0	0	0.05	
Adult (2)	6.67	0.01	–	5097.04	27.33	0.01	
							27.33
Twice Burned							
Seed (0)	1244.10	1.00	0.06	0	0	0.94	
Sapling (1)	75.42	0.06	0.02	0	0	0.05	
Adult (2)	1.51	0.0014	–	5097.04	6.95	0.01	
							6.95

DISCUSSION

We found the greatest abundance of MacNab cypress saplings in the 1999 burn site and the least in the 2015/2020 overlap site, supporting our hypothesis that fire frequency would decrease the abundance of fire obligate seeders. (Figure 3, Figure 4). The difference in MacNab cypress sapling abundance from the 1999 burn site to the 2015 burn site may have occurred because of the germination limitation caused by drought conditions from 2012 through 2015 (Luo et al. 2017). The only living MacNab cypress observed in the 2015/2020 overlap burn site were charred saplings with small patches of green foliage. These saplings did not have enough time to reach reproductive maturity before the second fire. The reduction in MacNab cypress density in the 2015 burn site may have allowed manzanita to successfully compete for space (Figure 4, Table 3). Despite their ability to establish themselves in 2015 burn sites, no living manzanita remained in the 2015/2020 overlap site (Figure 4, Table 3). The recently germinated saplings of the fire obligate seeders we surveyed were burned before reaching reproductive maturity, leaving their populations vulnerable to competition.

The total number of living chamise were similar between the 1999 and 2015 burn sites, suggesting that they rapidly recolonize burned landscapes due to their ability to resprout (Figure 5). With more time, we predict that chamise will return to their former population levels in the 2015/2020 burn site. It is possible that all facultative seeders will be more successful than fire obligate seeders in regions with frequent fires, altering the current composition of these fire-adapted communities.

In regions that burned twice within a five-year window, we calculated a four-fold decrease in the reproductive success of MacNab cypress, supporting our hypothesis that MacNab cypress population growth would decrease in such conditions. On average, each tree would have had only 7 recruits, instead of 27, because more saplings would have burnt before reaching reproductive maturity. When Mallek (2009) surveyed fire regimes in MacNab cypress populations, he found that short fire intervals were not a significant threat because 90% of the populations had not burned in 40 years, so they had time to reach reproductive maturity before burning. However, the 21st century has seen an unprecedented increase in fire frequency (Keeley 2003). Our study provides an updated insight into the reproductive success of MacNab cypress populations under current environmental conditions, which result in shorter fire intervals. Our calculated population growth rate suggests that, if fire frequency continues to increase or remains at this increased rate, overall MacNab cypress abundance will decrease.

Fire is essential to the reproductive success of endemic fire obligate seeders of California. Consequently, California's increasing fire regime has major impacts on fire-adapted communities. Fire obligate seeders require 10 to 20 years on average to replenish their seed bank (Zedler 1995). If regions continue to burn this frequently, we expect to see California landscapes decrease in fire obligate seeder abundance and become dominated by fire facultative plants and fire obligate plants with younger reproductive ages. The rapid changes in California's environmental conditions reveal a heightened need for conservation of California endemic plants. Expanding plant conservation policy to include single site endemics such as the MacNab cypress, would help prevent future extinction and irreparable shifts in fire-dependent ecosystems (Knapp et al. 2020). Unless proactive measures are taken to protect native adapted species, or to prevent this increased fire frequency, California's landscapes could be severely altered.

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REFERENCES

Esser, L. 1994. *Hesperocyparis macnabiana*. https://www.fs.fed.us/database/feis/plants/tree/hesman/all.html#BOTANICAL%20AND%20ECOLOGICAL%20CHARACTERISTICS.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. *Science of The Total Environment* **262:**221–229.

Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. fire and grazing impacts on plant diversity and alien plant invasions in the Southern Sierra Nevada. *Ecological Applications* **13:**1355–1374.

Knapp, W. M., A. Frances, R. Noss, R. F. C. Naczi, A. Weakley, and G. D. Gann. 2020, August 28. The Society for Conservation Biology. https://conbio.onlinelibrary.wiley.com/doi/full/10.1111/cobi.13621.

Koehler, C. 2021, February 23. Koehler fire map information.

Kozlowski, T. T., and C. E. Ahlgren. 2012. *Fire and Ecosystems*. Elsevier.

Krebs, C. J. 2009. *Ecology: The experimental analysis of distribution and abundance*. Fourth edition. Harpercollins College Div; 4th edition (November 1, 1993).

Kruckeberg, A. R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. *American Journal of Botany* **38:**408–419.

Lippitt, C. L., D. A. Stow, J. F. O'Leary, and J. Franklin. 2013. Influence of short-interval fire occurrence on post-fire recovery of fire-prone shrublands in California, USA. *International Journal of Wildland Fire* **22:**184.

Luo, L., D. Apps, S. Arcand, H. Xu, M. Pan, and M. Hoerling. 2017. Contribution of temperature and precipitation anomalies to the California drought during 2012–2015. *Geophysical Research Letters* **44:**3184–3192.

Mallek, C. R. 2009. Fire history, stand origins, and the persistence of McNab cypress, northern California, USA. *Fire Ecology* **5:**100–119.

Milich, K., J. Stuart, J. Varner, and K. Merriam. 2012. Seed viability and fire-related temperature treatments in serotinous California native *Hesperocyparis* species. *Fire Ecology* **8:**107–124.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. *Ecological Applications* **17:**1388–1402.

Pausas, J.G. and Keeley, J.E. 2019. Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment* **17(5):**289–295.

Zedler, P. H. 1995. Zedler, P.H. 1995. Fire frequency in southern California shrublands: biological effects and management options. Pp. 101–112 in: J.E. Keeley and T. Scott, editors. *Brushfires in California wildlands: ecology and resource management*. International Association of Wildland Fire, Fairfield, Washington, USA.

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