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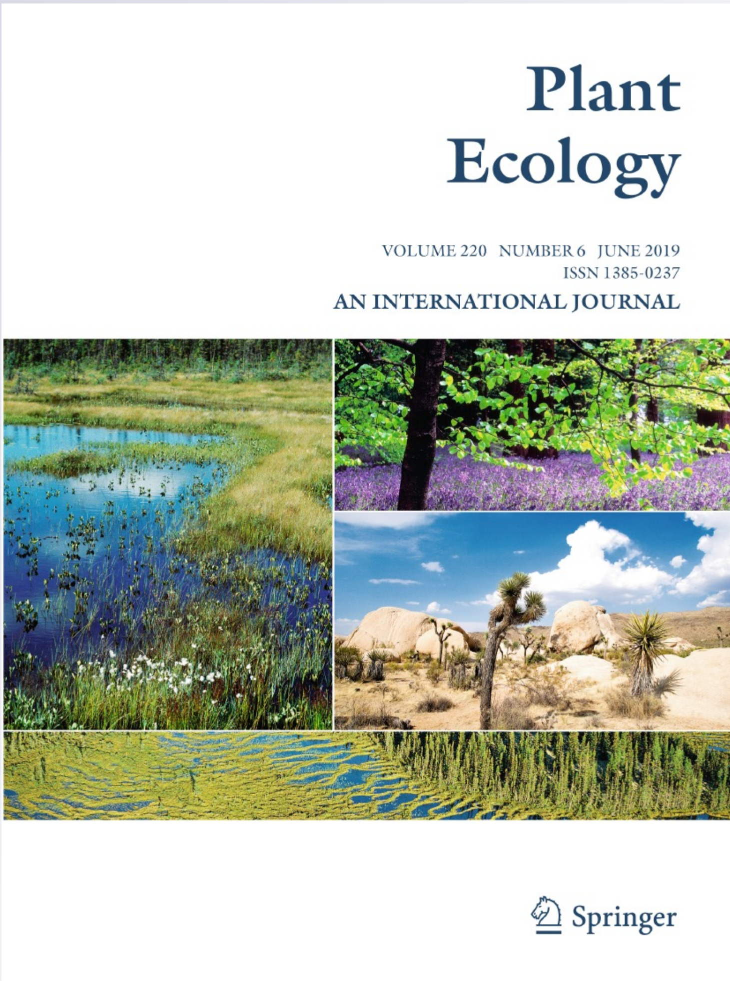
Plant Ecology
An International Journal

ISSN 1385-0237
Volume 220
Number 6

Plant Ecol (2019) 220:605-617
DOI 10.1007/s11258-019-00939-8



Springer

Plant Ecol (2019) 220:605–617
https://doi.org/10.1007/s11258-019-00939-8

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Received: 1 August 2018 / Accepted: 10 April 2019 / Published online: 10 May 2019

Abstract Tecate cypress *(Hesperocyparis forbesii)* is a rare species restricted to four metapopulations in southern California, USA and a few isolated populations in northern Baja California, Mexico. It is a closed-cone, fire-dependent tree of conservation concern due to an increase in human-caused wildfires that have shortened the interval between fires in many of their populations. In 2003, the Mine/Otay Fire burned 70% of the Tecate cypress on Otay Mountain in San Diego County, California providing an opportunity to evaluate the immaturity risk of this species and to examine its recruitment, survivorship, and reproductive maturity over a 14-year period from 2004 to 2017. Sixteen sites were established in burned stands of Tecate cypress with prefire ages that ranged from 7 to 53 years old. After 14 years, the overall density of Tecate cypress was still higher than before the fire, however, the areal extent of the species decreased due to the loss of locations where either there was low cone production or fire intensity was too high. The immaturity risk for this species, while a function of prefire stand age, is confounded by other factors including the reproductive capacities of trees based on their density and size and the climatic variables affecting their growth over time. The future management of Tecate cypress and other fire-dependent species requires a knowledge of all factors impacting their immaturity risk, as well as an understanding of the potential fire–climate interactions that may impact their persistence in a future of climate change and altered fire regimes.

Keywords *Hesperocyparis forbesii* · Tecate cypress · Closed-cone cypress · Fire frequency · Immaturity risk · Population dynamics

Communicated by Roland de Gouvenain.

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Introduction

Hesperocyparis forbesii, also known as Tecate cypress, is a closed-cone, fire-dependent tree that occurs in association with chaparral in the western Peninsular Ranges from Orange County in southern California, USA, to Rancho el Cipres in northern Baja California, Mexico (Dunn 1985). This species, formerly known as *Cupressus forbesii*, was recently transferred to the newly described *Hesperocyparis* genus, which includes 16 cypress species in the western hemisphere (Adams et al. 2009; Terry et al. 2016). Nearly half of the species are endemic to

California and many are considered relict populations of species that were formerly more widespread during earlier geological periods (Armstrong 1978). At present, there are four metapopulations of Tecate cypress in southern California and about 15 small scattered populations in northern Baja California. The northernmost metapopulation occurs on Sierra Peak in the Santa Ana Mountains of Orange County and the others on Otay Mountain, Guatay Mountain, and Tecate Peak in the southern portion of San Diego County (Fig. 1).

