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FORTY YEARS OF CHANGE IN PIUTE CYPRESS (*HESPEROCYPARIS NEVADENSIS*), A RARE CALIFORNIA TREE, AFTER FREQUENT FIRE AND DROUGHT

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ABSTRACT

Piute cypress (*Hesperocyparis nevadensis*) is a rare cypress species endemic to the Lake Isabella region in the southern Sierra Nevada in California. Piute cypress groves have not been quantitatively studied in the last 40 years and with recent fires (some in short succession) and observed mortality, we had questions surrounding conditions in groves recovering from fire compared to other groves with no recorded fire histories. Piute cypress rarely survive fire and are obligate seeders with serotinous cones and, as such, require sufficient time after fire to grow to reproductive maturity to be able to withstand future fire. We visited five of the 12 known groves of Piute cypress to evaluate current stand conditions and make comparisons with an assessment conducted 40 years ago. We evaluated two recently burned groves nine years post-fire. One grove with a shorter interval between fires (~20 years), has only limited regeneration and is at risk of local extinction. Based on our findings, we extrapolated to unstudied groves to conclude that five recently burned groves are vulnerable to immaturity risk if these stands were to reburn soon. We recommend aggressive fire suppression tactics to protect these groves if threatened by fire. Another recently burned grove with a longer period between fires (~90 years) appears to be recovering and capable of becoming a self-sustaining population that can survive another fire based on regeneration data. While the 90-year-old trees did not have nearly the level of canopy seed bank that older trees (~200 years old) did in another part of the grove, seedling and sapling regeneration after fire occurred at higher densities than tree densities in mature stands and were already developing cones. Though theoretically long-unburned groves also may be at risk, we found no evidence of age-related decline in this long-lived species and some non-fire induced regeneration. We did discover evidence of cedar bark beetle attack (*Phloeosinus* spp.), particularly in smaller trees at two unburned groves, which was correlated to high tree mortality (31.6%) at one site. While we found no evidence of encroaching non-cypress tree species threatening long-unburned groves among mature cohorts, we did document relatively high densities of regenerating non-cypress tree species in groves. We strongly recommend further monitoring in groves to assess fire, insect, and disease vulnerability in cypress populations.

Key words: drought mortality, fire frequency, *Hesperocyparis*, immaturity risk, reburn, stand-replacing fire

INTRODUCTION

Piute cypress (*Hesperocyparis nevadensis* (Abrams) Bartel) [syn. *Cupressus arizonica* var. *nevadensis* (Abrams) Little; *Cupressus nevadensis* Abrams] is a native California cypress species endemic to the region surrounding Lake Isabella in California in the southern Sierra Nevada (Fig. 1; Bartel 2019). The species is considered rare and endangered (CNPS 2021) because it has a highly restricted extant range and the population size is small (Terry et al. 2016; Rundel 2019). Modern interrelated threats such as climate change, drought, and more frequent wildfires threaten to reduce or eliminate these small populations (Bartel 2019).

In the Cretaceous, following the breakup of Pangea, a radiation of Cupressoideae occurred in both hemispheres. A few Cupressoideae clades, including *Hesperocyparis*, have evolved drought-resistant ecophysiological strategies for surviving in semi-arid seasonal climates on nutrient poor soils (Rundel 2019). *Hesperocyparis* Bartel & R.A. Price (Cupressaceae) or western cypress is a genus of 17 species in western North America, inclusive of Central America, that colonized the continent in the late Cretaceous or early Cenozoic (Terry et al. 2016). The common ancestor of all New World cypresses, *Hesperocyparis* and *Callitropsis*, likely diversified from north to south as the climate cooled and aridified beginning around 45 Mya (Terry et al. 2016; Mao et al. 2019). No *Hesperocyparis* species are older than 6 Mya and diversification within the clade is among the highest known for gymnosperms (Terry et al. 2016). Today, the species within the genus typically occur in small, isolated populations within geographically well-defined "groves" in chaparral or montane forests on azonal soils.

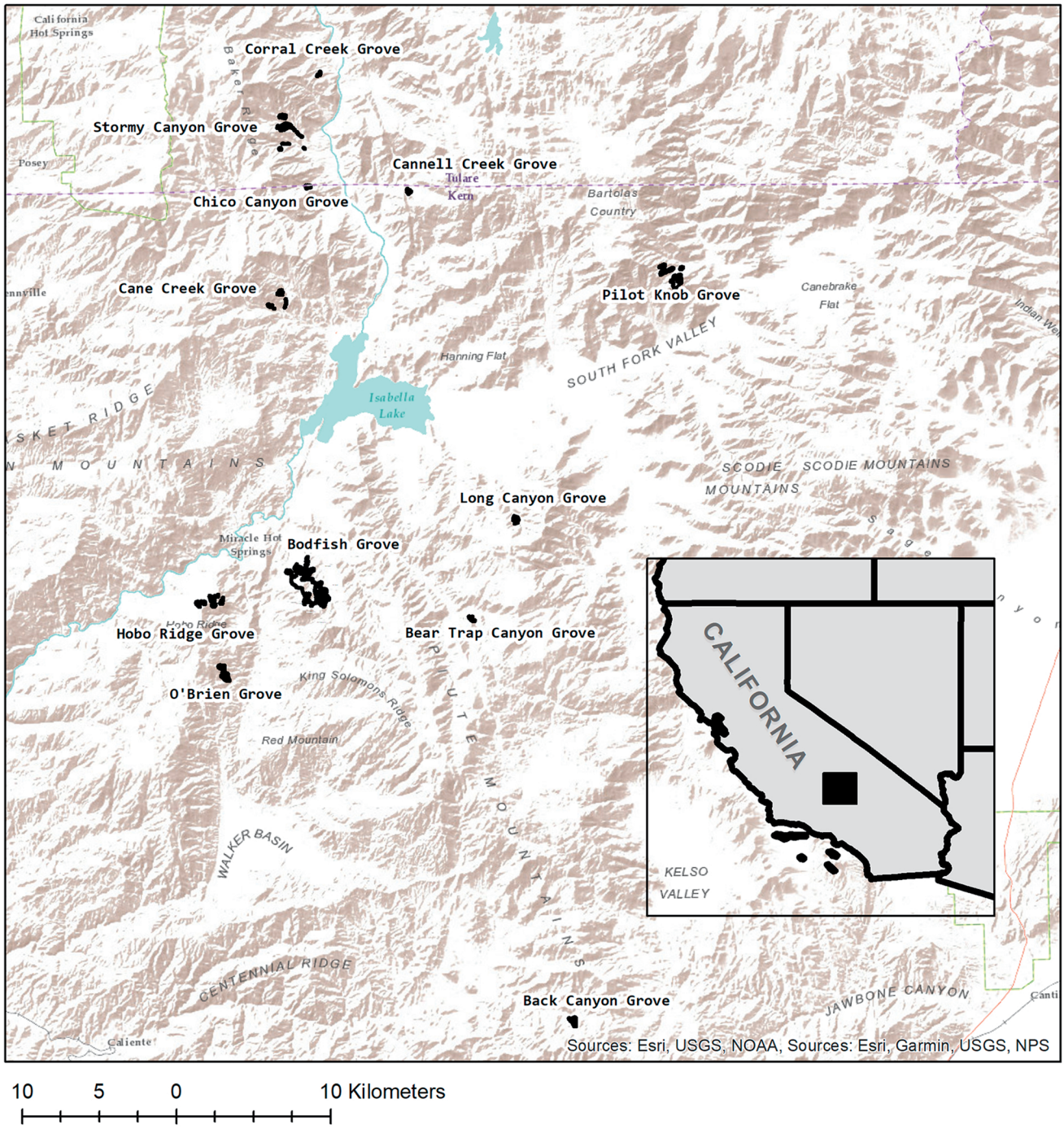

Fig. 1. Map of Piute cypress groves in Kern and Tulare Counties, California with inset of California State and bounding box around Piute cypress region.

Piute cypress grow in a dozen or so groves (~430 hectares total; Table 1) located between 1010 and 1800 meters in elevation, often in fire refugia (areas less prone to frequent fire, Bartel 1980), with most groves occurring in chaparral ecosystems in the Piute and Greenhorn Mountains. Because Piute cypress rarely survive fire and cannot resprout, populations are entirely reliant on the canopy seed bank to recover from fire (Bartel 2019). Like other California cypress species (Zedler 1977; Dunn 1985; Zedler 1995; Brennan and Keeley 2019) and serotinous species adapted to stand replacing fire in general (Keeley et al. 1999; Turner et al. 2019; Agne et al. 2022), Piute cypress face immaturity risk when fires occur more frequently than the time needed for reestablishing individuals to reach maturity and produce adequate seeds. Given the increasing size and frequency of fires associated with changing climate and higher temperature in the region (Wuenschel et al. 2021), the long-term future of Piute cypress is uncertain.

