Demographic processes underpinning post-fire resilience in California closed-cone pine forests: the importance of fire interval, stand structure, and climate

Michelle C. Agne · Joseph B. Fontaine · Neal J. Enright · Sarah M. Bisbing · Brian J. Harvey

Received: 15 September 2021 / Accepted: 4 February 2022 / Published online: 19 February 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract The resilience of serotinous obligate-seeding plants to fire may be compromised if increasing fire frequency curtails time available for canopy seed bank accumulation (i.e., immaturity risk), but how various drivers affect seed availability at the time of fire is poorly understood. Using field data from California closed-cone pine (Pinus attenuata and P. muricata) stands, we assess two critical demographic processes during the inter-fire period—reproductive capacity and mortality. At tree- and stand-levels, we test how these processes are affected by stand age and are mediated by biotic and abiotic factors. We found that stand age was the key driver of reproductive capacity; older stands had a greater proportion of reproductively mature individuals and greater closed cone density. Stand density mediated the effect of age; greater stand density resulted in greater closed cone density and a lower proportion of reproductively mature individuals, but reproductive capacity in low- and high-density stands converged over time. Increased moisture stress reduced the stand-level proportion reproductively mature trees but had no effect on closed cone density. Mortality was strongly associated with density-dependent thinning and increased in stands with high moisture stress. Reproductive capacity began to increase sharply 10 years post-fire and by 20 years immaturity risk was low. However, prior to 20 years, low-density stands with high moisture stress may be more susceptible to immaturity risk. Understanding these relationships is critical to predicting serotinous population persistence under changing climate and disturbance conditions.

Keywords Canopy seed bank · Cone production · Demographic shift · Pinus attenuata · Pinus muricata · Serotiny

Introduction

Widespread changes to climate and disturbance regimes are altering plant populations in terrestrial ecosystems globally (Johnstone et al. 2016). Changes in size, frequency, seasonality, or severity of a disturbance regime can have strong effects on ecosystem structure and function (Turner 2010).
Such changes can combine with direct effects of climate warming to erode resilience—the capacity of an ecosystem to absorb disturbance and reorganize without transitioning to an alternative state (Walker et al. 2004). Fire activity has increased in many temperate forest and woodland ecosystems during the period from 2000 to the early 2020s (Parks and Abatzoglou 2020; Boer et al. 2020), challenging resilience mechanisms that promote post-fire recovery and driving ecosystem type conversion (e.g., conversion from forest to non-forest; Coop et al. 2020). Such transitions are most likely where plant adaptations to fire are misaligned with fire characteristics (Pausas and Keeley 2014; Johnstone et al. 2016).

Serotinous obligate seeders—non-sprouting species that accumulate and store canopy seed banks over multiple years—depend upon predictable fire return intervals that exceed the time needed to develop a canopy seed bank sufficient for self-replacement (Lamont and Enright 2000). Although typically adapted to stand-replacing fires, serotinous plant populations may be threatened through three important mechanisms that collectively make up the interval squeeze framework of Enright et al. (2015). First, shortened fire-free intervals can lead to immaturity risk if populations burn before accumulating a sufficient canopy seed bank (Keeley et al. 1999). Second, stressful climate conditions during the first year post-fire—a crucial window for serotinous populations in which most recruitment occurs following en masse seed release (Turner et al. 1999; Harvey and Holzman 2014)—can result in recruitment failure even if sufficient seed is available (Enright et al. 2014; Hansen and Turner 2019). Third, warming and drying climate can directly affect demographic processes by delaying or decreasing reproductive capacity and increasing plant mortality (Enright et al. 2015). Shifts in demographic processes can combine with changing disturbance regimes to produce compound disturbance effects (sensu Paine et al. 1998), where multiple drivers create a synergistic effect on resilience. Shortened fire intervals and post-fire recruitment failure have been increasingly documented in recent years (Fairman et al. 2017; Stevens-Rumann et al. 2018; Davis et al. 2019; Turner et al. 2019). However, the effects of warming climate on demographic processes and the implications for seed availability at the time of fire are poorly understood, representing a key gap in understanding serotinous plant population persistence under future climate (Davis et al. 2018).

Demographic processes in plants are controlled by many drivers occurring at multiple levels of organization. The probability of producing seeds (i.e., reproductive maturity) strongly increases with plant age in perennial, obligate seeder species (Harper 1977; Viglas et al. 2013), as does individual seed production (Andrus et al. 2020). Seed production similarly increases with plant size (Davi et al. 2016), as greater access to resources generally results in greater seed production (Greene et al. 2002). However, trade-offs between vegetative growth and seed production can occur during early successional stages and when intraspecific competition is high (Climent et al. 2008). High initial population density can drive high intraspecific competition and delay age to reproductive maturity by years to decades (Borchert 1985), resulting in low individual seed production as compared with individuals in low-density stands (Esler and Cowling 1990; Alfaro-Sánchez et al. 2015). However, despite lower tree-level production, high-density stands may have greater stand-level seed production when compared with low-density stands (Moya et al. 2007; Turner et al. 2007). Moisture stress also affects plants via delayed maturity and chronic or acute reductions in seed production (Redmond et al. 2012) and by increasing mature tree mortality, thereby decreasing the population of reproductive individuals (Williams et al. 2013), especially where competition for resources is strong (Andrus et al. 2021). Warm and dry conditions can also trigger cone opening for some serotinous species, further depleting the canopy seed bank available at time of next fire (Borchert 1985; Verkaik and Espelta 2006). Compounding these climatic stressors, damage caused by biotic agents (e.g., insect pests, diseases) may further decrease seed production and seed availability for some tree species (Schaffer et al. 1983; Singh and Carew 1990). Understanding how these factors interact to influence demographic processes is critical to predicting how serotinous plant populations may respond following increasing fire frequency under a warming climate.

The closed-cone pine forests of California, USA, are a model system for understanding demographic mechanisms of serotinous forest resilience with climate warming and concomitant altered disturbance regimes. Typically, these forests are dominated by a
single cohort of closed-cone pines established following stand-replacing fire—similar to other serotinous forests in North America [e.g., lodgepole pine (*Pinus contorta*), jack pine (*P. banksiana*)]—but stand development occurs more rapidly (Vogl 1973; Harvey et al. 2011). California closed-cone pines reach reproductive maturity at a young age and proceed through the stages of stand dynamics quickly compared with other serotinous forests in North America (Keeley et al. 1999; Harvey and Holzman 2014). Stands are also short-lived with relatively short inter-fire periods (Sugnet 1985; van de Water and Safford 2011). Because of the rapid pace of stand development, empirical measurement of demographic processes across the inter-fire period is more logistically feasible than in other obligate seeding serotinous forests in North America with much longer fire return intervals (Romme 1982; Gauthier et al. 1996). Insights from California closed-cone pine forests may illuminate demographic mechanisms that control species persistence in forests in which these processes unfold across longer temporal scales.