The historical fire regime of Tecate cypress is unknown, although evidence from fossil charcoal indicates that chaparral plant associations might have developed approximately 8000 years ago under relatively long fire-free intervals (Byrne et al. 1977; Sauer 1977). As the climate shifted from cool with infrequent fires to warm and dry with frequent fires, the distribution of Tecate cypress became restricted to refugia or arboreal islands within the chaparral (Vogl et al. 1977) with a fire regime that was more likely controlled by the surrounding shrubs than by any inherent properties (Zedler 1995a). There is still much debate on what constitutes the natural range of fire frequency for chaparral in southern California (de Gouvenain and Ansary 2006), yet historical fire records for San Diego County indicate that the interval between fires in chaparral was likely between 30 and 50 years (Wells et al. 2004).

Tecate cypress, like many closed-cone conifer species, has evolved with fire and has adapted traits such as serotinous cones, resinous foliage, and thin bark to promote burning and the subsequent release of seeds from cones (Vogl et al. 1977; Keeley 2012). These traits alone, however, do not ensure the persistence of the species (Zedler 1977). Fire-

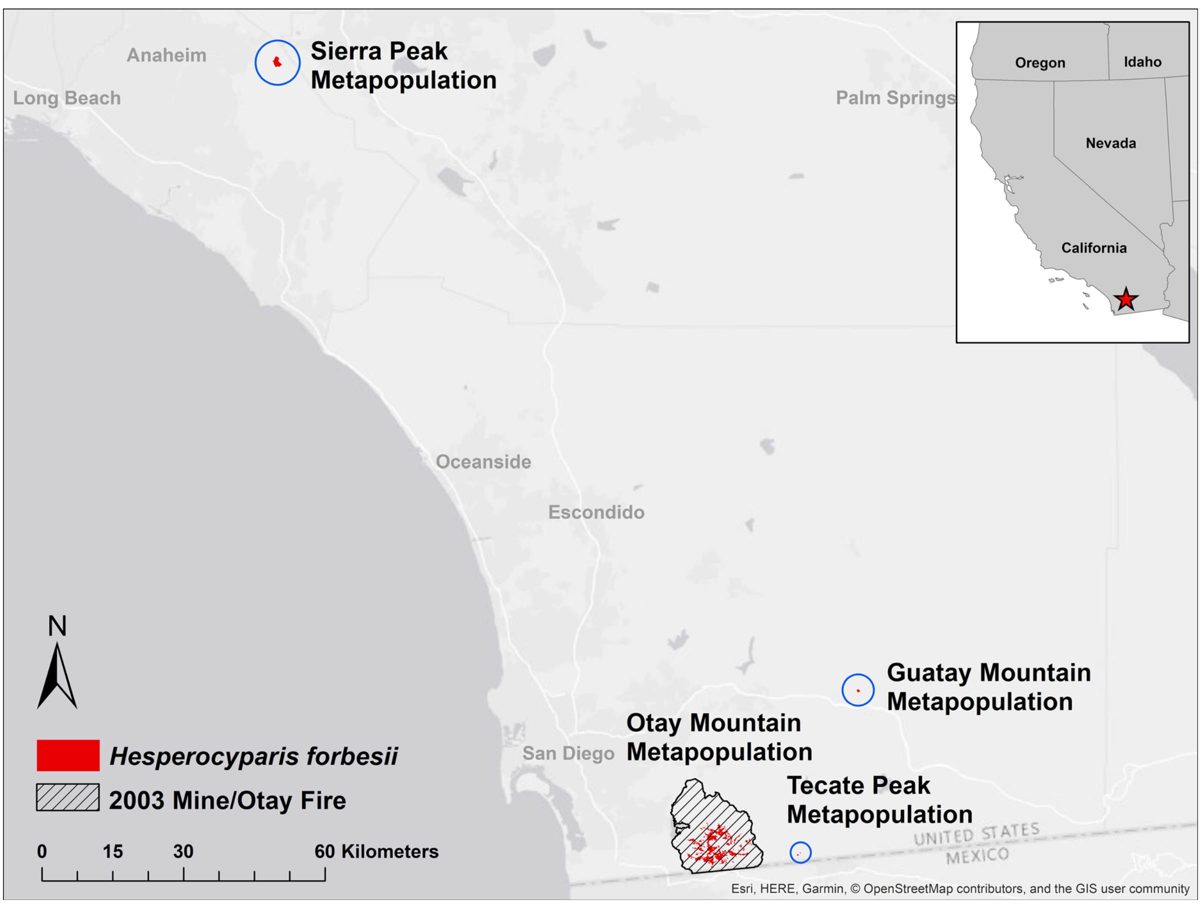

Fig. 1 Location of the four metapopulations of *Hesperocyparis forbesii* in Southern California, USA and the 2003 Mine/Otay Fire that burned the Otay Mountain metapopulation

dependent species face two potential threats in their life cycle; the risk of immaturity when the interval between fires is too short for a sufficient seed bank to accumulate and the risk of senescence when the interval between fires exceeds the longevity of the seeds stored (Lamont et al. 1991; Zedler 1995a; Keeley et al. 1999). The immaturity risk for Tecate cypress is high due to the length of time needed to establish a sufficient seed reserve for stand replacement (Zedler 1995a). It is an obligate seeder, reproducing exclusively from seed, and does not resprout basally or epicormically after fire like several Mediterranean species of the Cupressaceae family (Keeley and Zedler 1978; Zedler 1995b). Once established, the trees mature quickly with ovulate cone production commencing when trees are between 5 and 10 years old, yet production tends to be sporadic until the trees are at least 30 to 40 years old (Zedler 1977, 1981, 1995a; Dunn 1986). Annual cone production continues to increase beyond 90 years of age (Zedler 1995a) and specimens of Tecate cypress have been found in good living condition upwards of 200 years (Zedler 1995a; Vogl et al. 1977). The senescence risk for this species, comparatively, is low since there is a high likelihood that a stand will burn, based on its current association with chaparral, before the trees reach the end of their reproductive lifespan (Zedler 1995a).

