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Seed maturation and mortality patterns support non-serotinous conifer regeneration mechanism following high-severity fire

Madeleine A. Lopez^{1,2}, Jeffrey M. Kane^{1*}  and David F. Greene¹

Abstract

Background Climate warming increases fire activity for many regions around the world, prompting concern over the long-term persistence of conifer species that regenerate poorly from seed after high-severity fire. However, substantive regeneration of non-serotinous conifer species within a large high-severity patch, a process we refer to as conditional pyriscence, is possible if the fire occurs in the window following seed maturation but before cone opening, the enclosed seeds can withstand the heat range of the fire, and the non-serotinous cone crop is sufficient. To define this temporal window, we collected closed cones from June to September over two seasons, examining seed maturation as a function of the heat sum for four non-serotinous California conifer species: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). Additionally, we examined seed survival based on viability testing in closed cones following heat treatments ranging from ~ 20 to 600 °C. Finally, we overlayed the period of viability with the timing of fires for northern California to identify the proportion of fires that may be conducive to conditional pyriscence.

Results The accumulated heat sum was positively associated with seed maturity; the proportion of seeds that were viable varied by species but generally ranged from late-July (10%) to mid-September (90%) with heat sums ranging from 1285 to 2081 °C, respectively. Higher cone heat exposure was negatively associated with seed survival and some withstood temperatures as high as 400 °C for 150 s. Seeds of the smaller cone species tended to have lower survivability to heat treatments than the larger cone species. The period of availability of mature seeds overlapped with 60% of the area burned during wildfires for northern California.

Conclusions We identify circumstances suitable for conditional pyriscence following high-severity fires for four non-serotinous conifers in northern California. The temporal window that permits conditional pyriscence for these species may provide one explanation as to why some large high severity patches can result in substantive seedling regeneration. Inclusion of this information has potential to improve post-fire regeneration modeling and can aid forest management decision-making in fire-prone ecosystems containing non-serotinous conifers.

Keywords Conifer regeneration, Douglas-fir, Fire ecology, Incense cedar, Plant ecology, Ponderosa pine, Reproductive ecology, Seed viability, Sierra lodgepole pine

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Resumen

Antecedentes El Calentamiento Climático incrementa la actividad de los incendios en muchas regiones alrededor del mundo, instigando la preocupación sobre la persistencia a largo plazo de especies de coníferas que regeneran pobremente de semillas luego de incendios de alta severidad. Sin embargo, la regeneración sustancial de especies no serótinas dentro de grandes parches quemados a alta severidad, un proceso al que llamamos como una pirescencia condicional, es posible si el incendio ocurre en la ventana seguida a la maduración de la semilla pero antes de la apertura de los conos, en la cual las semillas encapsuladas pueden soportar el rango de temperaturas de ese fuego por lo que la cosecha de esos conos no seróticos sería suficiente. Para definir esta ventana temporal, colectamos conos desde junio a septiembre en dos estaciones, examinando la maduración de las semillas como una función de la suma del calor para cuatro especies no serótinas de California: pino ponderosa (*Pinus ponderosa*), pino contorta var. murrayana (*Pinus contorta* var. *murrayana*), cedro de incienso (*Calocedrus decurrens*), y pino oregón (*Pseudotsuga menziesii*). Adicionalmente, examinamos la supervivencia de semillas basados en la prueba de viabilidad en conos cerrados siguiendo tratamientos que variaron entre ~20 a 600 °C. Finalmente, superpusimos el período de viabilidad con el período de los incendios para el norte de California para identificar la proporción de los incendios que pueden ser conducentes a la pirescencia condicional.

Resultados La suma del calor acumulado fue positivamente asociada con la maduración de las semillas; la proporción de semillas que fueron viables difirieron por especies, pero generalmente variaron desde fines de Julio (10%) a mediados de septiembre (90%) con la suma del calor variando entre 1285 °C a 2081 °C, respectivamente. Una exposición de los conos a calores más elevados fue asociada negativamente con la supervivencia de semillas aunque algunos conos soportaron temperaturas de hasta 400 °C por 150 segundos. Las semillas de especies con conos más pequeños tendieron a tener menor supervivencia a los tratamientos de calor que las especies con conos más grandes. El período de disponibilidad de semillas maduras se superpuso con el 60% del área quemada durante los incendios en el norte de California.

Conclusiones Identificamos circunstancias posibles para la pirescencia condicional luego de fuegos de alta severidad para las cuatro especies no serótinas del norte de California. La ventana temporal que permite la pirescencia condicional para estas especies puede proveer de una explicación sobre cómo algunos grandes parches quemados a alta severidad pueden resultar en una regeneración sustantiva de plántulas. La inclusión de esta información tiene potencial para mejorar el modelado de la regeneración post fuego y puede ayudar en los procesos de decisión para ecosistemas propensos al fuego y que contengan coníferas no serótinas.

Background

Climate warming is contributing to current and projected increases in fire frequency, size, and severity for many regions globally (Moritz et al. 2012; Dennison et al. 2014; Senande-Rivera et al. 2022). Changing fire regimes have prompted concern over the persistence of many non-serotinous and non-resprouting woody plant species, especially for conifers that are less capable of adequately regenerating from seed within high severity fire patches. Many recent surveys of post-fire regeneration in areas dominated by non-serotinous conifers have shown that large high severity patches often have poor regeneration (e.g., Shive et al. 2018; Stevens-Rumann and Morgan 2019). Continued increases in the size and extent of high severity fire are therefore expected to substantially reduce the abundance of obligate seeder, non-serotinous woody plants with increased potential for transition to non-forested ecosystems (i.e., type conversion) over the coming decades (Enright et al. 2014, 2015). Increasing evidence in coniferous forests of the western United States suggests that such ecosystem transition

events may be underway (e.g., Tepley et al. 2017; Davis et al. 2018, 2019), and that these instances may accelerate as fire activity and warming continues to increase (Davis et al. 2023). While most studies demonstrate insufficient regeneration densities within large high severity wildfire patches, there are reported instances with considerable regeneration of non-serotinous conifer seedlings (100 to 4000 seedlings/ha) that may be capable of reestablishing forest stands to desired densities (e.g., Larson and Franklin 2005, Roccoforte et al. 2012, Crotteau et al. 2013, Pounden et al. 2014, Outz et al. 2015). However, the circumstances that contribute to these lower frequency incidences of higher regeneration following high severity wildfire are not well understood.

