Range-wide population structure and dynamics of a serotinous conifer, knobcone pine (*Pinus attenuata* L.), under an anthropogenically-altered disturbance regime

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ARTICLE INFO

ABSTRACT

There is growing concern that populations of fire-adapted species around the world are at risk of extirpation due to 20th century fire exclusion (i.e. senescence risk). Concurrently, increasing fire activity in many regions is prompting concern that repeated, short-interval fire poses a risk to young stands before trees reach reproductive maturity (i.e. immaturity risk). Conceptual models assessing vulnerability to both risks exist, yet there is a lack of empirically-based studies that assess the effects of anthropogenically-altered fire regimes across the entire range of a fire-adapted species. We used geospatial data on fire occurrence (1900–2015) and a systematic sample of recently re-measured (~2005–2015) forest inventory plots across the range of a serotinous conifer, knobcone pine (*Pinus attenuata*), in California and southwestern Oregon, U.S.A. to assess the relative threat of immaturity and senescence risk. We base our assessment on: (1) recent trends in area burned, (2) geographic variability and changes in stand-scale population structure, and (3) patterns of local colonization, extirpation, and population change. The area burned across the species range was lowest during the early and mid-20th century and increased in the early 1980s. Approximately 39% of the range burned between 1984 and 2015 and fire rotation was 81 years for the 25-year period ending in 2015. During this period, approximately 6% of the range of knobcone pine experienced repeated fire, and only 4% of the reburned area (~0.25% of the entire range) experienced multiple fires at an interval less than 10 years. Most populations of knobcone pine currently exist in a mature or decadent state and we found evidence of recent senescence-related extirpation across approximately 15% of its range. However, we also observed a cumulative expansion of knobcone pine during the last decade, and the rate of colonization (less than half of which was associated with fire) was almost double that of extirpation. Despite high rates of colonization and expansion of knobcone pine in response to recent fires, vulnerability to extirpation varies geographically and remains high in some parts of the species range where wildfire activity has been low. This study provides a rare empirically-based look at the contribution of extirpation and colonization to the range-wide dynamics of a serotinous tree. Our findings underlie the importance of recognizing the different temporal and spatial scales at which contemporary disturbance regimes threaten fire-adapted species, and highlight the potential for alternative pathways of persistence and expansion of serotinous species.

1. Introduction

Fire plays an important role in the evolution of life history strategies of many plant species around the world (Bond and van Wilgen, 1996; Enright et al., 1996; Keeley et al., 2011; Pausas and Schwilk, 2012). There is long-standing global concern that many populations of fire-adapted species currently exist in a decadent state and are at risk of local extirpation (i.e. "senescence risk") due to fire exclusion during the 20th century (Bond, 1980; Ne'eman et al., 1999; Gent and Morgan, 2007; Fry et al., 2012). At the same time, recent and projected increases in fire activity associated with longer fire seasons and increasing drought in many regions is prompting concern that repeated, short-interval fire poses a risk to young stands before trees reach reproductive maturity (i.e. "immaturity risk" or "interval squeeze") (Zedler et al.,
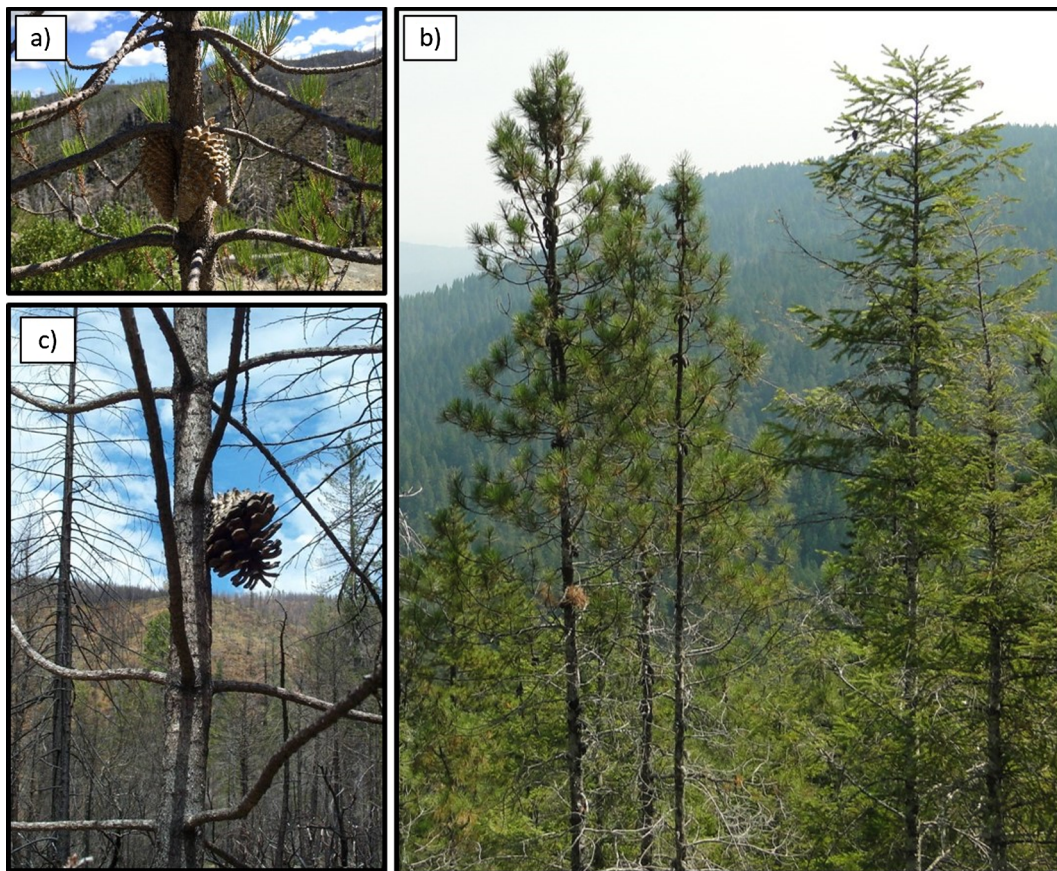

Fig. 1. Knobcone pine (*Pinus attentuata*) (a) with closed cones, (b) growing with Douglas-fir (*Psuedotsuga menziesii*) in the Klamath Mountains of northern California, and (c) open cones following stand-replacing fire. Photo credits E. Jules.