Over the last few decades, a number of *Hesperocyparis* species have become a conservation concern due to changes in the frequency of fire on the landscape (Zedler 1977, 1995a; Dunn 1985). Baker cypress (*Hesperocyparis bakeri*) and MacNab cypress (*H. macnabiana*), for example, are being negatively affected by the long-term exclusion of fire from their populations (Mallek 2009; Rentz and Merriam 2011; Bower and Hipkins 2017; McNamara 2018), whereas other species such as Tecate cypress and Sargent cypress (*Hesperocyparis sargentii*) are being threatened by shortened fire intervals due to an increase in anthropogenic ignitions (Zedler 1977, 1981; Dunn 1986; de Gouvenain and Ansary 2006). While none of these species have been officially listed as threatened or endangered by the California Department of Fish and Wildlife or the U.S. federal government as of 2018 (CDFW 2018), their conservation statuses are currently a matter of debate (de Gouvenain and Ansary 2006; Regan et al. 2012).

Research pertaining to the population dynamics of Tecate cypress, in particular, are limited and conflicting. There is no consensus on the minimum fire-free period required to sustain their populations and it is uncertain as to whether or not the present populations in southern California are stable. Estimates of the minimum fire-free period or immaturity risk threshold for Tecate cypress range from 18 years (Rodríguez-Buriticá and Suding 2013) to 40 years and beyond (Dunn 1986; Zedler 1977, 1995a; de Gouvenain and Ansary 2006) and its population status has been reported as both declining and increasing within the same populations. Empirical studies by Zedler (1977, 1981) and Dunn (1986), for example, have documented a substantial reduction in the density and size of Tecate cypress populations as well as the local extinction of the species in certain areas due to a shortened fire return interval, while others have reported that three out of the four southern California populations appear to be stable or potentially increasing based on results from demographic matrix models (de Gouvenain and Ansary 2006; Rodríguez-Buriticá and Suding 2013). Most studies have focused on the relationship between prefire stand age and postfire recruitment, yet little is known about how burn severity or other demographic and environmental site characteristics affect the recruitment of this species after fire. Furthermore, there are no long-term studies examining the recruitment and survivorship of Tecate cypress over time.

Studying population dynamics of fire-dependent species in the absence of a recent fire can be a significant challenge. However, in October of 2003 we were presented with the opportunity to study Tecate cypress when a large wind-driven fire burned nearly 70% of the populations on Otay Mountain (Marcovchick-Nicholls 2007). The Otay Mountain metapopulation is the largest of the four southern California metapopulations and accounts for 85% of the total Tecate Cypress in the US. It consists of several small populations representing various age classes due to the fire history in the area and was therefore ideal for studying questions pertaining to the immaturity risk of the species.

The specific objectives of our research were to:

1. Evaluate the temporal window of immaturity risk of Tecate cypress and to examine the effects of burn severity, environmental site characteristics,

and prefire stand demographics on postfire seedling recruitment.

2. Monitor the recruitment, survivorship, and reproductive maturity of Tecate cypress over time.

Methods

Study area description

This study was conducted in Tecate cypress stands within the Otay Mountain Wilderness area (6833 ha) following the 2003 Mine/Otay Fire (Fig. 1). Otay Mountain is located in the San Ysidro Mountain range just north of the United States Mexico border in the southwestern corner of San Diego County, USA. This region has a Mediterranean climate with mean January and July temperatures of 12 °C and 24 °C, respectively, and an annual average precipitation that ranges from 33 cm at the base of the mountain to 44 cm near the top and is concentrated in the months from November to May (https://www.wrcc.dri.edu). The terrain is rugged and steep with elevations from near sea level to 1087 m at the top of the mountain 27 km inland from the Pacific Ocean. This area is underlain by the Santiago Peak Volcanics of Late Jurassic age and has rocky metavolcanic soils (San Miguel-Exchequer rocky silt loams) (Todd et al. 1988) with a unique chemistry that supports a number of sensitive plant species including several that are endemic to Otay Mountain (Dunn 1985).

Tecate cypress is found between 400 and 1000 m in elevation on Otay Mountain and occurs within disjunct populations of varying sizes. These populations collectively represent the largest isolated metapopulation of Tecate cypress and were estimated to cover approximately 2400 ha prior to 2003 Mine/Otay fire (Marcovchick-Nicholls 2007). This species inhabits ravines as well as ridgetops and is found interspersed within a matrix of chaparral dominated by *Adenostoma fasciculatum*, *Arctostaphylos* spp., *Ceanothus* spp., *Pickeringia montana*, and *Quercus* spp. Its communities comprise a wide diversity of plants including nearly a dozen species considered rare or endangered by the California Native Plant Society (Dunn 1985) and they provide habitat for a number of birds, insects, small mammals, and herpetofauna (Fisher et al. 2002; Rochester et al. 2010; Brehme et al. 2011; Lucas et al. 2013).

