Fire Ecology

ORIGINAL RESEARCH

Persistent, viable seedbank buffers serotinous bishop pine over a broad fire return interval

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Abstract

Background In ecosystems where fire has been excluded, pyrosilviculture can restore some processes historically maintained by fire while mitigating risk where fire is inevitable. Pyrosilviculture in crown fire-adapted forests is, however, limited by insight into the temporal window of fire return matching canopy seedbank development. Here, we characterized demographic responses to fire and non-native pine pitch canker infection in a chronosequence of serotinous bishop pine stands burned at high-severity to quantify (1) temporal patterns of seedbank development given seed viability and density, cone production, and tree density, and (2) pine pitch canker incidence across tree ages and sizes to assess how infection might impact stand and seedbank development. We use our findings to elucidate pyrosilvicuture as a means of restoring fire given practical challenges of reintroducing high-severity fire in crown-fire adapted forests embedded within wildland urban interfaces (WUI).

Results Bishop pine produces an abundant, viable seedbank within eight years that persists across developmental stages and age classes. Seed abundance and viability are exceptionally high at even the earliest age (median > 600,000 seeds ha^{-1} and 97% viability at 6 years) and remain high, with the oldest stands (36 years) maintaining median densities of > 500,000 seeds ha^{-1} and viability of 95%. We additionally learned that pine pitch canker infection is most severe during the sapling stage (8–10 years post-fire), likely altering stand development trajectories as well as potentially limiting recruitment, and thus the aerial seedbank, into the canopy.

Conclusions In bishop pine and equally-fecund serotinous species, pyrosilviculture appears a viable management tool across a broad fire return window given the early development and persistence of a robust, viable seedbank, allowing managers flexibility in restoring fire to promote forest persistence while simultaneously mitigating wildfire risk. Moreover, pyrosilviculture in pine pitch canker infected stands may also provide disease mitigation. Although the long-term effects of pine pitch canker infection remain unknown, bishop pines' viable, persistent seedbank suggests that managers can ignite prescribed fire across a broad return interval — as short as eight years and as long as several decades — to promote bishop pine persistence, mitigate disease infection rates, and reduce wildfire risk in WUI-adjacent ecosystems.

Keywords Aerial seedbank, *Pinus muricata*, Fire management, *Fusarium circinatum*, Pine pitch canker, Prescribed fire, Silviculture, Forest management, Serotiny, Pyrosilviculture, Crown fire, Fire-adapted

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Resumen

Antecedentes En los ecosistemas en los que se ha excluido el fuego, la piro-silvicultura puede restaurar algunos procesos históricamente mantenidos por fuegos y a su vez mitigar el riesgo donde los incendios son inevitables. La piro-silvicultura en bosques adaptados a fuegos de copas, es asimismo limitada por la perspectiva de tener la ventana temporal del retorno del fuego coincidente con el desarrollo del banco de semillas del dosel. En este trabajo, caracterizamos las respuestas demográficas al fuego y a la infección del cáncer no nativo del pino tea en una crono-secuencia de rodales serótinos de pino del obispo quemados a alta severidad para cuantificar: (1) los patrones temporales del desarrollo del banco de semillas dados en viabilidad y densidad de semillas, producción de conos, y densidad de árboles, y (2) la incidencia del cáncer del pino tea a través de diferentes tamaños y edades de árboles para determinar cómo la infección puede impactar en el desarrollo de los rodales y en el banco de semillas. Usamos nuestros resultados para dilucidar si la piro-silvicultura sirve como una medida para restaurar el fuego dados los desafíos prácticos que implican el restaurar fuegos de copas de alta severidad en bosques adaptados a fuegos de copa e integrados dentro de áreas de Interfaz Urbano-Rural (WUI).

Resultados El "pino del obispo" produce un banco de semillas viable y abundante a partir de los ocho años y que persiste a través de los estados de desarrollo y clases de edad. La abundancia y viabilidad de las semillas son excepcionalmente altas aún a edades tempranas (mediana > 600,000 semillas ha-1 y 97% de viabilidad a los 6 años) y permanece alta en los rodales antiguos (36 años) manteniendo una densidad cuya mediana es > 500.000 semillas ha-1 y una viabilidad del 95%. Aprendimos además que la infección debida al cáncer del pino tea es más severa en el estadio de plántula o brinzal (8 a 10 años post-fuego), pudiendo alterar la trayectoria del rodal y también limitar su reclutamiento, y por ende el banco se semillas aéreo ubicado en el dosel.

Conclusiones En el "pino del obispo" y también en especies serótinas igualmente fecundas, la piro-silvicultura aparece como una herramienta de manejo viable a través de amplias ventanas de retorno de fuegos dado su desarrollo temprano y la persistencia de un banco de semillas robusto y viable, lo que permite a los gestores de recursos ser flexibles para restaurar el fuego y promover la persistencia del bosque y simultáneamente mitigar el riesgo de incendio. Además, la piro-silvicultura puede mitigar los efectos de la infección del cáncer del pino tea en rodales afectados. Aunque los efectos a largo plazo de la infección por cáncer del pino tea permanecen aún desconocidos, el banco de semillas viables y persistentes del pino del obispo sugieren que los gestores pueden iniciar las quemas prescriptas en un amplio rango de intervalo entre ellas, --tan corto como cada ocho años o tan largo como varias décadas–, para promover la resistencia del pino del obispo, mitigar la tasa de infección de la enfermedad, y reducir el riesgo de incendios en ecosistemas adyacentes a las WUI.

Background

Species' adaptations determine ecosystem responses to fire (Pausas et al. 2017), and species possessing traits adapted to a particular fire regime may be threatened when regime shifts render adaptations no longer advantageous (Keeley et al. 2011; Bowman et al. 2014; Pausas 2015). Regime shifts involving substantial changes in fire frequency and severity are increasingly common in fire-adapted ecosystems worldwide due to anthropogenically-driven climate change (Flannigan et al. 2009; Moritz et al. 2012), legacies of forest management and fire suppression (Stephens et al. 2014; Parks et al. 2015), exclusion of Indigenous burning (Kimmerer and Lake 2001; Cermak 2005), and introductions of non-native disturbance agents (Metz et al. 2013). Regime shifts are consequential, as ecological resilience — returning to a pre-fire state, function, or regime (Gunderson 2000) — is a key underpinning in persistence of fire-adapted species. Persistence potential may be challenged if, for instance, uncharacteristic fire frequency or severity diminishes post-fire seed availability

or overwhelms resilience mechanisms (Donato et al. 2009; Buma et al. 2013; Shive et al. 2018). Fire-adapted forests of the western US are particularly vulnerable to such mismatches between fire adaptations and contemporary fire regimes due to a massive fire deficit (i.e., less fire than historical climate and fuels dictate; Marlon et al. 2012, Parks et al. 2015). Yet, in fire-adapted forests, fire return is both inevitable and increasingly uncharacteristic (Hagmann et al. 2021; North et al. 2021).

There have thus been growing calls for (North et al. 2015, 2021; Kolden 2019; Stephens et al. 2020) and legislation directing (e.g., US Congressional National Prescribed Fire Act, California Senate Bill 332, California Executive Order B-52-18) the expanded use of managed and prescribed fire for reducing fuel loads and restoring fire-adapted forests of the West. California takes center stage in the deliberation over prescribed fire use, where, after more than a century of fire exclusion and suppression, ~8 million hectares of forest are in a fire deficit (Miller et al. 2020) and predisposed to wildfires

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misaligned with their historical regimes (Safford et al. 2022, https://www.fire.ca.gov/stats-events/). Concomitantly, wildfire risk has increased amidst growth of the wildland urban interface (WUI), with one-third of all California homes now located within the WUI (32%; Kramer et al. 2019) and the majority of US homes lost to fire between 1990 and 2020 residing in California (Kramer et al. 2018; Higuera et al. 2023). Reducing barriers to prescribed fire use in order to mitigate wildfire risk has been a focal point for policy development (Sugihara et al. 2006), but these efforts are complicated by the variability of ecosystems across the State — from those adapted to high-frequency/low-severity fires to those adapted to low-frequency/high-severity fires. Proactive management will be essential to reducing socio-ecological impacts where fire is inevitable (Moreira et al. 2020), but there remains a parallel need to develop ecosystem-specific burn plans that mimic the frequency, severity, and seasonality of the regime to which local species are adapted (Stephens et al. 2020).