Successful regeneration of non-serotinous conifers via seed following high-severity fires typically requires that there are large seed crops available within or near high-severity patches before seedbed quality deteriorates due to forest floor accumulation and competition for light increases due to post-fire vegetation recovery (Collins and Roller 2013; Hansen et al. 2018). The proximity to

living trees has been consistently identified as the most important factor determining the subsequent patch-wide density of non-serotinous conifer recruits (Agee 1993; Greene and Johnson 1996; Welch et al. 2016; Stevens-Rumann and Morgan 2019). The decline of seed or recruit density with distance from a living forest edge is essentially a negative exponential function over the first 200 m and flattens strongly at greater distances; the number of seeds at 200 m from the living edge will only be about 5–10% of the seed density nearest the edge (Greene and Johnson 1996).

Serotiny is a fire-adaptive strategy that maintains a large supply of viable seeds within the crown (aerial seed-bank) by retaining closed cones for more than 1 year after seed maturation. Following fire, cones open and seeds are deposited onto mineral soil (i.e., pyriscence; Lamont 1991), an optimal seedbed exposed by litter and duff consumption (Lamont et al. 1991; Johnson and Gutsell 1993; Marlin et al. 2024). Serotinous species can act as a seed source despite fire-caused tree mortality, resulting in high density recruitment even deep within a large high severity patch (Greene and Johnson 1999; de Groot et al. 2004; Turner et al. 2007; Maia et al. 2012; Fernández-García et al. 2019). However, serotiny is known to vary widely within and across species (Lamont 2021), thus, characterizing this trait as a simple dichotomy can be conceptually limiting and incidences of high-density recruitment following high severity fire may not be exclusive to serotinous species.

Non-serotinous species are also capable of having viable seeds within closed cones that survive fire and can function similarly to serotinous species without requiring long-term (i.e., > 1 year) on-plant seed storage. As with serotinous species, survival of mature seeds within non-serotinous cones following fire can relax the seed dispersal constraint and result in post-fire seedling regeneration that occurs far from a surviving conspecific mature tree. A modeling study demonstrated that a sufficient portion of viable non-serotinous seeds should survive a high-severity fire (Michaletz et al. 2013). Protection from fire is largely due to seed depth in the ovulate cone, which is known to proportionately increase with cone size, independent of being considered serotinous or non-serotinous (Greene et al. 2024). Thus, species that produce larger cones should experience lower rates of seed mortality due to fire. Non-serotinous species may also be exposed to lower temperatures than the average serotinous cone given that new cones tend to reside in the upper, cooler portion of the crown (Greene and Johnson 1994; Michaletz and Johnson 2007). Serotinous cones are often more evenly distributed throughout the crown and thus experience higher average temperatures during the passage of the flaming front. Unlike serotinous species

with their reliable supply of stored seeds, post-fire success of a non-serotinous species would depend greatly on the size of the cone crop that year. Therefore, the density of non-serotinous recruitment from burned trees will depend mainly on the size of the cone crop at the time a fire occurs, with mast years having far greater potential for high density regeneration following fire.

This alternative post-fire regeneration mechanism is also supported by field observations. As an empirical example of the mechanism, dense regeneration of the non-serotinous Douglas-fir (>4000 seedlings/ha) was observed in high-severity burn sites located several hundred meters away from the nearest living conspecific source when a mast crop coincided with fire (Larson and Franklin 2005). Given that non-serotinous species are normally limited to full restocking within approximately 100 m or less of the living seed source at the burn edge (Greene and Johnson 1996), it is improbable that seed dispersal by wind could be responsible for high density recruitment at such great distances away from the burn edges. Additionally, following mast events for the non-serotinous Engelmann spruce (*Picea engelmannii*), abundant regeneration far from living trees was likewise observed at two separate burn sites in the Rocky Mountains (Pounden et al. 2014). Similar findings of high-density post-fire regeneration far from a living edge have also been observed where young serotinous trees have not yet developed persistent closed cones (the first few years after the onset of sexual maturity) or within non-serotinous varieties of *Pinus*. For example, the serotinous Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) amply regenerated following a fire that burned in a stand of 16-year-old trees with almost entirely non-serotinous cones (Turner et al. 2019). Likewise, abundant regeneration within high severity patches was reported for the non-serotinous Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) following a reburn event (1984 and 2012) in northeastern California (Harris et al. 2020).

The abundance of post-fire regeneration via this mechanism is partially dependent on the timing of seed maturation and fire. Previous studies have established that the timing of seed maturation is a function of the accumulated heat sum > 5 °C (i.e., degree days), such that greater heat sum values promote more metabolic activity for seed development and maturation (Henttonen et al. 1986; Zasada et al. 1992; Sirois et al. 1999; Fedorkov 2001; Meunier et al. 2007; Michaletz et al. 2013). However, most prior studies have been conducted within higher latitude species, and the relationship between accumulated heat sum and plant phenological development is known to vary with latitude (e.g., Beuker 1994; Gao et al. 2023). Following seed maturation, the ovulate cone scale tissue dries and reflexes until the seeds are abscised (Song et al.

2015). Conifer seeds are primarily dispersed by wind in the autumn, with far fewer seeds abscising in the winter or spring (Oliver and Larson 1996; Tanaka et al. 1997). Scale flexing and seed abscission in many North American conifers begins in September (Schopmeyer 1974). Thus, as seed maturation progresses during the growing season, the potential for post-fire regeneration should increase until cone opening or seed release. Therefore, if there is sufficient overlap between the timing of fire and the presence of viable seeds within closed-cones, regeneration of non-serotinous species should be possible.

The likelihood of successful regeneration in non-serotinous species is also contingent on the ability of cones to sufficiently protect mature seeds from the high temperatures of a passing fire. During a fire, closed ovulate cones within the canopy are exposed to the prolonged heat from the flaming front. The temperatures associated with the flaming front will vary depending on fire type (surface or crown), intensity, and position within the crown. Field-based studies have reported temperatures in the canopy up to 1300 °C during crown fires and up to 750 °C during surface fires (Hobbs and Gimingham 1984; Butler et al. 2004). While lab-based studies indicate that serotinous and non-serotinous cones can maintain viable seeds with air or cone temperatures up to 500 °C for at least 1 min, species vary in their heat exposure tolerance (Habrouk et al. 1999; Reyes and Casal 2002; Milich et al. 2012). The high temperatures associated with fire rapidly dehydrate the cone, thus speeding up the cone opening schedule and promoting seed release through pyriscence (Johnson and Gutsell 1993, Greene et al. 2013). Given the limited empirical research that has examined the relationship between temperature and seed mortality, information on the heat exposure thresholds across a wider range of species, especially non-serotinous cones, is needed.