Fire is a natural process in these communities. However, in the last century, there have been over 45 recorded fires within the Otay Mountain Wilderness, 90% of which have occurred in the last 40 years and were primarily the result of human activities (https://frap.fire.ca.gov/data/frapgisdata). The largest of these fires was the Mine/Otay fire. This fire, which was preceded by four years of drought, started on October 26th, 2003 during a Santa Ana wind event where strong, extremely dry winds blow from high pressure air masses in the Great Basin of the United States westwards toward the coast. It burned more than 4,000 ha within the first 6 hours and continued to burn a total of 17,120 ha over a period of 3 days. Burn severity was high especially across the upper elevations of Otay Mountain dominated by chaparral and Tecate cypress. Two years after the fire, there was a record year of rainfall that was nearly four times the average annual precipitation, yet since then there have been two extended drought periods that occurred between 2006 and 2009 and between 2011 and 2017 (https://www.wrcc.dri.edu).

Field and lab methods

Our research design included 16 tenth-hectare sites established in separate populations of burned Tecate cypress within the Otay Mountain metapopulation in the spring of 2004 (Fig. 1). The study sites were established randomly in locations with at least ten visible dead trees at a distance of no less than 10 m from the burn perimeter to avoid edge effects. Our sampling design consisted of a 20 m × 50 m permanent site that was further subdivided into ten nested 100 m^2 plots. Site variables including elevation, incline, and slope aspect were recorded for each location and spatial coordinates were obtained from a global positioning system.

The density of Tecate cypress prior to the fire was estimated by recording the number of dead trees in each plot and the age of the stand at the time of the fire was determined by counting the growth rings of stem cross-sections taken from the two largest trees at each site. The presence or absence of cones on dead trees was also noted. Estimates of fire severity were conducted using a caliper to measure the diameter of the smallest remaining twig on the two *Adenostoma* *fasciculatum* skeletons nearest to the outer edge of each plot (Moreno and Oechel 1989). The foundation for this estimate is the demonstration that higher fire intensities are correlated with the diameter of terminal branches on burned skeletons of a number of species (Moreno and Oechel 1989). *Adenostoma fasciculatum* was used for this measurement because it was present in every plot.

Postfire recruitment of Tecate cypress was recorded and monitored in postfire years 1, 2, 6, 8, 11, and 14. In the first postfire year, the total number of seedlings was recorded in each plot and summed for a site total. In the second year the total numbers of one-year-old and two-year-old seedlings were recorded separately. In subsequent years, no seedlings were observed, therefore, only the total number of individuals was recorded. We also recorded the total number of new or resprouting shrubs within each plot in the first and second postfire years. Trees were inspected for cones every survey year and when observed the total number on each tree was recorded. Tree height was measured to the nearest tenth of a meter on every individual starting in year 6 and in year 14 the diameter of trees at breast height (1 m) was measured for a random selection of trees to determine the average height to diameter ratio. Climate data over the 14-year study period were procured from the Western Regional Climate Center for climate stations distributed within the range of sites (https://www.wrcc.dri.edu).

Statistical methods

Tecate cypress characteristics of prefire and postfire densities, height, percent of trees with cones and mean number of cones per tree were summarized for each site for every survey year. Bivariate regression analyses were conducted using the ordinary least-squares model to determine if there were significant relationships ($P < 0.05$) between the postfire recruitment of seedlings and prefire tree density, prefire stand age, burn severity, and postfire shrub density, as well as environmental site characteristics including elevation, incline, and insolation (sensu McCune and Keon 2009). Parent to seedling ratios were also calculated for Tecate cypress by dividing the total number of seedlings observed in a site by the total number of parent trees in the site prior to the fire.

Mortality rates over the study period were determined by subtracting the total density of individuals in one survey year from the total density of surviving individuals in the next survey year and multiplying the difference by 100. This total was then divided by the number of years between surveys to get an annual mortality rate when required. A continuous record of precipitation data were only available from one nearby station so we were unable to evaluate the relationship between annual precipitation and mortality on a site by site basis. Instead, we calculated the total mortality of recruits across all sites between survey years and used bivariate regression analyses to determine if there was significant relationships ($P < 0.05$) between mortality and the total accumulated annual precipitation between those same survey years.

To assess the long-term immaturity risk of Tecate cypress, we extrapolated the postfire densities of trees in our sites out over time. We did this by multiplying the average mortality rate observed across all sites in postfire year 14 by the density of trees in postfire year 14 to get an estimated density for postfire year 15. This was repeated for each successive year until the postfire stand density dropped below the prefire stand density for each site. If the extrapolated density of trees was above the prefire density of trees when the postfire site reached the prefire stand age that site was considered to have stand-replacing recruitment.

Results

Prior to the Otay/Mine Fire in October of 2003, our 16 Tecate cypress sites had stand ages that varied from 7 years old to 53 years old ($\bar{X}$ = 32, SD = 14) and stem densities that ranged from 10 trees per hectare to over 4,000 trees per hectare ($\bar{X}$ = 1253, SD = 1499). The younger sites typically had a higher density of trees than older sites (Table 1), however, there was not a significant relationship between prefire stem density and prefire stand age ($R^2 = 0.06$, $P = 0.358$). None of the trees within our sites survived the fire, however, ovulate cones were noted on dead trees within every study plot. Estimates of burn severity were variable across sites and tended to be higher in stands that were older at the time of the fire ($R^2 = 0.51$, $P = 0.002$). Burn severity, however, was not significantly influenced by the density of trees ($R^2 = 0.01$, $P = 0.927$) or by the elevation ($R^2 = 0.02$, $P = 0.576$), incline