Conversely, fires that occur too infrequently in *Hesperocyparis* groves may allow site takeover by other tree species,

Table 1. List of Piute cypress groves, their approximate sizes and the years they have burned in wildfire. Note some fires may have only burned portions of groves, and GIS perimeters on some fires may be incorrectly located. Bolded groves represent groves sampled in this study.

Piute cypress groves	Hectares	Years burned
Back Canyon Grove	14	NA
Bear Trap Canyon Grove	5	1952
Bodfish Grove	**257**	**1921, 2010**
Cane Creek Groves	**6**	**1915, 1924, 1961, 1968, 2021**
Cannell Creek Grove*	**3**	**1942, 2010**
Chico Canyon Grove	5	1924, 2010
Corral Creek Grove	2	1942
Hobo Ridge Grove*	**23**	**1921, 1966, 2010**
Long Canyon Grove	8	1942, 1954, 1984, 2016
O'Brien Grove	21	1928
Pilot Knob Grove	53	1928
Stormy Canyon Grove	**24**	**1924, 1990, 2010**

* While these groves experienced numerous fires, our plots were located in places with no fire scar evidence.

resulting in cypress mortality from competition, lack of cypress regeneration, and potentially cypress senescence risk (i.e., age related decline; Mallek 2009; Rentz and Merriam 2011; Bower and Hipkins 2017) although this situation has not yet been established for Piute cypress. One Piute cypress grove and portions of another grove have experienced little to no documented fire in the observable record. Fires have been abnormally low during the last century in the Sierra Nevada region due to fire suppression and cessation of indigenous burning. It should be noted, however, that Piute cypress is not entirely dependent on fire for regeneration. Regeneration can be observed in areas of open and disturbed ground, and Piute cypress are a long-lived species (trees as old as 650 years have been measured; Bartel 2019), suggesting that even infrequent fire-induced regeneration might sustain populations. Ne'eman et al. (1999) concluded that Sargent cypress (*H. sargentii* (Jeps.) Bartel), the most closely related species to Piute cypress (Terry et al. 2012), is not threatened by senescence, as even the low densities of seedling recruitment observed in mature stands were much greater than mature tree densities.

Warming climate, drought, and increasing precipitation variability are also threatening conifer species directly through mortality and their ability to regenerate. The 2012–2016 California drought, an uncharacteristically hot and severe drought, killed an estimated 129 million trees across the state (CDFFP 2018). Other California and Arizona cypress populations have demonstrated sensitivity to drought (Goforth 2009; Verrier 2022). However, no drought-related mortality observations have yet been made in Piute cypress groves—an infrequently studied species. Also, observations of increasing regeneration failure across conifer species (Kemp et al. 2019; Stevens-Rumann et al. 2019) call into question how well Piute cypress can recover from fires in our modern era and adapt to site changes given dispersal limitations (McNamara et al. 2019).

Little field work has been done on Piute cypress, with the exception of Bartel (1980) who studied the distribution and ecology of the species. Bartel (1980) mapped and described the nine groves known at the time of his field work. To characterize the associated woody species found within the groves, Bartel also separately sampled two groves for the frequency, density, dominance, and importance value of the woody species found within these stands. In light of repetitive wildfires that have reduced the extent of some groves over the last 40 years, Bartel (2019) updated the status of the species focusing on the distribution, topography, and geology that underlie the relative vulnerability fire poses to many of its smaller fragmented populations.

Because much is unknown about Piute cypress other than as described in Bartel (1980) and Bartel (2019) and the groves have not been studied in the last 40 years, we visited five groves in 2019. Because multiple fires have been documented in the groves since 1980, and significant cypress mortality was observed, our goal was to study general grove condition (e.g., reproductive maturity, regeneration, health status, species composition, structure) and change over the last 40 years using Bartel (1980) as a comparison. We wanted to see how grove conditions have varied with time since fire and compared to groves unaffected by recent fire.

With available information at the time, Bartel (1980) estimated the optimum fire return interval for Piute cypress to be between 60 to 200 years, and we now had the opportunity to test this estimate with a grove that experienced only 20 years between fires while another grove that experienced 90 years between fires. A refined understanding of the minimum fire-free period necessary for persistence of the species will enable land managers to assess risk to cypress groves as fires approach and thus inform decisions on employing fire suppression tactics for grove protection.

Our overarching objectives and related questions are summarized below:

1. **General grove characterization.** Characterize the tree and shrub species composition and structure of the groves and how they vary by fire history. What are the regional fire trends in fire numbers and burned area?
2. **Assess change over 40 years.** What are growth patterns and rates in Piute cypress? How have cypress densities changed over time? Have relative proportions of non-cypress tree species changed in groves over time?
3. **Evaluate post-fire recovery.** How do grove conditions vary by fire return intervals? Are Piute cypress exhibiting regeneration at densities higher than mature tree densities? At what age are Piute cypress bearing cones and appear ready to withstand another fire?
4. **Summarize conditions in unburned groves.** In groves (or portions of groves) with no record of fire, are Piute cypress senescing, is regeneration taking place, and what are the relative proportion of non-cypress species?

METHODS

To evaluate whether a significant increase in wildfires in the Lake Isabella region has taken place, we created a minimum bounding polygon around all of the Piute cypress boundaries and calculated the hectares burned each year within them (ArcGIS 10.7; ESRI 2019) since 1950. We chose the year

1950 based on the presumption that fire records before then were unreliable and may underestimate the amount and numbers of fires in that period, although we have documentation of earlier recorded fires in groves (Table 1). We acquired fire perimeters from the publicly available CAL FIRE Fire Resource and Assessment Program (FRAP) database (*https://frap.fire.ca.gov/*). We used a simple linear regression to evaluate the relationship between time since 1950 and the number of fires and hectares burned per year. We did not factor in fire severity as fire tends to be stand-replacing in Piute cypress (Bartel 1980). Both response variables (number of fires and hectares burned) had to be log-transformed to produce more normal distributions.

In 2019, we visited five of the Piute cypress groves; the Bodfish, Cane Creek, Cannell Creek, Hobo Ridge, and Stormy Canyon groves, all located on the Sequoia National Forest and Bureau of Land Management, Bakersfield Office lands near Lake Isabella. We chose groves based on recent fire history where recent fires were close in succession (Hobo Ridge and Stormy Canyon) and we also wanted to draw comparisons to measurements in unburned groves (or unburned stands within groves), which we prioritized by accessibility as many of the groves are in steep, difficult to access locations.

We used a 50 m grid randomized plot design (100 m spacing in Bodfish due to grove size). Some plots were dropped due to inaccessibility. We collected a total of 23 plots including five plots in Cannell Creek, five plots in Hobo Ridge, and 13 plots in Bodfish groves.

We located seven plots in the portion of the Bodfish Grove that burned in 1921 and 2010, and six plots in the portion of the grove with no recorded fire history. Plots in the Cannell Creek and Hobo Ridge groves occur within areas that have no recorded fire history. Clustered plot locations using a random, gridded design were identified prior to sampling. Some plots were dropped due to inaccessibility.

In each of the plots, we collected tree and sapling data for all species, and cypress seedling data. Tree and cover data were collected within 10 m radius circular plots. We collected seedling (shorter than 1.37 m) and sapling (<7.6 cm bole diameter and taller than 1.37 m) data for cypress and other tree species within 5 m of plot center. We counted seedlings in two categories, those >10 cm tall and those <10 cm. If no saplings existed in the smaller nested plot, the full plot was surveyed for saplings. Plot centers were marked with rebar and transects were laid out in 4-cardinal directions (N-S, E-W) from plot center. Plot centers were located by handheld GPS and photos were taken at the ends of each transect facing plot center.

At each plot, we visually estimated percentage of living and dead overstory cover (everything over 2-m in height), live and dead shrub cover by species, and ground cover (e.g., rock, litter, herbaceous). In addition to percent cover, we also recorded modal heights for shrubs. For each tree in the larger plot, we measured diameter at breast height (DBH) and live/dead status. For cypress only, we estimated cone number classes as 0 = 0 cones, 1 = 1–10 cones, 2 = 11–100 cones, 3 = 101–500 cones, and 4 = >500 cones. We also recorded number of downed cypress trees in a given plot. We identified all trees in the plot by species, and live/dead status.

