

Bishop pine (*Pinus muricata*) forest health



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Executive Summary

Bishop pine (*Pinus muricata*) is endemic to coastal California and Baja California. With a limited geographic distribution and several threats to its persistence, bishop pine is characterized as a ‘vulnerable.’ Bishop pine forests are adapted to high severity fire via post-fire seed release from serotinous cones, proceeding through early seral, mid-seral, and old-growth successional stages within approximately 100 years post fire. The structure and composition of bishop pine forests is expected to be distinct within each of three seral stages. Early seral (0-10 years post-fire) stands are characterized by very high tree density and species diversity with low fuel loads and low bishop pine seed availability. Mid-seral stands (10-50 years post-fire) are characterized by high tree density, low species diversity, high fuel loads, and moderate bishop pine seed availability. Old-growth stands (50-100 years post-fire) are characterized by low tree density, moderate species diversity, moderate to high fuel loads, and high bishop pine seed availability.

Key threats to bishop pine health include a potentially changing fire regime, increasing temperature and drought, non-native invasive plants, and non-native pine pitch canker disease—all which may alter bishop pine successional pathways and regional distribution. The relative importance of threats varies with seral stage. Resilience to fire is high in mid-seral and old-growth stands with live, seed-producing trees, but low in early seral stands that lack a seedbank or very old stands where bishop pine has senesced. Increasing temperature and drought may affect all seral stages, but effects may be strongest immediately following fire, during the establishment of post-fire tree seedlings. Invasive plant species can strongly impact the early seral post-fire period if they establish and compete with native vegetation. Pine pitch canker disease causes dieback and mortality in all seral stages. Currently, severity is greatest in mid-seral stands, but the disease is unlikely to be at equilibrium, posing substantial uncertainties regarding its effects on other seral stages. In addition, pine pitch canker disease is likely to cause changes to fuel profiles, fire behavior, and fire management operations in all seral stages; effects on post-fire regeneration and fire severity are less known and potentially minor.

Important knowledge gaps exist for all threats. Given the dynamic nature of these threats and the high level of uncertainty regarding their potential effects on bishop pine, six metrics are recommended to measure and monitor bishop pine forest health, with seral-stage specific target ranges. Metrics include bishop pine density, native plant species diversity, fuel profiles, bishop pine reproductive capacity, large snag and coarse woody debris abundance, canopy structure and texture. A key management recommendation is the implementation of a monitoring protocol that has been developed around these six metrics to measure bishop pine forest health in Point Reyes National Seashore. Additional management recommendations include:

- minimizing unplanned fire in early seral stands and raising awareness of potentially extreme fire behavior in stands severely affected by pine pitch canker
- avoiding density reduction for pine pitch canker mitigation due to unintended consequences
- implement monitoring following fuel reduction treatments in mid-seral stands near the WUI
- identify individual bishop pines with inherent genetic resistance to pine pitch canker disease
- applied experiments testing acceleration of development of mid-seral stands to old-growth
- applied burning experiments in old-growth to regenerate bishop pine prior to senescence

Managing for the conservation of bishop pine forests in and around the Point Reyes Peninsula will be well served by a combination of monitoring, applied experiments, and application of best practices that can mitigate threats to forest health.

Bishop pine background and natural history

Bishop pine (*Pinus muricata*) forests are an iconic ecosystem endemic to the coastal region of the Californian Floristic Province (Millar 1986a). Fossil evidence suggests bishop pine, along with closely related Monterey pine (*Pinus radiata*) and knobcone pine (*Pinus attenuata*)—collectively referred to as the California closed-cone pines (Barbour et al. 2007)—was once more widespread as part of the Madro-Tertiary flora in western North America (Axelrod 1967). The present-day distribution of bishop pine is restricted to relatively cool and moist sites near the Pacific coast, in isolated populations spanning from southwest Oregon to southern California (USA), as well as Baja California (Mex.) and the Santa Rosa and Santa Cruz Channel Islands (Axelrod 1967, Barbour et al. 2007). Bishop pine populations are divided into two mainland varieties, the northern var. *borealis*, which occurs north of Monterey, CA and the southern var. *muricata*, which occurs south of Monterey, CA; an island variety (var. *stantonii*) occurs on the Channel Islands (Millar 1986b, Millar 1983). Due to the relatively limited distribution of bishop pine, coupled with several threats to the persistence of the species (detailed below), it is listed as “vulnerable” on the Red List for the International Union for Conservation of Nature (<https://www.iucnredlist.org/species/34058/2841776>).

Bishop pine is a medium sized (approximately 12 to 24 m tall) and short-lived (typical life span of 80 to 100 years) tree with traits that are generally associated with strong adaptations to severe fire (Stuart and Sawyer 2001). Bishop pine possesses moderately serotinous cones, an adaptive trait where mature seeds are retained inside tightly sealed cone scales until the heat of fire (or extremely warm days) melts the resin bonds. Cone scales from southern populations of bishop pine remained closed at temperatures of 30 deg C, but 50% of cone scales opened at temperatures between 80 deg C and 130 deg C – above which no additional scales opened (Ostoja and Klinger 1999). Seed germination can be 80% successful when exposed to temperatures as high as 95 deg C, but germination fails when seeds are exposed to temperatures exceeding 125 deg C (Linhart 1978). Seeds within serotinous cones at the time of fire are typically protected from such extreme temperatures. Serotiny varies across the distribution of bishop pine, generally increasing in warmer and drier environments where cone production is prolific and serotiny is extreme (Millar 1986a). Further, bishop pine is reproductively mature at a young age (approx. 5 years old, Holzman and Folger 2005), has relatively thin bark, and retains low foliage that can easily carry fire into the crown (Davis and Borchert 2006)—all traits that are associated with adaptations to reproduce after severe fire (as opposed to resisting or surviving fire).

The typical fire regime in bishop pine forests is best understood as a stand-replacement, or high-severity (near 100% mortality of pre-fire trees) regime (Stuart and Stephens 2006). Fires likely occurred historically in the late summer or early fall when dry periods coincided with warm, dry winds originating from the east (e.g., Diablo winds in Northern California) and an ignition source. Due to relatively low frequency of lightning ignitions on and around the California coast (Keeley and Syphard 2018), anthropogenic ignitions from Indigenous peoples were likely an important component of the fire regime throughout the Holocene (Keeley 2002, Keeley 2005). However, as much of the documented practices of cultural burning were focused on promoting grasslands, it is unknown if fires were intentionally set in bishop pine forests or if fire transferred from adjacent grasslands. Historically, fire sizes were likely at least several hundred hectares; however, the exact fire history of bishop pine is difficult to reconstruct because of two reasons.

First, in stand-replacing regimes, there are very few, if any, trees that survive fires and retain fire scars—the absence of which makes it near impossible to reconstruct multiple past fire events. Second, in stand-replacing regimes, age/cohort reconstruction is typically used to reconstruct past fire patches by mapping the contiguous extent of the cohort of trees established since the last fire (Romme 1982, Hemstrom and Franklin 1982)—but comprehensive information on bishop pine age cohorts is lacking throughout the distribution of bishop pine (Stuart and Stephens 2006).

The combination of bishop pine traits and the general fire regime throughout most of its range leads to a general pattern of even-aged stands that originated as a single cohort of pulsed regeneration following the most recent stand-replacing fire. These stand dynamics have been documented in northern (e.g., Millar 1986a, Harvey et al. 2014c) and southern (e.g., Urza et al. in review) mainland populations of bishop pine, where high-intensity fires (prescribed fire and wildfire) can lead to post-fire seedling densities that are several orders of magnitude greater than the pre-fire stand density. Although some evidence suggests that low-intensity fires can also result in even-age stands through killing of canopy trees and releasing seed from serotinous cones (Sugnet 1985), most accounts of prescribed fire in bishop pine forests result in high-intensity crown fires that cause near 100% above-ground vegetation mortality and initiate a post-fire cohort (Urza et al. in review).

In the absence of fire, regeneration is possible, though more idiosyncratic and sparse than following fire (Millar 1986a). Bishop pine has moderate to low shade tolerance (McCune 1988) and is a poor competitor with neighboring shrubs (Harvey and Holzman 2014)—hence the high establishment success after severe fire when growing space is available. However, if seeds are released from open cones, bishop pine seedlings can germinate and establish in open, rocky sites with poor soil and sparse vegetation—where competition is low from other woody vegetation (Sugnet 1985, Millar 1986a). Such establishment is evident along roadsides and trail breaks that abut older stands. Regeneration of bishop pine in the absence of fire has been documented in var. *stantonii* on Santa Cruz Island, where low-productivity and rocky sites can provide refugia from competition by other woody vegetation (Walter et al. 2005). However, the Santa Cruz Island populations of bishop pine are distinct subpopulations with different ecological dynamics than the mainland populations (Millar 1986b) and may therefore have a different evolutionary relationship with fire (Linhart 1978). Recognizing these above exceptions, for purposes of this report and usefulness to managing for bishop pine forest health in Marin County, we focus hereafter primarily on the more general stand-replacing fire regime and even-age cohort stand dynamics of bishop pine forests.

Forest health attributes depend on seral stage

Similar to temperate and boreal forests elsewhere that are characterized by stand-replacing fire regimes, bishop pine forests proceed through generally consistent seral stages in the interval between stand-replacing fire events. Although these stages represent discrete points along a temporal continuum and there can be variability in forest structure and pathways at any point in time (Harvey et al. 2011, Harvey and Holzman 2014), it is nonetheless useful to organize stand dynamics into seral stages. Such concepts are applied in forests in other stand-replacing fire regimes such as subalpine forests in the Rocky Mountains, boreal forests in northern latitudes, and wet coastal forests in the Pacific Northwest (Donato et al. 2012, Franklin et al. 2018). As forest structure and function changes drastically among seral stages, this can provide a

framework for understanding the range of variability of key structural and compositional attributes that are within the natural range of variability (NRV) and would be presumed to be ‘healthy’ and resilient to stressors. The early- to mid-seral stages are the stages for which there is the most published literature on bishop pine forest dynamics. Much research followed the 1995 Vision Fire in Point Reyes, which burned through 5000 ha, of which nearly 500 ha was old-growth bishop pine forest. However, data from several monitoring reports on nearby old-growth stands that have not burned in more than half a century provides insight into old-growth characteristics of the bishop pine conservation target.

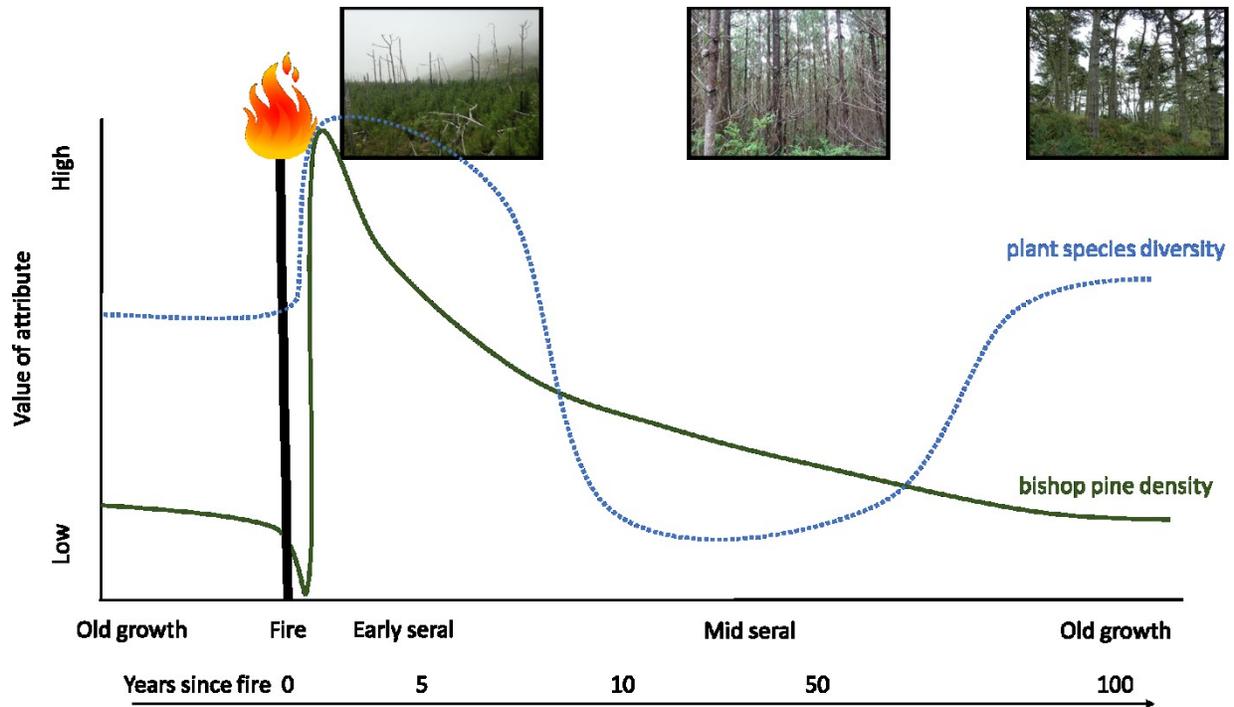


Figure 1. Generalized trends of key attributes of forest structure (Adopted from Franklin et al. 2018 and Harvey and Holzman 2014)

Disturbance and legacy creation stage

Severe (i.e., stand-replacing) fire that kills most or all of the above-ground vegetation is the characteristic disturbance that resets the sere, or creates early seral conditions. While such fires can be considered frequent on an absolute scale (e.g., 50-80 years apart) compared to other forests with infrequent, stand-replacing regimes (e.g., several centuries in subalpine forests), they are infrequent relative to the lifespan of bishop pine trees (approx. 80 to 100 years, Stuart and Sawyer 2001) and the pace of stand structural development. When fires occur, they leave myriad biological legacies—living or dead biologically derived structures that persist through disturbance (Franklin et al. 2000)—in the form of coarse woody debris, standing snags, and a range of reproductive structures (canopy seedbanks, soil seedbanks, underground root structures for re-sprouters).