In this study, we used field data collected in California closed-cone pine stands dominated by either knobcone pine (*P. attenuata*) or bishop pine (*P. muricata*) across the early stages of the inter-fire period to address these knowledge gaps about the demographic mechanisms underpinning post-fire resilience. Specifically, to assess the relative effects of multiple drivers on reproductive capacity and tree mortality—two demographic processes that are important for post-fire resilience—we asked: (1) How does reproductive capacity develop over time since stand-replacing fire? (2) How do biotic and abiotic factors drive variability in reproductive capacity at individual tree- and stand-levels? (3) How does stand-level density-dependent tree mortality vary across abiotic and biotic drivers, and what are the implications for the canopy seed bank? We expected that: (1) time to a high proportion of individuals within a stand reaching reproductive maturity is short and canopy seed bank production increases rapidly over time. (2) Tree size and stand age have the strongest effects on both measures of reproductive capacity at tree- and stand-levels, respectively. Increased stand density has negative effects on tree-level reproductive capacity and stand-level reproductive maturity, and positive effects on canopy seed bank production. Conversely, warmer, drier climate, disease incidence, shrub cover and stand density, and fertile soil have negative effects on both measures of reproductive capacity at both levels of organization. (3) Stand-level density-dependent mortality increases with warmer, drier climate, greater disease incidence, greater shrub cover and stand density, resulting in decreased reproductive capacity. Understanding the relative magnitudes of multiple drivers of demographic processes is key to anticipating serotinous population persistence with implications for conifer-dominated forests across North America.

**Methods**

**Study area and site selection**

This study was conducted in closed-cone pine stands in California, USA within the Klamath Mountains and Northern and Southern Coast Ranges in areas that have experienced stand-replacing fires since 1985 (Appendix S1 in the Electronic supplementary material). The region has a Mediterranean climate and covers a wide range of average winter (January) temperatures (3.3–12.2 °C), average summer (July) temperatures (14.9–26.9 °C), and annual average precipitation [467–1996 mm; 800-m gridded 30 year climate normals from 1981 to 2010 (PRISM Climate Group 2019)]. There is a strong seasonality in precipitation, with >90% falling between October and May, and summer fog produces a moderating effect across the study area (Vogl et al. 1977; Torregrosa et al. 2016). Bishop pine occupies areas that receive less annual precipitation (467–1034 mm), and lower seasonal variation (due in part to coastal proximity) in average temperature (8.8–12.2 °C in January and 14.9–18.7 °C in July) than knobcone pine (average annual precipitation of 785–1996 mm, mean temperatures of 3.3–9.9 °C in January and 20.7–26.9 °C in July).

The study area encompasses low elevation to lower montane zones [84–1344 m above sea level (asl)], with bishop pine occupying a narrower elevational zone (84–413 m asl) than knobcone pine (334–1344 asl). Stands are often characterized by steep slopes and soils are typically shallow and rocky, with serpentine substrate common for knobcone pine (Vogl et al. 1977). Closed-cone pine communities often occur as dense forest stands for several decades following establishment but can also be characterized by
low-density stands interspersed with chaparral. Common co-occurring shrub species include Adenostoma fasciculatum, Arctostaphylos spp., Ceanothus spp., Heteromeles arbutifolia, Vaccinium ovatum. Quercus spp. are also common, existing both in shrub and tree form. Herbaceous vegetation, where it is present, commonly includes Acmispon glaber, Lupinus spp., and Mimulus spp.

To establish a chronosequence of stand age in bishop pine and knobcone pine forests, we selected 15 fires that overlapped the target species’ ranges using Monitoring Trends in Burn Severity data (Eidenshink et al. 2007), species distribution maps, and local land management information. The sample fires occurred between 1985 and 2013 and contained patches of high-severity, stand-replacing fire. Plots were established in monodominant, even-aged stands of the target species that established following the previous fire, with stand ages ranging from 4 to 32 years, and we assumed that all trees had established within the first post-fire growing season. Although there is evidence of seedling establishment 2–3 years post-fire (Vogl et al. 1977), the vast majority (> 95%) of establishment following stand-replacing fire occurs in the first post-fire growing season for both bishop pine (Holzman and Folger 2005) and knobcone pine (M.C. Agne, unpublished data). The historical fire regime is characterized by mean return intervals between 30–90 years (Sugnet 1985; van de Water and Safford 2011), suggesting that the chronosequence covers the period during which immaturity risk is greatest (i.e., the first several decades post-fire). Plots were established at least 50 m from roads and had no evidence of management following the most recent fire. Plots covered the range of topographic features and stand densities within each fire perimeter and were separated by at least 100 m, except when on opposing aspects. During the summers of 2016–2020, we established 31 and 38 plots in bishop pine and knobcone pine stands, respectively. Two to ten plots were sampled in each past fire (each fire represented a single stand age), varying by area that met our sampling criteria.

Field data collection

We measured live, standing dead, and fallen trees from the most recent post-fire cohort within a central subplot at each plot. Central subplot radii were chosen to capture ~50 trees and thus varied with stand density, ranging from 2 to 18 m (total sampling area range: 12.6–1017.9 m²). All trees were assessed for disease presence (western gall rust, pitch canker) and measured for diameter at breast height (DBH; 1.37 m above ground). All mature cones were tallied by status: closed (majority of cone scales sealed), open (majority of cone scales open), or damaged (evidence of seed predation or mechanical damage). Full visibility of tree crowns allowed counting of all cones on each tree. Field work occurred in warm and dry weather, so scale contraction (and mischaracterization of cones) due to high relative humidity (Vogl 1973) was unlikely. We did not directly assess seed density within cones, but estimates of seed density within closed cones range from 61 to 95 and 62 to 78 mean seeds cone⁻¹ for knobcone pine (Fry and Stephens 2013) and bishop pine, respectively (S. Bisbing, unpublished data), with seed viability >60% upon reproductive maturity for both species. Tallies of trees and cones by status were scaled to the plot to obtain per hectare (trees ha⁻¹ and cones ha⁻¹) estimates. We measured understory and shrub cover along two 18-m transects at each plot using a point-intercept method (Fontaine et al. 2012). We tallied shrubs intercepting the transect at 1-m intervals (n = 36) and divided shrub interceptions by the number of points measured to obtain an estimate of shrub cover.