We also measured overhead canopy cover (a measure of how much light hits the surface) using a densitometer. We took canopy cover 'hit' readings at each of the four cardinal directions (N, W, S, E) at 5 m along the transects and at plot center with a densitometer.

We first characterized the groves according to structure and composition of live and dead trees, regeneration and shrub cover. Where we had data, we compared our 2019 measurements to those reported in Bartel (1980). Bartel (1980) used quadrat and point-quarter sampling techniques to sample tree and shrub vegetation. Within the Bodfish Grove, Bartel (1980) sampled structure and composition using seven 300 m long transects in the older section of the grove and four 275 m long transects that were divided into square quadrats of 25 m^2 placed every 25 m along the transect. Bartel (1980) reported size measurements for Piute cypress that represented the majority of trees in a stand, and we used median values with standard errors for comparison. To calculate growth rate, we used the mean of the Bartel (1980) height or DBH range and subtracted that from the 2019 median and divided by years the tree was growing between measurements.

We used tree measurements, shrub, and cover data to characterize the groves relative to one another and by disturbance history. We used the cone number class data and seedling and sapling regeneration data to evaluate Piute cypress grove resiliency, how well the groves were recovering from recent fire, and how well the groves are poised to recover in the event of future fire (i.e., if they appear to have cones and occur in densities equivalent to those of mature stands).

In two instances we were not able to collect full plot data as planned at groves due to dangerous conditions or unexpectedly long cross-country travel times. At those sites, we described the grove conditions and collected representative Piute cypress height and DBH data (stands tend to establish after fire in even-aged cohorts) to estimate the central tendency. We used median estimates of DBH and height and modal estimates of cypress cone number classes to be able to compare across groves. A linear regression model was developed to assess the relationship between Piute cypress tree height and diameter to cone number classes.

In some cases, Bartel (1980) estimated ages of trees within groves using increment tree cores. We simply added 39 years to those ages to develop a rough estimate of modal tree ages for each stand.

While we did not design the study to assess beetle activity within these groves, incidence of high levels of *Phloeosinus* spp. (a cedar bark beetle genus known to damage and kill cypress) at one grove prompted us to start recording evidence of beetles throughout the field study. It is possible we did not note low levels of insect attack evidence before we started looking for it systematically.

RESULTS

1. General Piute Cypress Grove Characterizations and Regional Fire Trends

1.1 What are the regional fire trends in fire numbers and burned area?

We found that more fires overall have occurred within the Piute cypress region ($p < 0.05$; Fig. 2). However, we did not

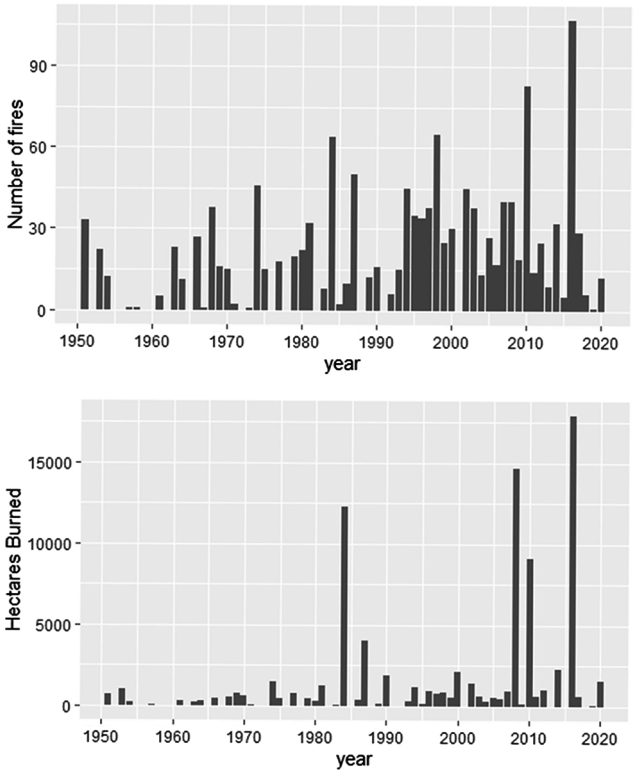

Fig. 2. Number of fires each year since 1950 (top) and hectares burned each year since 1950 (bottom) and within the bounding geography of Piute cypress groves. More fires overall burned within the Piute cypress region ($p < 0.05$), however no significant increase occurred in total area burned between 1950 and 2020.

find a significant increase in total area burned between 1950 and 2020 (p value = 0.14; Fig. 2).

1.2 Characterize the tree and shrub species composition and structure of the groves and how they vary by fire history

Bodfish Grove.—The Bodfish Grove is the largest Piute cypress grove at around 200 ha in size (Bartel 1980). When Bartel (1980) surveyed the groves for his 1980 thesis at California State University, Fresno, the grove was noticeably partitioned into an older and younger stands or sections due to fire history. Note throughout the document we use stands to describe sub-components of groves with differing characteristics (e.g., young stand versus old stand). In the older section with no recent fire, trees were mostly around 240 years of age with scattered individuals that were estimated to be 400–600 years old (Bartel 1980; Fig. 3C). The younger stand of the grove (Fig. 3D) has a 55-year fire return interval with fires occurring in 1921 and 2010 (30 years after Bartel's measurements). Because we sampled nine years post-fire (2019), we assumed that all regeneration occurred immediately after wildfire (~9 years old) and that fire-killed, mature trees were ~89 years old at the time of the 2010 fire.

The younger Bodfish stand had no live mature cypress that survived the 2010 fire (Fig. 3E), although we recorded an abundance of seedlings and saplings [see section 3.1]. Standing fire-killed 90-year-old cypress occurred in much lower densities and with lower variation in density than in the older stand (Table 2). However, we found very high numbers of downed fire-killed cypress (1777 ± 1285.4 per hectare), but these were driven by extremely high numbers of downed trees at one plot in particular.

While we found an overall low shrub cover in the unburned portion of the grove, we recorded a relatively high cover of *Cercocarpus betuloides* Nutt. (Fig. 4). Bartel (1980) described the understory of the older portion of the grove as being bare, other than a few scattered forbs and pinyon seedlings. However, measurements took place on the somewhat steeper and higher slopes above Saddle Springs Road, which may have limited vegetation cover. Higher abundances of diverse shrub species were found within the more recently burned portion of the grove (Fig. 4) than in the older portion. In the older portion of the grove, *C. betuloides* dominated with little representation from other shrub species. While the recently burned portion of the grove had more herbaceous cover and litter following the fire, the older portion of the grove had markedly more rock on the surface than the younger portion and all groves measured (Table 2).

Cane Creek Grove.—Cane Creek Grove has experienced the most frequent number of fires with fires occurring five times since 1915, with the most recent two fires being in 1968 and the 2021 French Fire. During our 2019 visit, we noted that the grove may be smaller than when delineated in Bartel (1980) with the easternmost portion of the southern grove cluster not having any cypress. In 2019, we noted high fuel loads within the grove and vegetation was too dense to conduct robust measurements in most places. Most of the cypress in this grove occur in the drainage bottom. Bartel (1980) noted that the largest, oldest cypress occurred along the creek here potentially due to moisture and the drainage-bottom location acting as a fire refugium. Cypress near the road had been managed for fire hazard and pruned. The modal height of Piute cypress was 5 m, the modal DBH was 15 cm and the majority of trees had around 11–100 cones. We also noted evidence of *Phloeosinus* spp., particularly on many of the dead cypress in close proximity to the creek bed.