Figure 2. Early seral bishop pine forest 4 years post-fire. Abundant bishop pine seedlings (approx. 100,000 ha⁻¹ are beginning to dominate and shade out post-fire colonizing herbaceous plants. Standing snags are the pre-fire bishop pine trees that were killed in the fire event but released seed necessary for the post-fire cohort to establish. Photo location: Diablo Canyon, CA. Photo credit: B. Harvey

Early seral stage (approximately 0-10 years post-fire)

The early seral stage of bishop pine forest-stand development is characterized by high plant species diversity, very high density of small bishop pine seedlings, dense and short stature vegetation, and standing snags from fire-killed trees (Figure 1, 2). Within months following fire, tree, shrub, and herbaceous regeneration from seed and re-sprouting structures rapidly colonize and/or begin to reoccupy burned stands (Ornduff and Norris 1997). The fire-catalyzed synchronous release of the bishop pine canopy-seedbank leads to extremely high seedling density 1 year post-fire, which can average as great as 250,000 seedlings ha⁻¹ (Holzman and Folger 2005). Species richness is high, mostly composed of disturbance adapted broad-leaf plants that have a range of adaptations to fire. Dominant plant forms (measured by percent cover) in the first year post fire are broadleaved herbaceous plants in the family Fabaceae (many of which have nitrogen-fixing symbioses with bacteria in their roots) and shrubs that sprout from fire-stimulated soil seedbanks (e.g., *Ceanothus thrysiflorus* and *Arctostaphylos* spp.) or resprout from roots (e.g., *Baccharis pilularis*). Re-sprouting trees (e.g., *Quercus agrifolia*, *Umbellularia Californica*, *Arbutus menziesii*, and *Notholithocarpus densiflorus*) are also present, but lower in percent-cover dominance in the early seral stage (Holzman and Folger 2005). Species richness typically peaks 2-yr post-fire and evenness is highest in the first year post-fire, before the

dominant trees and shrubs crowd out smaller statured and shade intolerant plants toward the later end (e.g., 10-yr post-fire) of the early seral stage (Holzman and Folger 2005, Harvey and Holzman 2014, Harvey et al. 2014c). Species diversity and bishop pine density (dominance) are inversely related in the early seral stage; that is, species diversity is greatest in stands where bishop pine dominance is lower –likely due to the low light environment under a dense canopy of bishop pine saplings (Harvey and Holzman 2014). Vegetation height is mostly less than 1-m in the first year post-fire, but can reach heights of 2-4 m by 10-yr post-fire. The first several years post-fire are characterized by high densities of fire-killed standing snags (~ 100-1000 snags per ha), which have mostly fallen by the end of the early seral stage. Throughout the early seral stage, bishop pine trees grow and come to dominate aerial cover by 10 to 15 years post-fire as they go through an intense period of density-dependent thinning (Harvey et al. 2011, 2014c, Harvey and Holzman 2014). With very little bishop pine seedling establishment occurring in the absence of fire, density steadily decreases from ~250,000 ha⁻¹ 1-yr post-fire to an average of ~5,000 ha⁻¹ in the second decade after fire (Harvey and Holzman 2014).



Figure 3. Mid-seral bishop pine forest 14 years post-fire. Bishop pine density (approx. 50,000 ha⁻¹) and canopy dominance is very high, excluding most understory vegetation except for shade tolerant shrubs and ferns (*Vaccinium ovatum* pictured here). Photo location: Inverness Ridge, CA. Photo credit: B. Harvey

Mid-seral stage (approximately 10-50 years post-fire)

By approximately 10 years post-fire and persisting until approximately 50 years post-fire, bishop pine stands are in a mid-seral stage, characterized by comparatively low plant species diversity and moderately high density (approximately 1,000 to 50,000 stems ha⁻¹) of mature bishop pine trees (Figure 1, 3). Canopy closure resulting from bishop pine dominance leads to dark conditions inside stands. Understory vegetation is sparse and composed of shade-tolerant evergreen shrubs (e.g., *Vaccinium ovatum*, *Frangula californica*, *Gaultheria shallon*, *Rubus ursinus*) where bishop pine density and canopy cover are high. Canopy gaps where initial bishop pine dominance was low are often dominated by *Ceanothus thrysiflorus* and support slightly greater understory plant diversity (Harvey et al. 2014c, Harvey and Holzman 2014). Most fire-killed snags have fallen by ~15 years post-fire, and high moisture in coastal regions leads to rapid decomposition of logs once on the ground. Little research has tracked the transition from mid-seral to old-growth stages of bishop pine forest development, but at some point several decades after fire, bishop pine trees reach their maximum height (~25 m) and crown width, resulting in a cessation of density-dependent mortality. Mortality from processes other than competition with neighboring trees (e.g., insect, fungi, physical damage from wind) then starts to cause opening of the otherwise uniform and dominant bishop pine canopy.



Figure 4. Old-growth bishop pine forest in an area that has not burned for approx. 80 years. Bishop pine density (approx. 100 stems ha^{-1}) and canopy cover is low, leading to greater co-dominance by broadleaf trees and a wider range of understory shrubs. Photo location: Inverness Ridge, CA. Photo credit: B. Harvey

Old-growth stage (approximately 50-100 years post-fire)

A sparse canopy of bishop pine, co-dominance by broadleaf evergreen trees, and moderately high plant species diversity, characterizes the old-growth stage of bishop pine forest stand development (Figure 1, 4). Density of tall (~ 25 m) and large diameter (50-80 cm DBH) bishop pine trees is approximately 50-500 stems ha^{-1} and accounts for less than 20% of the canopy cover. However, these relatively sparse bishop pine trees account for half or more of the total tree basal area, which averages approx. $25 \text{ m}^2 \text{ ha}^{-1}$ (Gaman 2019). The forest canopy is not closed as it is in the mid-seral stage, but is instead characterized by gaps between crowns of bishop pine and co-dominant broadleaf trees (*Arbutus menziesii*, *Quercus agrifolia*, *Umbellularia californica*, *Notholithocarpus densiflorus*). Since these broadleaf tree species can regenerate in the absence of fire, with more time since fire they will dominate more of the canopy. When shrub and herbaceous cover is high, bishop pine regeneration is rare in the absence of fire, resulting in fewer than 5 seedlings ha^{-1} on average in old-growth stands (Gaman 2019), and limited to rocky and open sites near a seed source (Millar 1986a). With the opening of the canopy, increased light availability leads to understory plant species diversity that is greater than the mid-seral stage, but not as diverse as the early seral stage. In addition to

seedlings of broadleaf trees, the understory is dominated by evergreen shrubs and ferns (*Polystichum munitum*, *Pteridium aquilinum*), which collectively can total to 80% cover in the understory (Gaman 2019).

Bishop pine on Point Reyes Peninsula

The bishop pine forests on the Point Reyes Peninsula are primarily restricted to the eastern (inland) and western (coastal) slopes of Inverness Ridge. Bishop pine forests are the dominant plant community at higher elevations on Inverness Ridge, but sparse stands (i.e., woodlands) intermix with some dense stands continuing down to sea level at Tomales Bay and the Pacific Ocean. Isolated stands occur throughout other locations on and around the Point Reyes Peninsula and further inland in Marin County that are relicts of a once more widespread local distribution (Millar 1986a). Bishop pine in Point Reyes is the northern variety (*Pinus muricata* var. *borealis*) though they are intermediate in their trait characteristics between populations in Northern California and Southern California (Millar 1983).

The Point Reyes Peninsula has been occupied by people for most of the Holocene epoch (since approx. 10,000 years BP) and the influence of humans on the vegetation and fire regimes continues today. Coast Miwok used fire as a land management tool to burn grasslands and charcoal evidence suggests that human-ignited fires were a major part of the local fire regime since approximately 3,500 years BP (Anderson 2005). Temporal data at high resolution (e.g., annual) are not available to reconstruct fire return intervals (FRIs) for the time when Coast Miwok occupied the Point Reyes Peninsula prior to European colonization. However, wide ranging FRIs from 3 to 188 years in coast redwood forests in the Santa Cruz Mountains suggest pre-colonization anthropogenic influences on the fire regime that were variable in space and time (Jones and Russell 2015). Frequent fall burning approaching annual frequency occurred in grasslands along the coast to promote prairie habitat, and would have likely spread into forest areas occasionally (Sugnet 1985). In the mid- to late-1700s, Spanish colonizers settled in the San Francisco Bay and by the 1820s had decimated Coast Miwok populations, changing human influence on the fire regime.

During the Spanish era, the primary land uses on the Point Reyes Peninsula were grazing and logging. Logging in the bishop pine forest would have been mostly for firewood, as opposed to harvesting of large Douglas-fir and coast redwood trees for dimensional lumber. Ranchers during the Spanish era intentionally set fires, but for the purpose of clearing shrubland and promoting grazing pasture (Sugnet 1985). Although anthropogenic fires were concentrated in the grasslands, fire scars on coast redwood and Douglas-fir trees demonstrate that fires also expanded into forested areas (Brown et al. 1999). Fire return intervals (FRIs) were 20 to 30 years in coast redwood (Brown et al. 1999), and likely at least some of these fires would have burned in bishop pine forests, resulting in a slightly longer FRI in bishop pine forests than in the adjacent coast redwood forests. Following the Spanish era, in the 1850s when California became a state, more than 30 dairies and cattle ranches occupied the peninsula, with larger ranches toward the north and east (Watt 2002). Several large fires in and around the peninsula are noted between the late 1880s through the 1940s, after which two small fires occurred in the mid-1950s and 1970 (Sugnet 1985, Brown et al. 1999). In 1962, the Point Reyes National Seashore (PRNS) was formed and further broad-scale active manipulation of vegetation within the unit boundaries was slowed.

The 1995 Vision Fire: summary of post-fire research on PIMU forests

The 1995 Vision Fire catalyzed research and understanding on the fire ecology, post-fire response, and general stand dynamics of bishop pine forests. In early October 1995, a wildfire ignited from an unattended campfire just outside the PRNS boundary on the east side of Mt. Vision. During a 4-day period of warm and dry easterly winds (Diablo Winds), the Vision Fire burned more than 5,000 hectares on the Point Reyes Peninsula, mostly within PRNS. Although initial concern was high regarding the capacity for the bishop pine forest to recover following fire, dense seedlings of bishop pine blanketed the burned area within months, and plant species diversity was higher than pre-fire in the bishop pine forest (Ornduff and Norris 1997, Ornduff 1998). Prior to the Vision Fire, bishop pine forest covered 756 ha; post-fire bishop pine expanded to cover 993 ha. Expansion within the burn perimeter, where the bishop pine forest extent nearly doubled in area (from 348 ha pre-fire to 584 ha post-fire) was concentrated primarily in areas that were pre-fire coastal scrub and grassland on the lower slopes of the Pacific side of Mt Vision (Forrestel et al. 2011).

Following the Vision Fire, several trends were characterized through research tracking succession and stand development (Harvey et al. 2014c). First, the Vision Fire demonstrated the interconnectedness of ectomycorrhizal fungi communities and bishop pine. Fire caused rapid turnover in the ectomycorrhizal fungi community (Baar et al. 1999, Grogan et al. 2000), and post-fire bishop pines colonized by *Rhizopogon* sp. fungi demonstrated enhanced growth compared to plants without ectomycorrhizal fungi (Kennedy and Peay 2007). Second, the bishop pine forest demonstrated tremendous resilience to fire. Bishop pine density and plant species diversity were extremely high in the first two years following fire (~250,000 seedlings per hectare and 34 plant species per plot, respectively) (Holzman and Folger 2005), and were immediately followed by a period of rapid successional change.

Over the next decade and a half, bishop pine sapling density decreased by >90% through intense and naturally occurring density-dependent thinning (to an average of ~15,000 stems per hectare), and plant species diversity decreased by nearly 40% (Harvey and Holzman 2014). The fire also served as a catalyst for bishop pine forest expansion, as the bishop pine forest extent nearly doubled (Forrestel et al. 2011) from a combination of expansion from the edge of existing pre-fire forest and new stand development from seeds provided by isolated pre-fire trees (Harvey et al. 2011). These newly established tree islands served as important locations for ectomycorrhizal fungi, where greater than 40 ectomycorrhizal fungi species were found on single isolated trees established post-fire (Peay et al. 2010). Finally, the bishop pine forest within the Vision Fire footprint has been one of the areas most severely affected by pine pitch canker disease (PPCD) in California, which has expanded from a few isolated stands in 2006 (Crowley et al. 2009) to most of the forest by 10 years later (Gordon 2017).

Current state of bishop pine and seral stage distribution

Currently, there are approximately 1,000 hectares of bishop pine forest on the Point Reyes Peninsula, which are primarily in two different stand development stages, depending on whether they were burned in the 1995 Vision Fire (Figure 5). Slightly more than half of the bishop pine forest on the Point Reyes Peninsula (578 ha) is in the mid-seral stage (25 years old), having originated immediately following the 1995 Vision Fire. Nearly all of the mid-seral bishop pine

stands are located on the southwest slopes of Inverness Ridge, stretching from the crest of the ridge to the Pacific Ocean.