Pyrosilviculture purposefully adopts prescribed or managed fire into objectives-based prescriptions as a tool for harmonizing management with the adaptations and disturbance history of local species (North et al. 2021; York et al. 2021). Purposefully burning implies a paradigm shift in forest management, however California's Indigenous peoples were the initial pyrosilviculturists (Codding and Bird 2013; Cuthrell 2013); frequent cultural burning had profound ecological effects, including generating fire-adapted ecosystems and mitigating fire severity through repeated fuel reduction (Blackburn and Anderson 1993; Lightfoot and Cuthrell 2015). Though limited in application over the last century, pyrosilvicultural approaches have been recently (and successfully) re-employed as a management alternative for restoring fire and reducing wildfire risk in California's seasonally-dry forests and oak woodlands adapted to low- or mixed-severity fire (Hankins 2015; North et al. 2021; York et al. 2021). Ongoing application will be critical to addressing the State's fire deficit, yet prescribed fire use in California remains nominal due to operational and societal barriers to implementation (Quinn-Davidson and Varner 2012; Miller et al. 2020; York et al. 2021). These constraints are acutely challenging in forests adapted to high-severity crown fires in proximity to the WUI (Barbour 2007; Mann et al. 2014). Despite the evident challenges, the need to restore fire or provide a functional alternative is nonetheless critical in crown fire-adapted systems where fire exerts strong selective pressure on demographic processes, including the degree of serotiny (i.e., long-term canopy seedbank released by heat) and the temporal window of seed viability for fire-obligate seeders (Crawford et al. 2011; Hernández-Serrano et al.

2013; Pausas and Keeley 2014). Long-term sustainability of crown fire-adapted forests will depend upon restoring the high-severity fire regime to which these ecosystems are adapted, however pyrosilviculture is limited by key ecological knowledge gaps on canopy seedbank development and viability. Of critical importance for designing pyrosilviculture in crown fire-adapted systems is understanding the rate of canopy seedbank development and its persistence following fire so that the repeated use of fire can be scheduled in a way that does not conflict with desired regeneration patterns of key species.

Here, we address these critical knowledge gaps using managed stands of crown fire-adapted bishop pine (*Pinus muricata* D. Don) on the Central Coast of California. Bishop pine is an endemic, serotinous conifer growing in ten disjunct populations from northern California to Baja California, Mexico (Millar and Critchfield 1988; Stephens and Libby 2006). Historical mean fire return is estimated at as frequent as ∼6 years to as long as ∼70 in northern California stands (Sugnet 1985; Finney and Martin 1989). Fire return intervals are unknown for Central Coast bishop pine, however these forests co-occur with coastal chaparral, a well-studied crown fire-adapted ecosystem with a mean fire return interval of 20 to 40 years (Byrne et al. 1977; Mensing et al. 1999). Across its range, bishop pine cone opening and regeneration are rare in the absence of fire (Sugnet 1985; Millar 1986; Harvey et al. 2011), though serotiny is variable and increases from north to south (Duffield 1951, Linhart et al. 1965, Millar 1986). Given the low density of lightning strikes on the Central Coast (2–3 strikes/100 km^2/year, Cuthrell 2013), fire was historically ignition-limited, and frequent fire would have been a product of regular Indigenous burning to meet cultural resource objectives (Keeley 2002a; Cuthrell et al. 2012, Lightfoot et al. 2013). Regardless of ignition source (lightning vs. anthropogenic), fires in bishop pine typically burn as high-severity, stand-replacing crown fires (Keeley and Zedler 1998), and stands exhibit rapid, high-density regeneration from a serotinous canopy seedbank (Linhart et al. 1965; Vogl et al. 1977; Harvey et al. 2011).

Managers have thus proposed returning fire to bishop pine stands to promote ongoing persistence of this fire-adapted species while simultaneously reducing wildfire risk to the adjacent WUI (see plans & decisions by: California State Parks, National Park Service, & PG&E). A distinct complication in management is the prevalence of the non-native pathogen pine pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell) (McCain et al. 1987), which may limit fire resilience if trees die prior to reproductive maturity and fail to contribute to the seedbank (Aegerter and Gordon 2006). On the other hand, fire has reduced non-native disease infection and mortality

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in other coastal, fire-adapted forests (e.g., sudden oak death, Simler-Williamson et al. 2021), and fire return may instead be an effective means of controlling infection. Yet, well-defined targets for fire return as well as the long-term implications of a pyrosilvicultural approach remain unknown for this crown fire-adapted system.

To better understand canopy seedbank development and support pyrosilviculture in crown fire-adapted forests, we characterized demographic responses to fire and pine pitch canker in bishop pine stands burned at high-severity across a chronosequence of wild- and prescribed fires ranging from 6 to 36 years. Prescribed fires were used to meet two objectives — (1) promote bishop pine regeneration following decades of fire exclusion and (2) reduce wildfire risk in this WUI-adjacent landscape. We leveraged this chronosequence of fires to identify the acceptable fire return window for bishop pine by quantifying: (1) the temporal pattern of post-fire canopy seedbank development given seed viability and density, cone production, and tree density and (2) the incidence of pine pitch canker infection across stand ages and tree size classes to assess how infection might affect stand development and thus pyrosilvicultural options. Although previous studies of serotinous species have estimated canopy seedbank development as a function of cone production and stand density (Keeley et al. 1999; Turner et al. 2007; Fry and Stephens 2013; Agne et al. 2022), here, we quantify both seed viability and density over a range of stand ages to provide a more accurate assessment of seedbank dynamics and to determine the temporal window of fire return promoting forest persistence. We use the results to discuss options for developing pyrosilviculture as a component of management in fire-obligate, crown-fire adapted forest types, such as serotinous bishop pine.

Methods

Study area

This study was conducted in the bishop pine forest surrounding the Diablo Canyon Nuclear Power Plant, a privately-owned 5090-ha property managed by Pacific Gas & Electric (PG&E) in San Luis Obispo County on the Central Coast of California. Bishop pine on the Diablo Canyon property grows adjacent to or intermixed with the coastal chaparral type dominated by *Adenostoma*, *Arctostaphylos*, and *Ceanothus* spp. (Pacific Gas & Electric Company 2007). This chaparral ecosystem type is composed predominantly of post-fire seeding and sprouting species that require fire for reproduction and survival (Hanes 1971; Keeley 1986, 1987), and Diablo is represented by a complex mosaic of this and other ecosystem types adapted to high-severity crown fire (Pacific Gas & Electric Company 2007). Climate on the Central Coast is characterized as Mediterranean

with mild temperatures, wet winters, and dry summers. Average annual temperature is ~15 °C (ranging from 8 to 18 °C), while precipitation falls as rain between December and March and averages ~58 cm (Ryan 1994). Here, as across the species' range, warm season precipitation (April–November) comes largely via fog drip from regular fog cover (Baguskas et al. 2016; Fischer et al. 2016), which supplements soil moisture, moderates air temperature, and reduces transpiration (Carbone et al. 2013).

PG&E took ownership of the Diablo Canyon property in 1985 after roughly 100 years of farming and grazing by private landowners (Spooner Family 1892–1942, Oscar Field 1942–1985) following exclusion of Chumash Indigenous peoples during the Mission Period (1769–1830; Pacific Gas & Electric Company 2007). With the exception of a wildfire in 1982, there is no written documentation of naturally- or anthropogenically-ignited fires on the property prior to PG&E ownership, and little is known about Indigenous burning practices beyond oral history that Chumash periodically burned to maintain a range of cultural resources and promote coastal grassland (Timbrook et al. 1982, Pacific Gas & Electric Company 2007). Cores takes from even-aged stands of mature bishop pine on the property ~2005 produced estimated stand ages of ~75 years (*personal communication, PG&E*), suggesting the bishop pine forest burned during Spooner Family ownership (1930−1940s). These fires were likely a product of fire escape from coastal grassland fires ignited by ranchers after rounding up cattle each fall; the last ranch hand out would tie a tire to a rope, light it on fire, and drag it behind a horse to promote vegetative response for the following year's grazing (*personal communication, PG&E*). Burning of bishop pine was not an objective but a likely consequence of uncontrolled burning in the adjacent coastal terrace.