Cannell Creek Grove.—Cannell Creek Grove, like Bodfish, has a more recently burned portion and a long-unburned portion. In juxtaposition to Bodfish, it is one of the smallest Piute cypress groves (Bartel 1980). The ridgetop portion burned in 1942 or 1943 (Bartel 1980) and potentially again in 2010. We conducted measurements within 5 plots in the long, unburned portion of the grove (Table 2) and found that Piute cypress was the only tree species present. Cypress measured at Cannell Creek were shorter than those measured in other unburned groves. Bartel (1980) noted that chaparral species in the portion that burned in 1942 were negatively impacting cypress saplings due to intense competition. We found that *Ceanothus cuneatus* (Hook.) Nutt. dominated the shrub composition at plots, but overall cover was low (2.6% ± 0.93 on average). We also documented *Artemisia tridentata* Nutt., *Cercocarpus betuloides, Ephedra viridis* Coville, *Fremontodendron californicum* (Torr.) Coville, *Garrya flavescens* S. Watson, and *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird. Although this grove currently has sparser understory vegetation with notably more bare ground (Fig. 5; Table 2) than unburned groves, the presence

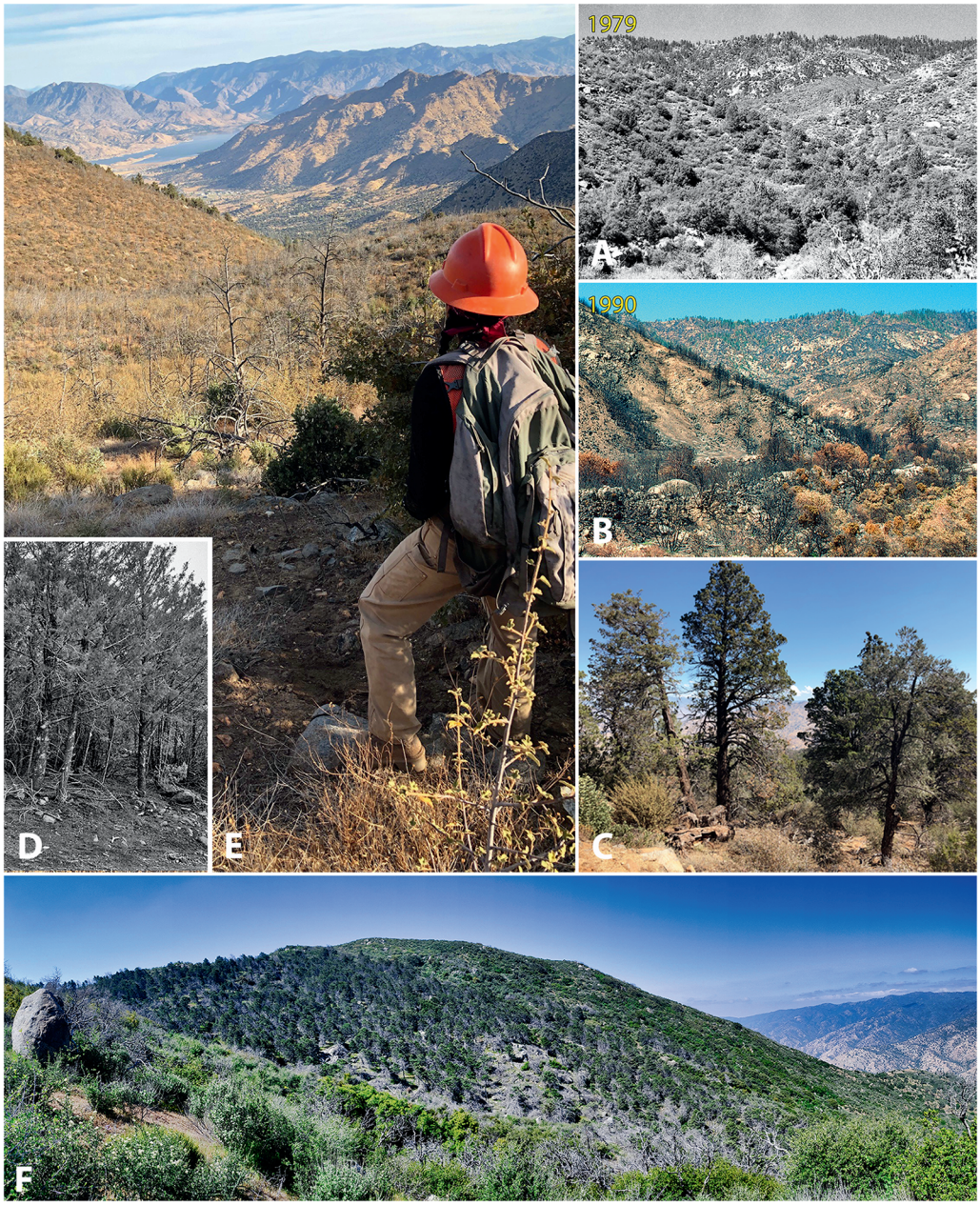

Fig. 3. Piute cypress groves before and after fire.—A. Stormy Canyon Grove in 1979.—B. Stormy Canyon Grove in 1990 immediately following the Stormy fire.—C. Piute cypress in the unburned portion of Bodfish Grove on the Sequoia National Forest.—D. The younger portion of Bodfish Grove in 1979 (~60 years old).—E. Alexis Bernal, UC Davis, looks out from another location of the same stand as shown in Fig. D in 2019, after the stand burned in the 2010 Canyon Fire.—F. Cypress mortality visible within a ~175-year-old stand of Hobo Ridge Grove in 2019.

of these species may be a hindrance to sustaining this small grove in the future should they persist for as many years (~38 years) as Bartel noted in 1980.

Hobo Ridge Grove.—Hobo Ridge Grove has burned three times in documented history (1921, 1966 and 2010); fires have ranged from only affecting portions of groves to nearly burning the entire grove. The grove (~23 hectares) is made up of seven distinct stands surrounded by chaparral (Bartel 1980). We conducted measurements in a stand that had not been burned in documented history (Bartel 1980). In viewing this stand from the trail in 2019, it seemed to be impacted significantly by mortality from either drought or insect damage (Fig. 3F). At the time of Bartel's measurements, most of the trees in this stand were at least around 136 years old (Bartel 1980), making them ~175 years old when we measured them. The stands within the greater grove were mostly even aged at the time of Bartel's measurements with ancient cypress potentially approaching 500 years in age in a small stand immediately east of the studied stand on Bureau of Land Management (BLM) lands. Though the large trees within this small stand were

Table 2. Piute cypress attribute findings and 1980 comparisons summarized by groves (or portions of groves).

			Bodfish old (~240 year) cohort	Bodfish mid (~ 90 year) cohort*	Bodfish young (~10 year) cohort	Cane Creek	Cannell Creek	Hobo Ridge (175 years)	Stormy Canyon (20 years old)*
		Plot #:	**6**	**7**	**7**	**Repr.**	**5**	**5**	**Repr.**
Cover	Bare ground (%)		6 (± 1.4)	NA	9.9 (± 4.3)	-	26.6 (± 10.9)	0.5 (± 0)	-
	Coarse woody debris (%)		2.2 (± 1.6)	NA	3.3 (± 2.4)	-	0.9 (± 0.3)	3.5 (± 1.8)	-
	Herbaceous cover (%)		20 (± 8.9)	NA	59.2 (± 9.6)	-	49 (± 8.6)	90 (± 2)	-
	Litter (%)		62.8 (± 8.6)	NA	80.3 (± 4.5)	-	66.4 (± 13.5)	81 (± 10.7)	-
	Rock (%)		33.3 (± 11.1)	NA	6.7 (± 2.1)	-	8.2 (± 2.9)	11.6 (± 7.3)	-
	Shrub cover (%)		24.2 (± 4.4)	NA	28.3 (± 6.9)	-	2.6 (± 0.9)	2.4 (± 1.9)	-
Density	HENE** trees per hectare (TPH)	All (live & standing dead)	477.4 (± 226.1)	259.9 (± 95.6)	NA	-	171.9 ± 78.3	318.2 ± 99.1	-
		Live	424.4 (± 202.6)	NA	NA	-	146. 4 (± 77.7)	241.9 (± 88.1)	-
		Standing dead	53 (± 31.5)	259.9 (± 95.6)	NA	-	25.5 (± 12)	76.4 (± 25.9)	-
		Downed dead	42.4 (± 31.5)	1777 (± 1285.4)	NA	-	318.3 (± 188.6)	0 (± 0)	-
	All other species live TPH		10.6 (± 6.7)	NA	NA	-	0 (± 0)	50.9 (± 29.5)	-
	TPH 1980		**297.6**	**1316**	**NA**	-	-	-	-
	Other species 1980		**57.5**	**88**	**NA**	-	-	-	-
	HENE seedlings per hectare		0 (± 0)	NA	9876.7 (± 3635.2)	-	1298.7 (± 941.2)	101.9 (± 74.2)	-
	HENE saplings per hectare	Live	63.7 (± 63.7)	NA	2200.9 (± 507.6)	-	7104.7 (± 3421.5)	229.2 (± 197.6)	-
		Dead	127.30 (± 127.3)	***	***	-	1273.2 (± 635.3)	0 (± 0)	-
	Other species seedlings & saplings		933.7 (± 339.5)	0 (± 0)	145.5 (± 145.5)	-	50.9 (± 31.2)	350.1 (± 164)	-
Size	Median HENE height (m)	Live	8.4 (±.0.7)	NA	NA	4	4.9 (±.0.6)	9.7 (±.1.1)	-
		Dead	8 (± 1.5)	3.3 (± 1.1)	NA	-	3.7 (± 0.7)	9.4 (± 2.2)	2
	HENE height 1980 (m)		**5–8**	**2–3**	**NA**	-	-	-	-
	Median DBH (cm)	Live	27.9 (± 4.9 cm)	NA	NA	15	26.2 (± 12.2)	25.5 (± 3.2)	-
		Dead	26.4 (± 8.9)	7.4 (± 2.4)	NA	-	20.7 (± 8.4)	23.0 (± 6.0)	3
	DBH 1980 (cm)		**20**	**3–10 (majority)**	NA	-	-	-	-
	Modal cone class (# of cones)		101–500	11–100	****	11–100	101–500	101–500	0–10
	Phloeosinus evidence?		-	-	-	Yes	-	Yes	-

Repr. = Representative.
* Fire-killed trees studied to assess attributes at age of death.
** HENE = *Hesperocyparis nevadensis*.
*** 1164.1 (± 865.5) HENE saplings were reported dead at the young Bodfish site but whether they died due to fire or in the 9 years following is unknown.
**** Did not systematically collect cone data for sapling sized cypress but we observed cones on a number of 9-year-old saplings.