Climate and site condition variables

We obtained climate data at a monthly resolution for our sites from ClimateNA, a software package that locally downscales historical climate data to scale-free point estimates (Wang et al. 2016). Given that our analysis seeks to understand climate effects on aggregate measures of demographic trends over the interfire period (e.g., canopy seed bank accumulation over multiple growing seasons), we aggregated annual climate variables as a mean value for the entire growing period (one year following the most recent fire to the year of measurement) for each plot. We considered growing season (March to October) mean annual precipitation and cumulative moisture deficit (CMD) as candidate predictors given the importance of water availability to reproductive capacity and demographic performance in seasonally dry forests (Redmond et al. 2012). The two predictors were strongly collinear, so we assessed parallel model forms with each climate
variable included during model evaluation (detailed under Statistical analysis).

In addition to regional climate, we characterized site-level topo-climate using three topographic predictors: heat load index (HLI), topographic position index (TPI), and topographic wetness index (TWI). HLI represents the amount of direct incident radiation to a site (McCune and Keon 2002), TPI represents its relative topographic position (i.e., ridge or valley) (Weiss 2001; De Reu et al. 2013), and TWI reflects a site’s potential moisture balance (Gessler et al. 1995). We calculated these indices from 30-m digital elevation models (U.S. Geological Survey 1999) using the Geomorphometry and Gradient Metric Toolbox (Evans et al. 2014) in ArcMap version 10.6.1 (ESRI 2018). Only HLI was retained as a candidate predictor for model fitting due to collinearity among topographic variables and poor interspersion of TPI and TWI across stand age.

We also obtained spatial data that reflected soil characteristics from the Probabilistic Remapping of SSURGO (POLARIS) database, a spatially contiguous soils dataset that provides a suite of ecologically relevant soils variables (Chaney et al. 2016). We extracted depth to bedrock and percent soil clay as two candidate predictors as they represent a proxy for soil fertility and can influence forest productivity (Romanyà and Vallejo 2004; Wall and Westman 2006). However, depth to bedrock was strongly collinear with mean growing season CMD, so only percent soil clay was retained as a candidate predictor for model fitting.

Statistical analysis

To address questions 1 and 2, we fit generalized linear mixed models for each of the following response variables: tree-level probability of reproductive maturity (cone presence/absence on individual live trees), tree-level cone production [total cones (of all classes) individual$^{-1}$ on live trees with ≥1 cone], stand-level proportion reproductively mature individuals (proportion of standing live and dead trees within a stand with ≥1 cone; hereafter, stand-level proportion mature trees), and stand-level closed cone density (closed cones on standing live and dead trees ha$^{-1}$). To address question 3, we fit a generalized linear mixed model for the response variable stand-level tree mortality of the post-fire cohort (standing and fallen dead trees ha$^{-1}$). Tree-level probability of reproductive maturity was fit with a binomial error structure while tree-level cone production was fit with a negative binomial error structure. Stand-level proportion mature trees was fit with a zero-inflated beta error structure as appropriate for proportion data (Zuur et al. 2009). Stand-level closed cone density and tree mortality were fit with zero-inflated negative binomial error structures and an offset term [log(plot area)] to account for variable sampling area (Zuur et al. 2009). All models fit with a negative binomial error structure were also fit with a Poisson error structure, but Poisson-distributed models were removed from consideration due to overdispersion. Stand-level models included a random effect of fire, and candidate models included the following suite of potential fixed predictor variables: stand age (years since last stand-replacing fire), species, stand density [density of the post-fire cohort, including live and dead individuals (log transformed trees ha$^{-1}$)], shrub percent cover, HLI, percent soil clay, mean growing period precipitation or CMD, and stand age—stand density interaction. Tree-level models included nested random effects of plot within sample fire, and candidate models included the stand-level fixed predictor variables assessed for the stand-level models and the following tree-level predictor variables: DBH, disease incidence, DBH—stand age, DBH—species, and DBH—stand density interactions. Predictor variables were assessed for collinearity prior to model fitting.

Models were fit using standardized predictors (mean-centered per two standard deviations) to discern relative effects of each predictor. Models with all terms included were fit for each response variable, and model diagnostic tests were conducted. When the full model did not meet assumptions, a suite of new models was fit, each with a single predictor term (all except stand age) removed. This process was repeated until a model was fitted that met assumptions. If two models with the same number of predictors met assumptions, the model with the lowest AICc was selected for inference. We interpreted $P \leq 0.01$ as strong, $P \leq 0.05$ as moderate, and $P \leq 0.10$ as suggestive evidence of an effect (Ramsey and Schafer 2012). Models were fit with the glmmTMB package (Brooks et al. 2017), diagnostics were conducted using DHARMa (Hartig 2021), and effects were visualized using broom (Robinson et al. 2021), ggeffects (Lüdecke 2018), ggplot (Wickham 2016), ggrepur
(Kassambara 2020), and jtools (Long 2020). Analyses were conducted in R version 4.0.5 (R Core Team 2021).

Results

We counted 68,400 cones on 4573 trees (2121 knobcone pine and 2452 bishop pine), 3855 of which were live when sampled (1960 knobcone pine and 1895 bishop pine). Stand structure varied widely both within and across stand age (Table 1). Stand density ranged from 147 to 82,800 live trees ha$^{-1}$. Live basal area and quadratic mean diameter were highly correlated with stand age, with median values of 0.5 m$^2$ ha$^{-1}$ and 2.0 cm at 6 years and 26.2 m$^2$ ha$^{-1}$ and 10.4 cm at 32 years (Table 1).

Reproductive capacity over time since fire

Cones were first present in stands by five years post-fire for bishop pine and six years post-fire for knobcone pine (Table 1), but time to reproductive maturity varied, with some stands lacking cones until eight years post-fire for both species. Average cone density remained under 10,000 cones ha$^{-1}$ for at least 10 years post-fire, after which there was a steep and continuous linear increase in cone production (Fig. 1). Incidence of cones on dead trees and damaged cones increased with time but closed cones represented the greatest proportion at all ages (Fig. 1A) and increased most steeply with age (Fig. 1B).