Burning of bishop pine is, however, a contemporary objective of management on the Diablo Canyon property. PG&E directs a land stewardship program that aims to manage and protect natural and cultural resources while reducing the risk of catastrophic wildfire (Pacific Gas & Electric Company 2007). The property lies immediately adjacent to the town of Avila Beach, a community deemed high or very high hazard due to its proximity to crown fire-adapted wildlands and its "one-way-in, one-way-out" road system that may impede evacuation during a wildfire (Avila Community Plan 2021). After a wildfire in 2007, PG&E began to actively manage the bishop pine forests surrounding the nuclear power plant to reduce wildfire risk, and high-severity prescribed fires were ignited in 2009, 2010, and 2012 as part of their vegetation management plan (Pacific Gas & Electric Company 2007).

All prescribed fires were ignited in mature bishop pine stands during dry windows of the Central Coast rainy season (December through March) to re-introduce fire prior to the dry season when escapement risk increases. The objectives of PG&E's pyrosilvicultural program are to (1) promote resilience by regenerating bishop pine and (2) burn at the appropriate fire return interval so that, in the long-term, bishop pine stand management will reduce fuel loads and mitigate the risk of catastrophic wildfire to the power plant and adjacent WUI (Pacific Gas & Electric Company 2007) (Fig. 1).

Field sampling

Data were collected on 50 permanent plots located within the boundaries of five fire perimeters (Fig. 2), including two wildfires that occurred in 1982 and 2007 and three prescribed burns that occurred in 2009, 2010, and 2012 (Table 1). All fires burned at high severity, with > 90% mortality within each fire perimeter. For the 1982, 2010, and 2012 burns, fire polygons were first stratified by aspect; plots falling on each aspect within each fire perimeter were then randomly selected in ArcGIS using the Sampling Design Tool (Buja and Menza 2013), with
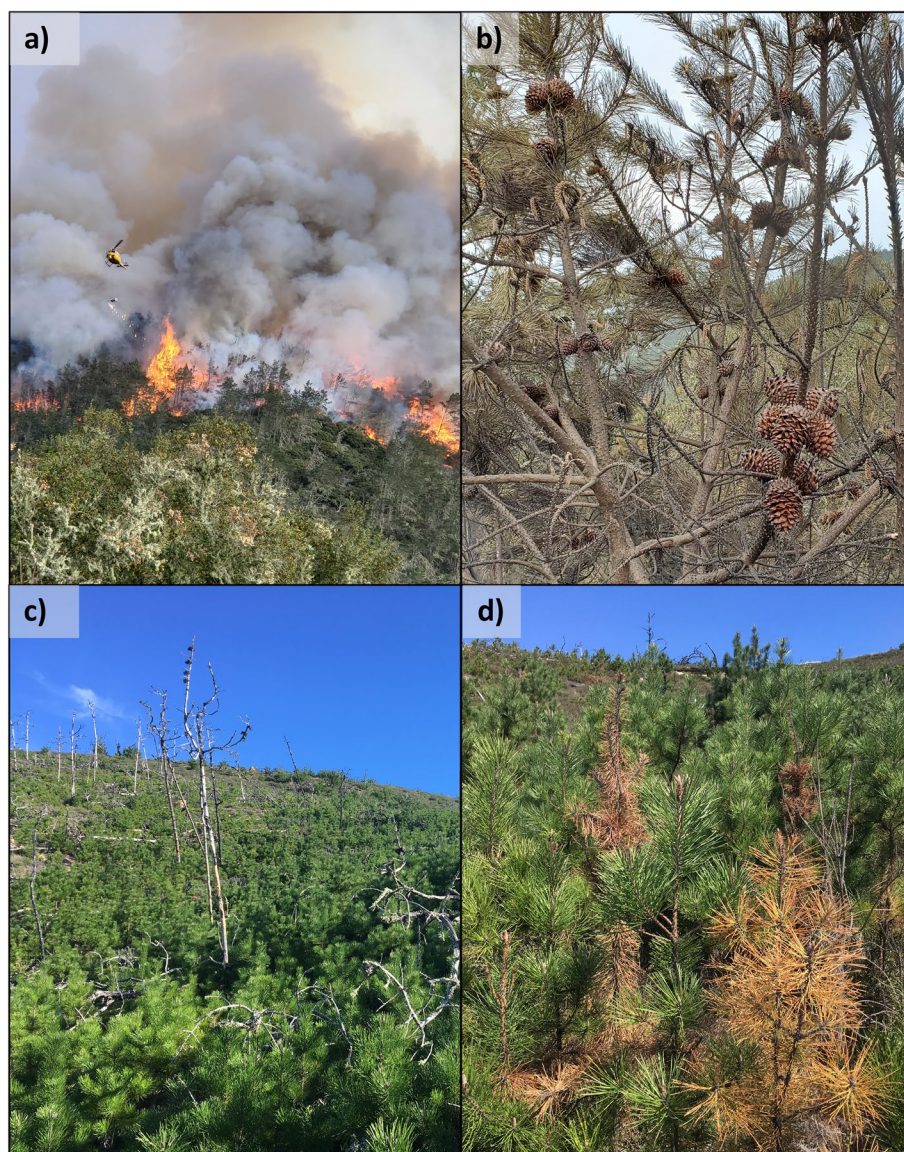

Fig. 1 Bishop pine stands in our study site. **a** Helitorch ignition during prescribed fire operations. **b** Opened cones following prescribed high-severity fire. **c** Post-fire bishop pine regeneration (photo taken 5 years after fire). **d** Stem dieback from pine pitch canker infection in bishop pine saplings. **a**, **b** Photo credit: Dan Stocks; **c**, **d** Photo credit: Sarah Bisbing

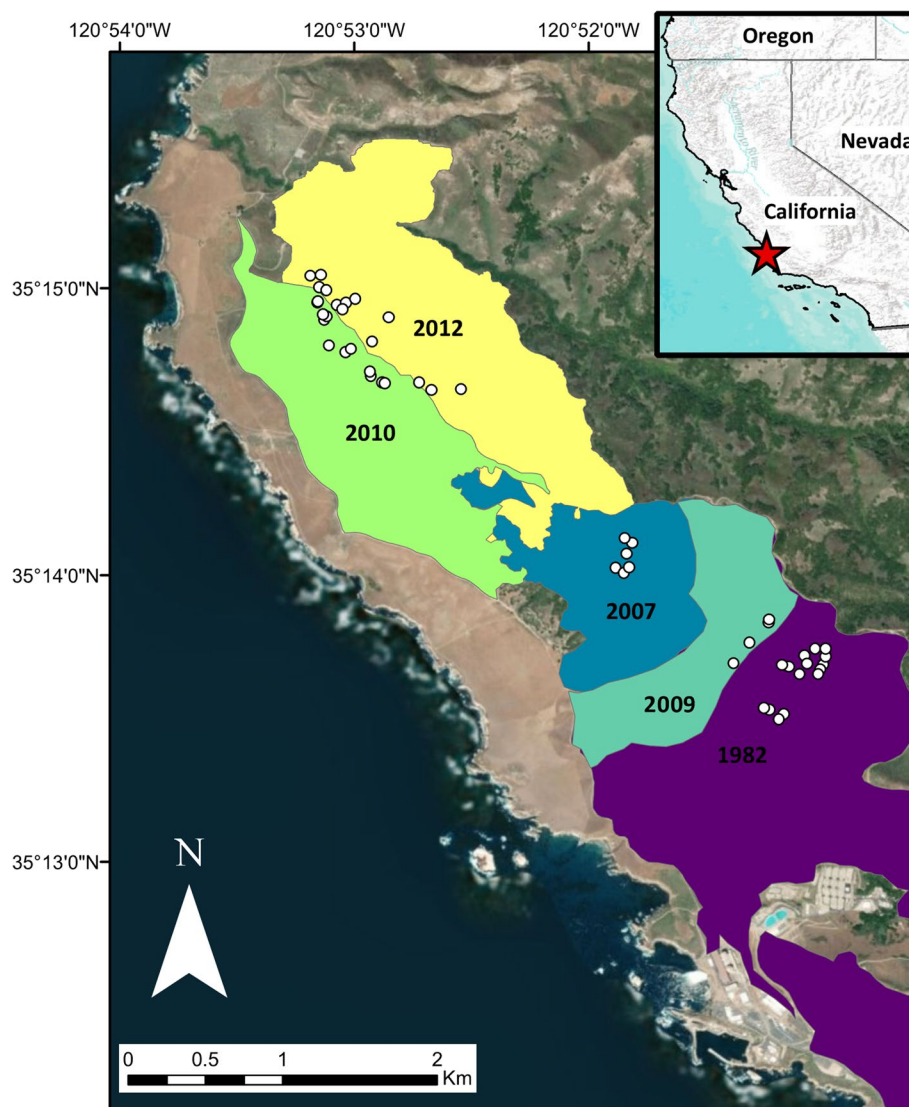Bisbing *et al. Fire Ecology*   (2023) 19:35