Table 1 *Hesperocyparis forbesii* prefire density, recruitment density, and postfire year 14 density, by prefire stand age including seedling to parent ratios for sixteen 0.10 hectare sites burned in the 2003 Mine/Otay fire on Otay Mountain in San Diego County, CA, USA, mean and (standard error)

Prefire stand age	# of sites	Prefire density #/ha (SE)	Recruitment density #/ha (SE)	Seedling to parent ratio	Postfire year 14 density #/ha (SE)
7	2	2205 (35)	0 (0)	–	0 (0)
24	4	48 (14)	10,000 (2345)	226:1	606 (52)
33	4	3430 (308)	18,500 (9385)	6:1	6788 (2814)
42	4	233 (136)	29,000 (18,443)	294:1	11,745 (8854)
53	2	400 (240)	182,000 (92,000)	927:1	22,562 (8451)

(R^2 = 0.02, P = 0.569), or insolation (R^2 = 0.01, P = 0.888) at the site.

The recruitment of Tecate cypress seedlings began in the spring of 2004 following the winter rains and occurred entirely within the first two postfire years. Over 90% of the recruitment was within the first postfire year ($\bar{X}$ = 34,563, SD = 67,597), although nearly half of the sites had a small, secondary pulse of seedlings in postfire year two ($\bar{X}$ = 2563, SD = 4618). No new seedlings were found after postfire year two throughout the remainder of the study. Recruitment density was highly variable between sites yet it was not significantly influenced by environmental site characteristics, burn severity, prefire tree density, or the postfire density of shrubs (Table 2). There was, however, a significant relationship between recruitment density and the age of the Tecate cypress stand prior to the fire. The youngest sites had zero recruitment whereas the oldest sites had seedling densities that were upwards of 90,000 seedlings per hectare. The average seedling to parent ratio across the 14 sites that had recruitment was 283 seedlings per parent tree with values that ranged from 0.24 seedlings per parent to 1,713 seedlings per parent. There was not a significant relationship between the seedling to parent ratio and either prefire stand age (R^2 = 0.23, P = 0.058) or prefire tree density (R^2 = 0.20, P = 0.079), however, the oldest sites at the time of fire tended to have the highest number of seedlings per parent tree and the densest sites at the time of the fire tended to have the lowest number of seedlings per parent tree (Table 1).

Postfire recruitment densities decreased over the 14-year study period with an average seedling survivorship rate of 25% across the 14 sites with recruitment (Fig. 2a). Seedling mortality tended to be the highest between the first and second postfire years yet was highly variable between sites (Fig. 2b).

Table 2 Relationship of *Hesperocyparis forbesii* seedling recruitment to environmental site characteristics, prefire stand demographics, and postfire shrub density for sixteen 0.10 hectare sites burned in the 2003 Mine/Otay Fire on Otay Moutain in San Diego County, CA, USA

	Hesperocyparis forbesii recruitment density (# / ha)		
	r	r^2	p
Elevation	− 0.415	0.172	0.110
Incline	0.067	0.005	0.805
Insolation	0.367	0.134	0.163
Prefire stand age	0.595	0.355	**0.015**
Prefire stand density	− 0.248	0.062	0.358
Burn severity	0.209	0.044	0.436
Postfire shrub density	− 0.463	0.214	0.071

Analyses were conducted using the ordinary least-squares model of bivariate regression analysis

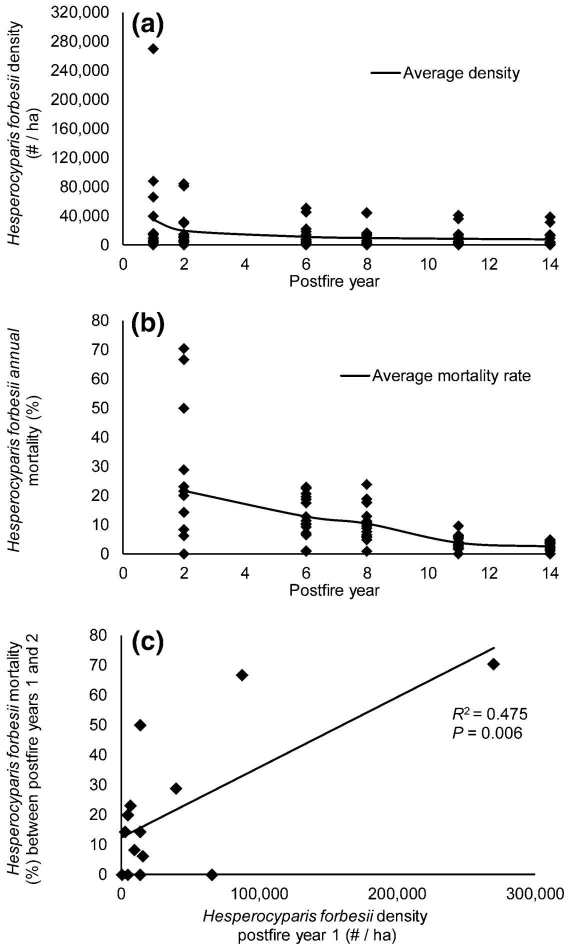

Fig. 2 *Hesperocyparis forbesii* density (**a**) and mortality (**b**) by postfire year for sixteen 0.10 hectare sites following the 2003 Mine/Otay Fire in San Diego County, CA, USA and the relationship of seedling mortality between postfire years one and two to the recruitment of seedlings in postfire year 1 (c) using the ordinary least-squares model of bivariate regression analysis