Here we propose the term *conditional pyriscence* to succinctly describe seedling regeneration that results from the intra-annual on-plant storage of viable seeds that survive within the cone and are released following the passage of a high severity fire that kills the parent plant. We refer to this process as “conditional pyriscence” to distinguish this mechanism from species that are more obligately pyriscent and to account for the suite of circumstances that are required for its occurrence. This process was previously termed facultative serotiny (Greene et al. 2024); however, the term serotiny is not strictly appropriate as these species are, by definition, non-serotinous because they reliably release their seed each year.

In this study, we determine the temporal window for conditional pyriscence based on the rate of seed maturation for four common, non-serotinous conifers: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine

(*Pinus contorta* var. *murrayana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*) throughout two growing seasons in northeastern California. Specifically, the objectives of this study were to (1) investigate and track conifer seed maturation to determine the probable temporal window of conditional pyriscence, (2) identify the capacity of seeds to survive increasing levels of heat exposure, and (3) estimate the proportion of burned area by wildfire in the region that overlaps the period that cones contain mature seed. This research is the first to examine the conditions necessary to support conditional pyriscence across multiple species and should provide information relevant to other fire-prone regions with non-resprouting, obligate seeding species.

Methods

Site location

All field collections were made along public roads within or adjacent to the Lassen National Forest near Burney, California (40.8432, −121.7088), at elevations ranging from 980 to 1680 m. Cone collections were made from young mature stands that had been planted for timber, or those that had encroached into adjacent meadows. Burney is located at the base of an inactive volcano in Shasta County, hosting scattered volcanic soils comprised of Holland, Bobbitt, Aquolls, and Skalan soils that support mixed conifer forests, scattered oaks, and meadows (NRCS 2020). The selected tree species for the study were limited to common species of commercial value in California and included ponderosa pine, Sierra lodgepole pine, incense cedar, and Douglas-fir. Developing female cones from these four species were collected in 2018 and 2019 for the seed maturation part of the study, and again in 2020 for the heat-induced seed mortality portion of the study. The average temperature during the summer collection months for 2018 (July–September) ranged from 17.5 to 23.6 °C, in 2019 (June–September) it ranged from 15.9 to 21.1 °C, and in 2020 (June–September) it ranged from 18.1 to 22.7 °C (PRISM 2020). The average annual precipitation across collection years was 93.2 cm in 2018, 139.5 cm in 2019, and 67.6 cm in 2020 (PRISM 2020).

Seed maturation

The ovulate cone collections for each species were made every other week in June, July, August, and September for both 2018 and 2019, except for Douglas-fir which was only sampled in 2019. Pole pruners were used to collect maturing cones within the crown that had closed cone scales and lacked obvious insect damage. The sampled trees varied in height from 2 to 10 m. The number of sampled cones and trees was dependent on the expected number of seeds per cone for each species. There were

four to five trees sampled for Douglas-fir and ponderosa pine, with a minimum of one cone collected per tree during each collection period in both 2018 and 2019. For lodgepole pine, there were ten trees sampled per collection period, and a minimum of one cone collected per tree in both 2018 and 2019. Additionally, five incense cedar trees were sampled with a minimum of 20 cones collected per tree in both 2018 and 2019. After each collection was made, the cones were transported to the lab and placed in a forced convection oven at 23 °C. Once the cone scales reflexed, all seeds were manually extracted from each cone.

Twenty-five seeds from each species and collection date were randomly selected to undergo viability testing. Some of the collections made early in the season had cones with immature seeds that were categorized as undeveloped and nonviable. A 1% tetrazolium solution was prepared using 2,3,5 triphenyl tetrazolium chloride, and the acidic solution was then neutralized to a pH of 7 with potassium chloride (AOSA 2008). The selected seeds for each collection date were scarified by nicking the seed coat with a razor blade, and then submerged in 5 ml of 1% tetrazolium solution in dark conditions for 72 h. This process allowed the solution to penetrate the megagametophytic tissue and promoted a hydrogen transfer that stained viable embryos red. After 72 h, the seeds were rinsed with deionized water, and longitudinally sectioned to excise the embryo. The embryos were then evaluated for stain patterns with a stereoscope and placed into three categories: viable—where the embryos stained an even and vibrant red; probably viable—where most of the embryo displayed a red or pink stain; and nonviable—which included seeds that were hollow and without embryos, or those that did not stain red or pink.

The heat sum was calculated for each cone collection date, specifically using localized 2018 and 2019 interpolated climate data for the grid cell that included the collection site (PRISM 2020). The heat sum is simply the cumulative sum of the mean daily air temperature ($T_{i,mean}$) that exceeded 5 °C (Eq. 1).

$$\text{Heat Sum} = \sum_{i=1}^n [(T_{i,mean}) - 5] \quad (1)$$

Temperatures above 5 °C are warm enough to allow for metabolic activity within woody plant species, such that gametophytes and embryos can develop (e.g., Meunier et al. 2007). By assigning a heat sum value to each collection date, we were able to examine the heat accumulation pattern across each year, such that it could be applied to future seasons despite variable annual temperatures. The annual heat sum was also calculated for this region spanning from 2000 to 2020, to identify the patterns of accumulation and associated variation of timing among years.

Heat-induced seed mortality

Additional cones were collected in 2020 to examine heat-induced seed mortality thresholds of the same four species. We determined the optimal cone collection date (period of maximum viability prior to seed abscission) based on the established relationship of accumulated heat sum and seed maturation from 2018 and 2019 data, and then we tracked the daily heat sum for 2020 using Eq. 1 and PRISM temperature data for the site. As such, the 2020 cone collections were made on September 5th when 2146 °C had accumulated. The developed ovulate cones were then collected with pole pruners from the canopy, following the same methods as the seed maturation portion of the study described earlier. We sampled a minimum of 50 cones from 2 to 13 trees for each species. The cones were kept cool until testing could be conducted to maintain cone closure and the state of seed maturity.