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Fig. 2 Permanent plot locations (white circles; *n* = 50) for bishop pine stands sampled on the Diablo Canyon Power Plant property in San Luis Obispo County, California, USA. Colored polygons show the perimeter of the most recent fire: 1982 wildfire (purple), 2007 wildfire (blue), 2009 prescribed fire (cyan), 2010 prescribed fire (green), and 2012 prescribed fire (yellow)

a 100-m minimum distance between plots. The 2007 and 2009 burns had less continuous bishop pine cover and steeper slopes, and, here, plots were selected in the field to represent the range of aspects and stand structure within each fire perimeter. Stratification by landscape position (i.e., aspect) was used because bishop pine abundance is well-documented to vary as a function of topographic factors (Harvey and Holzman 2014). Additionally, because the objective of this study was to assess bishop pine stand development and quantify seed production following fire, plots were only sampled if they contained bishop pine individuals (dead or alive), and plots were moved by up to 50 m if they did not meet

this criterion. The patchy distribution of bishop pine across the study area thus resulted in plot locations that were clustered within fire perimeters, but nearly all plots remained more than 80 m apart, consistent with spacing between uncorrelated plots in a previous study in this forest type (Harvey and Holzman 2014).

Nested, circular, fixed-radius permanent plots were established at each sampling location, and all plots were sampled in 2018. At each plot center, rebar was installed for future remeasurements, and data were collected on slope, aspect, and elevation. Large trees (diameter at breast height [DBH] greater than 20.0 cm) and small trees (12.5–20.0 cm DBH) were sampled for

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Table 1 Fire type, sample size, and stand characteristics for each wild and prescribed fire burned in bishop pine stands on the PG&E Diablo Canyon Power Plant property as of the 2018 sampling year

Fire year	Years since fire[a]	Fire type	No. plots	Tree density (ha^{-1})	Seed density (ha^{-1})	Cones per tree	Seeds per cone[c]	Seeds viable (%)[b]	Pine pitch canker infection (% of trees in plot)
				Median (min-max)					
1982	36	Wildfire	15	402 (30–1547)	$10^{5.7}$ ($10^{4.8}$–$10^{6.1}$)	20 (0–200)	60 (0–112)[c]	95 (86–98)[c]	10 (0–30)
2007	11	Wildfire	6	2653 (707–3537)	$10^{6.4}$ ($10^{5.4}$–$10^{6.8}$)	9 (0–275)	62 (3–141)	97 (64–99)	48 (10–100)
2009	9	High-severity prescribed fire	4	5128 (354–14,501)	$10^{5.8}$ (0–$10^{6.5}$)	0 (0–25)	49 (4–115)	94 (93–97)	100 (50–100)
2010	8	High-severity prescribed fire	12	10,257 (1415–63,308)	$10^{6.6}$ ($10^{5.2}$–$10^{7.2}$)	0 (0–303)	63 (0–146)	98 (77–100)	38 (4–100)
2012	6	High-severity prescribed fire	13	9196 (1840–102,920)	$10^{5.8}$ (0–$10^{6.5}$)	0 (0–41)	48 (0–154)	97 (90–100)	22 (0–81)

[a] Time since fire at the time of sampling in 2018

[b] Seed viability was quantified using pooled seed lots for each sampling plot and does not include plots in which no cones were found (five plots in 2012 fire and one plot in 2009 fire)

[c] In the 1982 fire, seeds per cone and seed viability were quantified from cones collected in three locations outside of permanent plots

species and DBH in a 0.1-ha plot (17.8 m radius), while saplings (> 1.37 m in height, 2.5–12.5 cm DBH) and seedlings (< 2.5 cm DBH) were tallied in a nested subplot. Nested subplot size varied as a function of post-fire density of tree seedlings, with sampling defaulting to 0.02 ha (8 m radius) but reduced to 0.007 ha (5 m radius) or 0.002 ha (3 m radius) when seedling densities exceeded 200 trees in the default subplot size. All trees (live or dead) falling within each respective plot were sampled and individually assessed for snag decay or damage agents and tagged so that individual tree cone production and health could be tracked into the future.

Each sampled live tree was evaluated for the presence of pine pitch canker infection, which results in resinous cankers and may be visible on branches, shoots, or boles (Storer et al. 1995). Although pine pitch canker may be a casual mortality agent in these stands, it is not possible to attribute mortality to infection, as symptomatic evidence is only visible on live trees. Trees considered symptomatic were those with evidence of: tree crown dieback from the leader, branch end dieback, resin-coated boles, and/or stem cankers (Gordon et al. 2001). The most common, and obvious, sign of infection is leader and branch dieback, usually within one or two whorls of the infection point, in which a girdling lesion kills an affected branch tip while causing little or no visible damage elsewhere on the tree (Gordon et al. 2001). These symptoms are consistent with infection in local populations of Monterey pine (*Pinus radiata* D. Don), a close relative of bishop pine and the most

well-documented regional host of the pathogen in which infection has been verified via genetic analyses (Bisbing, unpublished data).

We additionally quantified and sampled female cones to assess bishop pine seed availability. Across all recent fire years (2007, 2009, 2010, and 2012 burns), total cone abundance was documented for each individual tree, and three cones were collected for viability analysis from each of the ten bishop pine individuals closest to plot center (n_{cones} = 30 per plot). For the plots within the 1982 wildfire, for which cone abundance per tree was high, we counted cones on the ten closest bishop pine to plot center, with a maximum cone count of 200 (only three out of 110 sampled trees had 200 or more cones). Cones were collected from three locations on the perimeter of the stand boundaries for the 1982 burn due to stand and landscape conditions that limited safe and accessible cone collection within plot interiors. The location of cones high in the tree canopy required trees to be felled in order to access intact cones, and both steep terrain and dense forest conditions limited tree falling in stand interiors.

Canopy seedbank estimates

In the lab, cones were heated at 70 °C for 24–72 h until open. All seeds were manually removed from the opened cones, and seeds that appeared potentially viable (i.e., not cracked or shriveled) were counted for each collected cone and retained for seed viability testing. A random sample of seeds from each sampling plot, distributed

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proportionally across collected cones, was used to measure potential viability. The size of the seed lots varied based on total seed abundance for each plot, ranging from 120 to a target lot size of 400 seeds. Seed lots were pooled for each plot and sent to the Idaho State Department of Agriculture Seed Lab for tetrazolium staining, resulting in an estimated proportion of viable seeds at the plot level. Seed density was estimated for each plot based on established protocols (Tapias et al. 2001; Goubitz et al. 2004) by multiplying plot-level measurements of live tree density, mean cones per tree, mean seeds per cone, and proportion of viable seeds. Because cones from the 1982 fire were collected in three locations outside of permanent plots, the mean of the three seed viability values was used for calculations of stand-level seed density for all 1982 plots.