The remaining extent of bishop pine forest on the Point Reyes Peninsula (430 ha) is in the old-growth stage (exact stand age unknown, but approximately 80 years old or greater) likely having originated from fires in the 1940s or earlier. While records prior to the modern satellite era of fire databases (e.g., MTBS) are sparse, accounts exist for some fire events in the bishop pine forest on Point Reyes Peninsula between the late 1800s and the start of the satellite fire record in 1984. Newspaper reports note a large fire near Point Reyes in October 1887, though the spatial location within the peninsula is unclear (Sugnet 1985). In October 1927, a fire that was set to clear shrubs along the slopes of Inverness Ridge escaped into bishop pine stands on Mount Vision (Sugnet 1985). A 430 ha fire is mapped in Tomales Bay State Park with an unknown date between 1917 and 1934, which covered the approximate extent of bishop pine stands within the park (<https://data-nifc.opendata.arcgis.com/>). Smaller, isolated fires in bishop pine stands are recorded during the 1950s in and around Mt Vision, though perimeters are not known (Sugnet 1985). Nearly all of the old-growth bishop pine stands are located along the upper elevations of the west slope of Inverness Ridge (north of the Vision Fire perimeter) or on the northeast slopes of Inverness Ridge between the crest of the ridge and Tomales Bay.

Collectively, the fire history data and fire perimeters from Marin County Fire records suggest most of the old-growth forest in Point Reyes established following fires between the years 1917 and 1934, with some likely originating from the 1887 fire—though exact dates of some fires are unknown (Figure 5). Presumably, most or all of the historical fires were stand-replacing, high-severity fires, as even two accounts of low intensity prescribed surface fires in PRNS in the 1970s resulted in near 100% mortality of bishop pine (Sugnet 1985).

Currently there is no known bishop pine forest on the Point Reyes Peninsula in the early seral stage, because of no recent fires burning bishop pine stands since the 1995 Vision Fire. The Woodward Fire in 2020 burned southwest of the Vision Fire perimeter with a small area of overlap, however only a few isolated and very small stands of bishop pine were affected (Figure 5).

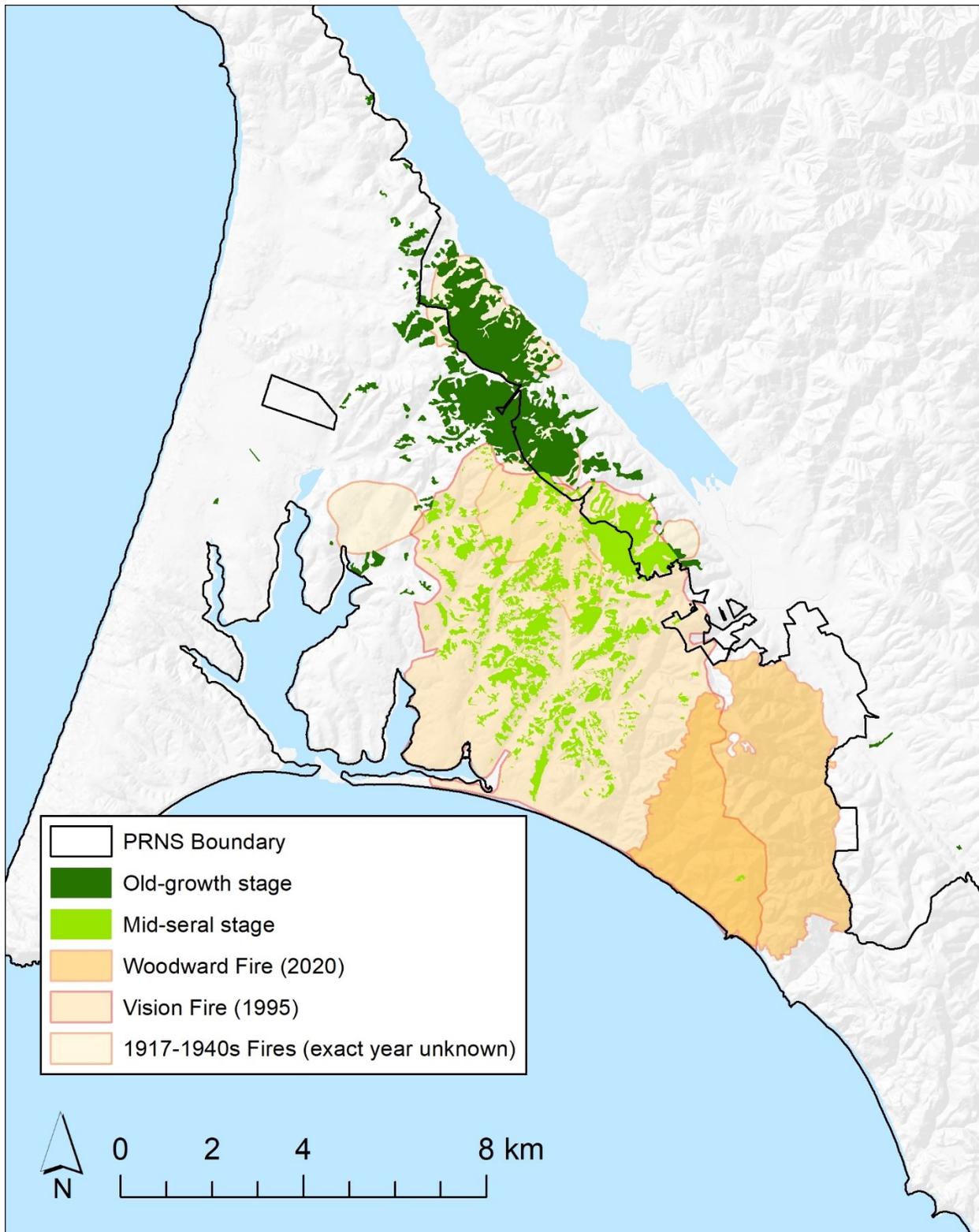


Figure 5. Bishop pine forest on the Point Reyes Peninsula by stand age, based on vegetation layers for GGNRA in 1995 and 2005 used in Forrester et al. (2011). Fire perimeters are overlain with darker colors signifying more recent fires. Perimeters are from the National Interagency Fire Center (<https://data-nifc.opendata.arcgis.com/>).

Several key threats to bishop pine forest health are summarized in Table 1; although many relate to knowledge gaps where further research is needed (see later section). The primary threat is the likely severe, but currently unknown, impacts to the population, physical structure, and ecological function of the bishop pine forest from mortality associated with PPCD. The second threat is potentially altered fuel structure and fire hazard, which is driven by PPCD-associated mortality. The third threat is the direct effect of climate warming and associated changes in precipitation and moisture availability for bishop pine forests. The fourth threat is forest resilience to fire associated with potential alterations to the natural range of variability (NRV) in the fire regime in bishop pine forests. The fifth threat is the potential effects of non-native invasive species on the bishop pine forest. Each threat and associated knowledge gaps are discussed in detail in the following section.

Table 1. Threats to bishop pine forest health.

Threat			
	Early seral	Mid-seral	Old-growth
	(~0-10 years post-fire)	(~10-50 years post-fire)	(~50-100 years post-fire)
Pine Pitch Canker Disease (PPCD)	Unknown, as pitch canker was not introduced in PRNS until stands were mid-seral	Pitch canker incidence (~75% of trees) and severity (~50% canopy dieback) is greatest in mid-seral stands	Pitch canker incidence and severity is lower in old-growth stands, though less well surveyed
Fuel structure / fire hazard altered from PPCD	Fuels within the NRV are limiting to fire and would have a low likelihood of supporting stand-replacing crown fire. Threat is high if fuels are sufficient to carry fire prior to reproductive maturity of bishop pine.	Fuels within the NRV are sufficient to carry stand-replacing crown fire but not support high intensity fire that would burn important ecological legacies (e.g., seeds). Pitch canker disease may alter fuel profiles and fire hazard.	Fuels within the NRV are sufficient to carry stand-replacing crown fire but not support high intensity fire that would burn important ecological legacies (e.g., seeds). Pitch canker disease may alter fuel profiles and fire hazard.
Climate warming and associated drought stress	Potential increased mortality of post-fire tree seedlings, lowering establishment rates	Potential increased drought stress in dense stands, accelerating density dependent mortality	Potential increased drought stress and mortality for old trees, shortening longevity of old growth stage
Resilience to fire under altered fire regime	Short-interval reburn prior to seed/cone production on bishop pine trees can lower resilience	Resilience to fire would be expected to be high with sufficient canopy seedbank	Fire exclusion or suppression could lead to senescence risk (mortality before fire) / low resilience
Non-native and invasive plant species	Likely high risk from abundant available space, firefighting operations, re-seeding for erosion control, especially for disturbance adapted and shade intolerant spp. such as Australian fireweed.	Potentially high risk for shade-tolerant understory plants such as English Ivy. Potential for stands impacted by PPCD to be more susceptible to non-native and invasive plant species.	Potentially high risk for species such as Himalayan blackberry and English Ivy. Potential for stands impacted by PPCD to be more susceptible to non-native and invasive plant species.

Threats and contributing factors

Pine pitch canker disease (PPCD)

Pine pitch canker disease (PPCD) is a major threat to the health of bishop pine forest via direct and indirect effects. Direct effects include fundamentally altering the population, physical structure, and ecological function of bishop pine forests, while indirect effects are via changes to fuel structure and fire hazard. Pine pitch canker disease is caused by the fungal pathogen *Fusarium circinatum*, which is suggested to be native to Mexico and introduced to pine forests in coastal California in the mid-1980s (Gordon et al. 1997, Wikler and Gordon 2000). *Fusarium circinatum* affects multiple host trees in the genus *Pinus*, and has been most notable on Monterey and bishop pine populations near the California coast (Storer et al. 1997). Localized infections, often aided by wounds caused by penetration of tree bark from native beetles (Storer et al. 2004) result in cankers, which then girdle conductive tissue and lead to branch or crown dieback (Storer et al. 1997).

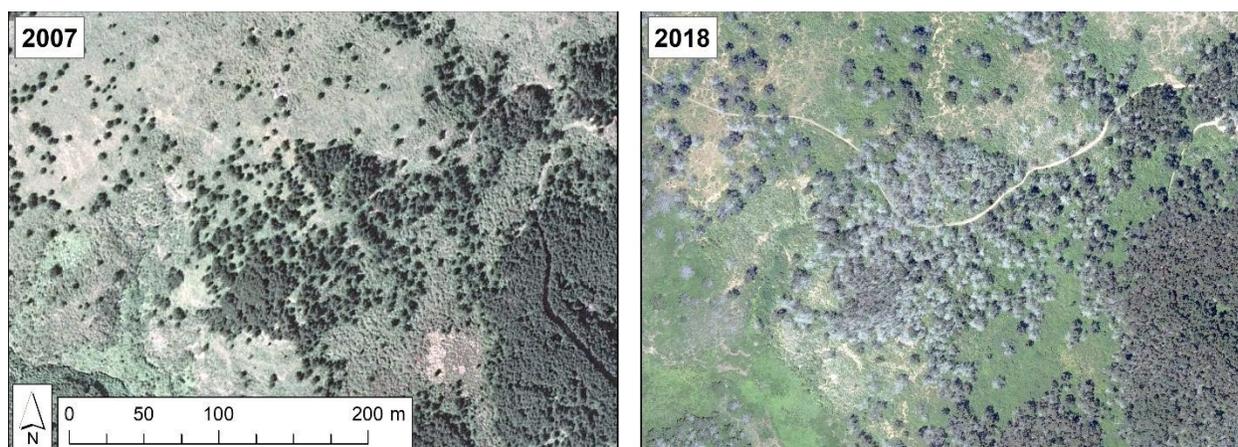


Figure 6. Progression of bishop pine mortality caused by PPCD along the Estero Trail north of Muddy Hollow in PRNS. In 2007, very few trees were infected (green crowns) and by 2018 mortality was near 100% (gray crowns) near the center of the aerial photograph (source: marinmap.org).

Across the Point Reyes Peninsula, the incidence (percentage of trees infected) and severity (degree of damage per tree summed across all trees in a plot) of PPCD has increased steadily since the early 2000s (Figure 6). First discovered in PRNS in 2006, in 2007, the aerial extent of PPCD in the PRNS bishop pine forest was less than approximately 5 ha, accounting for less than 1% of the bishop pine forest in PRNS (Crowley et al. 2009). Initial analyses of the spatial distribution of PPCD in 2007 indicated that PPCD presence was not strongly associated with topographic variables (e.g., elevation, slope, aspect, and distance from Drakes Bay). However, these analyses were from very early in pitch canker spread, and as the disease was far from equilibrium with the potential extent, inference for the eventual spatial distribution was limited (Crowley et al. 2009). Between 2011 and 2016, a series of 16 monitoring plots (each containing 20-30 bishop pine trees) distributed across the post-Vision-Fire bishop pine population were installed to track the progression of PPCD (Gordon 2017). Disease incidence and severity in 2011 were greater in low-density bishop pine stands, which tend to be lower elevation and in areas where the bishop pine forest expanded following the 1995 Vision Fire. In 2011, incidence

and severity were 55% and 28%, respectively, in low-density stands, compared to 6% and 2% in high-density stands (Gordon 2017). The initially higher incidence and severity of PPCD in low-density stands at lower elevations could relate to proximity to a potential introduction site – a Monterey pine plantation near Home Bay in Drakes Estero. From 2011 to 2016, incidence and severity monotonically increased in every plot between each re-measurement interval, and by 2016, incidence and severity were 95% and 79%, respectively, in low-density stands, and 47% and 23% in high-density stands (Gordon 2017). By 2020, observations indicate that the disease continues to spread and has caused canopy dieback exceeding 50% across broad extents of bishop pine forest.