The heat exposure tests were performed in a muffle furnace using a total of seven heat treatments: no heat (control, ~20 °C), 100 °C, 150 °C, 200 °C, 300 °C, 400 °C, 600 °C. These temperatures were selected to represent a wide range of air temperatures that a cone would experience during wildfires (Butler et al. 2004; Michaletz et al. 2013). We used Omega type K thermocouples (Omega Engineering, Norwalk, CT, USA), with a testable temperature range that spanned from 200 to 1250 °C, connected to a Campbell Scientific CR1000 data logger (Campbell Scientific Inc., Logan, UT, USA), to record the maximum temperature (± 10 °C) within the muffle furnace. For each heat treatment, five cones were randomly selected from each species, except incense cedar, which had 15 cones selected per treatment due to a maximum of four seeds produced per cone. Each cone was placed individually in a metal pan and placed into the muffle furnace at the designated temperature for 150 s. This exposure time was chosen because it represents the duration range of simulated fire (Michaletz et al. 2013) and observed data in an experimental crown fire (Butler et al. 2004). Following exposure, the cones were removed promptly from the muffle furnace. Increasing heat treatments were implemented for all species until complete seed death was observed. After removing cones from the furnace, all seeds were extracted and five seeds per cone were tested for viability. If the cone scales failed to reflex during the heat treatment (commonly found at low heat treatment levels), the cones were placed in a drying oven at 23 °C until the cone scales reflexed enough to free the seeds for manual extraction. In total, 25 randomly selected seeds across five or 15 (incense cedar) cones per heat treatment and species were examined for viability. Only seeds that were free of insect damage and appeared to have abundant megagametophytic tissue, indicating a high potential for a viable embryo, were selected to undergo viability

testing. Using the same viability test methods as the seed maturation portion of the study, the seed embryos from the mortality experiment were examined and categorized by viability. This data was obtained for all tested seeds in each treatment, with the number of viable and probably viable seeds combined to find the proportion of viable seeds per treatment and species.

Timing of fire

To estimate the temporal window that may permit post-fire regeneration via conditional pyriscence, we first obtained the 2000–2017 fire perimeter data of all wild-fires greater than 200 ha for the Klamath Mountains, northern Sierra Nevada, and southern Cascade ecoregions in northern California from the CalFire FRAP fire perimeter database (<https://www.fire.ca.gov/>). Each fire included a total area burned as well as the start and end date. From this data, we calculated the daily cumulative proportion of area burned for each year assuming a constant rate of fire growth based on fire size and duration. For example, if a fire began on July 20 and was declared as ended on July 27 then 1/7 of the area burned was assigned to the cumulative total for each of those days. However, it is important to note that this approach will tend to bias our cumulative area burned estimates towards later dates as the “mop-up” phase of a wildfire is often protracted despite little additional area burned. We then overlaid the temporal window of seed maturation with the window of fire activity to identify the proportion of area burned that could permit conditional pyriscence. We defined the window of conditional pyriscence as the period between the onset of seed maturation (10% viability) and 90% seed maturation based on our two study years. We expect that the ending period of this window should correspond to the typical time for cone opening and the onset seed abscission for these conifers which appears to be around early September (Schopmeyer 1974).

Data analysis

Data from the seed maturation and heat-induced mortality studies for all four species were analyzed in R (R Core Team 2022). Seed maturation data from 2018 and 2019, seed mortality data from 2020, and cumulative area burned data from 2000 to 2017 were all analyzed using a generalized linear model assuming a binomial distribution. The significance level ($\alpha=0.05$) of the main effects of each analysis were examined with the Anova function in the *car* package (Fox and Weisberg 2019). Both seed maturation and heat treatment analysis included relative seed viability as the response variable. Relative viability was calculated as the proportion of observed viability for each collection period divided by the maximum

observed viability for each species, with values ranging from 0 to 1 (Pereira 2020). With the wide variation in maximum absolute seed viability observed (Table 1), relativized proportions of viability were calculated to allow for comparisons among the examined species. The most parsimonious generalized linear model for the seed maturation study was selected based on the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2004), with consideration for the parameters of heat sum, species, and year. For the heat-induced seed mortality study, we considered the parameters of species and treatment and again selected the most parsimonious generalized linear model using the lowest AIC values. The same approach was used to examine the relationship of Julian date and year with cumulative area burned.

Results

Seed maturation

Seed viability across all four species increased over time in association with the increase in heat sum over the growing season (Fig. 1) for both 2018 and 2019 ($p=0.0013$, $z=3.23$, $df=42$). The best generalized linear model of seed maturation included an additive model with heat sum and species. The collection year was not included in the top model and did not quite have a significant effect ($p=0.061$, $z=-1.87$, $df=42$).

The onset and rate of seed maturation varied among species (Table 2). Species were informative in the best model, although we did not detect significant differences in relative seed viability with heat sum among species ($p=0.1749$, $\chi^2=4.96$, $df=3$). The onset of seed maturation (10% relative viability) was earliest for Douglas-fir (959 °C heat sum, early-July) and lodgepole pine (1205 °C heat sum, mid-July), and latest for ponderosa pine (1484 °C heat sum) and incense cedar (1491 °C heat sum) in early August. For the four species examined, 90% relative seed viability was reached with a cumulative heat sum between 1756 °C (Douglas-fir) and 2287 °C (incense cedar), which is typically mid-August to mid-September.

Table 1 The observed maximum absolute viability for the sampled seeds of each species in 2018 and 2019, collected in northeastern California. These values were used to calculate relative viability for each collection period for the seed maturation study

Species	Maximum viability (%)
Incense cedar	68
Douglas-fir	24
Lodgepole pine	76
Ponderosa pine	52

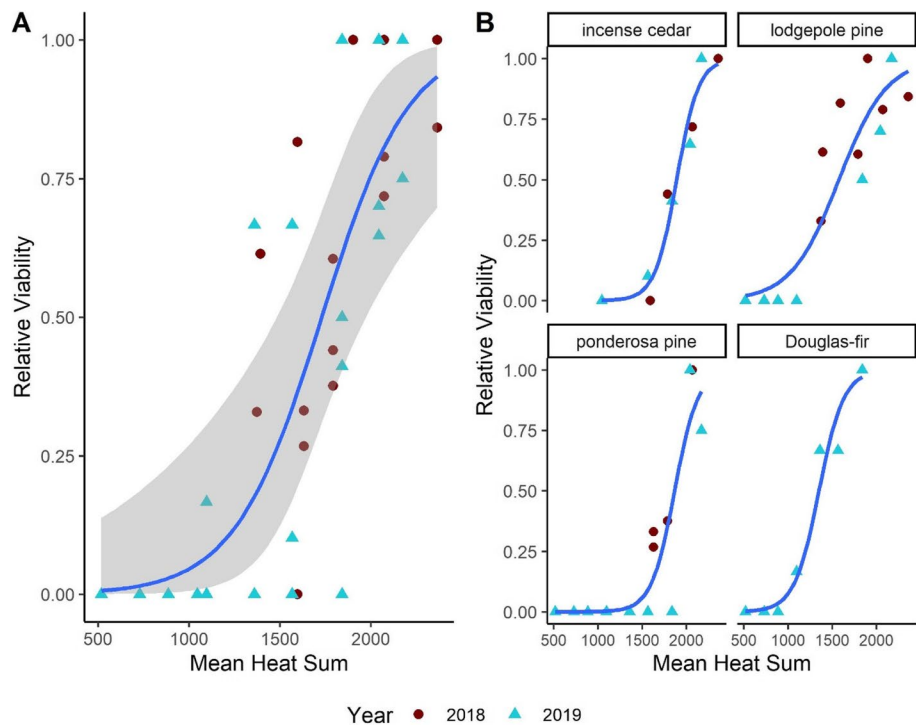


Fig. 1 The positive relationship between mean heat sum and mean relative viability ($p=0.0013$, $z=3.23$) in 2018 and 2019, based on a generalized linear model, with 95% confidence intervals in gray for **A** all species combined and **B** each individual species. All cone collections were from northeastern California