1983; Keeley et al., 1999; Buma et al., 2013; Enright et al., 2015; Bowman et al., 2016). Conceptual models for assessing vulnerability to both risks exist (Buma et al., 2013; Enright et al., 2015), yet there is a lack of empirically-based studies that assess the effects of anthropogenically-altered disturbance regimes across the entire range of a fire-adapted species.

Serotiny is a common trait and life history strategy of woody plants in fire-prone landscapes (Lamont et al., 1991). Serotinous species store seeds in closed-cones that reinitiate populations when a fire burns intensely enough to melt resins, open cone scales, and trigger the release of seeds into post-fire environments with open canopies and reduced cover of surface litter (Schwilk and Ackerly, 2001; Enright et al., 1998). This reinitiation is critical as long fire-free intervals relative to the life span of a species pose a risk of local extirpation as individual trees senesce and die. Many serotinous species exhibit partial serotiny where cones open in the absence of fire throughout all or some of their range (Tonnabel et al., 2012), potentially as a bet-hedging strategy to variability in fire return intervals (Enright et al., 1998) and adaptation to drought. However, seedling establishment is unlikely in the absence of fire which exposes bare mineral soil and reduces canopy cover (Bond and Keeley, 2005). A number of studies document decadent populations of serotinous species fire-prone regions of Australia, South Africa, and North America (Bond, 1980; Brose and Waldrop, 2006; Gent and Morgan, 2007; Fry et al., 2012), but most studies infer decadence and senescence risk from a static examination of live and dead stand structure. Empirically-based observations of local extirpation are rare for any species (Keil et al., 2018) and few if any studies quantify stand scale extirpation and how it contributes to population dynamics at the scale of the entire range of a serotinous species.

Immaturity risk and interval squeeze (Zedler et al., 1983; Enright et al., 1996; Keeley et al., 1999) have received considerable attention

and developed conceptually in response to changing disturbance regimes over the last decade (Buma et al., 2013; Enright et al., 2015). Multiple case studies demonstrate reduced regeneration of serotinous conifers and other tree species following repeated, short-interval fire at stand- and landscape-scales (Keeley et al., 1999; Brown and Johnstone, 2012; Bowman et al., 2014; Fairman et al., 2017). Concerns surrounding the local extirpations of serotinous species from both immaturity and senescence risk include losses of biodiversity, decreased resilience of forests to high-severity fire, and state changes from forest to non-forest conditions (Buma et al., 2013). However, little is known about the relative or combined contribution of these processes to range-scale dynamics of a serotinous species. Assessing this issue requires an unbiased, multi-temporal look at contemporary dynamics and fire activity at the scale of the entire range of a species.

We use geospatial data on historical fire occurrence (1900–2015) and a spatially balanced sample of current population structure from a national forest inventory to assess the relative threat of senescence risk and immaturity risk across the range of knobcone pine (*Pinus attenuata* Lemm.). Knobcone pine is a strongly serotinous species that reproduces only from seed and is endemic to parts of California and southwestern Oregon, U.S.A. This species is commonly associated with a developmental pathway characterized by establishment at high densities following stand-replacing fire (Keeley et al., 1999), though there is evidence of non-stand-replacing fire in some portions of its range (Fry et al., 2012). In the absence of subsequent fires, longer-lived, more shade-tolerant species eventually replace knobcone pine as individual trees senesce and die (Vogl, 1973; Zedler et al., 1983; Fry et al., 2012). Estimates of historical fire frequency across most of its range varied from approximately 10–50 years (see Van de Water and Safford, 2011; Reilly et al., 2017 for fire history summaries). Following a long period of fire exclusion during the 20th century, fire activity has increased
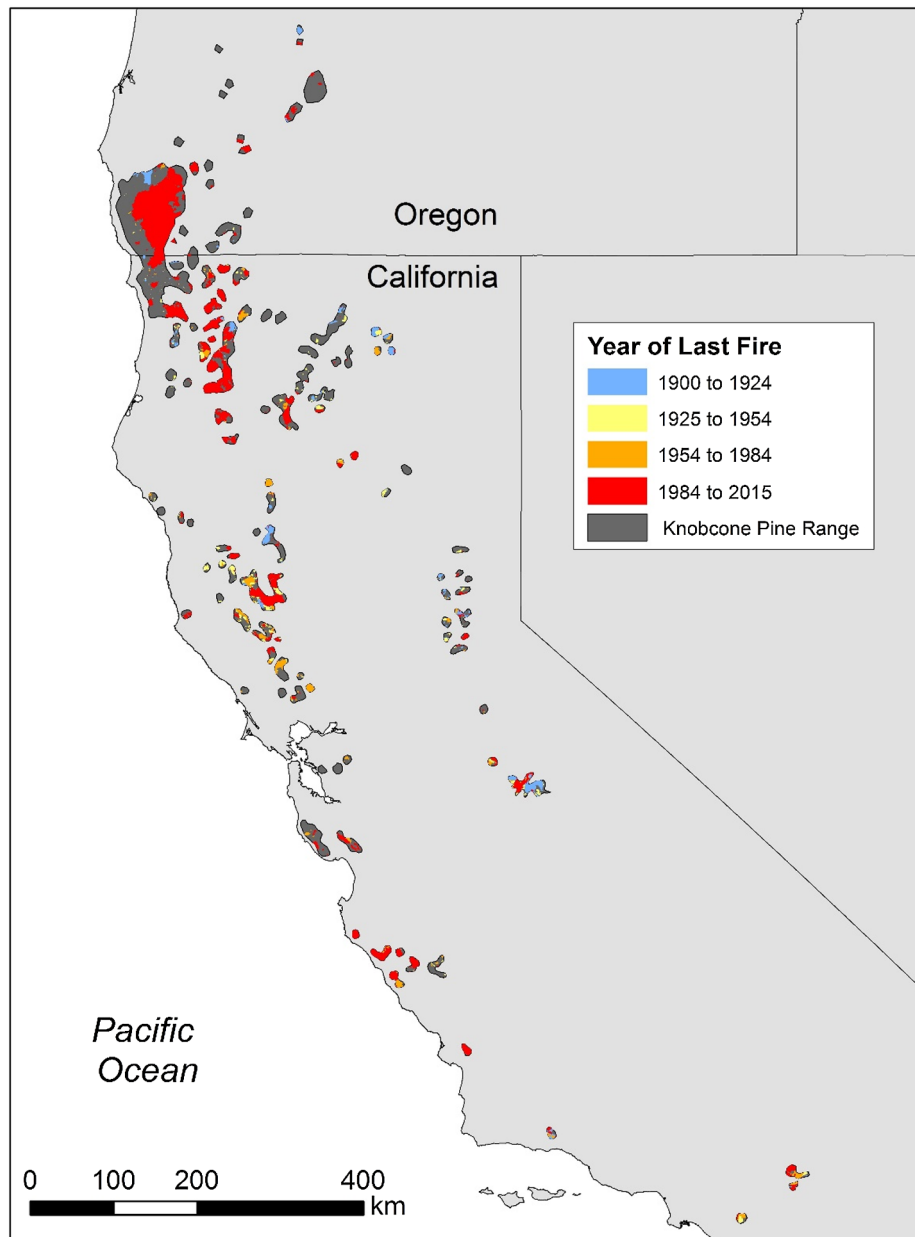
Fig. 2. Map of fire occurrence since 1900 within the range of knobcone pine (*Pinus attenuata*) in southwestern Oregon and California, U.S.A. Range map from E.L. Little, Jr. "Atlas of United States Trees" (USGS, 1999).