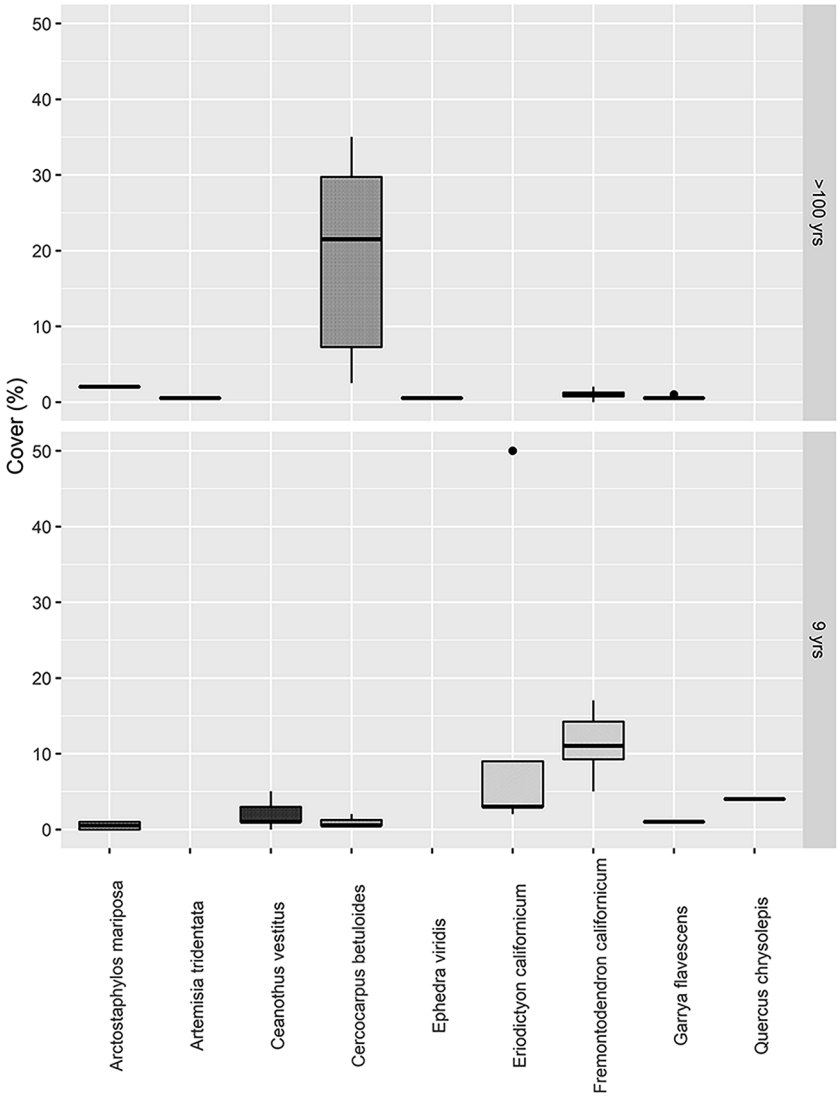

Fig. 4. Shrub composition in the older (burned > 100 years ago) and younger portions (burned 9 years prior to sampling) of Bodfish Grove.

not affected by the 1921 and 1966 fires, the 2010 Canyon Fire swept through this stand killing most of the ancient trees.

Piute cypress measured at Hobo Ridge trended larger than at the other unburned stands, though they were not significantly larger than trees measured in Bodfish but are around 65 years younger (Bartel 1980). [See section 4.3 on Piute cypress mortality measurements].

At Hobo Ridge, we noted a substantially higher amount of herbaceous (72% ± 18%) and litter cover (81.0% ± 10.7) relative to the other groves and to other ground cover types measured within Hobo Ridge, which illustrates the relatively open understory in the grove. Like the Cannell Creek Grove (and in contrast to the Bodfish Grove), we found relatively low amounts of shrub cover (2.4% ± 0.93).

Stormy Canyon Grove.—Stormy Canyon Grove is one of three groves on the eastern slope of the Greenhorn Mountains (Bartel 1980). The grove was first reported as "an extensive colony, nearly as large as the Bodfish colony" with an estimated 1000, mostly even-sized trees (Twisselmann 1967). Bartel (1980) reported the grove as being extensive on north-facing upper slopes with many larger trees near the creek. [See Section 3.1 for detail on fire impacts].

2. Assess Change Over 40 Years

2.1 What are growth patterns and rates in Piute cypress?

In the old stand of Bodfish (the portion with no recorded fire), cypress were slightly taller with wider diameter boles (Table 2). We estimate that these older trees (~240 years old) grew 0.03 m a year on average in height and 0.2 cm a year in diameter.

Within the twice-burned portion of Bodfish, Bartel (1980) measured the young cypress to be from 2 to 3 m in height and 3 to 10 cm DBH. In our 2019 sampling, the fire-killed cypress we measured were taller and wider in diameter (Table 2), representing the 30 years of growth between Bartel (1980) measurements and the 2010 fire. The 90-year-old cypress grew

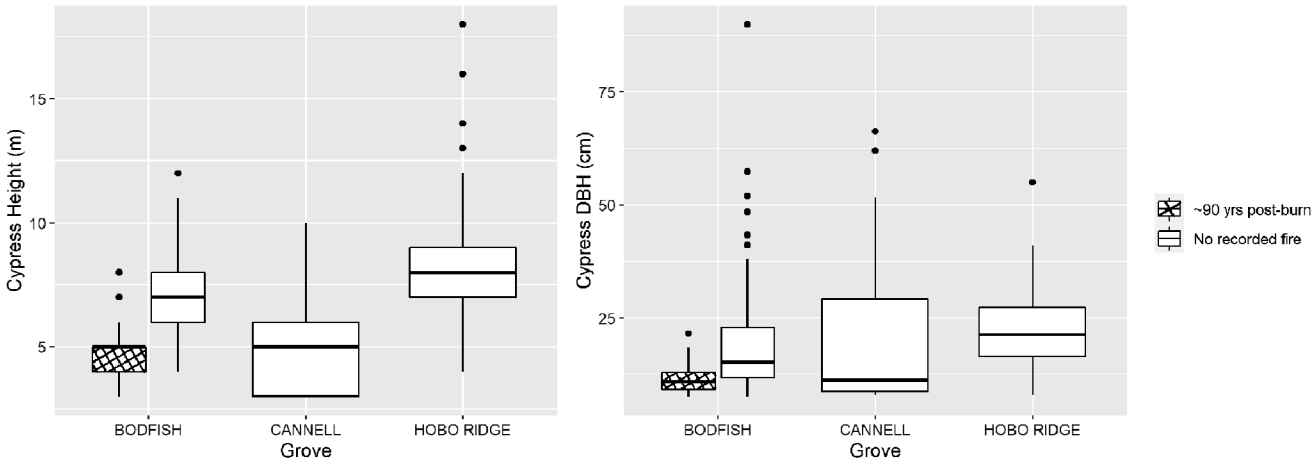

Fig. 5. Distribution of cypress heights and DBH measurements at three groves classified by fire history. Trees measured in Bodfish Grove shown in the '~90 yrs post-burn' class had recovered from the 1921 fire and were fire-killed in 2010. Note, we only measured heights and DBH on trees with a DBH of 7.6 cm or larger.

approximately 0.03 m a year in height and 0.03 cm a year in diameter.