Table 2 Accumulated heat sum at 10%, 50%, and 90% relative viability for four non-serotinous conifer species in Shasta County, California, as well as the seasonal timing for 10% and 90% relative viability. Heat sum values are based on predictions from the top selected model that included heat sum and species. Timing estimates for each species and viability category represent the average Julian dates associated with accumulated heat sums generated from modeled temperature data from 2000 to 2020 for the study site in northeastern California

Species	10% viability (°C)	50% viability (°C)	90% viability (°C)	Timing at 10%	Timing at 90%
Incense cedar	1491	1889	2287	Early-August	Late-September
Douglas-fir	959	1358	1756	Early-July	Mid-August
Lodgepole pine	1205	1603	2002	Mid-July	Early-September
Ponderosa pine	1484	1883	2281	Early-August	Late-September

Based on these findings, the temporal window for conditional pyriscence (10 to 90% relative viability) with cumulative heat sum values ranging from 1285 to 2100 °C typically occurred between the Julian dates of 200 and 260 or generally mid-July to mid-September.

Annual variation in the heat sum accumulation from 2000 through 2020 at the study site in northeastern California varied among years (Fig. 2). For instance, the heat sum for the average onset of viability (10%; 1285 °C) across all species had an average Julian date of 206 (± 4.0 days 95% CI), or late July. An accumulated heat sum of 1683 °C represented the average 50% viability across all species and occurred on the Julian date of

230 (± 4.3 days 95% CI), or mid-August. Our estimate of the closing period of conditional pyriscence (90% relative viability) occurred around an accumulated heat sum of 2100 °C and occurred on the Julian date of 259 (± 6.4 days 95% CI), or mid-September.

Heat-induced seed mortality

Seed survival was negatively associated with increasing convective heat (Fig. 3). As the heat treatment temperature increased, relative seed viability significantly decreased across all species ($p=0.0156$, $z= -2.42$, $df=27$). The most informative seed mortality model included heat treatment and species. While species was

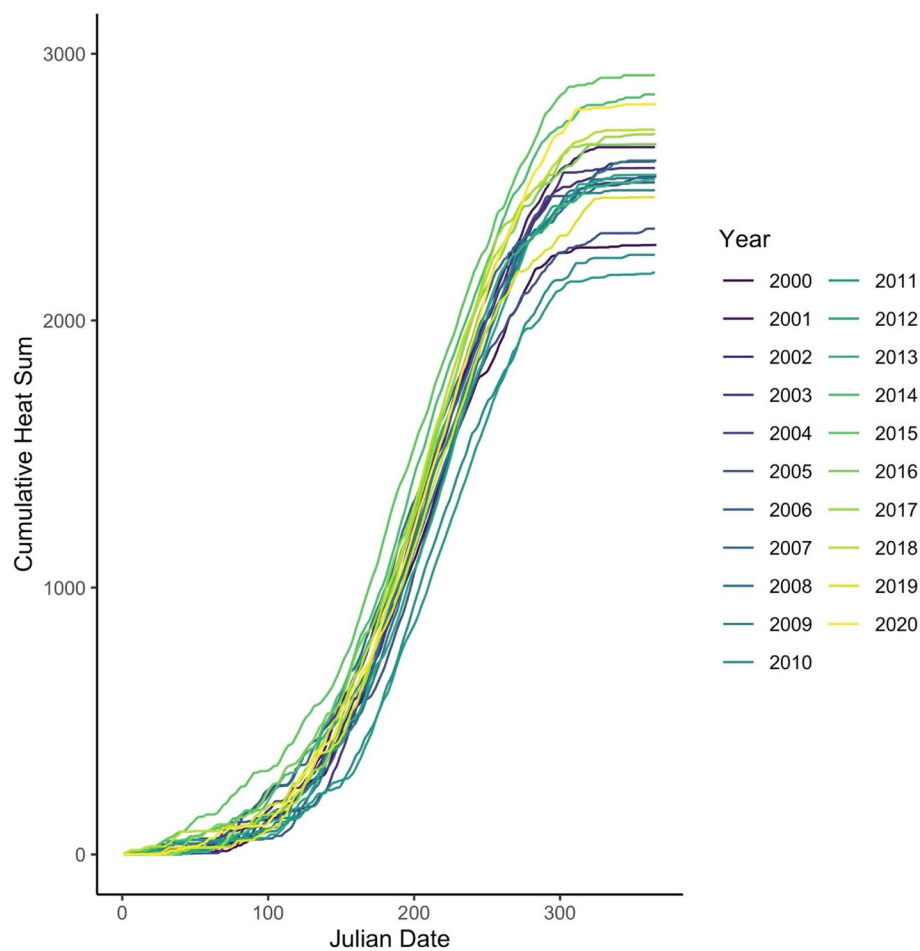


Fig. 2 The accumulated heat sum by Julian date for the study site in northeastern California demonstrating the variability in annual patterns of heat accumulation from 2000 through 2020 (PRISM, 2020)

informative in the most parsimonious model, it was not statistically significant ($p=0.1895$, $\chi^2=4.77$, $df=3$). Seeds of the smaller cone species, incense cedar and Douglas-fir, tended to have lower survivability to heat treatments than the larger cone species, lodgepole pine and ponderosa pine (Table 3). Douglas-fir and incense cedar were only able to maintain 50% relative seed viability at cone temperatures up to 60 °C and 105 °C, respectively. Ponderosa pine and lodgepole pine maintained 50% relative seed viability at cone temperatures of 215 °C and 240 °C, respectively. And ponderosa pine, our largest sampled cone, had some seeds that survived cone temperatures that reached as high as 400 °C.