across parts of the species range in recent decades (Miller et al., 2012; Reilly et al., 2017).

We focus on three specific questions: (1) what are recent trends in the area burned across the range of knobcone pine?; (2) how does the size-class structure of local populations vary across its range and how is it changing over time?; and (3) how do rates of colonization and local extirpation vary between burned and unburned portions of the range of the species?

2. Materials and methods

2.1. Study species

Knobcone pine (Fig. 1) is a serotinous tree distributed primarily across California and southwestern Oregon, U.S.A (Fig. 2). We used a map from E.L. Little, Jr. "Atlas of United States Trees" (USGS, 1999) to define the range of knobcone pine. Much of its range is in the Klamath

Mountains of California and southwestern Oregon, but it continues to southern California where several smaller, disjunct populations occur (USGS, 1999). A small disjunct population comprising less than 0.4% of its range also exists in Baja California, Mexico, at the extreme southern portion of its range, but is not included in this study due to data limitations.

Knobcone pine occurs across a range of elevations (< 300 m to > 1700 m). It may be found in pure stands following high-severity fire or in mixed stands with many other longer-lived conifer species including Douglas-fir (*Pseudotsuga menziessii*) and several species of pine (*Pinus* spp.) at low and middle elevations, and multiple species of true fir (*Abies* spp.) at higher elevations. Knobcone pine may also be found interspersed with and along the border of chaparral vegetation in hot and dry portions of its range. It is commonly found on low productivity serpentine soils, and is maintained by fire on more productive, non-serpentine sites capable of supporting forest vegetation (Vogl, 1973). Knobcone pine trees may begin producing cones as early as 4–14 years

of age and can continue producing viable seed in past age 70 (Fry and Stephens, 2013). Age-related decadence is apparent in trees < 75 years old (Vogl, 1973) and though trees rarely live more than 80 years (Howard, 1992) some may live more than 90 years (Keeley et al., 1999). Lab experiments indicate that closed-cones require temperatures of 93 °C for five minutes to open (Vogl, 1973). As most of the information on knobcone pine life history traits come from a few study sites scattered across its range, little is known about geographic variability in maximum age, time to maturity, or seed viability across its range. Knobcone pine exhibits some partial serotiny across some portions of its range (Newcomb, 1962, M. Reilly personal observation), but extremely little is known about how the degree of serotiny varies geographically or with age.

2.2. Fire occurrence data

We assembled a geospatial database of all known fires that occurred within the range of knobcone pine from 1900 to 2015 (Fig. 2). We acquired perimeters of all fires > 400 ha occurring between 1984 and 2015 from the Monitoring Trends in Burn Severity (MTBS) program (www.mtbs.com) (Eidenshink et al., 2007). We used the FRAPS database from the California Department of Forestry and Fire Protection (available at: http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download, downloaded 11/8/2017) for fires from 1900 to 1983 in California. In southwestern Oregon, we combined all available spatial data on historical fire occurrence including (1) a map of a known historical fires on USFS lands from 1900 to 1984, (2) a map of stand-replacing fire delineated from 1902, and (3) a map of "deforested burns" from the 1930's survey of forest resources in Oregon and Washington (Harrington, 2003). Because the first of the Oregon maps covered only United States Forest Service (USFS) lands and represented most but not the entire range of knobcone pine in this area, our map potentially misses some fires. Our confidence in the final map increases after 1950 when methods of documentation became more standardized. However, given the widespread and well-documented effects of fire exclusion over the last century, it is unlikely that we are missing any large fires and that our map is representative of general trends in 20th century fire activity.

We used the fire perimeter data to calculate the fire rotation for the 25-year period preceding each year from 1925 to 2015 following Miller et al. (2012). For example, the fire rotation in 1925 includes fires from 1900 to 1925, and the fire rotation from 2015 includes fires from 1990 to 2015. Fire rotation was calculated as the 25-year time period divided by proportion of the total range of knobcone pine that burned. Finally, we calculated the percent of the range of knobcone pine that experienced reburn at annual intervals from 1985 to 2015.