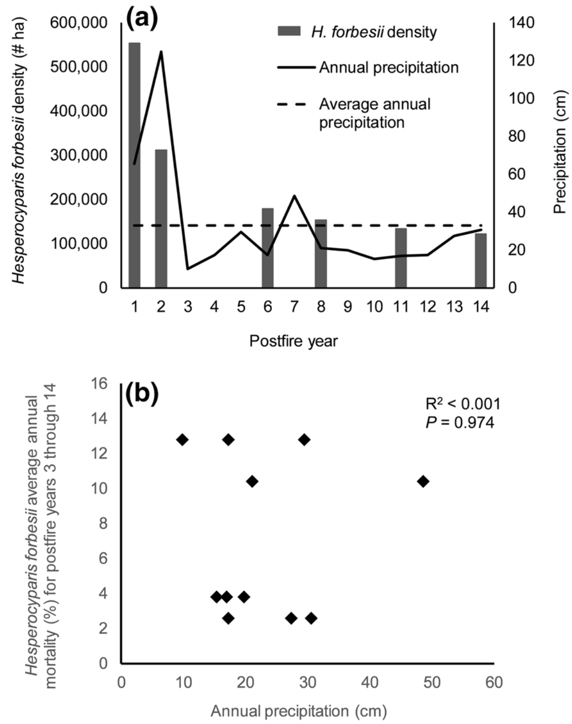

Fig. 3 *Hesperocyparis forbesii* density and annual precipitation by postfire year for study sites on Otay Mountain in San Diego County, CA, USA (**a**) and the relationship of average annual mortality rate of *Hesperocyparis forbesii* (%) to annual precipitation for postfire years 3 through 4 using the ordinary least-squares model of bivariate regression analysis (**b**)

There was a significant relationship between seedling density and the rate of mortality with the highest density sites having the highest rates of mortality between postfire years one and two (Fig. 2c). After postfire year two there was a fairly consistent drop in tree density over the remainder of the study period and by postfire year 14 the average mortality rate across sites was less than 3%.

During the course of our study annual rainfall was lower than average 11 out of the 14 years (Fig. 3a) and many species in our sites were showing signs of drought stress and subsequent mortality (personal observation).There was not, however, an obvious decline in the density of Tecate cypress in our sites associated with the two drought periods (Fig. 3a) and there was not a significant relationship between annual precipitation and the annual mortality rate of trees for postfire years 3 through 14 (Fig. 3b). Tree growth over the study period, on the other hand, was slow with only 15% of trees attaining a tree height greater than two meters by postfire year 14 (Table 3). The diameter of trees increased with tree height ($R^2 = 0.73$, $P < 0.001$) and there was a relatively consistent ratio between the two that decreased slightly as trees got taller. Ovulate cone production was first observed in postfire year 8 and by year 14 over 38% of the trees in our sites were producing cones. Cone production was significantly related to tree height ($R^2 = 0.30$, $P < 0.001$) with the number of cones nearly doubling with each meter increase in height. Most trees that were under a meter tall had yet to reach reproductive maturity by the end of the study.

Table 3 *Hesperocyparis forbesii* stand characteristics of tree height, diameter [at breast height of 1 m (dbh)], and cone production by height classes in postfire year 14 for sixteen 0.10 hectare sites burned in the 2003 Mine/Otay fire on Otay Mountain in San Diego County, CA, USA

	Tree height			
Postfire year 14	< 1 m	1–2 m	2–3 m	3–3.2 m
Percentage of trees	35%	50%	12%	3%
Mean dbh in cm (SE)	2.1 (0.1)	4.0 (0.2)	7.9 (0.6)	15.3 (1.3)
Ratio of tree height to diameter	324:1	338:1	280:1	203:1
Percent of trees with cones	3%	44%	81%	100%
Mean number of cones (SE)	3.5 (1.6)	5.9 (0.6)	15.0 (2.0)	36.9 (4.8)
Range in number of cones	1–8	1–51	1–91	1–86

In an effort to evaluate the long-term immaturity risk for Tecate cypress, we compared the recruitment densities at the end of our study to the densities of the parent cohort and found that 13 out of our 16 sites still had densities that were well above that of stand replacement in postfire year 14. Of the three sites with densities below that of stand replacement, the two youngest had no recruitment at all while the third had less than 10% of the trees that were in the plot prior to the fire. When we extrapolated the tree density in our sites out over time using the average mortality rate observed in postfire 14 we found that the four sites with the highest prefire densities were the first ones one that would have postfire recruitment densities fall below that of the parent cohort (Fig. 4). One of these sites would likely have a recruitment density that would fall below that of stand replacement 11 years before it reached that same age that it was at the time of the fire. The remaining sites, which had prefire stand ages that ranged from 24 to 53 years, would most likely have recruitment densities that were well above that of the parent cohorts long after they passed their prefire stand ages.

Discussion

Evaluation of immaturity risk is a common theme in many Tecate cypress studies. The immaturity risk threshold or minimum fire-free interval required for the persistence of stable populations is often estimated and a discrete year or range of years is reported, yet there is generally little discussion of other factors that may be affecting the recruitment of the species after fire. This study was therefore focused on evaluating the immaturity risk of Tecate cypress by examining a number of factors including the stand demographics prior to the fire, the severity of the burn, and the characteristics of the site. In addition, we have provided a much needed long-term account of the recruitment, survivorship, and reproductive maturity of Tecate cypress over time. Lastly, we have considered how our findings may better inform management decisions related to the conservation of this species.