Tree-level reproductive capacity

Tree-level reproductive capacity was strongly associated with tree DBH, with an effect size more than two times greater than other predictors (Figs. 2, 3). Tree-level probability of reproductive maturity increased from near zero for trees < 2 cm DBH to nearly 100% for trees > 9 cm DBH, irrespective of all other drivers (Fig. 2A). There was a similarly strong effect of DBH on tree-level cone production, where cone production increased slowly for trees < 10 cm DBH but increased exponentially for trees > 15 cm DBH (Fig. 3A, B). Trees of a similar DBH had a greater probability of reproductive maturity and greater cone production in older stands than trees with the same DBH in younger stands (Figs. 2D, 3D). For example, probability of reproductive maturity for a tree of 4 cm DBH increased by > 40% (Fig. 2D) and cone production for a tree of 10 cm DBH increased by a factor of

| Stand age |
|---|
| 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 |
| Plots (n) | 4 | 2 | 5 | 3 | 6 | 2 | 4 | 8 | 3 | 2 | 14 | 9 | 15 | 2 | 6 | 3 | 23 | 10 | 3 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 |
| Species | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT | PIMU | PIAT |
| Trees (n) | 276 | 114 | 122 | 95 | 585 | 150 | 225 | 464 | 475 | 456 | 110 | 341 | 189 | 769 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 | 202 |
| Mean cones per tree | 0 | 0 | 0.01 | 0.10 | 0.14 | 0.53 | 1.01 | 1.89 | 9.85 | 13.33 | 2.08 | 17.23 | 62.74 | 75.39 | 47.06 | 10.4 | 10.3–12.6 | 2785 | 2288–3183 | 26.15 | 21.95–28.67 |
| Quadratic mean diameter (cm) | NA | NA | 2.0 | 1.8–2.2 | 1.2 | 1.0–1.5 | 2.8 | 5.6 | 3.6 | 8.8 | 6.6 | 8.9 | 12.2 | 13.8 | 10.4 | 10.3–12.6 | 2785 | 2288–3183 | 26.15 | 21.95–28.67 |
| Stand density (live trees ha$^{-1}$) | 3932 | 7582 | 5659 | 1837 | 54,643 | 7112 | 6797 | 2763 | 1723 | 4106 | 3417 | 2412 | 2735 | 2910 | 47.06 | 10.4 | 10.3–12.6 | 2785 | 2288–3183 | 26.15 | 21.95–28.67 |
| Live basal area (m$^2$ ha$^{-1}$) | 1840–6068 | 6013–9151 | 3830–9549 | 640–3034 | 13,440–82,761 | 1890–29,412 | 643–16,977 | 671–11,332 | 553–3631 | 943–18,104 | 2236–4598 | 1297–16,043 | 603–3979 | 147–28,736 | 2288–3183 | 26.15 | 21.95–28.67 |

Table 1 Summary statistics for stand structure attributes by stand age

PIMU bishop pine, PIAT knobcone pine
Fig. 1 Stand-level cone density by stand age for A all cone class (closed, open, damaged) by tree status (live, dead) combinations, B closed cones (cones presumed to contribute to the canopy seed bank) by tree status. Colors represent average plot-level estimates by category for each stand age interpolated across the chronosequence using a loess smoother (span = 0.5)

Contrary to our expectation, stand density had a positive effect on tree-level probability of reproductive maturity (Fig. 2B). Trees in high-density stands were associated with a ~40% greater probability of reproductive maturity than trees in low-density stands at an age of 10 years, but this difference decreased to ~10% by 30 years (Fig. 2C). The positive effect of stand density was greatest for trees of larger DBH and there was no effect for trees < 2 cm DBH (Fig. 2E). As expected, trees in low-density stands had greater cone production, although this effect decreased in older stands (Fig. 3B, G). However, for trees with relatively large DBH, the effect of stand density on cone production was less than for smaller trees, with wide variation around the estimated effect (Fig. 3E). Holding other covariates constant, bishop pine individuals had double the cone production of knobcone pine, but there was no difference in probability of reproductive maturity between species (Figs. 2B, 3B, C). Cone production of trees in stands with high soil clay was double that of trees in stands with low soil clay (Fig. 3B, F). Disease incidence, HLI, mean growing season CMD or precipitation, and shrub cover had no effect on tree-level reproductive capacity (Appendix S2–S4 in the Electronic supplementary material).
Stand-level reproductive capacity

Stand-level reproductive capacity increased strongly with stand age. Stand-level proportion mature trees ranged from 0 to nearly 100%, with all observations of 0% occurring in stands < 10 years and all observations of > 90% occurring in stands ≥ 14 years (Fig. 4A). Estimated closed cone density increased by approximately two orders of magnitude between the initial years of reproductive maturity (5–6 years) and 30 years (Fig. 5A). The effect of stand age was mediated by stand density, with contrasting effects on each measure of stand-level reproductive capacity (Figs. 4B, 5B). There were strong negative effects of stand density and its interaction with stand age on proportion mature trees (Fig. 4B). For 10-year-old stands, proportion mature trees was estimated at > 50% for low-density stands, compared with < 25% for moderate to high-density stands, and the difference increased over time (Fig. 4C). Conversely, there was a strong positive effect of stand density on closed cone density, which declined with stand age (Fig. 5B). For young stands, estimated closed cone density was more than an order of magnitude greater in high-density stands than in low-density stands, but after ~ 20 years, closed cone densities were similar across stands of all densities (Fig. 5C). Effects of regional climate also varied by response variable. Mean growing season precipitation had a strong positive effect on proportion mature trees (Fig. 4B), while mean growing season CMD had no effect on closed cone density (Fig. 5B). Greater soil clay had positive
effects on both measures (Figs. 4E, 5D), although this effect was lower magnitude than other significant covariates in each model (Figs. 4B, 5B). Stand-level reproductive capacity did not differ between species (Figs. 4B, 5B; Appendix S5–S7 in the Electronic supplementary material). Stand density and stand age drove tree mortality (Fig. 6B); tree mortality in high-density stands was two orders of magnitude greater than that of low-density stands of the same age (Fig. 6D). Similarly, tree mortality increased by nearly two orders of magnitude between 10 and 30-year-old stands of the same density (Fig. 6A, D). Moisture stress further exacerbated tree mortality (Fig. 6B); high mean growing season CMD was associated with approximately one order of magnitude greater tree mortality compared with stands with low mean growing season CMD (Fig. 6E). Bishop pine also had significantly greater tree mortality than knobcone pine stands of a similar age and stand density.