2.3. Inventory data

We acquired field data from the USDA Forest Service Pacific Northwest Research Station Forest Inventory and Analysis program (FIA) PNW-FIA Integrated Database (IDB) for plots in California and Oregon. FIA plots are a spatially balanced sample across all ownerships with approximately one plot every 2428 ha in areas capable of supporting forest vegetation (Bechtold and Patterson, 2005). Since the FIA focuses on forested lands, the sample may underestimate knobcone pine occurrence where it grows interspersed in chaparral or shrubland vegetation types. The sample is broken down into ten spatially-balanced panels that are measured each year. Data collection began in 2001 and continued until 2017, so the entire sample was measured once, and the first seven panels were measured twice. The sample also included plots that were part of a spatial intensification on USFS lands in both states, as well as an off-panel temporal intensification in California. Knobcone pine was present as a live tree, a dead tree, or a seedling in a total of 391 plots from 206 locations during at least one measurement.

Plots consisted of a cluster of four nested variable radius subplots

(Fig. A.1). Live saplings and snags between 2.54 and 12.7 cm diameter at breast height (dbh) were tagged and measured in 2.1 m radius microplots (13.6 m^2 total area). The presence of seedlings with a height > 15 cm and dbh < 2.54 cm was also recorded in the 2.1 m radius microplots. Live trees ≥ 12.7 cm dbh were measured in 7.32 m radius subplots (168.3 m^2 total area). Live trees > 76.2 cm dbh in Oregon and > 61 cm in California, were measured in 18 m radius macroplots (4050 m^2 total area). Given the nested plot design, it is possible that individual trees were present in the footprint of the larger plot, but not in the subplots.

2.4. Classification of stand population structure

We used Ward's method (Ward, 1963) of hierarchical agglomerative cluster analysis based on Euclidean distances using the hclust function in R (R Core Team, 2018) to classify each of the plots with a live knobcone pine > 2.54 cm dbh into population structure types based on the size-class structure of trees. Agglomerative clustering works by iteratively merging the most similar plots into groups until all groups are merged. We based the classification on the number of trees in the following diameter at breast height (dbh) size classes: < 12.7 cm, 12.7–20 cm, 20–30 cm, 30–40 cm, and > 40 cm. We applied a square root transformation to the number of trees in each size class to equalize the relative importance of small and large trees (McCune et al., 2002). The classification included 249 samples from 160 plots with at least one live tree.

We used the randomForest package in R (R Core Team, 2018) to assess how well the cluster analysis discriminated among structural classes. Random forest is a machine learning algorithm for classification and regression (Cutler et al., 2007). When implemented for classification, random forest provides a confusion matrix with classification accuracies for the different population structural types.

2.5. Regional population structure and trends

To compare changes in the abundance of the structural types identified by cluster analysis and characterize population trends, we selected all plots that were measured twice over a ten-year period and had at least one live tree. This sample included 75 plots that were sampled first from 2001 to 2007, and second from 2011 to 2017. We characterized population trends in each plot based on changes in the number of trees (n) during the sample period: (1) gain ($n_{t2} > n_{t1}$), loss ($n_{t2} < n_{t1}$), stable ($n_{t2} = n_{t1}$), colonization ($n_{t1} = 0$ and $n_{t2} > 0$), and extirpation ($n_{t1} > 0$ and $n_{t2} = 0$). The nested sampling design with smaller subplots limited our ability to detect all colonization events, which is relative to the size of the plots, thus we likely underestimate colonization events.

3. Results

3.1. Fire trends

Approximately 63% of the range of knobcone pine burned between 1925 and 2015. The area burned was lowest during the early and mid-20th century and fire rotation peaked during the 25-year period ending in 1950. Fire activity increased in the early 1980s (Fig. 3). Approximately 39% of the range burned between 1984 and 2015 and fire rotation decreased to 81 years for the 25-year period ending in 2015. Most of the area burned since 1984 occurred over three years (1987, 2002, and 2008) in the Klamath Mountains in northern California and southwestern Oregon where the largest contiguous portion of the species range occurs. Throughout other portions of its range, specifically the smaller disjunct portions in coastal mountains of central California and the eastern portions of its range in the Cascade and Sierra Nevada Mountains of Oregon and California, populations of knobcone pine experienced little fire activity since the early 20th century. From 1985
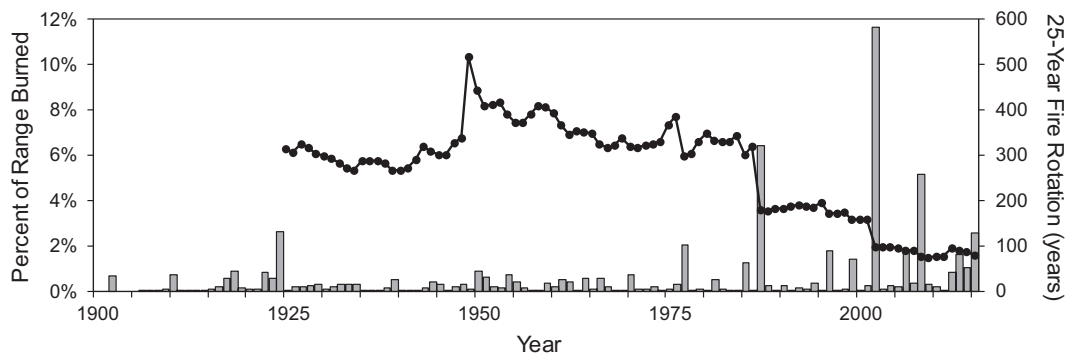
Fig. 3. Annual percent burned (gray bars) and fire rotation for twenty-five periods (dots) from known fire occurrence across the range of knobcone pine (*Pinus attenuata*) in southwestern Oregon and California.
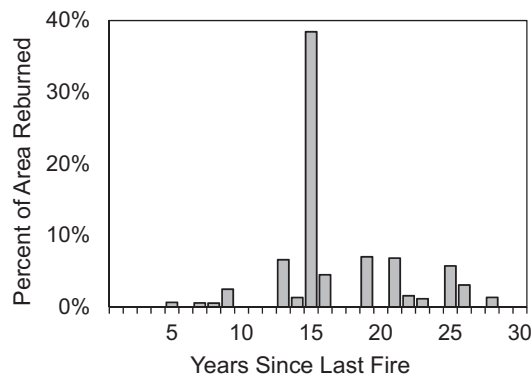

Fig. 4. Distribution of years since last fire as percent of total area reburned from 1984 to 2015 across the range of knobcone pine (*Pinus attenuata*) in California and southwestern Oregon.

to 2015, approximately 6% of the range of knobcone pine experienced repeated fire. Of the total area that reburned, most occurred at intervals greater than fifteen years and only 4% of the reburned area (~0.25% of the entire range) experienced multiple fires at an interval less than 10 years (Fig. 4).