2.2 How have Piute cypress tree densities changed over time? How have the relative proportions of non-cypress tree species changed?

Within the older unburned portion of Bodfish Grove, we found live cypress densities to be comparable to Bartel's 1980 measurements 40 years prior. The 2019 mean live cypress densities were higher than Bartel (1980) by 126.8 trees per hectare, but the standard error on the 2019 estimate are substantial indicating high variation in density patterns (Table 2). In terms of other tree densities, a comparison of Bartel (1980) to present revealed that the relative proportion of non-cypress tree species densities to cypress has dwindled by 82% (Table 2).

3. Evaluate Post-Fire Recovery

3.1 How do grove conditions vary by fire return intervals? Are Piute cypress exhibiting regeneration at densities higher than mature tree densities?

20-year fire return.—The Stormy Canyon Grove has burned three times in documented history (1924, 1990, and 2010). The impact of the 1990 fire can be seen in Fig. 3A and Fig. 3B. The 20-year interval between the last two fires is the shortest of all the groves. Our 2019 visit revealed no surviving adult trees (standing or down). Presumably, the dead adult cypress that burned in the 1990 fire were consumed in the 2010 fire along with the regenerating saplings. The modal height of the ~20-year-old dead saplings was around 2 m, with 3 cm DBH and 0–10 cones present. No cypress we observed had a DBH of greater than 5 cm. During our visit, nine years post-fire, we did observe seedlings that were mostly confined to rocky patches near the creek with no observable cones.

90-year fire return.—Within the recently burned portion of the Bodfish Grove, the majority of regeneration (81%) were seedlings taller than 10 cm, compared to saplings (18%) and seedlings shorter than 10 cm (1%). As expected, given the complete overstory mortality, the burned portion of the Bodfish Grove had little canopy cover (20% on average).

Piute cypress regeneration densities for all size classes 9-years post fire in the Bodfish Grove were 1.2 ± 0.34 stems per m^2 (12,077 stems per hectare; Table 2). For regenerating individuals to populate Bodfish Grove to the same densities that existed 90 years post-fire (standing and fallen), only 16.9% of the seedlings and saplings would need to survive to maturity. While present, other tree species' seedling and sapling numbers are very low relative to Piute cypress regeneration at Bodfish (Table 2).

3.2 At what size are Piute cypress bearing cones and appear ready to withstand another fire?

We found that many of the smallest diameter at breast height Piute cypress we measured (7.6 cm was our minimum cutoff) and the shortest cypress (~3 m) had cones. We did not systematically measure cone numbers on sapling trees, but we have many remarks in our field notes documenting cones on saplings. We also found a significant relationship ($p < 0.001$) between increasing Piute cypress size (e.g., DBH, height) and number of cones. The three oldest groves also had higher modal cone classes (e.g., 101–500 cones) than younger stands in Bodfish, Cane Creek, and Stormy Canyon Groves (Table 2).

Fewer cones were measured in the portion of the Bodfish Grove where the adult trees had been killed 90 years after the first burn compared to the older portion of the grove with no known fire history (Fig. 6). Most of the individuals in the younger, recently burned portion of the grove had less than 100 cones in contrast to the older portion of the grove where 28.7% of cypress trees had between 101 and 500 cones and 12.2% had more than 500 cones. These findings are similar to Bartel's (1980) report of observing substantially more cones on 122-year-old trees relative to 45-year-old cypress in the Hobo Ridge Grove.

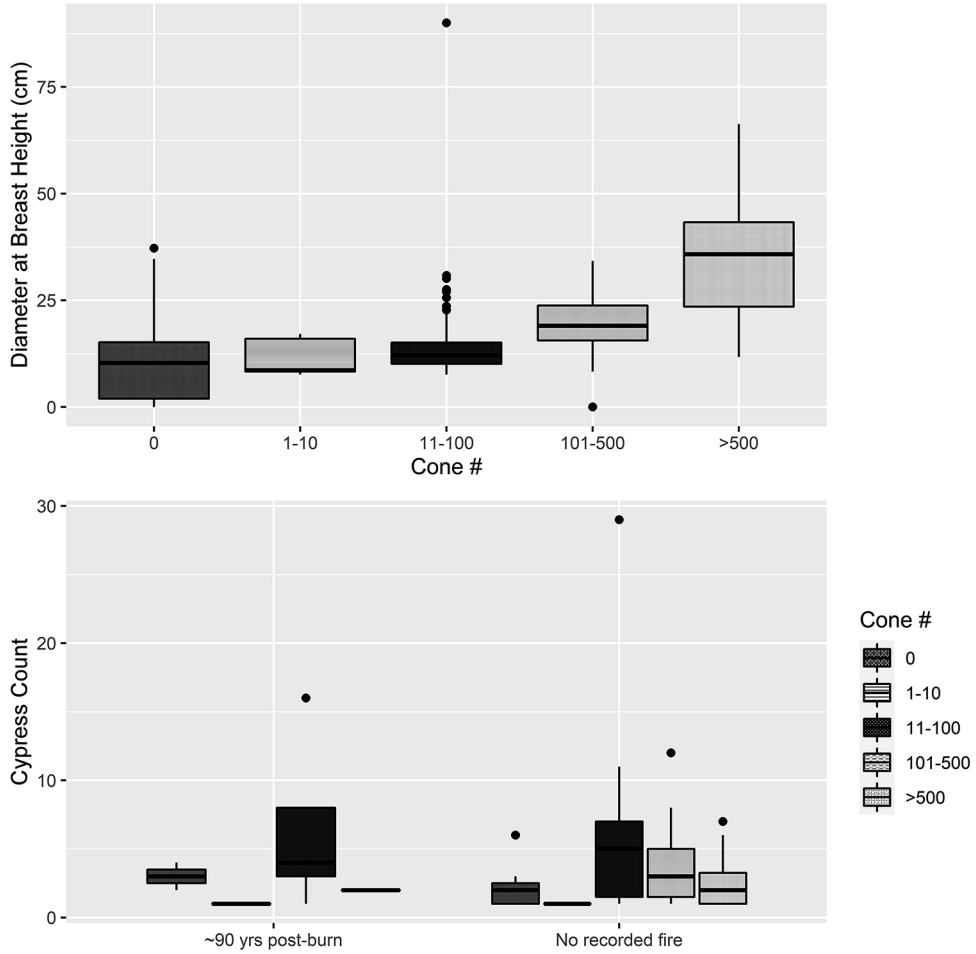

Fig. 6. [Bottom] Piute cypress diameter at breast height related to cone class across groves. [Top] Cone abundance measured on adult cypress (> 7.6 cm DBH) at Bodfish Grove. Cones measured on individuals in the younger portion of the grove were all dead (killed 90 years after the previous burn).

4. Summarize Conditions in Groves with no Record of Fire

4.1 What are the relative proportions of non-cypress tree species?

Of the unburned groves, we documented no species other than Piute cypress at Cannell Creek with no regenerating species other than Piute cypress. About 2% of the total tree densities were non-cypress species in the older portion of Bodfish, but about 94% of all regeneration was comprised of seedlings and saplings from non-cypress species. Piute cypress still dominated the unburned portions of Hobo Ridge at 318.2 ± 99.1 trees per hectare with about 13% of the total trees comprised of non-cypress species. However, we found abundances of non-cypress tree regeneration to be equivalent to Piute cypress. Other tree species present were *Quercus wislizeni* A.DC., *Q. chrysolepis* Liebm. and *Pinus monophylla* Torr. & Frém.

4.2 Is there regeneration in unburned groves?

While regeneration densities were lower than mature tree densities in the unburned Bodfish stand and at Hobo Ridge, the Cannell Creek Grove exhibited much higher regeneration densities than mature tree densities (Table 2). Of the three unburned portions of groves, Cannell Creek had marginally less canopy closure (1.4 canopy hits ± 0.4 of 5) compared with Hobo Ridge (2.2 canopy hits ± 0.97 of 5) and less than Bodfish Grove (2.6 canopy hits ± 0.67). Additionally, Cannell Creek had the highest relative number of individuals with large cone crops (>500) out of any of the groves.

Cone production among groves, when comparing the portions of the grove with no documented fire history, was comparable. The unburned portion of Bodfish Grove, which also has higher tree densities (Table 2) demonstrated higher numbers of cone-producing individuals, particularly in the 11–100 and 101–500 number of cones classes than other unburned groves. Cannell Creek Grove had the most individuals (38.7%) with greater than 500 cones per tree.