Factoring affecting immaturity risk

Like many prior studies on Tecate cypress, we found that the level of postfire recruitment was intrinsically tied to the age of the previous generation (Zedler 1977; Dunn 1986). In our study, some trees in all sites had reached reproductive maturity before the fire, however, the presence of cones was not a guarantee of recruitment, or of recruitment at stand-replacing densities. Over one-third of the dead trees in our two youngest sites, for example, had mature cones, yet there was zero recruitment and the species was extirpated from those locations. While our data did not reveal a relationship between recruitment density and the severity of the fire, possibly due to our low sample size, it's the most reasonable explanation for the total absence of recruitment in these sites. Fire intensity affects the mechanisms of seed release in Tecate cypress and if it is low, cones may not get heated at a high enough temperature or for a long enough duration to release seeds (Milich et al. 2012). The burn severities observed in these younger sites were the lowest recorded and it is possible that the

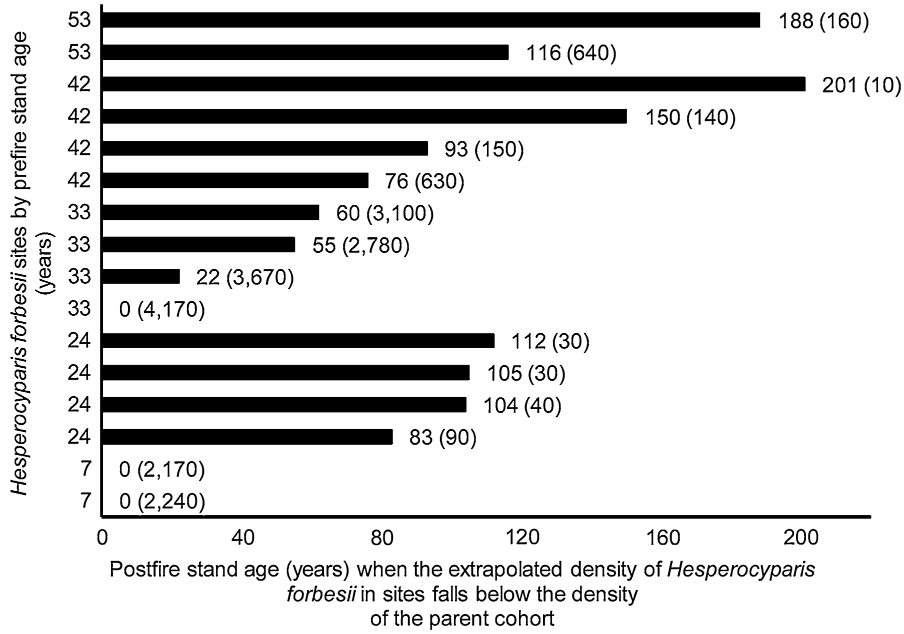

Fig. 4 Postfire stand age when the extrapolated density of *Hesperocyparis forbesii* trees will fall below the prefire stand density of the parent cohort for sixteen 0.10 hectare sites burned in the 2003 Mine/Otay Fire in San Diego County, CA, USA. Tree densities were extrapolated after postfire year 14 using the average mortality rate of 3% observed during the final year of the study. The first number to the right of the bar is postfire stand age and the number in parentheses is the prefire density of trees

intensity was just so low, in part due to the lower fuel load, that the cones were not opened. This would explain why there was zero recruitment even though mature cones were present.

The highest risk of immaturity for a closed-cone species occurs when a population is so young that it is has not yet produced cones and therefore is incapable of reproducing after a fire. However, even if reproduction does occur there is still a risk of immaturity if the recruitment density is initially low or falls below that of stand replacement over time. The recruitment of seedlings in one of our 33-year-old sites, for instance, was less than 25% of the parent density before the fire. This plot interestingly had the highest prefire density of trees as well as the highest recorded burn severity and it clearly burned hotter than the rest of our sites. In this particular case the intensity of the fire, which was likely extreme due to the high fuel load, probably caused some of the seeds to lose their viability due to prolonged heating (Milich et al. 2012) and it might have completely consumed others.

The recruitment densities in the remaining 80% of our sites were well above their parent densities in postfire year one, yet significantly decreased in the first few years after the fire due to density-dependent thinning. These results are similar to those of de Gouvenain and Ansary (2006) and Dunn (1986) who observed a 60% rate of mortality between the first and second postfire years in Tecate cypress stands on Tecate Peak. By the end of our 14-year study the average mortality rate across sites was less than 3% and all of the sites, with the exception of the three discussed above, still had densities that were above that of stand replacement. When we extrapolated the recruitment densities in our sites into the future we found that density of trees prior to the fire was more important than the age of stand when evaluating immaturity risk. A number of studies on various closed-cone species have found negative relationships between the prefire density of trees and cone size, as well as cone and seed yield (Arista and Talavera 1996; Karlsson and Orlander 2002; Ayari et al. 2012). This relationship was not captured in our data, although the most plausible explanation for the lower recruitment observed in our highest density sites may simply be that they were overcrowded and there were limited resources available for cone production. In this case, recruitment back to stand replacing density would not be ideal.

This study, like some other studies, confirms the relationship between immaturity risk and stand age, yet it also highlights that there are other factors contributing to immaturity risk that cannot be overlooked. The density of trees in a given area and their reproductive capacities based on variables affecting their growth are of particular importance, especially in a warming climate. Due to the variation in populations and the possible different interactions between these variables, it is difficult to estimate an immaturity risk threshold, or a minimum fire-free period for this species as a whole. If these type of estimates are to be useful, they need to be based on the population dynamics and specific conditions of a given location, otherwise they could potentially be misleading.