3.2. Classification

We identified five population structure types from the cluster analysis (Fig. A.2) with distinctive tree diameter size-class distributions (Fig. 5) and different fire histories (Fig. 6). Although fire histories vary among types, all types experienced some fire between 1984 and 2015. Population structural types also varied in terms of the basal area, density, and size of knobcone pine snags, as well as the density and basal area of other tree species (Table 1). Four of the structural types represent a generalized pathway of development following stand-replacing fire (e.g., Oliver and Larson, 1990). The first type, which we refer to as "stand-initiation," represents recently established populations consisting of very high densities of trees < 12.7 cm dbh (Fig. 5). The second type, "self-thinning," consists of moderately high densities of trees but with a much lower density of trees < 12.7 cm dbh. The third type, "mature," consists of moderate densities of trees 20–40 cm dbh. The fourth type, "old-growth," consists of very low densities of knobcone pine trees in the largest size classes (e.g. ≥40 cm dbh) and has the greatest proportion of dead knobcone pine basal area and highest proportions of other species. The final type, "woodland," consists of very low densities of trees primarily between 12.7 and 30 cm dbh.

Overall classification accuracy from the random forest model was extremely high at 98.4%, although individual class accuracy varied slightly (Table B1). Class accuracy was 100% for both the woodland

and self-thinning classes. Class accuracy for the old-growth class was 98.3% with two of 112 plots misclassified as mature. Class accuracy for the mature class was 97% with one of thirty-three plots misclassified as woodland. Class accuracy for the stand–initiation class was 92.2% with one of thirteen plots misclassified as self-thinning.

3.3. Temporal changes and population trends

Mature and old-growth population structural types made up approximately half of the plots at both sampling dates. Plots classified as stand initiation comprised less than 5% of all plots at both samplings and changed relatively little over the ten year-period (Fig. 7). The greatest increases occurred in the woodland type which almost doubled over the study period. The greatest losses occurred in the mature structural type (38%). The most abundant structural type at both times was the old-growth type, which increased slightly (8%). The number of plots with seedlings only (i.e. no trees or snags) was very low in the first sampling period but increased by ~450% over subsequent the ten-year period.

Populations of knobcone pine were extremely dynamic. Less than 30% of the plots were stable over the ten-year period and more plots experienced losses than gains (Fig. 8). Local extirpations occurred in approximately 12% of the plots, with 8% occurring in the absence of fire. Colonization occurred across almost 25% of the plots, indicating a cumulative expansion of knobcone pine.

4. Discussion

While recent fires are associated with stand-initiation and expansion of the knobcone pine, most populations currently exist in a mature or old-growth state. A few individual years that accounted for most of the area burned in our study area (e.g. 1987, 2002) left some populations of knobcone pine vulnerable to local extirpation via immaturity risk in landscapes affected by very large fires. However, relatively little reburn occurred over the last three decades, and ultimately senescence played a much greater at the scale of the entire range of the species. Despite relatively low rates of fire activity during the decade long period of re-measurement, we observed a cumulative expansion of knobcone pine as the rate of colonization was almost double that of extirpation. Our findings provide a rare look at ten years of population dynamics of a serotinous tree species under anthropogenically-altered fire regimes, and demonstrate how the complexity of processes operating at local scales may be manifest across the range of a fire-adapted species.

The dominance of mature and old-growth stands is consistent with overall patterns of fire activity during the last 30 years and suggests the potential for widespread extirpation across the range of the species as decadent trees approach their maximum lifespan and senesce in the absence of fire. Although fire rotation has been decreasing, a fire rotation of 80 years during the most recent period (1985–2015)
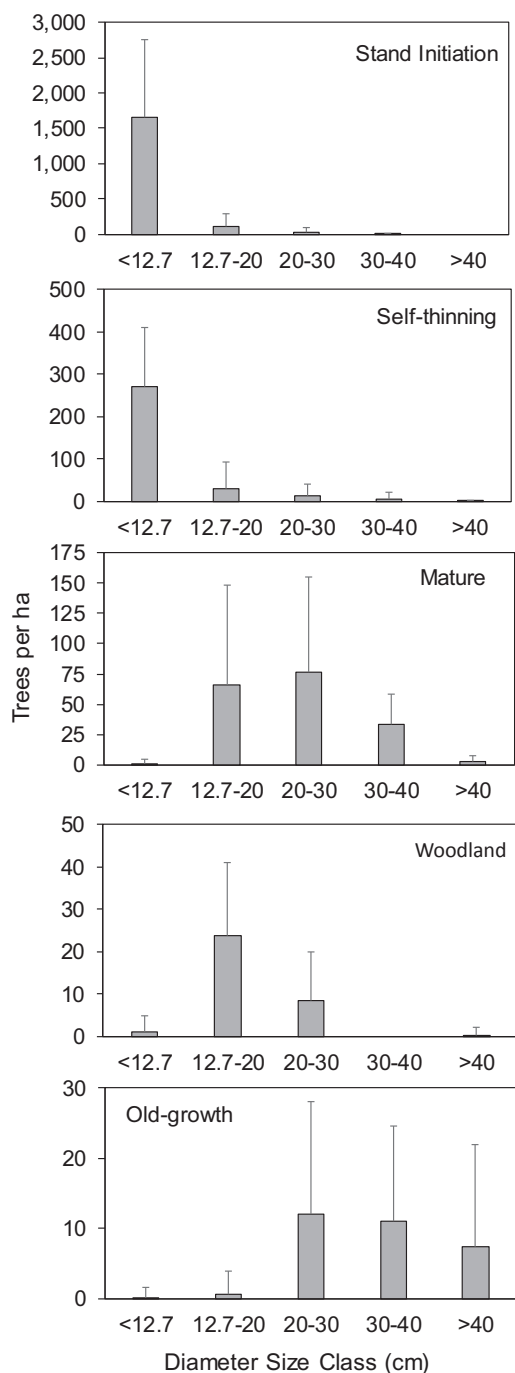
Fig. 5. Size class distributions (mean and standard deviation) of five population structural types for knobcone pine (*Pinus attenuata*) derived from a cluster analysis of 249 inventory plots systematically distributed across the range of the species in California and southwestern Oregon.