Stand-level tree mortality

For stands ten years and older (n = 47), observed stand-level tree mortality in the post-fire cohort ranged from 0 to 85,100 dead trees ha⁻¹, and was strongly positively correlated with stand-level proportion dead trees (Appendix S8 in the Electronic supplementary material). 

Fig. 3 Effects of covariates from the tree-level cone production model. 

**A** Partial effect of DBH. Each point, shaded by stand age, represents a tree (n = 1806). 

**B** Effects of covariates on tree-level cone production. 

**C–H** Change in stand age and cone production across gradients of significant covariates. Symbols are described in Fig. 2.
Our study identifies three critically important drivers of demographic processes in serotinous forests as they develop following stand-replacing fires. First, stand age is the key driver of reproductive capacity—older stands have greater reproductive capacity regardless of all other drivers. Second, intraspecific competition associated with stand density mediated tree- and stand-level reproductive capacity at a given stand age, while interspecific competition from shrubs had no detectable effect. Third, there were modest decreases in reproductive capacity and increases in tree mortality associated with warm and dry regional climate, although topo-climate had little effect. Collectively, these findings have important implications for serotinous forest resilience in a changing climate. Overriding other factors is the minimum fire-free period necessary for serotinous population persistence—change in other drivers cannot compensate for the importance of the fire interval. However, once stands exceed the minimum fire-free period, differences in stand structure produce divergent outcomes in reproductive maturity for stands of the same age. Our results are also consistent with the demographic shift described by Enright et al. (2015) suggesting that warming and drying conditions constrain the reproductive output of serotinous populations during the fire-free period. Although the demographic mechanisms underpinning
resilience are aligned to current conditions, continued climate warming and increased fire activity may have profound effects on serotinous forest persistence.

Rapid post-fire canopy seed bank accumulation suggests that the window for immaturity risk is brief for California closed-cone pine species. Closed cone development first occurred at five and six years for bishop pine and knobcone pine, respectively, suggesting that complete loss of these species from a site would occur if fire return intervals were shorter than this period—currently a rare occurrence. Early onset of cone production is common in strongly serotinous species adapted to frequent stand-replacing fire (Enright et al. 1996; Turner et al. 2007; Climent et al. 2008), serving as an important mechanism of resilience to population loss to short-interval fire (Tapias et al. 2001). Population self-replacement, however, requires a considerably longer fire-free interval (Burrows 2008; Gosper et al. 2013). Estimates for knobcone pine suggest the mean cone to seedling conversion ratio is 1:1 (M.C. Agne, unpublished data), or ~60 to 100 seeds for one established seedling (Fry and Stephens 2013). Therefore, mean canopy seed bank accumulation to regenerate at 1500 seedlings ha\(^{-1}\) [low seedling density for closed-cone pine (Keeley et al. 1999)] and at 15,000 seedlings ha\(^{-1}\) [moderate seedling density for closed-cone pine (Holzman and Folger 2005)] does not occur until 10 and 20 years, respectively. Although self-replacement is dependent on a variety of factors, we expect that the seedling density associated with self-replacement

**Fig. 5** Effects of covariates from the stand-level closed cone density model. **A** Partial effect of stand age. Each point, shaded by stand density (log-transformed), represents a plot (n=69). **B** Effects of covariates on stand-level closed cone density. **C, D** Change in stand age and closed cone density across gradients of significant covariates. Symbols are described in Fig. 2.
is toward the high end of this range. Canopy seed bank accumulation may begin to slow near the end of our chronosequence (~30 years; Fig. 1a), suggesting that sufficient seed is stored and available to regenerate the stand before three decades post-fire (Lamont et al. 1991). Thus, seed limitation is likely prior to 10 years and is unlikely after 20 years post-fire. Additional factors can alter seed availability for stands of any age, but their effects are most important between 10 and 20 years post-fire. Further, although our study focused on factors in the post-fire environment that control demographic processes, differences between pre-fire stand structure, fire intensity or fire season may have important effects on the post-fire cohort and could be considered in future studies.

Although stand age is the key driver of reproductive capacity in California closed-cone pines, strong effects of intraspecific competition suggest buffering against immaturity risk differs with stand structure. Negative effects of intraspecific competition on tree-level cone production are common for serotinous species (Esler and Cowling 1990; Moya et al. 2008). However, we found that this applied most strongly to trees with the smallest DBH. Tree-level reproductive capacity was greatest for relatively large trees, regardless of other factors, suggesting a synergy rather than trade-off between vegetative and reproductive growth.

**Fig. 6** Effects of covariates from the stand-level tree mortality model. A Partial effect of stand age. Each point, shaded by stand density (log-transformed), represents a plot (n = 47). Note: Two points at 49,400 and 85,100 trees ha\(^{-1}\) were omitted for interpretability. B Effects of covariates on stand-level tree mortality. C–E Change in stand age and tree mortality across gradients of significant covariates. Symbols are described in Fig. 2.
(Alfaro-Sánchez et al. 2015). These tree-level effects scaled up to delay the peak in stand-level reproductive maturity, similar to findings for *P. coulteri* and *P. halepensis* (Borchert 1985; Moya et al. 2008). Despite negative effects on tree-level cone production, high stand densities during the first two decades of stand development increased the canopy seed bank, with the increase in cone-bearing trees outweighing the decrease in cones per tree, similar to other serotinous species (Esler and Cowling 1990; Moya et al. 2007; Turner et al. 2007). Despite strong intraspecific competition, high post-fire stand densities provide a buffer against immaturity risk should a subsequent fire occur prior to the mean fire return interval, as well as a post-fire environment with low interspecific competition (Harvey and Holzman 2014). Short-interval fire activity is common within the study area (Reilly et al. 2019) and fire intervals < 20 years may increase with continued climate warming. By ~20 years, closed cone density converges across levels of stand density, indicating that the range of stand structural development pathways that occur for serotinous species (Harvey and Holzman 2014; Turner et al. 2016) can lead to sufficient canopy seed bank development, given adequate time.