The effects of PPCD on bishop pine are most concentrated in mid-seral stands, and impacts to stands of other stages are either unknown or potentially less severe. The timing of the first discovery of PPCD on Point Reyes Peninsula coincided with the period in which most forest stands were transitioning from early seral to mid-seral; therefore impacts in early seral bishop pine forests are unknown. In populations of bishop pine near San Luis Obispo (CA), PPCD has been documented in early seral stands, though incidence and severity are much lower than observed in the mid-seral stands in PRNS (Urza et al, in review). In old-growth bishop pine stands on the Peninsula (i.e., those not burned in the 1995 Vision Fire), incidence and severity of PPCD is also low (Gaman 2019). However, old-growth stands further north in the bishop pine distribution (Mendocino and Sonoma Counties) are experiencing dieback with unknown proximal causes. Drought mortality is suspected, but PPCD has been observed on dead and dying bishop pine trees (Lee et al. 2019).

The effects of the drastic expansion of PPCD are a major threat to bishop pine forest health at PRNS, with many knowledge gaps. Such a widespread mortality event in the absence of fire could be detrimental to local bishop pine forest health for several reasons. First, the natural disturbance regime for bishop pine forests is characterized by population cycles that are driven by fire. Populations increase by several orders of magnitude following a stand-replacing fire and release of seed from serotinous cones, and then steadily decrease as stands thin out through density-dependent mortality (Harvey et al. 2014c, Harvey and Holzman 2014). This process results in the largest trees outcompeting their neighbors, with mortality restricted primarily to smaller trees—all resulting in relatively steady live tree basal area among stands that have full canopy closure (Harvey et al. 2011).

However, mortality caused by PPCD in mid-seral stands is occurring across all tree size classes, which represents a substantial departure from population dynamics within the natural disturbance regime with unknown consequences. Second, the widespread canopy dieback caused by PPCD likely causes important changes to the physical structure and microclimate with bishop pine forests. The increase in resource availability likely provides opportunities for compensatory growth in shrubs and herbs and may provide establishment opportunities for bishop pine if seed are released. However, the vegetation dynamics following severe PPCD-caused canopy dieback have not been documented. Finally, a key mechanism of resilience to fire for bishop pine is sufficient viable seed stored in the canopy seedbank when fire occurs. PPCD may influence the number of live reproductive individuals present in the canopy at the time of fire, producing unknown effects on seed availability. Further, whether seed in cones of trees impacted or killed by PPCD remain viable is unknown, but critically important.

In addition, there are still many unknowns about the dynamics of PPCD itself, which have important consequences for bishop pine forests in the future. Trends in fog cover and PPCD incidence and severity on Monterey pine forests on Central California suggest that duration of fog cover (and associated moisture) is a key requirement for *Fusarium circinatum*, and that warmer and drier conditions with less fog may halt the spread of PPCD, which declined with respect to new infections following substantial mortality (Gordon et al. 2020). If, as the climate warms, fog cover duration decreases in the Point Reyes Peninsula, PPCD incidence and severity may decrease. Alternatively, warmer and drier conditions with less fog cover have been linked to bishop pine stress and widespread mortality in Channel Islands populations (Baguskas et al. 2014, 2016, Fischer et al. 2016), and may offset the effects of fog reduction on PPCD. Interactions among stress from PPCD and drought stress associated with changes in fog regimes are also likely important, but are currently unknown.

There is evidence of variation in susceptibility of bishop pine to PPCD. Results from a single laboratory study suggest 27% of individuals inoculated with *F. circinatum* did not develop significant lesions, demonstrating inherent genetic resistance to PPCD (Schmale and Gordon 2003). Further, for trees that developed lesions, lesion size declined with multiple inoculations, suggesting that systemic induced resistance, or the ability for individual trees to develop disease resistance over time, is common in bishop pine. Studies have shown similar findings for *Pinus radiata* with respect to inherent genetic resistance (Gordon et al. 1998) and systemic induced resistance (Reynolds et al. 2016) to *F. circinatum* and PPCD. Recent findings from *P. radiata* indicate that individual trees that were infected became free of symptoms over a period of <15 years, with new infections also declining over that period (Gordon et al. 2020). These findings suggest that breeding programs could be initiated in the future to improve genetic resistance in these species (Wingfield et al. 2008), and that susceptibility may also vary temporally. Greenhouse trials suggest that exposure of *P. radiata* seeds to soil containing *F. circinatum* expressed greater resistance to disease than individuals that were not exposed (Swett and Gordon 2017). Furthermore, two fungal endophytes of several *Pinus* spp. have been identified for possible use as biological control agents, as they are associated with reduced disease severity in hosts (Martinez-Alvarez et al. 2016). However, operational feasibility of seed exposure or use of endophytes as biological controls have not been shown in the field.

Potentially altered fuel structure and fire hazard from PPCD

(contributing factor: PPCD)

Virtually no information exists on the potential effects of PPCD on fuel profiles or fire hazard, making this a critical knowledge gap. However, insights can be gained from much research in other conifer forest systems with similar fire regimes that have experienced widespread tree mortality from other agents. Bark beetles in the genus *Dendroctonus* have caused widespread mortality across large swaths of forest in North America (Raffa et al. 2008, Meddens et al. 2012), and much research has focused on the effects of beetle-caused tree mortality on subsequent fuel structure and fire hazard (Hicke et al. 2012). While key differences between tree mortality caused by beetle outbreaks and PPCD exist (and are explained in detail below), until there is more empirical study of the interactions of PPCD and fuels/fire, information from bark beetle outbreaks and fire likely serves as the best potential surrogate. Bark beetles and PPCD are both

agents that cause mortality primarily via girdling of the bole and stem conductive tissue of the affected tree, leading to some probable similarities in how fuels are changed in affected stands. Further, the effects of PPCD on fuels and fire hazard, similar to those of bark beetle outbreaks, likely change over time since tree mortality.

Therefore, we describe potential effects using the stages developed for beetle outbreaks with stages that represent the post-outbreak structural trajectory characterized as “red,” “gray,” and “silver” (Simard et al. 2011, Hicke et al. 2012, Donato et al. 2013). The red stage occurs 0-2 years following tree mortality, when dead trees retain dead (red) needles. The gray stage occurs 3-10 years following tree mortality, as trees have shed needles and begin to shed smaller branches, but retain larger branches and remain standing as snags. The silver stage occurs 2-3 decades following tree mortality and characterizes the time when most dead trees remain standing as snags with few to no branches, or fall to the forest floor. We use these stages because as the disease impacts spread, all stages will be present on the landscape until the spread has completed and stages all go toward silver and later. One key difference between beetle outbreaks and PPCD is the time over which each causes tree mortality across a landscape. Beetle outbreaks typically result in relatively synchronous tree mortality (occurring over 2-3 years) among stands, whereas the effects of an introduced pathogen are more protracted (occurring over 3-10 years) among stands.

This section is organized into the following subsections, each with a temporal progression of how effects are likely to unfold as stands progress through stages of PPCD-caused mortality (e.g., red, gray, and silver stages): Fuels/fire hazard; potential changes to fire behavior; effects on fire severity (if fire were likely to occur); and post-fire forest recovery. For each section, a brief summary of the effects of bark beetle outbreaks is presented first, immediately followed by a discussion of likely similarities and differences with PPCD.

Changes to fuels driven by tree mortality

Red stage (0-2 years following tree mortality)

The red stage of post-beetle outbreak is characterized generally by changes to fine fuels in the canopy with correspondingly minor changes to other components of the fuel profile (e.g., live surface fuels or downed woody fuels) (Hicke et al. 2012, Jenkins et al. 2014). In the period following initial attack from beetles and leading up to tree death, needles immediately lose moisture and increase in flammability, with these changes greatest at the point when the tree is dead and needles turn from green to red (or yellow, depending on tree species) (Jolly et al. 2012). Counteracting the increased flammability of canopy fuels is the decrease in canopy fuel amount when foliage biomass decreases as dead needles drop from dead tree crowns, leading to a decrease in available canopy fuel load and canopy bulk density (Simard et al. 2011, Schoennagel et al. 2012, Donato et al. 2013, Jenkins et al. 2014). Changes to surface fuels in the red stage are minimal, with slight increases possible as needles fall and before they decompose (Jenkins et al. 2008, Simard et al. 2011, Schoennagel et al. 2012, Donato et al. 2013).

Effects of PPCD on fuel profiles in red-stage bishop pine forests likely follow similar trends as beetle outbreaks, with a few key differences. First, whereas beetle-caused tree mortality kills a tree over the course of one year (Amman and Cole 1983), PPCD-caused mortality is more protracted and can last multiple years (Gordon 2017). Therefore, the length of time that PPCD-

affected stands remain in the red stage may be longer than following beetle outbreaks. However, the magnitude of this effect may be diminished if a lower proportion of the canopy is in the red stage at any given time. Second, the amount of pitch/resin exuded by bishop pine trees affected by PPCD is greater and covers more of the tree (e.g., main bole and branches) than pitch tubes on beetle-killed trees (just the main bole). While the contribution of resin/pitch as a fuel has yet to be quantified in beetle-killed trees, the contribution is likely greater in PPCD-killed trees due to the greater amount of resin material exuded. Finally, beetle outbreaks are a selective mortality agent, typically killing trees that are greater than 12-15 cm diameter (Raffa et al. 2008, Hart et al. 2014, Buonanduci et al. 2020), whereas PPCD can affect trees of all sizes (Wikler et al. 2003). Therefore, potential effects to canopy fuels can be greater where nearly all trees are affected (Hoffman et al. 2012), as opposed to only trees that are large enough in diameter for a selective agent like beetles to attack.

Gray stage (3-10 years following tree mortality)

The gray stage of post-beetle outbreak is characterized by modest decreases in canopy fuels from the red stage (as all needles have fallen and some branches begin to fall), with corresponding increases to dead surface fuels. In addition, increases occur in live surface fuels as graminoids, herbs, and shrubs respond to the increase in resource availability (Hicke et al. 2012, Jenkins et al. 2014). Canopy fuel loads reach their lowest point over the course of the outbreak as dead trees have lost their fine fuels and regeneration or other vegetation has yet to ascend to the canopy. While snags remain standing, there are little-to-no changes to dead coarse surface fuels, and changes to fine surface fuels from fallen needles and fine branches may be offset by decomposition, depending on site conditions (Klutsch et al. 2009, Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012, Donato et al. 2013, Jenkins et al. 2014). With increasing time since tree mortality (and more breakage of branches from snags), dead surface fuels continue to accumulate on the forest floor while the mass and height of live fuels (primarily herbs and shrubs) increases (Jenkins et al. 2008, Klutsch et al. 2009).

Effects of PPCD on fuel profiles in gray-stage bishop pine forests are likely to be similar to bark beetle outbreaks; however, the potential for increases in live and dead surface fuels are likely greater following PPCD for two reasons. First, because PPCD kills trees across diameter size classes, there is likely to be more fine (e.g., 10-hr and 100-hr) canopy fuel that accumulates on the forest floor from the combination of branches from larger dead trees and boles + branches from smaller dead trees. Second, woody shrubs compose more of the total woody biomass in bishop pine forests than in many of the forest types affected by *Dendroctonus* beetle outbreaks. Therefore, the capacity for the shrub component to respond via compensatory growth is likely greater in bishop pine forests affected by PPCD and may lead to greater live surface fuels in the gray stage.

Silver stage (decades following tree mortality)

The silver stage of post-beetle outbreak is characterized by substantial increases in coarse surface fuels as snags fall, advanced tree regeneration ascends to the canopy, and herbaceous/shrubby vegetation peaks in dominance (Hicke et al. 2012, Jenkins et al. 2014). Canopy fuels begin to increase in amount and connectivity again as surviving canopy trees, shrubs, and any advanced regeneration increase in foliar and fine branch biomass (Jenkins et al. 2008, Collins et al. 2012, Woolley et al. 2019). Coarse surface fuels (1000-hr fuels) reach their greatest mass over the time

since tree mortality, in some cases nearly doubling from background levels pre-outbreak (Donato et al. 2013). Depending on forest composition, increasing growth in advanced and post-outbreak tree regeneration can eventually outcompete shrubs and lead to increasing ladder fuels as regenerating trees link the understory live and dead fuels to the canopy fuels of trees that survived the outbreak (Jenkins et al. 2008).

Effects of PPCD on fuel profiles in silver-stage bishop pine forests likely differ in some important ways. First, because of high moisture and relatively rapid decomposition rates, coarse surface fuels likely persist for a shorter time than following beetle outbreaks that occur in more generally drier environments. Combined with the greater range in sizes of dead tree boles following PPCD-caused mortality, this may shift biomass more quickly from coarse woody debris to duff than post-beetle-outbreak. Second, similar to the gray stage, the increase in shrub woody biomass is likely to be greater than following beetle outbreaks, as shrubs make up a greater proportion of background biomass, and the capacity for shrubs to encroach from nearby chaparral patches is greater than in montane and subalpine forests where beetle outbreaks occur. Finally, in beetle outbreaks, many of the surviving canopy and advance regeneration trees are other conifer species, with fuel profiles that are similar in nature to the host pine or spruce trees killed in the outbreak. However, in bishop pine forests, the tree species not affected by PPCD are broadleaf trees (e.g., *Quercus agrifolia*, *Umbellularia californica*) with very different canopy architecture and fuel profiles.