approximates the expected life span of knobcone pine (Howard, 1992) and is much longer than would be expected under the historical fire regimes to which this species is adapted. Estimates of historical fire frequency across most of its range varied from approximately 10–50 years (see Van de Water and Safford, 2011; Reilly et al., 2017 for fire history summaries). Risk of local extirpation appears to be especially high in the Cascade Mountains of Oregon in the northeastern portion of the species range, as well as in the central Sierra Nevada in California where the knobcone pine has experienced little fire activity since the early 20th century (Fig. 2).

Our results are consistent with landscape-scale studies documenting

primarily decadent populations of knobcone pine (Vogl, 1973; Fry et al., 2012) and other serotinous species around the world that are threatened by anthropogenic alteration of historical fire regimes (Bond, 1980; Brose and Waldrop, 2006; Gent and Morgan, 2007). Snags made up an average of 21% of all knobcone pine tree density and 16–18% of the basal area in our study area. Seedlings were reported in very few of these stands, and primarily only in those stands that experienced recent fire (i.e. post 1984). In addition to the lack of regeneration, knobcone pine made up less than 6% of the total tree density and 13% of the total basal area in populations classified as old-growth. Cumulatively, these results are consistent with widespread risk of senescence in decadent populations of knobcone pine that will likely be replaced by more shade-tolerant and longer-lived species as stands mature in the absence of fire.

Although many studies document the decadent state of populations of serotinous species, empirically-based observations of local extirpation are rare for any species (Keil et al., 2018). Plots with knobcone pine snags but no live trees and no evidence of recent fire provide evidence of recent extirpations from senescence across approximately 7% of its range prior to the first sampling. During the decade long sampling period, another 8% of the plots experienced recent extirpations with no evidence of fire. Senescence and extirpation had little effect on the overall population structure at the scale of the entire range, but these processes may reduce stand and landscape resilience to future fire as extirpation is linked to the death of mature trees and the loss of an in-situ seedbank for future recruitment in the event of fire. Many serotinous species exhibit necriscence, or the opening of cones upon death of an individual, but successful regeneration in this situation is far less likely than by seed release following fire when establishment is optimized by exposure of mineral soil and reduction in shade and competition (Lamont et al., 1991).

Immaturity risk from short-interval reburn (< 10 years) contributed very little to range scale dynamics of knobcone pine during the plot remeasurement period. Between 1984 and 2015, only 0.25% of the range experienced reburn at an interval shorter than a relatively conservative estimate of time it takes for knobcone pine to begin producing cones (~ 10 years). Correspondingly, we observed a single plot that burned twice during the study period. The presence of seedlings in this plot was consistent with some studies documenting that short-interval reburn may not always result in local extirpation of serotinous tree species but can drastically reduce population density (Keeley et al., 1999; Brown and Johnstone, 2012). Pre-fire tree density can be an important predictor of post-fire seedling density (Tinker et al., 1994), thus loss of stored seed in the canopy may decrease overall forest resilience to future fire activity and even a single high-intensity fire may have detrimental effects on cone viability if seeds are killed in crown fires (Alexander and Cruz, 2012).

Although short-interval reburn was extremely rare at the scale of the entire range of knobcone pine, some landscapes were vulnerable to immaturity risk following few exceptionally large wildfire events in 1987 and 2002. Recent and projected increases in fire size (Stavros et al., 2014) suggest an increased potential for immaturity risk to contribute to stand and landscape scale extirpation in the future. Such events may not pose the risk of extinction at the scale of its entire range, but landscapes with small, disjunct populations may be subject local extirpation. For example, repeated wildfires affected large areas of southeastern Australia from 2003 to 2014 (Fairman et al., 2016), and threatened landscape-scale collapse of an obligate seeder, *Eucalyptus delegatensis* (Bowman et al., 2014; Bowman et al., 2016). In one of the most extreme cases, approximately half of the range of *Banksia hookeriana*, a serotinous shrub in Australia, burned in a single 117,000 ha fire, part of which reburned again seven years later (Enright et al., 1996). Such examples substantiate the threat of short-interval fires on biodiversity and forest resilience, and are particularly salient given that several large wildfires in 2018 (the Mendocino Complex ~ 185,000 ha and the 93,000 ha Carr Fire) burned across much of knobcone pine's
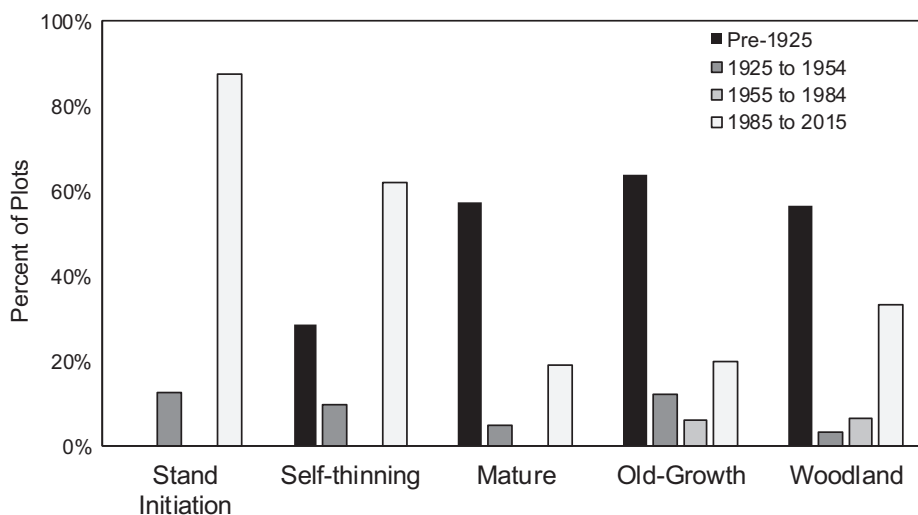
Fig. 6. Fire history for each of the five knobcone pine (*Pinus attenuata*) population structural types derived from a cluster analysis of 249 inventory plots systematically distributed across the range of the species in California and southwestern Oregon.