Tree mortality associated with regional moisture stress suggests a demographic shift is expected with climate warming in California closed-cone pine forests. Stand-level tree mortality was primarily associated with stand age and density, suggesting the dominant process controlling mortality was density-dependent thinning, consistent with expected stand dynamics (Harvey et al. 2011). However, an additional effect of high growing season cumulative moisture deficit suggests that warming climate may exacerbate background mortality, similar to findings in subalpine forests (Andrus et al. 2021). Increased tree mortality could decrease the reproductive capacity of stands if live trees cannot compensate for the loss of reproductively mature trees through increased cone production. Our assessment of tree mortality necessarily underestimates mortality rates due to disappearing evidence of mortality of small trees over time; future studies that track stands over time may provide more precise estimates. Stand-level reproductive maturity was also delayed where growing season precipitation was low, signaling some evidence of direct climate effects on reproductive capacity. However, there was no evidence of depressed canopy seed bank availability due to regional or local climate. Climate can also influence seed density within cones and seed viability (Moya et al. 2007), which were not evaluated in this study. Further research on annual cone and seed production responses to annual variation in climate is needed to predict future demographic trends.

Our findings have broad implications for demographic mechanisms underpinning serotinous forest persistence across North America. We expect that while rates of cone production vary among species, the period prior to reproductive maturity is brief relative to the historical mean fire return interval (Tapias et al. 2001; Turner et al. 2007). However, time to canopy seed bank accumulation sufficient for self-replacement is considerably longer and varies with stand density (Moya et al. 2007). Rapid development of a large canopy seed bank in high-density stands suggests that high establishment densities exhibited by serotinous conifers (Verkaik and Espelta 2006; Harvey and Holzman 2014) represent a resilience mechanism to short-interval fires. While serotinous populations may be able to persist at lower densities following a single short-interval severe fire (Keeley et al. 1999; Turner et al. 2019), they are unlikely to withstand recurrent short-interval fire activity (Espelta et al. 2008; Bassett et al. 2015). Demographic rates must be assessed in the context of the expected shortening of the fire-free interval to understand when erosion of serotinous forest resilience to fire may occur. While not investigated here, demographic trends for longer fire intervals are also needed to determine how the potential for senescence risk affects long-term persistence of serotinous conifers.

**Conclusion**

Reproductive capacity recovered rapidly following high-severity fire in California closed-cone pine forests, suggesting that the window for immaturity risk is brief. Differences in the canopy seed bank among stand trajectories suggest that high-density stands are more buffered against immaturity risk than are low-density stands during the critical early post-fire window. Evidence of decreased reproductive capacity and increased tree mortality associated with moisture stress suggest that a demographic shift may further dampen seed availability. Although the demographic
mechanisms we investigate here are aligned to relatively frequent high-severity fires, continued climate warming and increased fire activity may overwhelm these mechanisms. Understanding how fuels and associated fire hazard develop in tandem with reproductive capacity is critical for predicting serotinous forest persistence under future conditions.

Acknowledgements We thank J. Gibson, E. Engber, S. Kren, and K. Kephart for supporting this research. We received analytical advice from M. Buonanduci and K. Rodman. Field and logistical support were provided by D. Canestro, D. Chapman, J. Hulbert, A. Link, F. Nelson, T. Sterberg, K. Stork, A. Ubaka-Sampson, and W. Veber. Comments from two anonymous reviewers greatly improved this manuscript. This research was funded by the Australian Research Council award DP170101288, a Murdoch University Strategic PhD Scholarship, a U.S. Geological Survey Northwest Climate Adaptation Science Center award G17AC000218, the Achievement Rewards for College Scientists (ARCS) Foundation, the Graduate Research Innovation Award from the Joint Fire Science Program (award #19-1-01-16), and the University of Washington.

Authors’ contributions All authors contributed to the study conception and design. Data collection and analysis were performed by MCA. The first draft of the manuscript was written by MCA and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This research was funded by the Australian Research Council award DP170101288 to NJE and JBF and a Murdoch University Strategic PhD Scholarship to MCA, a U.S. Geological Survey Northwest Climate Adaptation Science Center award G17AC000218 to BJH and MCA, the Achievement Rewards for College Scientists (ARCS) Foundation to MCA, the Graduate Research Innovation Award from the Joint Fire Science Program (award #19-1-01-16) to BJH and MCA, and the University of Washington.

Availability of data and material All data presented in this study are available from the first author upon reasonable request.

Code availability The code used for analysis is available upon reasonable request.

Declarations

Conflict of interest All Authors declare that they have no competing interest.

References

Alfaro-Sánchez R, Camarero JJ, López-Serrano FR, Sánchez-Salguero R, Moya D, Heras JDL (2015) Positive coupling between growth and reproduction in young post-fire Aleppo pines depends on climate and site conditions. Int J Wildland Fire 24:507. https://doi.org/10.1071/WF14045
Andrus RA, Harvey BJ, Hoffman A, Veblen TT (2020) Reproductive maturity and cone abundance vary with tree size and stand basal area for two widely distributed conifers. Ecosphere. https://doi.org/10.1002/ecs2.3092
Andrus RA, Chai RK, Harvey BJ, Rodman KC, Veblen TT (2021) Increasing rates of subalpine tree mortality linked to warmer and drier summers. J Ecol 109:2203–2218. https://doi.org/10.1111/1365-2745.13634
Bassett OD, Prior LD, Slijkerman CM, Jamieson D, Bowman DMJS (2015) Aerial sowing stopped the loss of alpine ash (Eucalyptus delegatensis) forests burnt by three short-interval fires in the Alpine National Park, Victoria, Australia. For Ecol Manag 342:39–48. https://doi.org/10.1016/j.foreco.2015.01.008
Boer MM, Resco de Dios V, Bradstock RA (2020) Unprecedented burn area of Australian mega forest fires. Nat Clim Chang 10:170–172. https://doi.org/10.1038/s41558-020-0710-7
Borchert M (1985) Serotiny and cone-habit variation in populations of Pinus coulteri (Pinaceae) in the southern Coast Ranges of California. Madroño 32:29–48
Brooks ME, Kristensen K, van Bentheim KJ, Magnussen A, Berg CW, Nielsen A, Skaug HJ, Maecheler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400
Burrows ND (2008) Linking fire ecology and fire management in south-west Australian forest landscapes. For Ecol Manag 255:2394–2406. https://doi.org/10.1016/j.foreco.2008.01.009
Chaney NW, Wood EF, McBratney AB, Hempel JW, Nauern TW, Brungard CW, Odgers NP (2016) POLARIS: A 30-meter probabilistic soil series map of the contiguous United States. Geoderma 274:54–67. https://doi.org/10.1016/j.geoderma.2016.03.025
Climent J, Prada MA, Calama R, Chambel MR, de Ron DS, Alia R (2008) To grow or to seed: ecotypic variation in reproductive allocation and cone production by young female Aleppo pine (Pinus halepensis, Pinaceae). Am J Bot 95:833–842. https://doi.org/10.3732/ajb.2007354
Coop JD, Parks SA, Stevens-Rumann CS, Crausby SD, Higuera PE, Hurteau MD, Tepley A, Whitman E, Assal T, Collins BM, Davis KT, Dobrowski S, Falk DA, Fornwald PJ, Fulé PZ, Harvey BJ, Kane VR, Littlefield CE, Margo-lis EQ, North M, Parisien M-A, Prichard S, Rodman KC (2020) Wildfire-driven forest conversion in western North American landscapes. Bioscience 70:659–673. https://doi.org/10.1093/biosci/biaa061
Davi H, Cailleret M, Restoux G, Amm A, Pichot C, Fady B (2016) Disentangling the factors driving tree reproduction. Ecosphere 7:e01389. https://doi.org/10.1002/ecs2.1389
Davis KT, Higuera PE, Sala A (2018) Anticipating fire-mediated impacts of climate change using a demographic framework. Funct Ecol 32:1729–1745. https://doi.org/10.1111/1365-2435.13132
Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, Maneta MP (2019) Wildfires and climate change push low-elevation forests across...
a critical climate threshold for tree regeneration. Proc Natl Acad Sci USA 116:6193–6198. https://doi.org/10.1073/pnas.1815107116