Statistical analyses

All statistical analyses were conducted in R (R Core Team 2018). We used AIC_c for model selection (Anderson et al. 2000), comparing among a full model and nested sub-models using the "dredge" function in the R package "MuMIn" (Barton 2015). Candidate predictor variables for each model are described below. For linear models with fixed effects only, we calculated adjusted R^2 for the highest-ranking model using the "rsq" package (Zhang 2018). Mixed effects models were run using R package "lme4" (Bates et al. 2015), and marginal and conditional R^2 values were calculated using the *r.squaredGLMM* function in the "MuMIn" package (Barton 2015).

Canopy seedbank development

To characterize bishop pine seedbank development as a function of time since fire (TSF) and topographic variability, we developed linear models predicting multiple characteristics that determine seed availability: stand-level seed density, seed viability, seeds per cone, cones per tree, and tree density. We modeled seed density at the plot level ($n=50$), using a linear model to predict total seed density ($\log_{10}$-transformed; Gaussian distribution) as a function of the following candidate predictor variables: TSF (factor), topographic wetness index (TWI; see Supplementary Materials S1), and TSF*TWI. We then modeled plot-level seed viability (Gaussian distribution) as a function of TSF (factor), excluding six plots in which no cones were present ($n=32$). Because cones from the 1982 fire were collected from locations outside the permanent plots, we could not link seed viability data to site-specific measurements of TWI, so the seed viability model did not include these predictors.

Seeds per cone were analyzed at the scale of individual cones (Gaussian distribution; $n=443$) and modeled as a function of tree size class with a nested random intercept

terms for maternal tree, plot, and fire year to account for spatial clustering among the collected cones. Similar to the seed viability model, we could not include other site-specific measurements as predictors due to the cone collection strategy in the 1982 fire. We used a generalized linear mixed effects model to predict cones per tree (Poisson distribution; $n=3225$) as a function of the following candidate predictor variables: tree size class, TWI, and bishop pine tree density. Plot nested within fire year was included as a random intercept to account for spatial clustering of observations. The model of tree density is described in Supplementary Materials S2.

Pine pitch canker infection

To characterize pine pitch canker infection as a function of TSF and topographic variability, we used a generalized linear model (binomial distribution) predicting the proportion of trees infected in each plot ($n=50$) as a function of the same candidate predictor variables described above for the model of tree density: TSF (factor), TWI, and TSF*TWI. To characterize the probability of individual tree infection by pitch canker, we used a generalized linear mixed effects model (binomial distribution) predicting the infection status of individual trees (0/1 representing absence or presence of infection signs; $n=3225$) as a function of tree size class, with a random intercept for plot nested within fire year to account for spatial clustering of observations.

Results

Canopy seedbank development in post-fire stands

Tree age structure transitioned from many small trees to fewer large trees with time since fire (Figs. S2 and S3), with median live tree densities ranging from >9000 trees ha^{-1} in the most recent fire to ~400 trees ha^{-1} in the oldest fire (Table 1). Median seed densities were relatively consistent across time since fire at >600,000 seeds ha^{-1} in the 2012 burn and >500,000 seeds ha^{-1} in the 1982 burn (Table 1). Seed viability was also consistently high across stand ages, ranging from 94 to 98% across fire years and tree size classes (Table 1; Fig. 4a). Seeds per cone averaged 47 for seedlings, 61 for saplings, and 55 for large trees (Fig. 4b). Small trees were not sampled in the random cone collection (10 trees closest to plot center) and thus not represented in the cone and seed estimates presented here. Six plots (out of 50) had no observed cones and thus a total seed density of zero. Of these, five plots (out of 13) were in the most recent 6-year-old fire and one plot (out of five) was in the 9-year-old fire.

Seed density was significantly related to time since fire (Fig. 3; $F=4.82$; $P=0.003$; adjusted $R^2=0.24$), and TSF was the only predictor variable retained in the highest-ranking model (Table S3). Only plots from the most
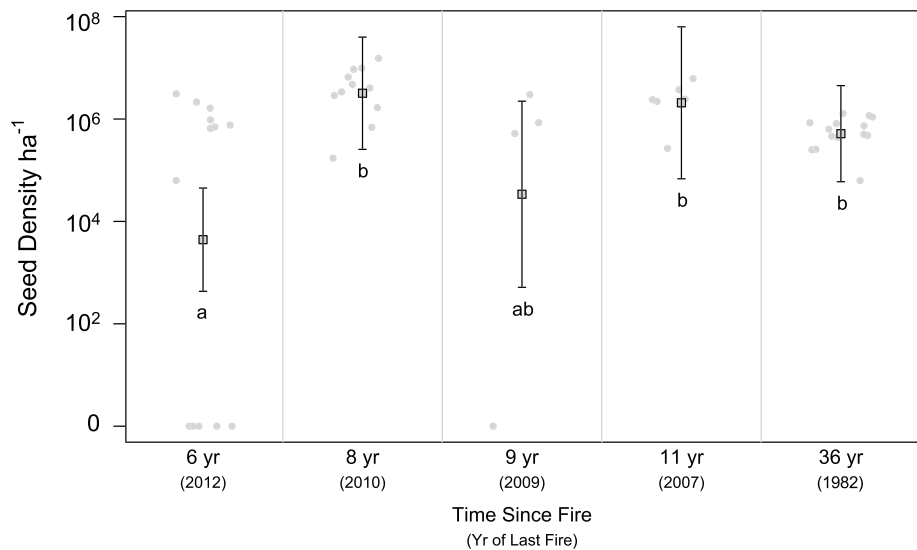
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Fig. 3 Model estimates of plot-level seed density as a function of time since fire (TSF) (coefficient estimate ± 95% confidence interval). Gray dots show the data points (*n* = 50). Plot-level seed density was calculated as the product of mean seed viability, mean seeds per cone, mean cones per tree, and tree density
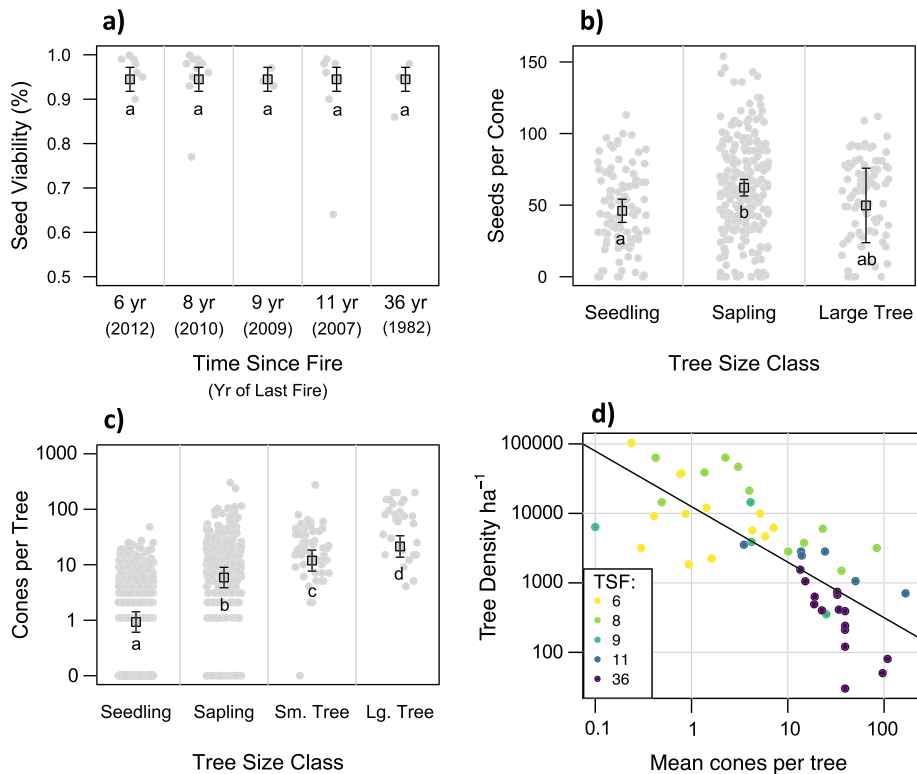