Potential changes to fire behavior and resistance to control

Despite the changes to fuel profiles brought about by tree mortality events such as beetle outbreaks (and similarly PPCD), there is little evidence to suggest that fires are more likely to occur or are larger in beetle-affected forests than in unaffected areas. Several studies across a range of spatial scales in the western US have shown that the likelihood of fire occurring (Bebi et al. 2003, Kulakowski and Jarvis 2011, Meigs et al. 2016) and area burned (Kulakowski and Veblen 2007, Hart et al. 2015, Hart and Preston 2020) are not statistically related to insect outbreaks. In historically frequent low- and mixed-severity fire regimes of the Southern Sierra Nevada Mountains, recent fire activity has been reported to be unpredictable in stands where a large proportion of trees were killed by pre-fire drought, though current research is underway to quantify potential effects—and may differ from findings in high-severity fire regimes of the Rockies. In any case, when fires do burn in areas with high levels of dead trees (from beetle outbreaks or other causes), there are potential operational concerns regarding fire behavior and resistance to control (Jenkins et al. 2014, Moriarty et al. 2019).

Red stage (0-2 years following tree mortality)

Several metrics of modeled fire behavior and on-the-ground operational concerns can be affected by tree mortality caused by beetle outbreaks in the red stage. Crown fire potential can be greater while red needles are retained on tree (Jolly et al. 2012), but increased flammability is offset by a reduction of fine fuels in the canopy as needles are shed (Simard et al. 2011). Outbreak-caused increases in crown fire potential (Schoennagel et al. 2012) are likely a result of two key factors: the proportion of trees in the red stage simultaneously (Hoffman et al. 2012) and the pre-outbreak surface fuels complex (Hoffman et al. 2013). With greater synchrony in red-stage trees and pre-outbreak fuel loads, crown fire potential in the red stage increases. Surface fire potential is likely less affected by canopy tree mortality in the red stage as the addition of dead needles to

the surface fuel profile represents a minor contribution to potential surface fire behavior. Operational concerns are primarily focused on the increased danger associated with numerous snags that are much more likely to fall than live trees when burned, as well as the potential for torching on snags that retain high levels of red needles (Page et al. 2013).

Effects of PPCD on potential changes to fire behavior and resistance to control in the red stage are likely similar. That is, fire is probably not more likely to occur or burn a larger area in PPCD-affected stands relative to unaffected stands, but when it does occur, crown fire potential may be greater when high levels of red needles are still retained in tree crowns. Further, safety and navigation through already dense stands of bishop pine may be more dangerous because of the increased potential for snag fall when dead bishop pine trees are burning.

Gray stage (3-10 years following tree mortality)

In the gray stage, crown fire potential is lower than unaffected stands due to the reduction in canopy fuels (canopy bulk density, available canopy fuel load) and less horizontal continuity (Jenkins et al. 2008, Klutsch et al. 2011, Hicke et al. 2012). Surface fire potential is modestly increased compared to unaffected stands, with the magnitude depending on the amount of fine and coarse fuels fallen from the canopy. As more canopy fuels fall to the forest floor in the form of branches and some snags, the potential for surface fire intensity and flame length increases (Jenkins et al. 2008, Klutsch et al. 2009). Operational concerns are elevated in the gray stage as standing snags are more likely to fall during a fire because of reduced structural integrity compared to the red stage (Page et al. 2013). In addition, standing snags with weakened branches can produce large firebrands with long burnout times, increasing potential for spot fires (Page et al. 2013). Effects of PPCD on potential changes to fire behavior and resistance to control in the gray stage are likely similar to those from beetle outbreaks.

Silver stage (decades following tree mortality)

Decades following tree mortality caused by beetle outbreaks, active crown fire potential remains low due to the sustained reduction in crown fuel amount and continuity, though surface fire potential and several operational concerns are at their highest levels. Fireline intensity, rate of spread, and flame lengths can be increased from the combination of high levels of coarse fuels and increased windspeeds with an open canopy (Jenkins et al. 2008, Klutsch et al. 2009). Operational concerns are primarily associated with extremely challenging navigation through forests as snag fall contributes to high loads of downed coarse woody debris and logs stacked on the forest floor, as well as increased resistance to control from high potential surface fire intensity and fireline intensity driven by high coarse surface fuel loads (Page et al. 2013)

Effects of PPCD on potential changes to fire behavior, operational concerns, and resistance to control, are likely similar to those from beetle outbreaks, with some potential differences. The higher dominance of shrubs in bishop pine stands compared to beetle-affected forests may lead to more of a mixing of downed coarse woody fuels and live surface fuels, with more fallen snags partially suspended above the ground (as opposed to flush on the forest floor). This may increase drying of coarse fuels and affect surface fire potential, as well as increase operational and navigational challenges through areas with high levels of mortality.

Potential effects on fire severity

From the mid-2000s to the mid-2010s, fires that burned through varying levels of pre-fire mortality from bark beetles led to many studies examining the effects of beetle outbreaks on subsequent fire severity—defined as the ecological effect of fire, often measured as fire-killed vegetation or fire-caused change (Keeley 2009).

Red stage (0-2 years following tree mortality)

Burn severity has been mostly similar between beetle-impacted and unaffected forests when fires have burned through the earliest outbreak phases. In the green-attack stage (when trees are attacked by beetles and in the process of dying, but before needles have turned red), some measures of burn severity increased modestly when weather conditions were moderate, but under extreme weather conditions (warm, dry, and windy), burn severity was mostly unaffected by beetle outbreaks (Harvey et al. 2014a). In the red stage, most measures of burn severity were unaffected by pre-fire beetle outbreaks under moderate or extreme weather conditions, with the exception of deep charring on trees that were dead pre-fire (Harvey et al. 2014b). Compared to the effects of topography and weather conditions, beetle outbreaks had relatively minor effects on burn severity in the green-attack and red stage (Harvey et al. 2014a, 2014b). Remotely sensed burn severity analyses of multiple fires throughout the Pacific Northwest and Northern Rockies have also found little effect of beetle or defoliator outbreaks on burn severity, and in some cases burn severity is decreased following outbreaks (Meigs et al. 2016). Effects of PPCD on burn severity in the red stage are likely similar to those of beetle outbreaks; that is, relatively minor compared to other drivers of burn severity (e.g., weather and topography).

Gray stage (3-10 years following tree mortality)

Effects of beetle outbreaks on burn severity in the gray stage have been more varied and depend on weather conditions at the time of fire. Several studies in a range of forest types and beetle outbreaks have found no effect of beetle outbreak severity on burn severity under extreme or moderate weather conditions (Harvey et al. 2013, Andrus et al. 2016, Agne et al. 2016). In gray stage mountain pine beetle outbreaks in the Northern Rockies, however, burn severity decreased with beetle outbreak severity under moderate weather conditions (Harvey et al. 2014a), but increased with beetle outbreak severity under extreme weather conditions (Harvey et al. 2014b). Under extreme weather conditions, when severe fire is expected in lodgepole pine forests, beetle-killed snags in the gray stage were more prone to deep charring and partial consumption of bole and branch mass than were live or red-stage trees (Harvey et al. 2014b, Talucci and Krawchuk 2019).

Effects of PPCD on burn severity in the gray stage are likely similar to those of beetle outbreaks, with a potential increase in effects of deep charring and partial-to-whole consumption of branches and boles. Such effects have been documented in Santa Cruz Island bishop pine stands that burned in the gray stage following drought-induced mortality (Walter et al. 2005). The smaller diameter branches and boles of bishop pine, especially in the mid-seral stages most severely impacted by PPCD, make combustion more likely during extreme weather conditions when fire potentials are high.

Silver stage (decades following tree mortality)

Not enough time has elapsed following recent beetle outbreaks in North America to have an opportunity to study the effects of silver-stage beetle outbreaks on subsequent burn severity.

Potential effects on post-fire recovery

Red stage (0-2 years following tree mortality)

In serotinous lodgepole pine forests that experienced beetle outbreaks followed by fire, post-fire regeneration has been unaffected by pre-fire beetle outbreak severity. That is, post-fire lodgepole pine seedling density was not statistically different between areas with severe beetle outbreaks pre-fire or areas where most trees were alive pre-fire (Harvey et al. 2014a, 2014b). Instead, post-fire tree regeneration was driven strongly by the pre-fire abundance of serotinous cones and burn severity. Seeds can remain viable inside serotinous cones of dead trees for more than a decade (Aoki et al. 2011, Teste et al. 2011). Further, cones from beetle-killed lodgepole pine open slower in a fire than cones on live lodgepole pine, potentially providing added protection to seeds from encountering lethal temperatures (Sharpe and Ryu 2015). Therefore, trees killed pre-fire that still retain closed cones in the canopy may contribute substantially to post-fire tree regeneration if cones are not consumed by fire. Effects of PPCD on post-fire bishop pine regeneration are expected to be similar if seeds contained in closed cones on trees killed by PPCD remain viable after tree death.

Gray stage (3-10 years following tree mortality)

Similar to the red stage, no effect of pre-fire beetle outbreaks has been detected on post-fire tree regeneration in lodgepole pine forests that burned in the gray stage post-outbreak (Harvey et al. 2014a, 2014b, Edwards et al. 2015, Agne et al. 2016, Talucci et al. 2019). Reasons for the lack of effect are interpreted as similar to those explained above for the red stage (i.e., viable seeds are still retained in closed cones on dead trees). Effects of PPCD on post-fire bishop pine regeneration are expected to be similar if seeds contained in closed cones on trees killed by PPCD remain viable after tree death.

Silver stage (decades following tree mortality)

Not enough time has elapsed following recent beetle outbreaks to have an opportunity to study the potential effects of beetle outbreaks on post-fire tree regeneration when fires burn through the silver stage. However, as beetle-killed trees fall, cones are moved to the forest floor where they are more likely to be consumed by fire, removing the potential seed source that could be provided by dead trees. Effects are expected to be similar in bishop pine forests, where dead and fallen trees (boles, branches, cones) are more susceptible to consumption in fire (Walter et al. 2005), or if not consumed, exposed to lethal temperatures greater than 125 deg C (Linhart 1978).

Summary of effects of PPCD on fuels, fire behavior, operational concerns, fire severity, and post-fire recovery

A key difference between bark beetle outbreaks and PPCD is that stand-level crown dieback and subsequent mortality occur within several years in bark beetle outbreaks but may develop over longer time spans for PPCD. Trees with PPCD are likely to experience partial crown dieback for years to a decade or more before dying. This suggests that at the aggregated scale of a stand, PPCD is unlikely to follow a progression of discrete phases (e.g., red, gray, and silver stages) and is more likely to contain trees in each phase at a single time.

Effects of PPCD on fuels will depend on the proportion of trees in each phase. Infected or dead trees with recent crown dieback (dead needles remain in the crown) may increase canopy flammability, but if substantial standing dead trees without needles exist in a stand, this effect

could be counteracted due to decreased canopy fuel amount. In general, canopy fuels are expected to decline in areas with PPCD, except for in the early phases of symptom expression and decades following mortality where hardwood species have entered the canopy layer. Additionally, the contribution of pitch/resin may serve as an important fuel component in PPCD-affected stands, but this has yet to be quantified. Surface fuels are likely to be elevated in areas where PPCD-killed trees have lost their needles and/or fallen to the forest floor. Live surface fuels are likely to accumulate rapidly following crown dieback through compensatory growth of shrubs. Downed woody surface fuels may also be elevated, although rapid decomposition may counteract this effect when mortality occurs over a protracted time.

Fire is probably no more likely to occur or burn a larger area in PPCD-affected stands relative to unaffected stands. Potential changes to fire behavior following PPCD are likely to differ depending on the proportion of dead trees in various phases. Where PPCD-affected stands have high levels of red needles retained in tree crowns, crown fire potential may be increased. Where stands have many standing dead trees that have experienced branch loss and fallen dead trees, surface fire intensity and flame lengths are likely to increase. Where stands contain a mix of recently dead trees with red needles, standing dead and fallen trees, both surface fire intensity and crown fire potential are likely to increase.

Resistance to control and operational concerns vary with the proportion of trees in each phase. Where standing dead trees are abundant, navigation through dense bishop pine stands may be more dangerous because of the increased potential for snag fall, especially where trees have been dead for several years. Standing dead snags can also increase potential for spot fires. Where trees killed by PPCD have fallen, mixing of downed coarse woody fuels and live surface fuels from the shrub layer may increase navigational challenges through areas with high levels of mortality. However, rapid decomposition of coarse woody debris combined with asynchronous tree mortality may render these concerns minor in comparison with bark beetle-killed forests.

Effects of PPCD on burn severity are likely to be relatively minor compared to other drivers of burn severity (e.g., weather and topography), although deep charring and increased combustion of dead trees in the gray stage are likely. Post-fire recovery is unlikely to be affected by PPCD if seeds contained in closed cones on trees infected with or killed by PPCD remain viable after crown dieback and tree death. However, as the proportion of dead trees in the silver stage increases within a stand, post-fire bishop pine regeneration is expected to decrease as long dead cones may lack viable seed and are more susceptible to consumption by fire.