Timing of wildfire

Recent fires in the Klamath Mountains, northern Sierra Nevada, and southern Cascade ecoregions of northern

California from 2000 to 2017 mostly burned between June and September, with both lightning and human-caused fires having their highest area burned in August. However, a secondary peak was observed in June for lightning fires. During this same time and geographic area, the cumulative proportion of burned area varied significantly among years ($p<0.0001$, $z=-5.4$), with the cumulative area burned in more recent years occurring slightly later than in earlier years. Almost all the area burned (>99%) across the years examined occurred between 125 and 350 Julian days (Fig. 4). A total of 60% ($\pm 7.6\%$ 95% CI), of the cumulative area burned was within our estimated window of conditional pyriscence (200 and 260 Julian date); that is, more than half the area burned had the capacity for in situ regeneration by non-serotinous conifers following high severity fire.

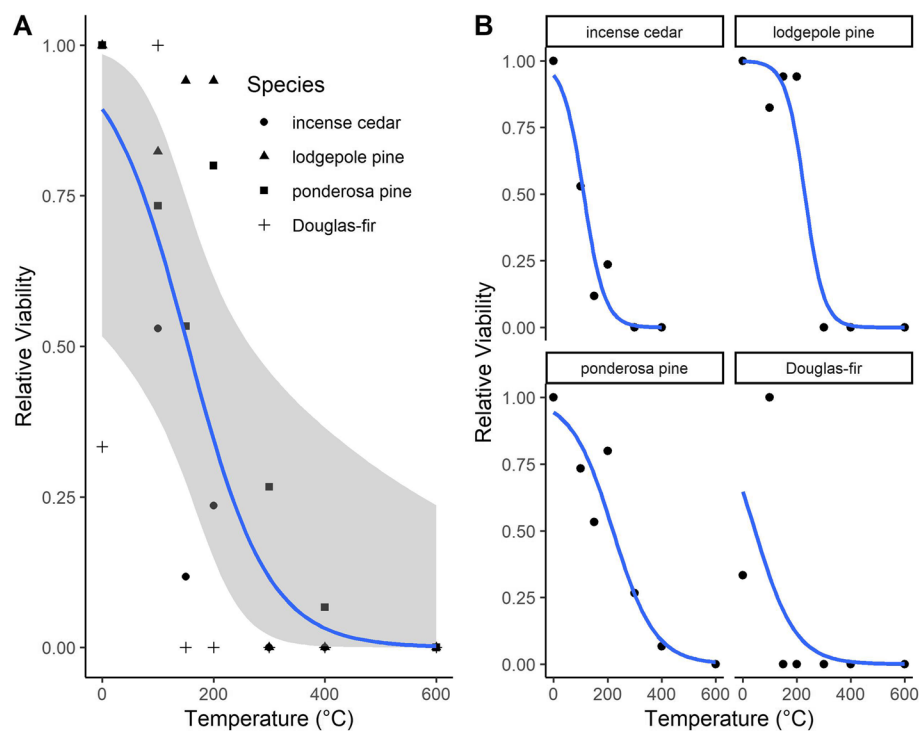


Fig. 3 A negative relationship between relative seed viability and cone heat exposure temperature ($p=0.0156$, $z=-2.42$), based on a generalized linear model, with 95% confidence intervals in gray for **A** all species combined and **B** each individual species. Cones were collected in 2020 from northeastern California

Table 3 The temperature of heat exposure permitting 10%, 50%, and 90% relative seed survivorship for the four conifer species studied in northeastern California. These values are based on predictions from the top generalized linear model, containing heat treatment and species

Species	10% survival (°C)	50% survival (°C)	90% survival (°C)
Incense cedar	230	105	20
Douglas-fir	185	60	20
Lodgepole pine	360	240	120
Ponderosa pine	340	215	90

Discussion

Here we provide support for the possibility of conditional pyriscence in northeastern California across the four conifer species examined. Within this region, we demonstrated that the timing of seed maturation (approximately mid-July to mid-September) coincided with the time when most fires occur (60% by area) and that seeds within cones can be protective of the heat experienced during wildfires. In combination, these results are aligned with our expectations that non-serotinous conifer species

can colonize the interior portions of high severity burn patches from seed that survives in the canopy. Yet, the temporal and geographic extent of conditional pyriscence remains uncertain as its occurrence will depend on several factors including the probability of a fire occurring when closed cones contain viable seed, the number of cones and viable seeds available, cone characteristics of the species (e.g., size and placement), and the intensity of the fire.

Seed maturation

We provide the first known study to examine the relationship between heat sum and seed maturation in lower latitude temperate forests across multiple conifer species. While our findings align with previous research that seed viability increases with accumulated heat sum (Henttonen et al. 1986; Zasada et al. 1992; Sirois et al. 1999; Fedorkov 2001; Meunier et al. 2007; Michaletz et al. 2013), there were marked differences in the timing and duration of seed maturation from other studies. The onset of seed maturation in our study began in late July with heat sums ranging between 959 and 1491 °C and closed around mid-September with heat sums ranging between 1756 and 2287 °C. However, other studies have demonstrated a more abbreviated schedule where