De Reu J, Bourgeois J, Bats M, Zwertiaeghe A, Gelorini V, De Smedt P, Chu W, Antrop M, De Maeyer P, Finke P, Van Meirvenne M, Verniers J, Crombé P (2013) Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49. https://doi.org/10.1016/j.geomorph.2012.12.015

Eidenshink J, Schwind B, Brewer K, Zhu Z-L, Quayle B, Howard S (2007) A project for monitoring trends in burn severity. Fire Ecol 3:3–21. https://doi.org/10.4996/fireecology.0301003

Enright NJ, Lamont BB, Marsula R (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, Banksia hookeriana. J Ecol 84:9. https://doi.org/10.2307/2261695

Enright NJ, Fontaine JB, Lamont BB, Miller BP, Westcott VC (2014) Resistance and resilience to changing climate and fire regime depend on plant functional traits. J Ecol 102:1572–1581. https://doi.org/10.1111/1365-2745.12306

Enright NJ, Fontaine JB, Bowman DM, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front Ecol Environ 13:265–272. https://doi.org/10.1890/140231

Environmental Systems Research Institute [ESRI] (2018) ArcGIS Release 10.6.1. ESRI, Redlands, CA

Esler KJ, Cowling RM (1990) Effects of density on the reproductive output of Protea leptophloecarpodendron. S Afr J Bot 56:29–33. https://doi.org/10.1016/S0254-6299(16)31107-3

Espelta JM, Verkaik I, Eugenio M, Lloret F (2008) Recurrent wildfires constrain long-term reproduction ability in Pinus halepensis Mill. Int J Wildland Fire 17:579. https://doi.org/10.1071/WF07126

Evans JS, Oakleaf J, Cushman SA, Theobald D (2014) An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0–0. http://evansmurphy.wix.com/evansspatial

Fairman TA, Bennett LT, Tupper S, Nitschke CR (2017) Frequent wildfires erode tree persistence and alter stand structure and initial composition of a fire-tolerant subalpine forest. J Veg Sci 28:1151–1165. https://doi.org/10.1111/jvs.12575

Fontaine JB, Westcott VC, Enright NJ, Lade JC, Miller BP (2012) Fire behaviour in south-western Australian shrublands: evaluating the influence of fuel age and fire weather. Int J Wildland Fire 21:385–395. https://doi.org/10.1071/WF11065

Fry D, Stephens S (2013) Field note: Seed viability and female cone characteristics of mature knobcone pine trees. West J Appl For 28:46–48. https://doi.org/10.5849/wjaf.11-046

Gauthier S, Bergeron Y, Simon J-P (1996) Effects of fire regime on the serotiny level of jack pine. J Ecol 84:539–548. https://doi.org/10.2307/2261476

U.S. Geological Survey (1999) National elevation dataset. ned.usgs.gov. Accessed 1 Feb 2021

Gessler PE, Moore ID, McKenzie NJ, Ryan PJ (1995) Soil-landscape modelling and spatial prediction of soil attributes. Int J Geogr Inf Syst 9:421–432. https://doi.org/10.1080/02693799508902047

Gosper CR, Prober SM, Yates CJ (2013) Estimating fire interval bounds using vital attributes: implications of uncertainty and among-population variability. Ecol Appl 23:924–935. https://doi.org/10.1890/12-0621.1

Greene DF, Messier C, Asselin H, Fortin M-J (2002) The effect of light availability and basal area on cone production in Abies balsamea and Picea glauca. Can J Bot 80:370–377. https://doi.org/10.1139/b02-020

Hansen WD, Turner MG (2019) Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. Ecol Monogr 89:e01340. https://doi.org/10.1002/ecm.1340

Harper JL (1977) Population biology of plants. Academic Press, London

Hartig F (2021) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.0. https://CRAN.R-project.org/package=DHARMa

Harvey BJ, Holzman BA (2014) Divergent successional pathways of stand development following fire in a California closed-cone pine forest. J Veg Sci 25:88–99. https://doi.org/10.1111/jvs.12073

Harvey BJ, Holzman BA, Davis JD (2011) Spatial variability in stand structure and density-dependent mortality in newly established post-fire stands of a California closed-cone pine forest. For Ecol Manag 262:2042–2051. https://doi.org/10.1016/j.foreco.2011.08.045

Holzman BA, Folger K (2005) Post-fire vegetation response in the bishop pine forest at Point Reyes National Seashore. Vision fire, lessons learned from the October 1995 fire. U.S. Department of the Interior, Washington, DC, pp 49–57

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GL, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378. https://doi.org/10.1002/fee.1311

Kassambara A (2020) ggpubr: “ggplot2” Based Publication Ready Plots. R package version 0.4.0. https://CRAN.R-project.org/package=ggpubr

Keeley JE, Ne’eman G, Fotheringham CJ (1999) Immaturity risk in a fire-dependent pine. J Mediterr Ecol 1:41–48

Lamont BB, Enright NJ (2000) Adaptive advantages of aerial seed banks. Plant Spec Biol 15:157–166. https://doi.org/10.1046/j.1442-1984.2000.00036.x