Climate warming and associated drought stress

In addition to acting as a contributing factor for other threats to bishop pine, direct effects of climate warming may threaten bishop pine. Direct effects of climate change on forests include the effects of changing temperatures and moisture availability on plant physiological function. Heatwaves and drought events are predicted to increase in many regions as the climate continues to warm and have been linked to widespread and severe forest die-off events (Williams et al. 2013, Allen et al. 2015). Further, reproductive capacity may be delayed and decreased as moisture stress on plants increases (Redmond et al. 2012, Enright et al. 2015). In California, the occurrence of drought events has been exacerbated by anthropogenic climate warming (Williams et al. 2015) and will become significantly more likely as climate warming continues to occur

(Diffenbaugh et al. 2015, Swain et al. 2016). For bishop pine, mortality caused by moisture stress is possible, especially as drought events become more frequent. Some old-growth bishop pine stands in Mendocino and Sonoma Counties are experiencing dieback attributed to drought (although PPCD may be involved). Further, fog drip is an important supplemental moisture source for bishop pine through summer drought (Fischer et al. 2016, Baguskas et al. 2016). If fog cover and duration decrease in tandem with increasing temperature and frequency of drought events, bishop pine mortality may increase, especially in small to moderate-size trees (Baguskas et al. 2014). Relatively small and late-developing canopy seedbanks may also result, leading to decreased reproductive capacity (Enright et al. 2015).

Resilience to fire under altered fire regime

(contributing factor: altered fire regime and interaction with warming climate)

Altered fire regimes threaten bishop pine forest persistence by potentially eroding their resilience to fire (defined as the capacity to experience fire and return to a bishop pine forest at some point following fire). As the primary regeneration opportunity for bishop pine forests is stand replacing fire, the forest stand condition at the time of fire, as well as the climatic conditions following fire are key factors affecting resilience.

If the fire regime changes such that the time between fires becomes anomalously short or long, the reproductive capacity of bishop pine stands may not be sufficient to regenerate a forest (Keeley et al. 1999, Buma et al. 2013, Enright et al. 2015). The typical fire return interval of bishop pine forests of approx. 40-70 years coincides with the time period where cone abundance is likely greatest. Although bishop pine trees as young as 5 years old can produce cones, stand level cone abundance likely remains below the point required to regenerate a stand if fire were to occur within the first decade or two post-fire. If fire were to occur at anomalously short intervals, bishop pine is at risk of “immaturity risk” (Keeley et al. 1999), and bishop pine may be replaced post-fire by other vegetation communities. Such dynamics have been documented in the Northern Rockies with serotinous lodgepole pine, where short-interval severe fires have led to drastic reductions in post-fire seedling density (Turner et al. 2019). Conversely, if fire return intervals approach or exceed the maximum lifespan of bishop pine (approx. 100 years), the canopy seedbank that is key to post-fire regeneration may deteriorate, and seed abundance may become insufficient to replace the stand if fire were to occur at anomalously long intervals (i.e., ‘senescence risk’). At every seral stage of bishop pine stand development, any factor such as PPCD that potentially reduces the abundance of viable seed may compound the effects of altered fire return intervals on bishop pine resilience to fire.

Further decreases in resilience to fire are likely if post-fire conditions are warm and dry during the first 1-3 post-fire years, when seedlings are particularly vulnerable to drought (Enright et al. 2015). Reductions of several orders of magnitude of post-fire seedling establishment have been observed when fires are followed by drought in the Rocky Mountains (Harvey et al. 2016), and in extreme cases have led to post-fire tree regeneration failure (Stevens-Rumann et al. 2018). In California, drought events have increased in recent decades and will become significantly more likely as climate warming continues to occur (Diffenbaugh et al. 2015, Swain et al. 2016). While average precipitation in California may remain similar, the window in which precipitation occurs is likely to become compressed, while extreme dry and wet years will become more common

(Swain et al. 2018). Both of these phenomena may have important implications for seedling establishment and survival. Furthermore, as the climate warms, trees will experience increased drought stress, even in the absence of changes in precipitation amount (Diffenbaugh et al. 2015). For bishop pine, impacts of drought more strongly negatively affect small trees in dry landscape positions (Baguskas et al. 2014), which may have important implications for post-fire seedling establishment. Fog drip is an important supplemental moisture source for bishop pine through summer drought and is particularly important for smaller seedlings and saplings (Fischer et al. 2016, Baguskas et al. 2016). If fog cover and duration decrease in addition to warmer and drier conditions following future fires, post-fire resilience of bishop pine may be further eroded.

Non-native and invasive plant species

(contributing factor: vectors of introduction)

Non-native invasive plant species are a threat to bishop pine forest health and likely interact with the previous threats. Following the Vision Fire, there was heightened concern about non-native Australian fireweed (*Erechtites minima*), which is an aggressive post-fire colonizing annual herb or sometimes perennial plant. Australian fireweed cover was as great as 20% in some post-fire plot locations, and aggressive removal along with succession toward shrub and tree cover reduced incidence through the early seral stage (Holzman and Folger 2005, Harvey and Holzman 2014). As Australian fireweed can produce a persistent seedbank that remains dormant in the soil, the long-term impacts of the post-fire cover following the Vision Fire are unknown. In the absence of fire, aggressive shade tolerant species such as English Ivy (*Hedera helix*) have been documented in the understory of the mid-seral bishop pine forest, particularly under tall fire-killed snags where birds may disperse seeds (personal observation, B. Harvey). Additional invasive plant species of concern in bishop pine forests include pampasgrass species (*Cortaderia spp.*), cotoneaster species (*Cotoneaster spp.*), panic veldtgrass (*Ehrharta erecta*), and English holly (*Ilex aquifolium*).

While non-native invasive plant species are not currently dominating bishop pine forests on the Point Reyes Peninsula, a key knowledge gap is how future fire or the current tree mortality caused by PPCD may affect establishment and spread of non-native species. Fire and disease-caused mortality of the dominant canopy trees (bishop pine) makes available light, water, and nutrient resources that may benefit non-native species.

Future desired conditions

The primary attribute of future desired conditions, based on input from GGPNC, CA State Parks, NPS, and One Tam Partnership, is to sustain local populations of bishop pine in Marin County in a mosaic that includes patches in each of the seral stages. As bishop pine is a fire-adapted species, fire is the key natural process that governs the distribution of seral stages across time and space. The natural range of variability in the abundance / proportion of seral stages is not known at this time, though the natural fire regime likely would have resulted in a shifting mosaic of stand ages across populations in Marin County. As each seral stage provides relatively unique conditions and functions, maintaining a diversity of seral stages is likely important for biodiversity as well as promoting resilience to disturbance and stressors.

Early seral stage: The presence of early seral bishop pine forests is strongly dependent on fire activity, which ‘resets’ stands to early seral conditions. It is currently unknown if there are surrogate disturbance processes (e.g., harvesting) that can create early seral conditions, and fire is likely to remain the primary driver of early seral stands. Desired conditions in the early seral stage are outlined in Table 2 below, but generally are characterized by extremely high bishop pine seedling density (though a wide range of seedling density is common), open forest canopy with large snags, low fuel loads, and high native plant species diversity.

Mid-seral stage: After approximately 10 years post-fire, early seral stands will transition to mid-seral, where desired conditions are high density of bishop pine trees proceeding through intense and naturally occurring density-dependent thinning, though density and the intensity of natural thinning are variable, depending on a wide range of initial post-fire bishop pine seedling densities. Currently, most bishop pine stands in Point Reyes are in this seral stage. Desired conditions in mid-seral stands are generally characterized by continuous canopy cover, low understory plant diversity, and a moderate to large canopy seedbank. High fuel loads are expected in this stage and it is uncertain whether treatments to reduce fuel loads would significantly reduce fire hazard, or what trade-offs with other measures of forest health might exist.

Old-growth stage: By approximately 50 years post-fire, bishop pine stands transition from mid-seral to old-growth. This transition occurs following a period of heavy density-dependent mortality, with desired conditions for density of old-growth stands 2-3 orders of magnitude lower than those of mid-seral stands. In general, desired conditions in old-growth stands include low density stands with canopy gaps that facilitate increased understory plant diversity, and a large canopy seedbank. As old-growth bishop pine stands meet or surpass 100 years since experiencing fire, trees may naturally (i.e., in the absence of pitch canker or other threats outside of the historical range of variability for this species) may begin to senesce. In the absence of fire, bishop pine is unlikely to persist in a stand after all mature trees senesce.

Condition and trends assessment

Six forest attributes are identified that can be used as potential metrics to assess and track forest health (Table 2). Each metric is described below and separated out by what would be expected within the NRV in each of the three key seral stages and is presented in context of how threats are likely to potentially affect metrics.

Table 2. Forest health attributes (metrics) and expected range of values under the NRV across each seral stage of bishop pine stand development. Values are ranked from 1-4 (and color-coded) where 1 = low (green), 2 = moderate (yellow), 3 = high (orange), 4 = extreme (red).



Forest Health Attribute (Metric)	Early seral (~0-10 years post-fire)	Mid-seral (~10-50 years post-fire)	Old-growth (~50-100 years post-fire)
Bishop pine live tree density (stems ha⁻¹)	4. Extreme (~100,000 to 500,000) from post-fire, even-aged, cohort establishment.	3. High (~1,000 to 50,000) as stands proceed through a period of heavy density-dependent mortality.	1. Low (~100 to 500) as stands have occupied maximum growing space and mortality is not replaced by ingrowth.
Native plant species diversity and dominance of life forms	3. High (herb and shrub-dominated with small stature bishop pine seedlings). Native plant diversity a27pprox. 30 species per 100 m ² and >90% cover.	1. Low (bishop pine dominated w/ few evergreen shrubs in understory). Native plant diversity a27pprox. 8 species per 100 m ² and >99% cover.	2. Moderate (shrub and herb diversity increasing again in canopy gaps). Native plant diversity a27pprox. 15 species per 100 m ² and >99% cover.
Fuel profiles and fire hazard	1. Low canopy fuel loads.	3. High canopy fuel load and continuity as soon as canopy closure occurs.	3. High canopy fuel load, but continuity likely lower than mid-seral stage.
	1. Low live surface fuels until substantial vegetation regrowth occurs.	2. Moderate live surface fuels are from shrubs.	3. High live surface fuels are from shrubs.
	1. Low dead surface fuels until fire-killed snags begin to fall and/or fragment.	3. High dead surface fuels that accumulate from density dependent thinning (fine) and fallen snags (coarse).	3. High dead surface fuels continue to accumulate from fallen branches and needles (fine) and snagfall (coarse).
Bishop pine reproductive capacity	1. Low as the canopy seedbank from pre-fire has been exhausted and young trees are just beginning to produce cones.	2-3. Moderate (increasing to high over the stage) as the canopy seedbank accumulates with time.	3-2. High (decreasing to moderate over the stage) as the canopy seedbank declines with time through eventual mortality of the canopy bishop pines.
Large snag and coarse woody debris abundance	3. High large snag abundance (from fire-killed cohort).	1. Low large snag abundance.	2. Moderate large snag abundance (increase in snags from density independent mortality).

	2. Moderate coarse woody debris from fallen snags.	1-2. Low (increasing to moderate over the stage) coarse woody debris (increase in small dead trees from density dependent mortality).	2. Moderate (gradually accumulating) coarse woody debris.
Canopy structure texture (LIDAR signature)	3. High fine grain (e.g., < 1m) variability with low (~2m) live canopy hei and standing snags (~10m).	1. Low variability at fine and moderate grain with continuous canopy cover (~3-20m).	3. High coarse grain (e.g., ~5m) variability with shrubs (~1m) and canopy trees (~20m).

Metric 1 – Bishop pine live tree density (stems ha⁻¹): stand dynamics that are in line with NRV and fire regime

Research on post-fire bishop pine stand dynamics outlined in the section above suggests general expectations for characterizing the condition and assessing trends in bishop pine population dynamics. Similar to other moderately or strongly serotinous fire-adapted conifers, bishop pine populations go through cycles of boom and bust. That is, fire catalyzes seed release and establishment of seedlings at the point in time where the population is greatest, after which the population monotonically declines over time through early-, mid- and old-stages, until the next fire occurs (Figure 1). Therefore, within stands, live bishop pine density in the range of several hundred thousand seedlings/saplings per hectare in early seral stages, several thousand to tens of thousands of medium sized trees per hectare in mid-seral stages, and several hundred old trees per hectare in old-growth stages would be considered healthy (Table 2). At any given stage, a wide range of density (and naturally occurring density-dependent mortality) is expected, driven primarily by initial post-fire seedling densities. As density-dependent mortality is the result of larger trees outcompeting smaller trees, mortality through the early- and mid-seral stages should be dominated by poorly competing trees with small diameter and height. Deviations from these patterns of stand dynamics expected under the NRV and fire regime may signify poor forest health. For example, especially in early- and mid-seral stages, mortality in a healthy bishop pine stand would be dominated in frequency by small-diameter and shorter trees. However, mortality across all sizes of trees (e.g., caused by PPCD) in early- and mid-seral stands would represent a deviation from ‘healthy’ stand dynamics undergoing competitive density-dependent mortality.

With specifics of the NRV for fire regime parameters (e.g., size, frequency) unknown, it is difficult to construct expectations for age/stage class diversity among stands. However, even though within-stand structure is relatively homogenous (e.g., single-age cohorts), heterogeneity in fire effects across any moderately sized landscape of bishop pine such as those on the Point Reyes Peninsula would create some heterogeneity among stands. That is, at any given point in time it would be normal to expect some mix of stands in early-, mid-, and old-stages across a landscape forested by bishop pine. Given the duration of each stage, the relative proportions at any time would likely be greater for old-growth and mid-seral stages, and less for early seral stages. As the threats to bishop pine forest health vary in nature and magnitude across seral stages, greater diversity in seral stages across a forested landscape would likely provide more resistance to stressors and disturbance.