4.3 What are Piute cypress mortality rates within stands with no recorded fire?

Almost 20% of the overall Piute cypress densities in the unburned portion of Bodfish were dead (standing and fallen). About 72% of the total Piute cypress densities measured at Cannell Creek were dead with the sizable majority having

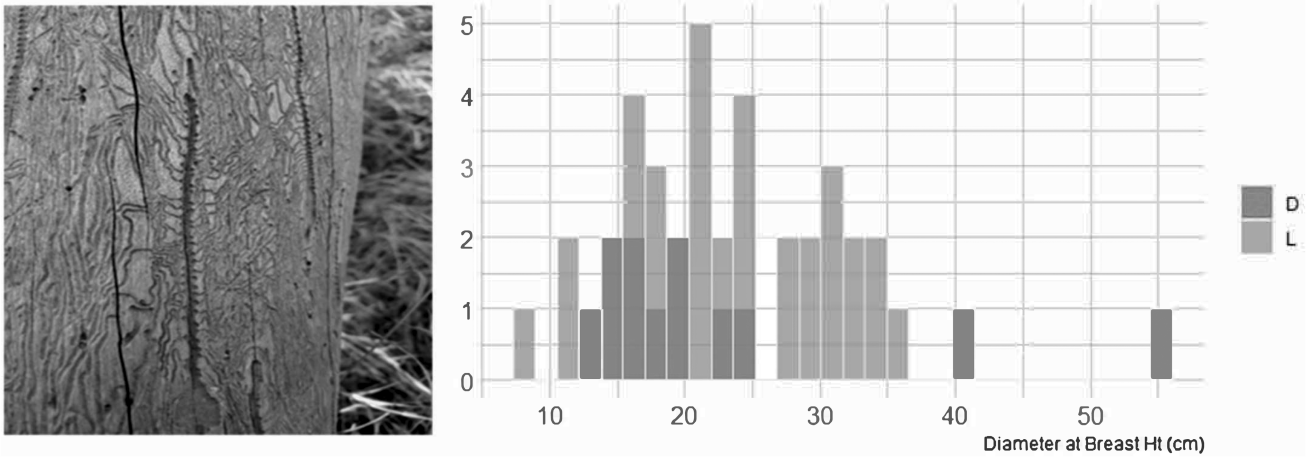

Fig. 7. *Phloeosinus* galleries present in a dead Piute cypress tree at Hobo Ridge (left) and histogram of diameter at breast height distributions among live (L) and dead (D) Piute cypress at Hobo Ridge.

fallen. Standing dead cypress measured at Bodfish and Cannell Creek were both on the smaller end of the diameter and tree height distribution of all Piute cypress measured.

At Hobo Ridge, relatively 24% of the cypress densities measured were dead. When evaluating total numbers of trees killed, nearly a third (31.6%) of all adult cypress (n = 206) measured at Hobo Ridge were dead. On every plot that we measured, we found evidence of *Phloeosinus* spp. beetle activity (Fig. 7). Trees that were dead had beetle galleries present and showed signs of over 50% of the bole being attacked. Generally, the dead trees at Hobo Ridge were at the smaller end of the diameter at breast height and tree height distributions (Fig. 7), with two exceptions being the two largest individuals measured on any of the plots. *Phloeosinus* spp. was also documented at the Cane Creek Grove, but their galleries covered a substantially smaller portion of those tree boles (~5%).

DISCUSSION

Increases in fire numbers may be related to more anthropogenic ignitions in the region (e.g., heavy summer tourism at the Lake Isabella area in summer months), which is a rising issue nationally (Balch et al. 2017). Fire occurrences and area burned may have been abnormally low during the early period of our dataset given the cessation of indigenous burning practices and fire suppression practices. The patterns we observed in more fires in the region are consistent with Mallek's (2009) dendrochronology study of McNab cypress where he found more frequent fires (2.6 times a decade) within cypress populations up until 1940, when the fires were reduced to once a decade, and then in the early 1990s where he found a resurgence in fires. Mallek (2009) attributed the trends to a wet period within the region and the advent of effective fire suppression.

Other studies have documented increases in numbers of fires and area burned for the Sierra Nevada ecoregion (Miller et al. 2009; Westerling 2016; Williams et al. 2019). With rising temperatures and decreased fuel moistures, the likelihood of fire is further expected to increase non-linearly in the Sierra Nevada region, with a 1°C increase projected to yield a 19–22% increase in fire occurrence (Gutierrez et al. 2021). Temperature increases (from 0.82 to 1.65°C) have already been documented at weather stations around the Piute cypress region in the Southern Sierra Nevada (Wuenschel et al. 2021). These predictions are dire for species not adapted to high frequency fire regimes.

Bartel (1980) estimated the optimum fire return interval for Piute cypress to be between 60 and 200 years, and our observations in this study further substantiate this. After only 20 years between fires in the Stormy Canyon Grove, we found near location extinction of Piute cypress. Conversely, Bodfish, which has not experienced fire in 90 years, appears well-poised to persist given high regeneration densities and cone presence in live saplings if it doesn't burn again soon. About 16.9% of the seedlings and saplings measured at the site would need to survive for the stand to reach pre-fire densities, which is a much lower threshold compared to all the other stands we measured where fire frequency was higher. While a study in Tecate cypress (*Hesperocyparis forbesii* (Jeps.) Bartel) estimated there was only an 8% survival rate from seedling to mature adult (de Gouvenain and Ansary 2006), the Bodfish Piute cypress seedlings and saplings are already 8–9 years old and showing signs of sexual maturity. Although, we did find cones on 9-year-old trees, and hence it is possible that groves may be sustaining with fire return even less than 60 years. This is consistent with Bartel (1980) who observed Piute cypress to generally begin developing cones around 10 years after fire. At Hobo Ridge, Bartel (1980) also observed no cones on trees 11 years post-fire but a number of cypress with cones two years later (13 years post-fire). However, we found larger diameter and taller trees bore a higher number of cones across the groves (Fig. 6), which increased as fire return interval increased (i.e., more years between fires). This stark contrast between groves with differing fire frequencies suggests that too-frequent fire and subsequent immaturity risk is a serious concern for this species.

In comparison with fire return intervals in other cypress species, Tecate cypress was found to be extremely vulnerable to fires more frequent than 30–40 years (Zedler 1977, 1995; de Gouvenain and Ansary 2006). However, in Sargent cypress (*Hesperocyparis sargentii* (Jeps.) Bartel), researchers reported that regeneration of a large population was substantial in stands as young as 20 years, which suggests a fire return

interval shorter than 20 years would be needed to pose a significant risk to the species (Ne'eman et al. 1999).

Timing of fire return may not wholly explain post-fire Piute cypress recovery. Fire intensity, cone combustion, seed age, and climate factors may all lead to varying regeneration rates. While high mortality in cypress stands takes place with fire generally, the most intense fires may also burn up canopy seed banks. Heat intensity and exposure times have been shown to influence seed germination in Piute cypress (Milich et al. 2012). Of five *Hesperocyparis* species studied in a germination/heat exposure experiment though, Piute cypress seeds were the least sensitive to very high temperatures, but germination was affected by prolonged exposure to high temperatures (Milich et al. 2012). We found evidence of high-levels of combustion at the site where we saw evidence of immaturity risk, perhaps due to fuel loading from residual downed trees from the previous fire. Additionally, post-fire regeneration may have perished at Stormy Canyon (∼20 years between fires) due to the 2012–2016 California drought, although this did not noticeably impact the other grove we studied that was also recovering from a 2010 fire.

Though a fire may miss or marginally singe an individual cypress, as expected we found no examples of mature Piute cypress having survived recent fires given the known patterns of stand-replacing fire in the groves (Bartel 1980). The Bodfish grove provided an opportunity to compare Piute cypress populations that occur adjacently with different fire histories. Rockiness within the older portion of the grove may have reduced fire spread by virtue of limiting ignitable herbaceous cover and litter (found at higher abundances in the twice-burned portion of Bodfish). These findings may be due to known edaphic and topographic differences (steep northeast facing versus gentler southeast facing) between the two stands (Bartel 1980). These natural barriers that limit fire behavior supports the notion that Piute cypress persist in areas where fire refugia exist (Bartel 1980).

Both stands within the Bodfish Grove featured markedly higher shrub cover than other groves, with the recently burned stand showing more representation from diverse shrub species possibly signifying a sudden opportunity with disturbance for shrub species to establish. *Cercocarpus betuloides* dominated the unburned stand, has been found to prefer open sites (Keeley 1992) and perhaps does well in older successional cypress stands that tend to be more open (Bartel 1980).