Population dynamics over time

Fire-dependent obligate seeding species, such as Tecate cypress, have evolved to persist under a fire regime of recurrent disturbance by having long-lived seeds that readily germinate on bare mineral substrates (Pausas and Keeley 2014; Bond and Keane 2017). The density of recruitment following a fire event is partially a function of the accumulated seedbank and the postfire growing conditions (Enright et al. 2015) and it typically occurs as a single pulse in the first postfire year (Pausas and Keeley 2014). Results from our study, which are similar to those of Zedler (1977) and Dunn (1986), found that the recruitment of Tecate cypress occurred primarily within the first postfire year as was expected, however, we also observed a pulse of recruitment in the spring of the second postfire year. While this is not typical, the extremely wet winter that occurred between the first and second postfire years might have supported a secondary pulse of recruitment when the spring conditions were optimal.

The postfire recruitment of most closed-cone species is usually substantially higher than the carrying capacity of the site resulting in a high rate of mortality immediately after the fire (Clark 1992). The mortality in our sites following the initial pulse of recruitment was highest between the first and second postfire years and was significantly affected by recruitment density. These results are consistent with the concept of density-dependent thinning where biotic factors such as inter- and intraspecific competition drive mortality versus abiotic factors related to climate and the physical environment (Clark 1992). Once a homeostatic state was reached the mortality across our sites dropped to less than 3% a year. After the second postfire year there were two substantial back to back drought periods (Fig. 3a) and we noticed that many of the shrub species in our sites were experiencing stress and subsequent mortality (personal observation), which was widespread across the region (Jacobsen and Pratt 2018), yet the Tecate cypress trees appeared unaffected. A study by Schenk & Jackson (2002), in water-limited ecosystems, found that the rooting depth and lateral root spreads of different plant growth forms were positively related to their typical above-ground size and thus this might explain why we were seeing drought stress in shrub species but not in Tecate cypress.

Many species such as Tecate cypress that have evolved within fire-prone ecosystems tend to mature early in their life cycle to ensure their persistence beyond that of the next disturbance event (Enright et al. 2015). We first observed cones on young trees in our sites in postfire year eight, which fits within the five to ten year window reported by Zedler (1977, 1981) and Dunn (1986). As the trees got older and taller the number of cones increased however the average number of cones by tree size in our study was substantially lower than that observed by de Gouvenain and Ansary (2006). They reported that trees 5 cm in diameter had an average number of cones that ranged from 33 to 60 across the four southern California Tecate cypress subpopulations and that trees 10 cm in diameter had an average number of cones that ranged from 75 to 400 per tree. In our study, the average number of cones on trees with mean diameters of 8 cm and 15 cm was 15 and 37, respectively. The large dissimilarity in these observations is probably due to differences in growing conditions. The young trees in our sites, for example, have experienced drought conditions over most of their lifespan, which most likely limited tree growth as well as cone production. The most commonly used predictor of cone-crop potential is stand age, yet our results and those of others (de Gouvenain and Ansary 2006; Redmond et al. 2012; Enright et al. 2015) suggest that tree height and growing conditions are equally if not more important in predicting cone-crop potential.

Management considerations

At present, nearly all of the populations of Tecate cypress in California are less than 40 years old (Marcovchick-Nicholls 2007) and there is concern over their conservation due to an increase in the number of human-caused wildfires over parts of southern California (Keeley and Syphard 2018) and the potential effects of a warming climate (Redmond et al. 2012; Enright et al. 2015; Jacobsen and Pratt 2018). A number of potential management strategies have been proposed in prior studies, some of which include the protection of refugia that sustain lower fire frequencies, the use of fuel treatments to stop the spread of wildfire into sensitive areas, and the assisted colonization of the species into new areas of suitable habitat (de Gouvenain and Ansary 2006; Marcovchick-Nicholls 2007; Rodríguez-Buriticá et al. 2010; Regan et al. 2012).

While these recommendations are prudent, they may not be enough to ensure the persistence of Tecate cypress. Many of the refugia areas on Otay Mountain are in ravines, which tend to support the highest density of trees, and therefore, could potentially already be at risk of overcrowding, especially if the current drought conditions become the norm (Enright et al. 2015). If the reproductive capacity of trees in these areas were assessed on a regular basis (Bond and Keane 2017), estimates of the optimal density of trees for the area could be determined and stands could potentially be thinned to avoid overcrowding and to enhance cone-crop potential. Conversely, trees could be planted in areas of low density, which may be more feasible than assisted colonization of new areas. Having different ages trees within stands could also help combat disease or insect infestations that may become more prominent due to climate change (Craig et al. 2010).

Conclusion

The results of our study suggest that the immaturity risk associated with Tecate cypress is not only a function of the stand age but also of the reproductive capacities of trees in an area based on their density and size structure, as well as the climatic variables that affect their growth. The future management of this species will require a knowledge of all of the factors that impact immaturity risk, some of which have probably not been identified, and it will need to be focused on the characteristics of individual populations in order to be the most successful. These findings and those of other studies on fire-dependent species highlight the need to better understand the possible fire–climate interactions that will potentially impact their persistence in a future that is predicted to have higher temperatures and more frequent fire.

Acknowledgements We are grateful to the numerous field biologists that helped us procure data over the 14 years study period and we thank the Bureau of Land Management for their cooperation, with special thanks to Joyce Schlacter for her help in logistical matters. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

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