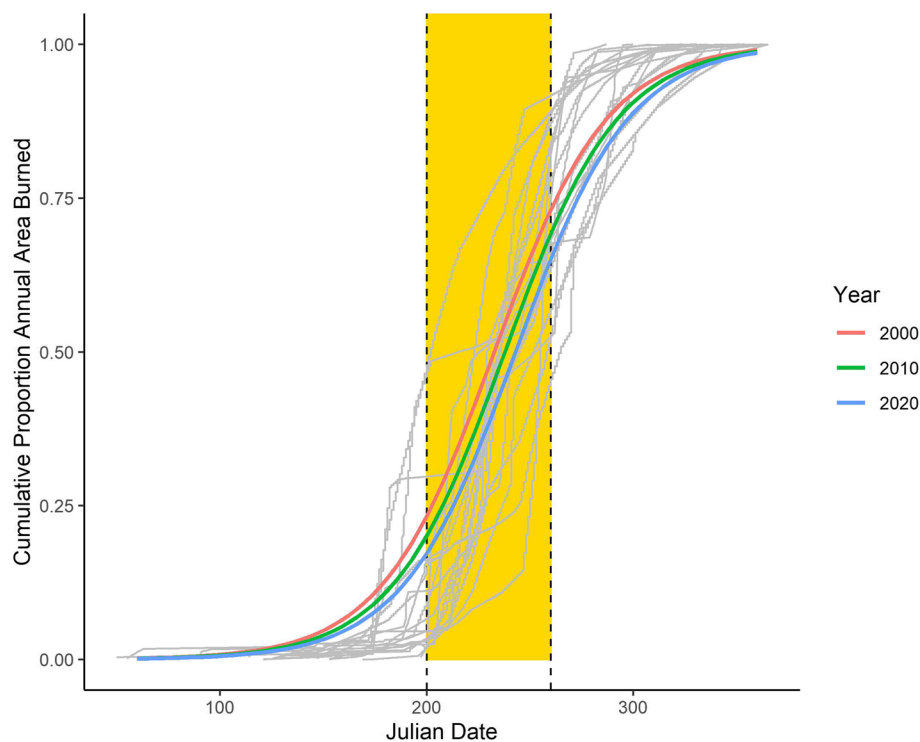


Fig. 4 Cumulative proportion of annual area burned from 2000 to 2017, based on start dates, in northern California (Klamath, northern Sierra Nevada, southern Cascade ecoregions). The yellow area represents the temporal window of conditional pyriscence (using 10% relative viability as the start and 90% viability as the end), which encompassed 60% (annual range: 33 to 86%) of the burns. The temporal window for conditional pyriscence includes the Julian date of 200 through 260 (late-July to mid-September). Gray lines represent cumulative area burned by year and colored lines represent the generalized linear model results of the year effect

seed maturation began with heat sums around 600 °C and closed around 1100 °C (e.g., Henttonen et al. 1986; Michaletz et al. 2013). A tendency for the required heat sum for a phenophase to decrease with latitude has been reported elsewhere for phases such as budburst or leaf fall (e.g., Beuker 1994; Gao et al. 2023), and it is likely that these observed differences are attributable to latitudinal variation across reported study sites. These differences highlight the importance of considering the local climatic (i.e., temperature) and topographic (i.e., elevation and latitude) context when examining seed maturation schedules and the potential for conditional pyriscence.

Our estimated temporal window for conditional pyriscence (late-July to early-September) will vary annually. Based on the examination of 20 years of recent temperature data at our site, the window of conditional pyriscence can vary by 4 to 7 days. We also note that the closing period of our estimate is based on the timing of 90% seed viability, which may represent a conservative estimate considering that cones may not open and release seeds until later. While reports indicate that seed abscission commonly begins in early-September for many species (Schopmeyer 1974), direct examination of cone opening and seed release schedules would provide

better estimates and is an area of future research we are pursuing.

The lack of a substantial influence of species on the relationship between cumulative heat sum and seed maturation in our study suggests that the timing of seed maturation, and thus the propensity for conditional pyriscence, may be relatively consistent across conifer species in northeastern California. While we were unable to detect a strong influence of species, it was informative in our best model of relative seed viability, suggesting that species may differ in their maturation schedules. Future studies that consider larger sample sizes may increase the power to detect differences among species.

Seed survival relative to heat exposure

The observed decline in seed survival with increasing cone temperature corroborates previous studies across a wide range of species (e.g., Zasada et al. 1979; Johnstone et al. 2009; Milich et al. 2012; Michaletz et al. 2013). While differences in seed survival among species were subtle in our study, we observed that species with smaller cones tended to have lower heat tolerances than species with larger cones. These observations confirm recent results from a fire simulation study that found

smaller cones with less protected seeds (i.e., shallower seed depth) experienced higher potential seed mortality rates (Greene et al. 2024). While the cone temperatures examined in our study were consistently applied to each species, the temperatures that seeds experienced likely differed based on cone size. Smaller cone species presumably reached higher seed temperatures at a given cone temperature due to more rapid heat transfer to the seed compared to larger cone species. However, our findings are somewhat limited due to relatively small sample sizes in only four species. Future studies might consider examining more species across a wider range of cone sizes with larger sample sizes to better examine the potential relationships among cone traits, heat transfer rates to seeds, and seed mortality due to heat exposure.

We note that our heating treatments do not fully reflect the heat flux cones typically experience during high severity crown fire conditions. Maximum temperatures associated with high intensity fires within the mid- to upper canopy can be over 1000 °C (Butler et al. 2004). Based on our study, this implies that most seeds would not survive these upper temperatures. However, these temperatures rarely last more than 10 to 20 s. Cones in high severity wildfires likely experience a wider range of temperatures and durations that could permit seed survival, especially if heat pulses are shorter than the 150 s we tested. Additionally, the heat pulses from wildfire are difficult to reproduce in a lab setting and the static temperatures of a muffle furnace are unlikely to replicate the dynamic heat fluxes experienced during a wildfire. A recent comparative experiment that examined different heating regimes in two serotinous obligate seeder species found lower seed mortality following dynamic heating than static heating treatments that were exposed to consistent heat intensity (Tada et al. 2024). However, our study included a high of 600 °C for 150 s to reflect the potential upper bounds of heat exposure during high intensity fire, which is higher than the rapid heat flashes over 1000 °C experienced for 10 to 20 s (Butler et al. 2004). That is, survival may be more likely in the rapidly varying temperature regime of a flaming front than in the static heating of a muffle furnace. Furthermore, most ovulate cones are in the upper portion of the crown, which can result in lower heat-induced seed mortality due to exposure to lower or more variable plume temperatures and durations when compared to cones in the lower and middle crown positions (Splawinski et al. 2019).

Our finding that viable seeds should be able to survive fire within cones must be tempered by the fact that seed survival will be highly dependent on fire intensity. One study in black spruce estimated 86% seed survival following fire (Zasada et al. 1979). In another study, seed

viability of black spruce following fire similarly ranged between 61 and 81% based on crown position, such that the side of the crown with more intense charring had greater seed mortality (Splawinski et al. 2019), although a separate study with black spruce indicated much lower seed viability (<10%) following the highest severity fires examined (Johnstone et al. 2009). Similarly, a computational study for white spruce cones estimated that only 12% of the seeds should survive representative crown temperatures during fire (Michaletz et al. 2013). Given this wide range of empirical outcomes, it is likely that post-fire seed survival will depend on the intensity of fire. Additional research is needed to determine the thresholds and circumstances that contribute to this variation.

Timing of wildfire

Sixty percent of the area burned in northern California forests from 2000 to 2017 occurred from late-July to early-September (our estimated window for conditional pyriscence) with lightning fires contributing to a higher proportion of this total area than human ignitions. Our findings are similar to the estimated 50% of the area burned in lightning fires that overlapped seed maturation in white spruce in Canada (Michaletz et al. 2013). Given that lightning-ignited wildfires tend to result in lower intensities than human-caused wildfires (i.e., accidental or arson fires; Hantson et al. 2022), it is plausible that conditional pyriscence may be more common following high severity lightning-ignited fires. Human-caused wildfires tend to occur at lower elevations and slope positions and burn when conditions are often drier (i.e., higher energy release component). These differences can allow for more rapid rates of spread up slopes in mountainous areas and contribute to higher intensities that may cause more heat-induced seed mortality within cones.