Lamont BB, Maitre DCL, Cowling RM, Enright NJ (1991) Canopy seed storage in woody plants. Bot Rev 57:277–317

Long JA (2020) jtools: Analysis and Presentation of Social Scientific Data. R package version 2.1.0. https://cran.r-project.org/package=jtools

Lüdecke D (2018) gggeffects: tidy data frames of marginal effects from regression models. J Open Source Softw 3:782. https://doi.org/10.21105/joss.00772

McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606


Moya D, Espelta JM, Verkaik I, López-Serrano F, Las Heras J (2007) Tree density and site quality influence on Pinus halepensis Mill. reproductive characteristics after large fires. Ann for Sci 64:649–656. https://doi.org/10.1051/for-est:2007043

Moya D, Espelta JM, López-Serrano FR, Eugenio M, Heras JD (2008) Natural post-fire dynamics and serotiny in 10-year-old Pinus halepensis Mill. stands along a geographic gradient. Int J Wildland Fire 17:287. https://doi.org/10.1071/WF06121

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1:535–545. https://doi.org/10.1007/s100219900049

Parks SA, Abatzoglou JT (2020) Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. Geophys Res Lett 47:e2020GL089858. https://doi.org/10.1029/2020GL089858

Pausas JG, Keeley JE (2014) Evolutionary ecology of resprouting and seedling in fire-prone ecosystems. New Phytol 204:55–65. https://doi.org/10.1111/nph.12921

PRISM Climate Group (2019) Oregon State University. http://prism.oregonstate.edu. Accessed 12 Dec 2019

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramsey F, Schafer D (2012) The statistical sleuth: a course in methods of data analysis, 3rd edn. Cengage Learning, Boston, MA

Redmond MD, Forcella F, Barger NN (2012) Declines in pinyon pine cone production associated with regional warming. Ecosphere 3:art120. https://doi.org/10.1890/ES12-00306.1

Reilly MJ, Monleon VJ, Jules ES, Butz RJ (2019) Range-wide population structure and dynamics of a serotinous conifer, knobcone pine (Pinus attenuata L.), under an anthropogenically-altered disturbance regime. For Ecol Manag 441:182–191. https://doi.org/10.1016/j.foreco.2019.03.017

Robinson D, Hayes A, Couch S (2021) broom: Convert Statistical Objects into Tidy Tibbles. R package version 0.7.6. https://CRAN.R-project.org/package=broom

Romanyà J, Vallejo VR (2004) Productivity of Pinus radiata plantations in Spain in response to climate and soil. Forest Ecol Manag 195:177–189. https://doi.org/10.1016/j.foreco.2004.02.045

Romme WH (1982) Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52:199–221. https://doi.org/10.2307/1942611

Schaffer B, Hawksworth FG, Jacobi WR (1983) Effects of comandra blister rust and dwarf mistletoe on cone and seed production of lodgepole pine. Plant Dis 67:215–217

Singh P, Carew GC (1990) Inland spruce cone rust of black spruce: effect on cone and seed yield, and seed quality. For Pathol 20:397–404. https://doi.org/10.1111/j.1439-0329.1990.tb01154.x

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252. https://doi.org/10.1111/ele.12889

Sugnet PW (1985) Fire history and post-fire stand dynamics of Inverness bishop pine populations. Master’s thesis, University of California, Berkeley

Tapia A, Gil L, Fuentes-Utrilla P, Pardos JA (2001) Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between Pinus halepensis Mill., P. pinaster Ait., P. nigra Arn. and P. pinea L. J Ecol 89:629–638

Torregrosa A, Combs C, Peters J (2016) GOES-derived log and low cloud indices for coastal north and central California ecological analyses. Earth Space Sci 3:46–67. https://doi.org/10.1002/2015ES005019

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849. https://doi.org/10.1890/10-0097.1

Turner MG, Romme WH, Gardner RH (1999) Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park. Wyoming Int J Wildland Fire 9:21. https://doi.org/10.1071/WF99003

Turner MG, Turner DM, Romme WH, Tinker DB (2007) Cone production in young post-fire Pinus contorta stands in Greater Yellowstone (USA). For Ecol Manag 242:119–126. https://doi.org/10.1016/j.foreco.2006.12.032

Turner MG, Whitby TG, Tinker DB, Romme WH (2016) Twenty-four years after the Yellowstone Fires: are postfire lodgepole pine stands converging in structure and function? Ecology 97:1260–1273. https://doi.org/10.1890/15-1585.1

Turner MG, Brazuinhas KH, Hansen WD, Harvey BJ (2019) Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc Natl Acad Sci USA 116:11319–11328. https://doi.org/10.1073/pnas.190241116

del van Water KM, Safford HD (2011) A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecol 7:26–58. https://doi.org/10.4996/fireecology.0703026

Verkaik I, Espelta JM (2006) Post-fire regeneration thinning, cone production, serotiny and regeneration age in Pinus halepensis. Forest Ecol Manag 231:155–163. https://doi.org/10.1016/j.foreco.2006.05.041

Viglas JN, Brown CD, Johnstone JF (2013) Age and size effects on seed productivity of northern black spruce. Can J For Res 43:534–543. https://doi.org/10.1139/cjfr-2013-0022

Vogel RJ (1973) Ecology of knobcone pine in the Santa Ana Mountains, California. Ecol Monogr 43:125–143. https://doi.org/10.2307/1942191

Vogel RJ, Armstrong WP, White KL, Cole KL (1977) The closed-cone pines and cypress. In: Barbour MG, Major J (eds) Terrestrial vegetation of California. Wiley, New York, pp 295–358

Walker B, Holling CS, Carpenter SR, Kinzig AP (2004) Resilience, adaptability and transformability in social-ecological systems. Ecol Soc. https://doi.org/10.5751/ES-00650-090205

Wall A, Westman CJ (2006) Site classification of afforested arable land based on soil properties for forest production. Can J For Res 36:1451–1460. https://doi.org/10.1139/x06-031

Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially customizable climate data for
historical and future periods for North America. PLoS ONE 11:e0156720. https://doi.org/10.1371/journal.pone.0156720

Weiss AD (2001) Topographic position and landforms analysis. In: ESRI Users Conference. San Diego

Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York

Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD, Dean JS, Cook ER, Gangodagamage C, Cai M, McDowell NG (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nat Clim Chang 3:292–297. https://doi.org/10.1038/nclimate1693

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology and R. Springer, New York

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.