Threats to bishop pine health pose several key questions regarding Metric 1. First, the impacts of PPCD have likely caused substantial deviation from stand dynamics within the NRV of bishop pine. The degree to which areas affected by PPCD are experiencing mortality patterns deviating from the expected density-dependent (e.g., mortality constrained to mostly smaller trees) remains an un-characterized, but important knowledge gap. Second, recent fire activity is likely the primary driver in variability in seral stages among stands. Prior to the 1995 Vision Fire, most of the bishop pine forest on the Point Reyes Peninsula was in the later mid-seral stage or the old-growth stage, with presumably relatively low among-stand diversity in seral stages. Currently, seral stage diversity is relatively evenly split between mid-seral (post-Vision Fire) and old-growth (unburned in the Vision Fire) stands, in proportions that are likely within the expected range given the fire regime. Despite heterogeneity in seral stages at the aggregate level, the spatial arrangement of seral stages is homogenous, as they are dictated by areas burned in the Vision Fire—within which most to all bishop pine stands were reset to early seral. Whether PPCD is potentially accelerating stand development from mid-seral to old-growth, reversing development from mid-seral to early seral, or sending stands on an alternative and novel trajectory is an important knowledge gap with implications for Metric 1.

Metric 2 – Native plant species diversity and dominance of life forms

Baseline information on trends in native plant species diversity and dominance suggest that over time, plant species diversity follows somewhat predictable trends (Figure 1 and Table 2). Diversity is highest in early seral stages (when herbs, shrubs, and small tree seedlings co-dominate) and native plant species richness is approx. 30 species per 0.01 ha with >90% cover. Diversity is lowest in mid-seral stages (when few evergreen shrubs are present) and native plant species richness is approx. 8 species per 0.01 ha with >99% cover. Diversity increases to moderate levels in old-growth stages (when shrub and herb diversity increases again as bishop pine canopy gaps open) and native plant species richness is approx. 15 species per 0.01 ha with >99% cover. Similar to (and related to) variability in bishop pine density, variability exists among stands at any seral stage, where the greater the canopy dominance by bishop pine, the lower the diversity of other plants (herbs, shrubs, and broadleaf trees).

Several threats to bishop pine health may potentially affect Metric 2 and pose important questions. First, the widespread and severe bishop pine mortality caused by PPCD in mid-seral stands is likely affecting the plant community in important, but unknown (i.e., yet to be documented) ways. The removal of dominant bishop pine trees in the canopy layer opens up light, water, and nutrient resources for other plants, which may increase plant diversity relative to what would otherwise be expected in mid-seral stages. However, depending on the native plant diversity nearby or in the understory, the canopy disturbance caused by PPCD and likely resulting effects on the understory microclimate may facilitate spread of non-native invasive species. If non-native / invasive species establish and/or spread in areas affected by PPCD, effects on native plant diversity could be negative. In sum, the effects of PPCD on the plant community, especially understory herbs and shrubs in bishop pine forests remains a critical knowledge gap with strong implications for Metric 2.

Metric 3 – Fuel profiles and fire hazard: values in line with NRV and fire regime

Fuel profiles and fire hazard in bishop pine forests change substantively over time (Agne et al. in review) (Table 2). In the early seral stage, fuels are not typically sufficient to support stand-

replacing fire, as fine dead fuels consumed by the previous fire have yet to recover, and most fuels are large coarse fuels and live, small-statured vegetation. By the time stands enter mid-seral and old-growth stands, fuels within the NRV are typically sufficient to carry stand-replacing crown fire, but presumably at intensities that do not consume important biological legacies for post-fire regeneration (e.g., bishop pine canopy seedbank, soil seedbank, underground root structure for resprouting shrubs and broadleaf trees). Fire intensity that produces temperatures of ~130 deg C outside of cones, but does not expose seeds to sustained temperatures greater than 105 deg C would open most bishop pine cones without damaging seeds. However, temperatures greater than 130 deg C do not yield any additional benefit for cone opening, and temperatures of 125 deg C are lethal to bishop pine seeds.

The key threat to bishop pine health regarding metric 3 is the likely effects of PPCD on fuel profiles and potential effects on fire behavior (specifically heat duration and intensity). Measurements of fuel profiles in PPCD-impacted stands can be compared to measurements in stands unaffected by PPCD to assess if, and how far, deviated fuel profiles are from expectations under the NRV. In addition to fuel amount, unknowns about the quality of fuels on dead trees (e.g., effusive pitch streaming on PPCD-killed trees) are important considerations for potentially altered fire behavior in bishop pine stands. The effects of PPCD on fuel profiles and fire behavior remain a critical knowledge gap, as basic information on fuel profiles in bishop pine forests are not widely documented (but see Agne et al. in review), and to our knowledge, no information exists currently on the effects of PPCD on fuel profiles for any forest type.

Metric 4 – Bishop pine reproductive capacity: sufficiently high when fire occurs

Post-fire persistence of bishop pine populations requires the presence of an ample on-site seed source at the time of fire. Observations and research in progress (Agne et al. in prep) suggest that bishop pine reproductive capacity, measured as the abundance of closed serotinous cones in a live stand containing viable seed peaks somewhere toward the end of mid-seral stages or in the early old-growth stages. In early seral stands, reproductive capacity is low until the post-fire cohort of trees has been reproductively mature for several years or more, and the canopy seedbank is replenished. As stands age, the canopy seedbank likely peaks at some point around 40-50 years post-fire, after which a slow but gradual depletion of the canopy seedbank likely follows the gradual mortality of bishop pine trees through old-growth stages (Table 2).

Several threats to bishop pine health are likely to affect Metric 4. First, the effects of PPCD production and retention of viable seed in cones on infected or killed trees are unknown. If PPCD has negative effects on viable seed production and storage, reproductive capacity could be lessened across all stages of stand development. Second, if PPCD alters fuel profiles and/or fire behavior to increase heat intensity or duration, viable seeds in serotinous cones may be damaged or consumed by fire. In both cases, PPCD is likely to lessen reproductive capacity at the time of fire. Third, if fire return intervals that are either anomalously short or long and fire occur in early seral stands or in late old-growth stands, reproductive capacity is likely low from immaturity risk and senescence risk, respectively, and may lead to low post-fire recruitment. Finally, increasing temperatures and drought stress may lead to delayed reproductive maturity and decreased annual cone production, diminishing the overall reproductive capacity of bishop pine forests. Understanding how reproductive capacity is affected by any of these factors is an important knowledge gap.

Metric 5 – Large snag and coarse woody debris abundance

Large snags and coarse woody debris are important contributors to wildlife habitat and woody carbon storage in bishop pine forests and likely follow somewhat predictable patterns through seral stages. In early seral stages, large snag abundance is expected to be at its greatest level, since stand-replacing fire immediately creates snags from the pre-fire cohort of trees. The size of the snags will depend, in part, on the seral stage at the time of fire. Coarse woody debris is expected to be moderate, consisting primarily of pre-fire downed and burned logs until the fire-killed cohort of snags begins to fall. In mid-seral stages, large snag abundance is expected to be very low, as the fire-killed snags have mostly (or all) fallen, and dead trees from the post-fire cohort killed through competition are primarily small diameter. Coarse woody debris levels are low-to moderate as fire-killed snags fall and decompose, and little-to-no coarse woody debris is produced from small-diameter trees killed by density dependent mortality. In old-growth stages, large snag abundance is moderate, as density-independent mortality becomes the primary driver of bishop pine tree death. As snags fall, coarse woody debris levels correspondingly increase.

Several threats to bishop pine forest health have implications for Metric 5. First, widespread PPCD in mid-seral stands is decreasing capacity for large snag and coarse woody debris production by killing trees that would otherwise outcompete neighboring trees and become dominant canopy trees (i.e., large snags and coarse woody debris after death). Second, changes to fuel profiles or fire behavior resulting from PPCD that increases consumption of dead wood will likely drive reductions in post-fire snags and/or coarse woody debris in future early seral (post-fire) forests. Third, shortened FRIs can drastically reduce large snag and coarse woody debris abundance in serotinous lodgepole pine forests in the Rocky Mountains (Turner et al. 2019), and similar effects in bishop pine forests could occur with short-interval fires.

Metric 6 – Canopy structure texture: LIDAR signature

Canopy structure (height, roughness/rumple, and density) as measured by LiDAR (Kane et al. 2010) can aid in mapping expected characteristics for each seral stage (Table 2). In early seral stages, canopy surface texture would be expected to be highly variable (high rumple) at a fine spatial grain (e.g., <1m) with a low live canopy height (approx. 2m) as shrubs, herbs, and trees co-dominate a short-statured canopy. Standing snags (approx. 10-15m tall) would be expected to contribute to canopy roughness/rumple with peaked height signature separated by several meters horizontally. In mid-seral stages, canopy surface texture would be expected to have low variability (low rumple) at fine (e.g., <1m) and moderate (e.g., 2-4 m) spatial grain, as canopy cover would be fairly homogenous and dense at heights of approx. 3 to 20m (Figure 7, left image). Few snags may be present and would be sharp anomalies extending several meters above the continuous canopy. In old-growth stages, canopy texture would be expected to have high coarse grain (e.g., approx. 5m) variability (high rumple) with irregular patches of canopy heights dominated by widely-spaced canopy bishop pine trees (approx. 20m tall) interspersed with canopy heights dominated by shrubs (approx. 1m tall) (Figure 7, right image).

The primary threat to bishop pine forest health that has implications for Metric 6 is PPCD. Through canopy dieback and mortality, PPCD is expected to increase canopy surface roughness in any seral stage, but most notably in mid-seral stages where canopy surface roughness would otherwise be very low.

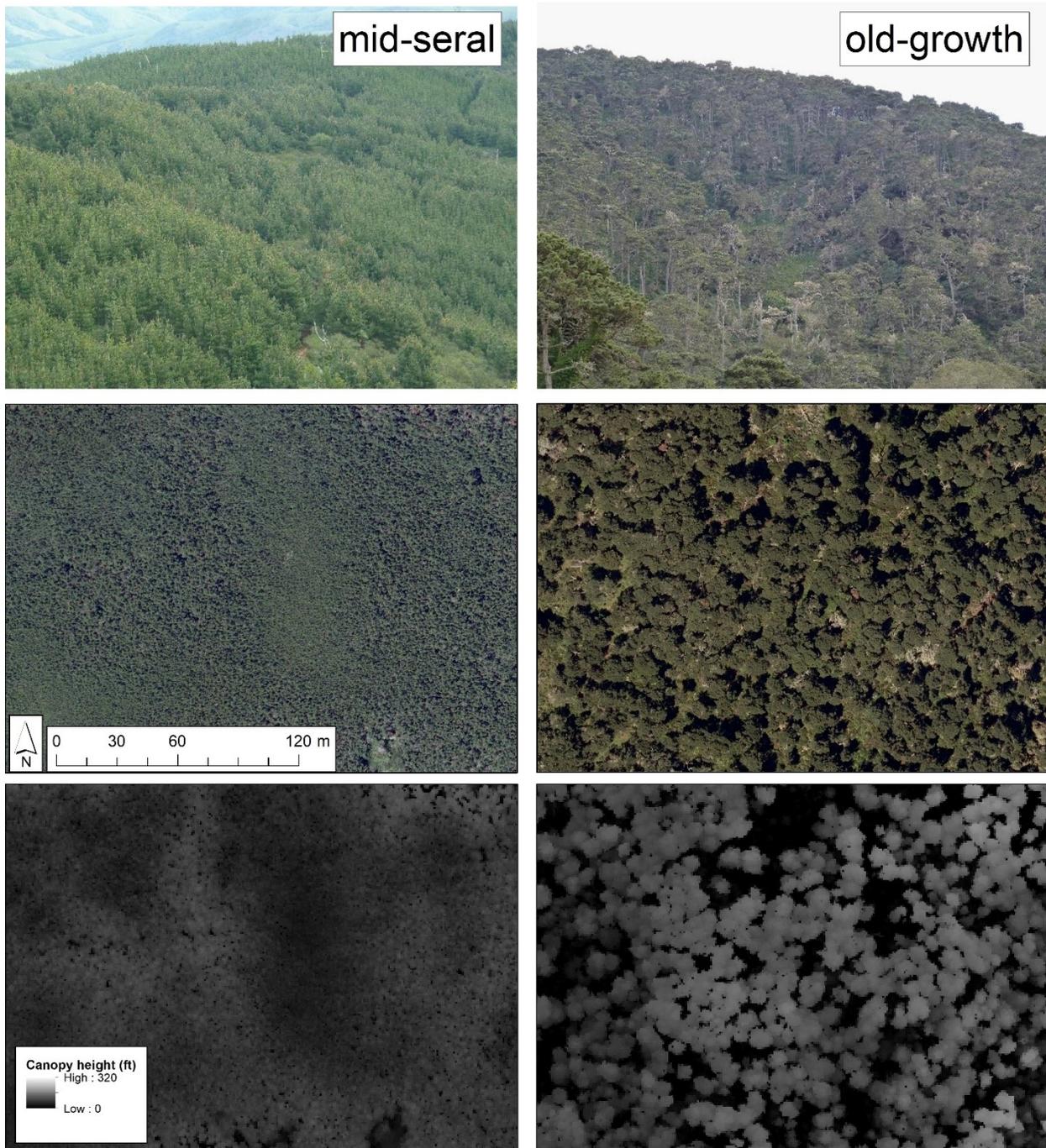


Figure 7. Visual difference in aerial canopy roughness (texture) between smooth and even texture in mid-seral stands (left) and rough texture with gaps between tree crowns in old-growth stands (right). Top row is an oblique photograph, middle row is an aerial photograph, and bottom row is LiDAR-derived canopy height at 1m pixel size. All images in each row are of the same location. (source: top row – B. Harvey; middle row – marinmap.org; bottom row – onetam.maps.arcgis.com).