range in the central portion of California where immaturity risk will be high in the coming decade.

Despite evidence of recent extirpations and the decadent status of most knobcone pine stands, the species appears to be expanding in geographic extent and we document the potential for rapid expansion of this species during a period of increasing fire activity. Most recent fire activity was located in the northwestern portion of the range where fires, notably the 2002 Biscuit Fire, re-initiated stands of knobcone pine in southwest Oregon (Donato et al., 2009a; Donato et al., 2009b). The re-initiation of young knobcone pine stands in landscapes composed primarily of decadent populations suggests a high degree of latent resiliency to fire exclusion (Larson et al., 2013). Our results also highlight the importance of landscape recolonization following long-distance dispersal events given the light wind-dispersed seeds of knobcone pine. In addition to in-situ seedbanks, long distance colonization is another important mechanism for regeneration and may enhance resiliency of forest landscapes in the future to large patches of high-severity fire and short, interval reburns that may occur under projected future climate change scenarios.

Increases in the woodland population structural type indicates the potential for alternative pathways of stand development, species persistence, and population expansion of serotinous trees. Some of the increase observed in the woodland structural type was associated with non-stand-replacing fires in mature and old-growth stands that left mature residual trees and could promote regeneration. We also observed non-stand-replacing fire in approximately 20% of the plots classified as mature and old-growth. In some cases the 10-year sampling period may be too short to capture recruitment of new cohorts, but there is evidence of cohort establishment following non-stand-replacing fire in mixed age-class knobcone pine in some parts of northern California (Fry et al., 2012). Non-stand-replacing fires and mixed age class structures have also been documented in Table Mountain pine,

another strongly serotinous pine in North America (Brose and Waldrop, 2006). Even if fires are not necessarily hot enough to melt resin and dehisce cones, dispersal from stands in close proximity that experienced more intense fire could a provide a local seed source.

In the absence of fire, increases in woodland population structure in knobcone pine represent an alternative mechanisms of population persistence for knobcone pine, most likely through partial serotiny into shrublands, chaparral, or low productivity serpentine soils. Parker et al. (2001) document the expansion of sand pine (*Pinus clausa*), a partially serotinous tree in some portions of its range, into previously non-forested ecosystems in the absence of fire. Observations of partial serotiny in knobcone pine are rare, but open cones occur on trees across a range of ages (M. Reilly personal observation). The opening of cones during drought conditions, or xeriscence (Nathan et al., 1999) can accelerate cone dehiscence, especially in portions of a species range where serotiny is weak or variable (Martin-Sanz et al., 2017). Such dynamics may result in phenotypic divergence among populations of serotinous species (Pausas and Schwilk, 2012) that may be maladaptive given projections of increased fire activity in the future (Martin-Sanz et al., 2016). As fire return intervals become more variable, individuals are expected to exhibit lower levels of serotiny (Enright et al., 1998; Tonnabel et al., 2012). Given the current lack of knowledge of geographic variability in serotiny in knobcone pine, more research is needed to better understand the evolutionary effects of continued fire exclusion on serotinous species.

5. Conclusions

This study provides a rare empirically-based study on how stand scale extirpation and colonization contribute to range wide populations dynamics of serotinous tree, and highlights the importance of recognizing the different temporal and spatial scales at which

Table 1

Attributes of forest structure in five knobcone pine (*Pinus attenuata*) population structural types derived from a cluster analysis of 249 inventory plots systematically distributed across the range of the species in California and southwest Oregon.