The occurrence of conditional pyriscence will also be influenced by changing climatic conditions given the likelihood of continued warming and further seasonal shifts in fire activity, but the direction and magnitude of this change remains uncertain. Increased warming will likely result in earlier seed maturation and abscission, shifting the window of conditional pyriscence to earlier in the year. Conversely, it is presumed, based on previously described shifts in fire activity, that fires will increasingly burn more frequently later in the season (Westerling 2016). This observation is consistent with our results that cumulative area burned for northern California between 2000 and 2017 has shifted to slightly later in the year. If both trends hold true, we expect that the incidence of conditional pyriscence would increase under future climate and fire conditions if a greater proportion of fires overlap the period when a large fraction of seeds are mature within closed cones. Although it is possible that if

a sufficient shift in the proportion of fires occurring after seed abscission, we may expect a decline in the incidence of conditional pyriscence.

Many regions in western North America have experienced increases in fire frequency and severity (Westling 2016, Parks and Abatzaglou 2020), resulting in a greater need to consider reforestation (North et al. 2019). However, given the limited availability and increasing demands on nursery stock (Fargione et al. 2021), improved post-fire regeneration modeling that considers conditional pyriscence may better inform replanting efforts. For instance, areas resulting in regeneration from conditional pyriscence could represent a lower priority for reforestation.

Areas for future inquiry

While we have demonstrated that conditional pyriscence is mechanistically supported across multiple conifer species, it is uncertain how frequently this process occurs. We can expect that the incidence of conditional pyriscence is much less than the 60% of fires that would permit its occurrence or else it would have been more commonly documented in previous studies. The incidence of this regeneration mechanism is likely lower than 60% of fires due to variation in cone production and fire intensity. Cone production in most non-serotinous conifers is highly right-skewed, with most years having lower levels of cone production with less frequent mast years (Greene and Johnson 2004). Thus, the more frequent occurrence of low cone producing years would expectedly result in low post-fire regeneration density that may be indistinguishable from long-distance dispersal. It is also likely that the intensity of high severity fires often exceeds the ability of cones to protect seeds, and so we would also expect lower incidence and detectability of conditional pyriscence, especially in species with very small cones such as *Tsuga* or *Larix* (Greene et al. 2024). Future research that examines the role of cone production and fire intensity are necessary to advance our understanding of the thresholds with which this mechanism occurs.

Still, we think that conditional pyriscence is not entirely rare either. It is likely that conditional pyriscence has been underrepresented in the literature due to the limited number of deliberate studies intended to examine it. Here we suggest several methods for detecting this regeneration mechanism in locations where the timing of fire and seed maturation are conducive. The first method would be to monitor seedling regeneration in non-serotinous species along transects perpendicular to the living forest edge and extending deep (> 300 m) into a large high severity patch (e.g., Pouden et al. 2014). Conditional pyriscence will be evident where seedling

densities do not steeply decline with distance from the living edge. A second method would be to examine regeneration around stands of isolated conspecifics in a matrix of other species within a high severity patch. One could extend transects from the center of each stand outward, counting recruits as well as recently fallen and still-appended cones. If conditional pyriscence is apparent, then there will be a positive relationship between recruit density and cone density throughout the high severity patch. Third, one could promptly (before seed abscission) visit a recently burned site and cut burned trees down, collect the cones, and test the seeds for germinability (e.g., Splawinski et al. 2019). This approach must be done very soon after the burn because the heat from fire greatly accelerates the drying of the scales and thus the rate at which they open. In serotinous pines, Marlin et al. (2024) and Greene et al. (2013) reported that most of the seeds were on the ground within 2 months. Summarizing, we feel that if researchers started employing these methods or others, the number of reported examples of conditional pyriscence would increase.

Conclusions

Our research provides support for the potential of conditional pyriscence to contribute to substantive post-fire regeneration following high severity fire across four non-serotinous species in northeastern California, with the potential to more broadly apply to other conifer-dominated fire-prone regions globally. While more research is needed to determine the extent and magnitude of conditional pyriscence, the development of future post-fire conifer regeneration models would likely benefit from considering factors such as cone and seed production, timing of wildfire, and fire intensity. Inclusion of these factors could explain observed incidences of sufficiently high post-fire regeneration density far from the living forest edge (e.g., Larson and Franklin 2005, Roccoforte et al. 2012, Crotteau et al. 2013, Pouden et al. 2014, Outz et al. 2015) that are not adequately captured by current post-fire regeneration models (e.g., Shive et al. 2018; Stevens-Rumann and Morgan 2019). While important, we acknowledge that many western US coniferous forests have experienced increased probability of regeneration failure following high severity wildfires that have potential to transition to non-forested ecosystems (Tepley et al. 2017; Davis et al. 2018, 2019) and that these trends are likely to continue increasing over the coming decades without substantive management intervention (Davis et al. 2023). However, our study indicates that determining the circumstances that may promote resistance to this trend provides insights that can also inform place-based forest management decisions regarding wildfire response

strategies, mitigation treatments, and post-fire restoration activities, although we also recognize that areas that experience conditional pyriscence may still be subject to transition to non-forested ecosystems over the long-term if subsequent fires occur before established trees reach maturity.

Throughout this paper, we have emphasized the central role of timing in determining the density of post-fire recruits. Particularly, the timing of fire and seed maturation are key. We conclude that the mechanism should be uncommon but not rare. We normally think of the fire-prone, conifer-dominated landscape as one where the serotinous species are found at high density in the younger stands while the non-serotinous species are mainly in the older patches or the edges of more recent fires, due to limited dispersal. Conversely, conditional pyriscence allows a non-serotinous species to occasionally develop high recruit densities across a high severity patch if, as with serotinous species, it was a major component of the site before fire. The emphasis on timing also underscores that the subsequent composition of the canopy decades later is contingent on the weather-driven dynamics of cone production and fire. Early arrival of regeneration after fire confers an advantage in the subsequent competition for light and the probability of becoming a canopy tree. The size of the crop and fire activity are differentially weather-dependent, with fire patterns influenced by weather of the current summer (Williams and Abatzoglou 2016) and cone production influenced by weather in the preceding two growing seasons (LaMontagne et al. 2020).

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Authors' contributions

MAL: investigation, supervision, formal analysis, writing—original draft, writing—review and editing; JMK: conceptualization, funding acquisition, supervision, formal analysis, writing—review and editing; DFG: conceptualization, funding acquisition, supervision, writing—review and editing.

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Data Availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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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