Fig. 4 Effects of time since fire (TSF) and tree size classes on seed viability, seed production, and cone production. **a** Model estimates of seed viability (*n* = 32) from the highest-ranking intercept-only model, shown in relation to TSF. **b** Model estimates of seed count per cone as a function of tree size class (*n* = 443). The 'small-tree' size class was not represented by the collected cones, which were sampled from the ten closest trees to plot center. **c** Model estimates of cone count per tree as a function of tree size class (*n* = 3225). **a–c** Boxes and arrows show the coefficient estimate ± 95% confidence interval, and gray symbols show the data points. **d** The relationship between tree density and plot-mean cones per tree. Colors indicate TSF, with yellow representing the most recently burned plots and dark purple representing the oldest post-fire plots. The black line shows the estimated linear relationship between plot-level tree density and cones per tree (values $\log_{10}$-transformed)

recent fire year (6-year TSF) had seed densities that were significantly different (based on non-overlapping 95% confidence intervals), with lower seed density than all older stands except for the 9-year TSF burn plots. The highest-ranking model of seed viability included only an intercept term (Table S3), and viability was very high for all fire years, including after only 6 years post-fire (median viability = 97%; Table 1; Fig. 4a). The best model of seeds per cone included tree size class as a predictor variable (Table S3), and cones from seedlings had significantly fewer seeds than cones from saplings (Table 2; Fig. 4b). However, the fixed effect of tree size only contributed a marginal R^2 of 0.05, while the addition of the random effects from maternal tree, sampling plot, and fire year resulted in a conditional R^2 of 0.50. The fact that neither seed viability nor seeds per cone were related to time since fire or tree size beyond the seedling size class (Table 2; Fig. 4a–b) suggests that trees produce cones of a consistent size and quality very quickly during stand development and then maintain a viable cone bank for at least three decades.

At the individual tree scale, cone abundance was related to tree size and tree density (Table 2; $P < 0.001$; marginal $R^2 = 0.27$). Cone counts increased with tree size, and large trees generally had more than ten times as many cones as smaller trees (average of 76 cones

Table 2 Model estimates (β) and 95% confidence intervals (CI) from the analysis of cone-level seed production and tree-level cone production. Nested random effects for tree, plot, and fire year were included for the "seeds per cone" model, and nested random effects for plot and fire year were included for the "cones per tree" model. Marginal R^2 represents the marginal contribution of fixed effects only, whereas the conditional R^2 is the contribution of both fixed and random effects. Continuous fixed effects bolded where 95% CI did not overlap 0. Topographic wetness index (TWI) was not retained in the best model for either analysis

Predictor	Seeds per cone (cone-level; Gaussian)		Cones per tree (tree-level; Poisson)	
	β	95% CI	β[a]	95% CI
Seedling size class[b]	46.04	37.95–54.13	0.93	0.61–1.42
Sapling size class[b]	62.18	56.40–67.96	5.88	3.85–8.99
Small tree size class[b]	n/a	n/a	11.89	7.68–18.42
Large tree size class[b]	49.79	23.79–75.79	21.34	13.69–33.25
Tree density ($\log_{10}$; ha^{-1})[c]	n/a	n/a	**0.66**	**0.54–0.83**
TWI	–	–	–	–
Marginal R^2	0.05		0.27	
Conditional R^2	0.50		0.99	

[a] Exponentiated coefficient estimates (odds ratios)

[b] Absolute estimates shown for each size class

[c] Continuous tree density variable has been standardized, and regression coefficient gives the effect of a change of 1 standard deviation

per large tree compared to 31 cones for small trees, 17 cones for saplings, and 1 cone for seedlings; Fig. 4c). Cone production was negatively related to plot-level tree density (Table 2; β [odds ratio] = 0.66; $P < 0.001$) after accounting for the effects of tree size. The nested random effect of sampling plots and fire year explained much additional variation in cone production, and the conditional R^2 was 0.99.

Increasing cone production with tree size corresponded to an increase in plot-mean cone production with time since fire (Fig. 4d), because large trees that tended to have more cones represented a greater proportion of the stand in older fires (Fig. S2). The fact that plot-level total seed density remained relatively consistent with time since fire (Fig. 3), despite these tree-level increases in cone production through time, reflects the strong relationship between plot-level tree density and cones per tree (values $\log_{10}$-transformed; $R^2 = 0.56$). With increasing time since fire, the bishop pine stands studied here quickly developed and then maintained an abundant seedbank while transitioning from extremely high tree density with few cones per tree towards lower tree density with many cones per tree (Fig. 4d).

Pine pitch canker infection rate as a function of time since fire and tree size class

Plot-level infection by pine pitch canker varied with time since fire, and the highest plot-level infection rates were observed in intermediate-aged stands (Fig. 5a). The highest-ranking model of plot-level pitch canker infection rate (proportion of plot infected; Table S4) included only TSF as a predictor variable ($\chi^2 = 9.72$; $P = 0.045$; adjusted $R^2 = 0.33$). There was, however, broad overlap among model predictions, and the only significant pairwise difference was a lower infection rate in the 36-year-old stands (average 11% of trees infected) compared to 9-year-old stands (average 87% of trees infected). At the scale of individual trees, infection probability was highest for trees in the sapling size class (Table 3; Fig. 5b), although there were no significant pairwise comparisons among size classes. Given that trees in the sapling size class represented the greatest proportion of the stand in intermediate-aged stands (Fig. S2), the plot-level and individual-level results are consistent in showing that pine pitch canker infection is greatest for stands that are differentiating in structure, with smaller, less-competitive trees succumbing to pitch pine canker while larger trees recruit into upper canopy positions. Yet, there was high variability in infection probability among and within plots, shown by wide confidence intervals in model estimates and low proportion of variance explained by tree size class in the individual-tree model (marginal $R^2 = 0.01$). The relatively large contribution of the random
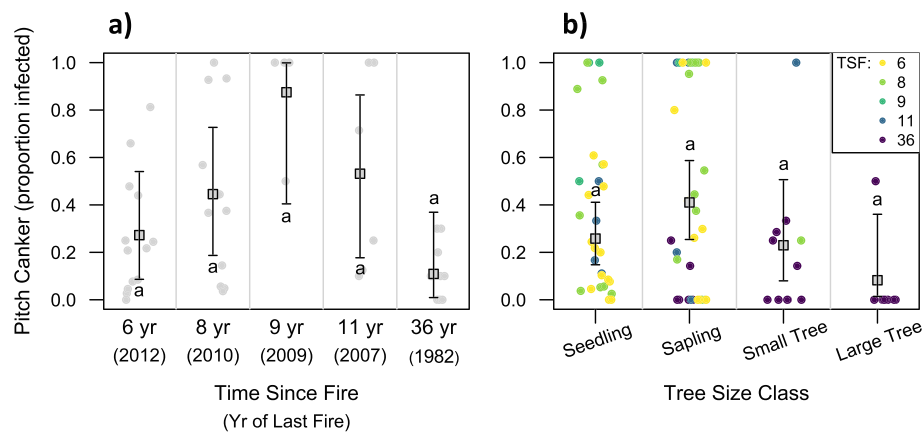
Fig. 5 Effects of time since fire and tree size class on pine pitch canker infection. **a** Model estimates of the proportion of trees infected per plot (*N* = 50) as a function of TSF (factor). Gray dots show the data points. **b** Model estimates of individual-tree probability of infection by pine pitch canker (Binomial presence/absence; *n* = 3225) as a function of tree size class. Colored dots show the proportion of trees in each size class infected by pine pitch canker in each plot (for visualizing tree size effects; *n* = 86), and the colors indicate time since fire. Large trees defined as >20.0cm DBH; small trees those between 12.5 and 20.0cm; saplings >1.37m in height and between 2.5-12.5cm DBH; and seedlings <1.37m in height and 2.5cm DBH. Boxes and arrows show the coefficient estimate ± 95% confidence interval

Table 3 Model estimates (β) and 95% confidence intervals (CI) from the analysis of tree-level infection by pine pitch canker. Plot nested within fire year was included as a random intercept. Marginal R^2 represents the marginal contribution of fixed effects only, whereas the conditional R^2 is the contribution of both fixed and random effects

	Pitch canker infection (tree-level; binomial)	
Predictor	β[a]	95% CI
Seedling size class[b]	0.26	0.15–0.41
Sapling size class[b]	0.41	0.25–0.59
Small tree size class[b]	0.23	0.08–0.51
Large tree size class[b]	0.08	0.01–0.36
Marginal R^2	0.01	
Conditional R^2	0.50	

[a] Back-transformed coefficient estimates

[b] Absolute estimates shown for each size class

intercept term in the individual-tree model (conditional R^2 = 0.50) indicates an important role of plot characteristics that were not represented by the predictor variables included in our models.