Of the cypress groves with no recorded history, Piute cypress measured at Cannell Creek were shorter and more sparsely populated with relatively higher numbers of fallen dead cypress. These characteristics could indicate that this grove was burned in the 1942 fire, of which we have some observational evidence (e.g., fire damage, char, fuels, etc.) to support this but lack spatial data to confirm. Shallow soils at Cannell Creek (Bartel 1980) may also contribute to growth and mortality patterns; there was notably more bare ground at Cannell than other groves measured, perhaps indicative of low productivity. Despite having fewer mature trees, Cannell Creek boasted the highest numbers of saplings compared to other unburned sites, and they could be older than size attributes belie, perhaps stunted due to site quality.

Within our study, we found no evidence of Piute cypress densification or thinning over 40 years within an already mature stand where we had the 1980 comparison data available. Although, when comparing densities in ∼90 year-old trees with densities in ∼240 year-old trees at the same grove, we found evidence of thinning with time since fire, which was also noted in Sargent cypress (Ne'eman et al. 1999).

Piute cypress regeneration in groves with no recorded fire occurred at higher numbers than mature trees are dying, indicate potentially increasing densities in some groves. Notably, though, variation in regeneration was very high, which indicates a patchy distribution that we may not have adequately captured in our small study. The Cannell Creek Grove, which had by far the highest regeneration numbers among unburned groves, was more open, had lower shrub cover and which potentially created conditions suitable for regeneration. Additionally, Cannell Creek had the highest relative number of individuals with large cone crops (>500) out of any of the groves. These findings do support the premise in Bartel (1980) that Piute cypress stands are not necessarily dependent on fire to sustain these long-lived populations, which is often an assumption in species that exhibit serotiny.

The absence of fire in cypress groves does lead to concerns related to encroachment by other tree species, lack of sustaining regeneration and age-related decline (Mallek 2009; Rentz and Merriam 2011; Bower and Hipkins 2017). Increased encroachment was not observed in Piute cypress stands where we had long term data available and there was a notable decline in non-cypress species over 40 years. Across the unburned stands studied, the relative species composition was largely dominated by Piute cypress (> 85%). None of the slow-growing tree species that occur within the Southern Sierra chaparral matrix are particularly aggressive or shade tolerant, which may protect Piute cypress from the site-takeover that's been observed in cypress that occur with more mesic forest environments (Rentz and Merriam 2011). It's also possible that the azonal soil conditions that Piute cypress tend to occur on preclude significant competition from other species. It should be noted that Bartel (1980) did find encroachment by *Pinus* spp. and *Quercus* spp. at Back Canyon Grove which also exhibited cypress senescence. However, this grove is the southernmost grove that is low in elevation and substantially drier than other groves, which may provide a competitive advantage to other species. Based on this and our observations of high proportions of non-cypress tree species occurring in two of the groves we measured, we recommend future monitoring to better assess composition trajectories within groves.

While we documented substantial Piute cypress mortality at all three unburned stands measured, dead trees tended to be on the smaller end of the height and diameter distribution for cypress at each site, implying that the cause of death was generally not age-related decline. Furthermore, our records of mortality may be inflated in cypress relative to those of other conifer species due to the rot-resistant nature of their wood and the arid nature of the southern Sierra habitat. Piute cypress are known to live as long as 600 years (Bartel 1980). Growth rates as measured over 30 and 40 years between younger trees (∼90 years old) versus older trees (∼240 years old) were remarkably similar for height but the older trees experienced faster radial growth. Faster growth rate in older trees may indicate that growth rates are slowing in areas that experience higher frequency fire relative to the unburned portions of the

grove. Even after a century of growth, younger trees were still markedly smaller than old trees measured in unburned groves indicating no evidence of a growth slowdown and Bartel (1980) found evidence of very large Piute cypress (2.3 m DBH). However, cypress size measurements were comparable between ~240-year-old trees and ~175-year-old trees, indicating differences in site quality and/or a leveling off of growth prior to 175 years of age.

However, anecdotal observations of recent mortality at Hobo Ridge (Fig. 3D) do suggest an uptick in death rates there that were substantiated by our measurements. We recorded high non-fire (potentially drought) mortality (31.6%) across all trees measured at Hobo Ridge. There was evidence of *Phloeosinus* spp. galleries both at Hobo Ridge and at Cane Creek. Other site-level factors, such as density or prevalence of other tree species that attract *Phloeosinus* spp., may also have been factors in the beetle presence at Hobo Ridge, but we did not design the inventory to evaluate this. Presence of *Phloeosinus* spp. galleries does not necessarily mean beetles were the primary mortality agent as they may have entered after the tree was significantly weakened or killed by another mechanism such as drought or disease (Beverly Bulaon, US Forest Service Entomologist, pers. comm.). The 2012–2016 drought, which killed hundreds of millions of trees across the Sierra Nevada (Brodrick and Asner 2017; CDFP 2018) may have been the prevailing factor in mortality observed at Hobo Ridge.

However, *Phloeosinus* spp. are widely known to damage trees and are potentially a risk for Piute cypress populations that will increase with future drought and warming temperatures (Fettig et al. 2019). Even higher levels (46%) of cypress mortality and evidence of *Phloeosinus* spp. attack were observed recently in Arizona cypress (*Hesperocyparis arizonica* (Greene) Bartel) and was correlated to a hot drought at the site (Verrier 2022). We recommend the Piute cypress groves be monitored for insect attack and non-fire mortality. While we know of no management technique to effectively mitigate drought-related mortality, understanding how the populations are doing overall may help inform how aggressively to protect groves vulnerable to compounding disturbances.

Based on our findings in five studied Piute cypress groves, known fire occurrences in groves, and observations in Bartel (1980), we estimated vulnerability to reburn for all Piute cypress groves. Stormy Canyon is highly vulnerable to local extinction and reburn given the limited numbers of Piute cypress following the previous fire, which also lacked cones. The Cane Creek Grove also is highly vulnerable to reburn given it has experienced a recent 2021 fire and is adjacent to a road and hence human-related ignition sources. Given the presence of cones and that the size of the cypress were similar to pre-burn densities at Bodfish, a grove with seemingly adequate recovery, we anticipate recovery of the Cane Creek Grove in the absence of fire returning soon. Portions of Cannell Creek, Chico Canyon, Hobo Ridge and Bodfish groves, which are recovering from 2010 fires, are also moderately vulnerable to reburn within the next 50 years.

Given the potential vulnerability of five of the Piute cypress groves to immaturity risk, we recommend employing fire suppression tactics to protect groves recently burned during wildfire operations. Groves that have had adequate time since last fire (at least 60 years, Bartel 1980) are likely to be resilient to wildfire and should be allowed to burn. During suppression activities, care should be taken within groves to avoid harming these uncommon populations (e.g., fuel breaks should be built around and not through them).

As groves recover from fire, if dense chaparral regenerates, experimental management to reduce shrub cover in vulnerable groves might be considered. While Piute cypress can compete with chaparral, the repetitive fires (10–40 years) chaparral systems are prone to, may threaten the tree species. Fire patterns in chaparral systems are becoming increasingly frequent with climate change and human ignition sources creating type conversions to annual grasslands that can, in turn, burn even more frequently (Park and Jenerette 2019; Safford et al. 2021) and these trends threaten the tree-species that live within the chaparral matrix. Any experimental reduction of shrubs must be carefully implemented outside of grove boundaries. Shrub removal may injure cypress, and shrubs are known to facilitate cypress growth particularly during drought (Gomez-Aparicio 2009).

Based on our study of groves with no documented fire history, Back Canyon, Bodfish (unburned portions), Cannell Creek (unburned portion), Corral Creek, O'Brien, and Pilot Knob groves are all poised to recover well from the next wildfire and no precautions need to be taken to protect them from fire (although it may be impossible to simultaneously protect a recently burned portion of a grove while allowing fire through an adjacent unburned area). Although we did not measure at Back Canyon Grove, evidence of fire exclusion-related decline (Bartel 1980) may warrant the use of fire for its continued persistence.

Because of the small and isolated nature of Piute cypress populations and increasing interrelated climate change, drought and wildfire-related threats, we recommend storing seeds from and propagating Piute cypress in nursery settings. Land managers should consider replanting in groves not adequately recovering from recent fire or after drought-related mortality events. These actions are particularly important to conserve the species given the increase in wildfire occurrences we are already observing in the region. Piute cypress seeds should also be preserved for posterity at the California Botanic Garden's California Seed Bank.

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