|	% of all knobcone pine that is dead	% of all knobcone pine basal area that is dead	% of all trees that are knobcone pine	% of all tree basal area that is knobcone pine	% with knobcone pine seedlings present: all/burned
Stand-initiation (n = 14)	0.1% (0–1%)	2% (0–27%)	76% (35–100%)	57% (12–100%)	73%: 8/11
Self-thinning (n = 36)	1% (0–20%)	4% (0–95%)	41% (2–100%)	31% (1–100%)	33%: 9/27
Mature (n = 33)	21% (0–68%)	16% (0–65%)	13% (3–100%)	42% (7–100%)	4%: 1/25
Old-growth (n = 112)	21% (0–93%)	18% (0–92%)	6% (0–86%)	13% (1–83%)	8%: 6/77
Woodland (n = 54)	10% (0–75%)	10% (0–72%)	12% (1–99%)	11% (1–99%)	3%: 4/44
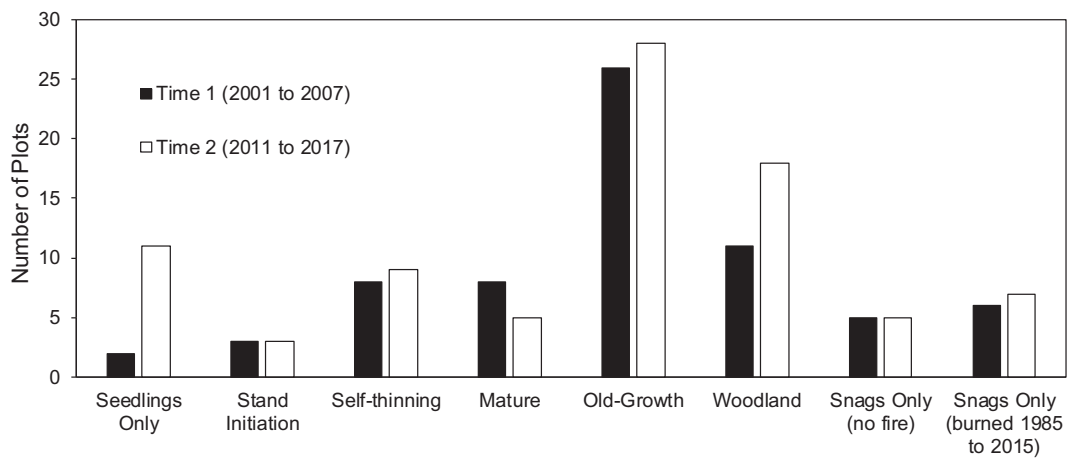
Fig. 7. Changes in the abundance of five knobcone pine (*Pinus attenuata*) population structural types over a ten-year period (2001–2007 and 2011–2017) from a systematically distributed sample across the range of the species.
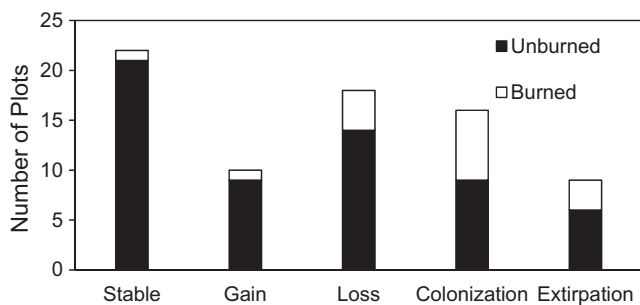

Fig. 8. Extirpation, colonization, and population trends of knobcone pine (*Pinus attenuata*) over a ten-year period (2001–2007 and 2011–2017) in seventy-five plots systematically distributed across the range of the species. Bars are color coded to indicate the occurrence of fire in a plot during the measurement interval with the exception of colonization, which includes whether or not a plot burned after 1984.

anthropogenic alteration of disturbance regimes threaten fire-adapted species. Despite the prevalence of decadent populations and high rates of stand scale extirpation, our results demonstrate the potential for

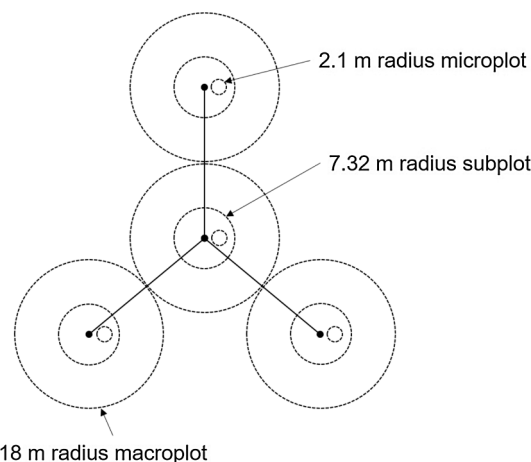some serotinous species to respond positively to increases in fire activity following long periods of fire exclusion. Abrupt changes in fire regimes may increase immaturity risk in landscapes following very large wildfires, but repeated, short-interval fires were rare during the study period. In the absence of fire, increases in knobcone pine woodlands suggest expansion of serotinous trees as an alternative pathway of development that is likely associated with partial serotiny. Even though we observed overall expansion of knobcone pine in response to recent fires, our results indicate that vulnerability to extirpation varies geographically and remains high in parts of its range where wildfire activity has been low. Judicious use of prescribed and wildland fire in the near future could help ameliorate negative effects of fire suppression by maintaining in-situ seedbanks to promote landscape resilience and the adaptive capacity of serotinous species such as knobcone pine (Enright et al., 2015).

Appendix A

See Figs. A1 and A2.

Fig. A1. Forest Inventory and Analysis (FIA) plot design consisting of four sets of spatially nested subplots.
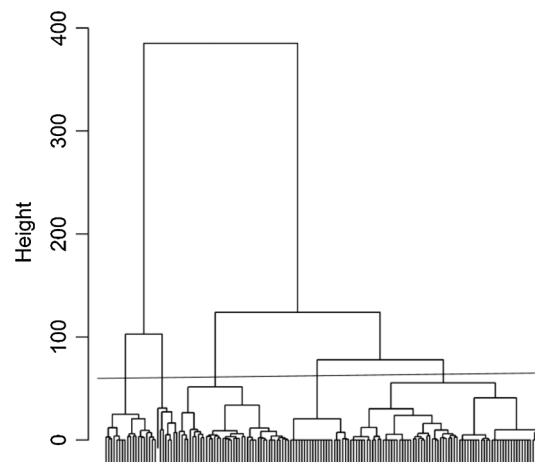
Fig. A2. Cluster analysis of five knobcone pine (*Pinus attenuata*) population structural types from 249 field inventory plots systematically distributed across the range of the species in California and southwestern Oregon, U.S.A.

Appendix B

See Table B1.

Table B1
Classification accuracies for a random forest model predicting five knobcone pine (*Pinus attenuata*) population structural types derived from a cluster analysis of 249 field inventory plots systematically distributed across the range of the species in California and southwest Oregon, U.S.A.

	Stand-initiation	Self-thinning	Mature	Old-growth	Woodland	Accuracy
Stand-initiation	13	1	0	0	0	92.9%
Self-thinning	36	0	0	0	0	100%
Mature	0	0	32	0	1	97%
Old-growth	0	0	2	110	0	98.3%
Woodland	0	0	0	0	54	100%
Overall accuracy	–	–	–	–	–	98.4%

Appendix C. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.03.017.

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