Discussion

In fire-adapted ecosystems where fire activity has been reduced or eliminated, pyrosilviculture can be used to purposefully return fire to the landscape to restore altered fire regimes while simultaneously lowering wildfire risk. Knowing the temporal window of fire return that matches canopy seedbank development and viability is, however, critical to matching prescriptions to species' adaptations, particularly in crown fire-adapted ecosystems dominated by fire-obligate seeders. Here, we leveraged a chronosequence of wild- and prescribed high-severity, crown fires in serotinous bishop pine to inform pyrosilvicultural techniques for reducing wildfire risk in this WUI-adjacent forest type while concurrently promoting bishop pine persistence. This study provides the first quantitative assessment of post-fire canopy seedbank development and viability for a crown-fire adapted tree species, and, here, we outline strategies for incorporating these findings into pyrosilvicultural prescriptions for managing crown-fire adapted forests. Of critical importance to pyrosilvicultural prescriptions, we discovered that bishop pine is capable of producing an abundant, viable canopy seedbank within 8 years of high-severity crown fire, with variable cone production yet consistently high seed densities over the 30-year fire window studied here. Although an abundant, viable seedbank is present within 6 years, some areas burned in the 2012 prescribed fire lack cones (5 of 13) and may thus not be resilient to fire return, indicating that 8 years is the conservative minimum acceptable fire return for bishop pine. We also learned that pine pitch canker infection is most severe during the sapling stage (8–10 years post-fire), likely altering stand development trajectories as well as potentially limiting recruitment, and thus the aerial seedbank, into the canopy. Our findings suggest that pyrosilviculture may be a viable management tool for regenerating this serotinous conifer across a broad fire return window — as short as 8 years to as long as several decades — while concurrently mitigating pine pitch canker infection and reducing wildfire risk in coastal California's growing WUI.

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Mapping adaptations to application

This science fills a critical knowledge gap on the appropriate window of prescribed fire application for a crown fire-adapted, serotinous conifer by quantifying canopy seedbank development and the temporal window of seed viability. In serotinous species, resilience is closely tied to the aerial seedbank, and, when fire matches the regime to which species are adapted, enhances fitness and promotes persistence by releasing seed onto an optimal postfire seedbed (Causley et al. 2016). Development of a sufficient aerial seedbank must occur prior to the recurrence of fire (Enright et al. 1996; Tapias et al. 2001), and this resilience mechanism may fail if fire return is too short (i.e., immaturity risk) or too long (i.e., senescence risk) (Zedler 1995; Keeley et al. 1999). The Central Coast bishop pine stands assessed here regenerated to extremely high densities (median ~ 9000 trees ha^{-1}) and became both reproductively mature and highly viable within 8 years (median > 3,900,000 seeds ha^{-1} and 98% viability), a strategy suggesting low immaturity risk and in line with the onset of reproductive maturity elsewhere in the species' natural and planted ranges (Fielding 1962; Agne et al. 2022) and in other serotinous species (Enright et al. 1996; Tapias et al. 2001; Turner et al. 2007; Climent et al. 2008). Viability, in particular, was exceptionally high in even the earliest age class (median of 97% at 6 years), providing the first verification of the assumption that cone production is equivalent to viable seed production. Notably, bishop pine's amassing of a substantial canopy seedbank in early successional phases is attributable to high densities of young trees that individually produce few, high viability seeds but collectively produce many. Low density stands under climatic stress may still be vulnerable to immaturity risk for up to 20 years (Keeley et al. 1999; Agne et al. 2022), and we found that more than one third of 6-year-old stands had not produced cones. Nonetheless, the large, viable seedbank and high post-fire stand densities documented here suggest bishop pine's window for immaturity risk is brief and buffers stands against risks associated with early or more frequent fire.

Beyond this narrow window for immaturity risk, bishop pine maintains its large, viable aerial seedbank across a range of stand ages. Stand-level seed availability remains consistently high as stands shift from high densities with low individual reproductive output to low densities with high individual reproductive output, a pattern common in serotinous pines (Tapias et al. 2001; Agne et al. 2022). Long fire-free periods that approach a species' lifespan are generally expected to diminish seed availability due to tree mortality or seed loss to decay, predation, and disease (Lamont et al. 1991), however the oldest stands studied here (36 years) maintain high seed densities (median > 500,000

seeds ha^{-1}) and viability (median 95%) in spite of time-related reductions in tree densities and cones. Bishop pine forest persistence can thus likely be promoted across a fire return window spanning many decades, and, despite limited insight into historical fire return, this finding is consistent with the acceptable range of fire return for bishop pine's most common neighboring ecosystem, coastal chaparral. Co-occurring chaparral is resilient to high-severity crown fire return as frequent as every 10 years to as long as every 100 (Hanes 1971; Keeley 1986, 1987). Generally, ~ 20 to 40 years is the best estimate of fire return (Byrne et al. 1977; Mensing et al. 1999), though chaparral communities tracked over 90 + years of varying fire frequency (once, twice, or thrice burned) remain compositionally equivalent to unburned communities (Franklin et al. 2004). Chaparral resilience is most inhibited under short fire return intervals (< 5 years) wherein fire occurs prior to seedbank development for obligate seeders (Zedler et al. 1983; (Keeley 2002b), an outcome also likely for bishop pine burned at a shortened return interval (< 6 years). Our findings in post-fire bishop pine add to the body of evidence suggesting that variable burning regimes occurring after establishment of a viable canopy seedbank but across a wide range of fire return intervals are likely the best strategy for maintaining the diverse mosaic of fire-adapted plant communities and age structures common to this intermixed pine-chaparral landscape (Keeley 1987; Odion and Davis 2000; Keeley et al. 2005).

Of note, though, is that the bishop pine stands burned and assessed here were all of similar age (~ 75 years) and stand structure (even-aged), thus limiting our scope of inference across stand developmental and structural phases. Experimentally burning across the temporal profile of stand developmental stages (i.e., burning across ranges of stand ages and surface fuel loads) is an important area of further study given the anticipated shifts in fuel profiles from live to dead and canopy to surface over time (He et al. 2004; Scott 2005). Live fuels sustain and spread fire differently than dead fuels due to varying moisture content and chemistry (Finney et al. 2012), while shifts in the abundance of canopy versus surface fuels have the potential to significantly alter fire intensity and severity (O'Brien et al. 2016; Kiefer et al. 2018; Banerjee et al. 2020; Skowronski et al. 2020). In addition, experimentally burning at varying intensities, potentially during different seasons, could reveal if it is feasible to burn under intensities that release seeds from cones but do not kill canopy trees and instead result in two-cohort stands (Enright and Lamont 1989; Knox and Clarke 2006; Clarke et al. 2010). Burning at lower intensities may be more palatable to managers igniting prescribed fires

in WUI or WUI-adjacent ecosystems and, accordingly, increase the use of this silvicultural tool. As with all fire-adapted species, understanding bishop pines' particular "ecology of fuels" will also be critical to developing pyrosilvicultural prescriptions (Mitchell et al. 2009) and may be more so with the prevalence of a novel disturbance agent altering the timing and development of fuel profiles.

Compounding effects of a non-native pathogen

The consequences of non-native pine pitch canker infection on bishop pine persistence remain unknown, but this novel, compounding disturbance agent is likely to alter post-fire stand trajectories and, ultimately, canopy seedbank development. In the bishop pine stands studied here, density-dependent self-thinning was, as expected, underway in the intermediate-aged stands in the years following post-fire establishment (Harvey et al. 2011), however the high concurrent incidence of pine pitch canker infected trees in these stands (90% median infected at 9 years) suggests that pine pitch canker has the potential to drive additional mortality and impact stand development. Selective pine pitch canker infection in saplings could, for instance, shift the live:dead and canopy:surface fuel ratios to earlier successional stages and increase the probability of higher fire intensity, as documented in other coastal California forests impacted by a non-native pathogen (Metz et al. 2013). Infected saplings may also be less likely to survive and recruit to larger size classes than uninfected saplings, thus altering stand development processes by reducing the number of individuals recruiting into the canopy, a bottleneck common in pine pitch canker-infected Monterey pine stands (Aegerter and Gordon 2006). This bottleneck could challenge bishop pine persistence potential as well as the timing of prescribed fire ignition if this differential mortality hinders development and persistence of the abundant, high viability seedbank documented here.

It is worth noting, however, that little is known about pine pitch canker disease dynamics in bishop pine, and our study design did not allow us to directly link infection with observed mortality, making it hard to predict long-term stand trajectories following infection. Pine pitch canker was discovered in the region in the mid-1980s (McCain et al. 1987) and has only become widespread in bishop pine over the last two decades (Schmale and Gordon 2003). The condition of the oldest stands assessed here (burned in 1982) may therefore not represent the fate of forests in the context of this disease agent. High levels of unexplained variability in infection rates within and among stand age classes highlights the role of stochastic processes, unaccounted-for environmental differences, and individual variation in susceptibility to

infection (Schmale and Gordon 2003). Additionally, our understanding of the effect of pine pitch canker infection on stand processes is limited by the space-for-time approach of this study. Specifically, we were unable to test the interacting effect of pine pitch canker infection and time since fire on plot-level variables, because stand development processes have coincided with a general increase in the presence of the disease on the landscape (Gordon et al. 2020).

Prescribed fire may nonetheless remain a viable management option for mitigating pine pitch canker infection, as, in other coastal forests infected by a non-native pathogen, burned forests have a lower incidence of infection that is attributed to the dampening of pathogen transmission (Simler-Williamson et al. 2021). Pyrosilviculture in pine pitch canker infected bishop pine may provide the same disease mitigation, and the rapid development and persistence of a viable canopy seedbank allows for flexibility in a fire return interval that will simultaneously promote bishop pine persistence. Trees tagged as part of this permanent plot network will provide valuable insight into long-term disease dynamics across bishop pine age classes and time since fire. Further experimentation with varying pyrosilvicultural techniques as well as prescribed burning at different stand ages, fuel structures, and seasons will be needed to refine our understanding of how to prescribe fires in bishop pine stands in order to mitigate both pine pitch canker infection and wildfire hazard without risking regeneration failures.

The case for pyrosilviculture

Irrespective of the regime, fire return to coastal California's fire-adapted pine-chaparral landscape is inevitable (Hanes 1971; Safford et al. 2018). Thus, the task at hand becomes one of mitigating risk while maintaining natural ecosystem functioning and integrity, and pyrosilvitulture is our best shot at meeting these seemingly competing objectives. Regular use of high-severity prescribed fire in densely populated areas, such as the bishop pine WUI studied here, will likely require restructuring of both risk analysis and wildfire mitigation programs (Calkin et al. 2014) as well as pairing of prescribed fire with alternate pyrosilvicultural methods to limit risk (Hanes 1971; Potts et al. 2010; Safford et al. 2018). Mastication, for instance, has been identified as a functional surrogate for fire that maintains species richness while providing an alternative in areas where prescribed fire may be risky (Potts et al. 2010). Strategically placed prescribed fire or fuel treatments could also be managed on a rotation (i.e., pyrosilviculture mimicking uneven-aged silviculture) to return fire to some portions of the landscape while protecting adjacent lands (WUI or wild) from a large, severe fire and

concurrently maintaining a mosaic of native plant communities and age classes (Safford et al. 2018; North et al. 2021).

Waiting on the inevitable wildfire is one alternative to pyrosilviculture, and one which adequately regenerates bishop pine and co-occurring chaparral at even the oldest stand ages (Odion and Davis 2000; Franklin et al. 2004; Forrestel et al. 2011; Harvey et al. 2011). This strategy may, however, be incongruent with the objectives of mitigating wildfire risk in the WUI, as increasing the time between fires increases the risk of accumulating combustible, high heat yield fuels and thus greater wildfire hazard (Odion and Davis 2000). Extensive fuel breaks cut along roads, on ridges, and around housing developments could buffer risk for when wildfire occurs, but these treatments have a high environmental cost (e.g., increased non-native species, erosion, and runoff; Safford et al. 2018), and, because these alternate treatments do not include fire, they are not, by definition, pyrosilviculture but rather a means for mitigating human risk. Without the fire component of these treatments, fire-obligate seeders, such as bishop pine and many co-occurring chaparral species, may senesce or decline.

Prescribed fire is the most effective means of restoring the natural ecosystem dynamics that have evolved with fire while concurrently reducing wildfire risk (Fernandes and Botelho 2003; Kolden 2019), and prescribed fire escapement is rare (~1–2%, Dether and Black 2006, Miller et al. 2020). There will always be more to learn as ecosystems, knowledge, and management evolve, but the fire deficit will inevitably self-correct on its own and is likely to do so under severities and extents undesirable for both natural and human systems. There are inherent risks and barriers to prescribed fire implementation (Quinn-Davidson and Varner 2012; Miller et al. 2020), particularly in WUI-rich California, however we argue, along with many other forest and fire ecologists (e.g., Kolden 2019, McWethy et al. 2019, Stephens et al. 2020, Hessburg et al. 2021, North et al. 2021, Prichard et al. 2021), for a proactive return of fire to the West's fire-adapted landscapes.

Conclusions

Long-term sustainability of crown fire-adapted forests will depend upon restoring the high-severity fire regime to which these ecosystems are adapted. Here, we quantified the temporal pattern of canopy seedbank development, as well as the impacts of a non-native pathogen, to identify viable options for developing pyrosilviculture as a component of management in fire-obligate, crown-fire adapted forest types, such as

serotinous bishop pine. This is the first study to move beyond cone counts as a surrogate for viability assessments and additionally quantify both seed viability and density over a range of stand ages to enumerate a more accurate assessment of reproductive capacity and the temporal window of fire return promoting crown fire-adapted forest persistence. We learned that bishop pine produces an abundant, viable canopy seedbank within 8 years of fire that persists across age classes from seedlings to mature trees and for at least a few decades following fire. We also learned that non-native pine pitch canker infection has differential effects on stand dynamics and that intermediate-aged stands dominated by saplings have the highest incidence of infection. Although the long-term effects of pine pitch canker infection remain unknown, bishop pines' viable and persistent seedbank suggests that managers can ignite prescribed fire across a broad return interval — as short as 8 years and as long as several decades. These findings may be generally applicable to equally-fecund serotinous species in which burning across a broad fire return interval is feasible given early development of a robust, viable seedbank and addressing two common management challenges in fire-adapted forests — restoring fire to promote persistence while mitigating wildfire risk to the WUI.

Author' contributions

SMB conceived of the idea and designed the study, organized and oversaw data collection, and led manuscript writing. AKU analyzed data with assistance from LEK. All authors contributed to manuscript writing and editing and approved of the final manuscript.

Availability of data and materials

Data will be made available upon publication.

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Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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