Management recommendations and guidance on addressing knowledge gaps

Based on the information above, here we discuss potential treatment options in the bishop pine forest with objectives of reducing fire risk, reducing exposure to negative effects of PPCD, fostering ecological resilience and supporting desired future condition (e.g., addressing threats identified in Table 1). We break these out into recommendations for each seral stage, focusing on ideas for adaptive management and research for continued learning. While these recommendations are at present for the bishop pine forests on the Point Reyes Peninsula, they are likely to be applicable to other bishop pine forests in the region.

Early seral stands

Management actions

- Minimize unplanned fire in early seral stands, especially if bishop pine are reproductively immature. Unplanned fire can be limited by decreasing ignition sources from roads adjacent to early seral stands. Specific actions include avoiding parking heavy equipment on adjacent roads, eliminating brush cutter work during the dry season, trimming grasses on adjacent roadsides (both within and outside the defensible space rotation), and coordinating with PG&E to prioritize areas adjacent to early seral stands for power pole replacements and undergrounding or removal of power lines where possible.
- When fire occurs in early seral stands prior to reproductive maturity and continued bishop pine presence is desired, closed cones can be collected from nearby mature stands, opened in the oven to release seeds, and planted in recently burned stands. Note that this action is not strictly ecological restoration, and its feasibility may be limited if fire in early seral stands increases.

Knowledge gaps

- Characterization of seed dispersal distance and rate from unburned, reproductively mature stands, with implications for natural regeneration of burned early seral stands from an adjacent seed source if the on-site seed source is not present post-fire.

Mid-seral stands

Management actions

- Applied experiments with thinning could be considered in limited locations to accelerate succession toward old-growth conditions, mitigate PPCD, and/or alter fuel profiles. Ideally, experimental thinning should be conducted in areas that are planned to be thinned for other purposes, as several unintended consequences could arise including: increased PPCD severity in low density stands (as suggested by observations) and loss of the process of forest self-thinning, which may select for traits in ways that are not yet understood.
- Target density and basal area of a thinning to accelerate succession toward old-growth conditions can be developed from reference stands that are currently in old-growth seral stage (e.g., approx. 100 to 500 stems ha⁻¹). However, a somewhat higher retention density (e.g., the higher end of this range, or a gradient of densities far exceeding this target) could buffer against the possibility that a considerable number of retained individuals may be lost to PPCD following treatment. The exact number or proportion of stems to be removed would vary on initial pre-treatment density, as stands 23-years post-fire ranged

from approx. 2,000 to 30,000 live trees ha⁻¹. Timing of thinning should occur when stands have well exceeded the age of reproductive maturity for trees that are retained, to avoid substantial loss of the canopy seedbank and therefore potential eroded resilience to subsequent fire. Additional prescription details include avoiding wounding of retained (unharvested) trees as PPCD develops most readily through wounds, or otherwise creating conditions that could facilitate the spread of PPCD.

- Fuels treatments should be prioritized in the WUI vs. more remote areas, as fuel treatments that retain a significant component of bishop pine forest are unlikely to prevent the occurrence of high severity crown fire. Fuel breaks should be implemented around values at risk with the understanding that when these forests experience fire under extreme conditions, crown fire remains highly likely.

Knowledge gaps

- Identify individuals with inherent genetic resistance to PCCD in the field; longer term/larger effort could initiate seed collection for a resistance breeding program.

Old-growth stands

Management actions

- Applied experiments with prescribed burning or other fire surrogate (raking) to regenerate bishop pine prior to canopy senescence.
- Within treated areas, disperse seed from cones opened in the oven; seed dispersal from open cones on live trees within or adjacent to the plot could also provide a source of regeneration.

Knowledge gaps

- Effects of PPCD on old-growth bishop pine are observationally less severe than in mid-seral stands, monitoring is needed to ensure this is a true effect over time vs. delayed demonstration of symptoms in older trees.
- Potential for seeds that germinate in soil containing *F. circinatum* to demonstrate greater PPCD resistance as seedlings—monitoring of regeneration in areas where PPCD is present and absent (or if opening cones in the oven, could experiment with exposing them to inoculum in the lab before outplanting).

Proposed field measurements and forest health monitoring

A separate field plan has been drafted to install and augment existing field plots to measure current conditions and set up future monitoring to assess conditions related to several questions of forest health in the post-fire (Mt Vision) Fire cohort of bishop pine that has now been affected by non-native PPCD. Plots will be designed to answer the following research question:

1. How does the level of PPCD affect the following measures of forest health:
 - a. Fuel profiles (e.g., surface and canopy fuel amount and configuration)?
 - b. Vegetation dynamics (e.g., tree regeneration and understory vegetation community shifts)?
 - c. Reproductive capacity in the event of a subsequent fire (e.g., viable PIMU seed abundance)?

Plots will be installed in stands that originated following stand-replacing fire in the 1995 Vision Fire (mid-seral stands composed of a ~25 year old cohort), as well as old-growth stands. Plots will be installed across a gradient of PPCD severity for each seral stage (ideally ranging from unaffected to nearly 100% overstory mortality, or as close to these extremes as exist in the study area). For logistical ease, plots will be given a quick field ID of an ocular estimate of PPCD severity (0-25%, 25-50%, 50-75%, and 75-100% canopy dieback) prior to plot establishment and an attempt will be made to sample 6-8 plots within each of the four categories in each seral stage (24-32 plots per seral stage). Plots will be installed in areas with near complete canopy closure (e.g., > 75% bishop pine canopy dominance) of bishop pine in the forests established after the 1995 Vision Fire (e.g., excluding more open scattered trees in coastal scrub and woodland areas).

For old-growth plots, the canopy may be more open due to the successional state of these stands, but bishop pine should be the dominant canopy species. For both seral stages, bishop pine canopy cover may be lower today because of mortality from PPCD, but would be reconstructed to the pre-PPCD canopy dominance of bishop pine. Plots will be stratified across a range of stand densities, across topographic positions, and at varying distance from the coast to capture a range of conditions that may influence disease severity.

The protocol is intended to be flexible enough to be implemented as additional stand structures and seral stages arise on the landscape including following wildfire to monitor recruitment and pitch canker effects on early seral stands or following the implementation of hazardous fuels reduction, Rx burning, or removal of infected trees. Potential areas for monitoring early seral stands established following the 2020 Woodward Fire are being scouted for inclusion in the initial monitoring efforts outlined in the field plan.

At this time, there is no recommendation to treat stands to mitigate effects of pitch canker. However, if treatments are implemented for other purposes or in the context of an experiment, this protocol can be implemented in such stands, ideally prior to treatment and following treatment.

The protocol will be modified from existing plot protocols (Alison Forrestel fuels plots) and similar plot design (Agne et al. in prep design has similar plots across a time since fire chronosequence in bishop pine and knobcone pine forests throughout CA and southern OR).

Conclusion

Bishop pine forests are an emblematic ecosystem endemic to the coastal region of the Californian Floristic Province. From a combination of introduced fungal pathogens, a warming climate, and potentially altered fire regimes, bishop pine forests face a number of threats and are a high priority for conservation throughout their distribution. This report can serve as a state of the condition, published research, identification of threats, and suggested management actions to aide in conserving bishop pine forests. Also identified are several key knowledge gaps that, if addressed, can provide critical information for augmenting management actions with the goal of fostering bishop pine forest health and resilience to stressors.

References:

- Agne, M. C., T. Woolley, and S. Fitzgerald. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *Forest Ecology and Management* 366:73–86.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:art129.
- Anderson, R. (2005). *Contrasting Vegetation and Fire Histories on the Point Reyes Peninsula During the Pre-Settlement and Settlement Periods*. Flagstaff, AZ, Northern Arizona University: 31.
- Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests: Part II. Population dynamics. General Technical Report INT-145. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Andrus, R. A., T. T. Veblen, B. J. Harvey, and S. J. Hart. 2016. Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. *Ecological Applications* 26:700–711.
- Aoki, C. F., W. H. Romme, and M. E. Rocca. 2011. Lodgepole Pine Seed Germination Following Tree Death from Mountain Pine Beetle Attack in Colorado, USA. *The American Midland Naturalist* 165:446–451.
- Axelrod, D. I. 1967. Evolution of the Californian closed-cone pine forest. Pages 93–149 in: *Proceedings of the Symposium on the Biology of the California Islands*, ed. Philbrick, R. N. Santa Barbara Botanic Garden, Santa Barbara, CA.
- Baar, J., T. R. Horton, A. M. Kretzer, and T. D. Bruns. 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *New Phytologist* 143:409–418.
- Baguskas, S. A., S. H. Peterson, B. Bookhagen, and C. J. Still. 2014. Evaluating spatial patterns of drought-induced tree mortality in a coastal California pine forest. *Forest Ecology and Management* 315:43–53.
- Baguskas, S. A., C. J. Still, D. T. Fischer, C. M. D’Antonio, and J. Y. King. 2016. Coastal fog during summer drought improves the water status of sapling trees more than adult trees in a California pine forest. *Oecologia* 181:137–148.
- Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. *Terrestrial Vegetation of California*, 3rd Edition. 3rd edition. University of California Press, Berkeley, CA.
- Bebi, P., D. Kulakowski, and T. T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84:362–371.
- Brown, P. M., D. Buckley, and M. W. Kaye. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. *Northwest Science* 73:205–216.
- Buma, B., C. D. Brown, D. C. Donato, J. B. Fontaine, and J. F. Johnstone. 2013. The Impacts of Changing Disturbance Regimes on Serotinous Plant Populations and Communities. *BioScience* 63:866–876.
- Buonanduci, M. S., J. E. Morris, M. C. Agne, and B. J. Harvey. 2020. Neighborhood context mediates probability of host tree mortality in a severe bark beetle outbreak. *Ecosphere* 11.
- Collins, B. J., C. C. Rhoades, M. A. Battaglia, and R. M. Hubbard. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *Forest Ecology and Management* 284:260–268.

- Crowley, B.J., Harvey, B.J., Holzman, B.A. 2009. Dynamics of pitch canker disease in bishop pines (*Pinus muricata*) at Point Reyes National Seashore, CA. Annual Meeting, Association of American Geographers, Las Vegas, NV. Poster presentation.
- Davis, F. W., and M. I. Borchert. 2006. Central Coast Bioregion. in *Fire in California's Ecosystems*, ed. Sugihara, N. G., J. W. Van Wagtenonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, pp. 321-349. Berkeley, CA: University of California Press.
- Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences* 112:3931–3936.
- Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science* 23:576–584.
- Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecological Applications* 23:3–20.
- Edwards, M., M. A. Krawchuk, and P. J. Burton. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. *Forest Ecology and Management* 338:163–175.
- Enright, N. J., J. B. Fontaine, D. M. Bowman, R. A. Bradstock, and R. J. Williams. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* 13:265–272.
- Fischer, D. T., C. J. Still, C. M. Ebert, S. A. Baguskas, and A. P. Williams. 2016. Fog drip maintains dry season ecological function in a California coastal pine forest. *Ecosphere* 7:e01364.
- Forrestel, A. B., M. A. Moritz, and S. L. Stephens. 2011. Landscape-Scale Vegetation Change following Fire in Point Reyes, California, USA. *Fire Ecology* 7:114–128.
- Franklin, J. F., K. N. Johnson, and D. L. Johnson. 2018. *Ecological Forest Management*. Waveland Press Inc, Long Grove, IL.
- Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. *Conservation in Practice* 1:8–17.
- Gaman, T., 2019. Tomales Bay State Park Forest Inventory. Report produced for California State Parks. 37p.
- Gordon, T. R. 2017. Surveys of pitch canker on the Monterey Peninsula and at Pt. Reyes National Seashore. Page 11. University of California, Davis, CA.
- Gordon, T., G. Reynolds, S. Kirkpatrick, A. Storer, D. Wood, D. Fernandez, and B. McPherson. 2020. Monterey pine forest made a remarkable recovery from pitch canker. *California Agriculture* 74:169–173.
- Gordon, T. R., K. R. Wikler, S. L. Clark, D. Okamoto, A. J. Storer., and P. Bonello. 1998. Resistance to pitch canker disease, caused by *Fusarium subglutinans* f. sp. *pini*, in Monterey pine (*Pinus radiata*). *Plant Pathology* 47, 706–711.
- Gordon T.R., K. R. Wikler, A. J. Storer, and D. L. Wood. 1997. Pitch canker and its potential impacts on Monterey pine forests in California. *Fremontia* 25:5–9.
- Grogan, P., J. Baar, and T. D. Bruns. 2000. Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. *Journal of Ecology* 88:1051–1062.

- Hart, S. J., and D. L. Preston. 2020. Fire weather drives daily area burned and observations of fire behavior in mountain pine beetle affected landscapes. *Environmental Research Letters* 15:054007.
- Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences* 112:4375–4380.
- Hart, S. J., T. T. Veblen, and D. Kulakowski. 2014. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? *Forest Ecology and Management* 318:44–53.
- Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94:2475–2486.
- Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecological Applications* 24:1608–1625.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proceedings of the National Academy of Sciences* 111:15120–15125.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography* 25:655–669.
- Harvey, B. J., and B. A. Holzman. 2014. Divergent successional pathways of stand development following fire in a California closed-cone pine forest. *Journal of Vegetation Science* 25:88–99.
- Harvey, B. J., B. A. Holzman, and J. D. Davis. 2011. Spatial variability in stand structure and density-dependent mortality in newly established post-fire stands of a California closed-cone pine forest. *Forest Ecology and Management* 262:2042–2051.
- Harvey, B. J., B. A. Holzman, and A. B. Forrester. 2014c. Forest resilience following severe wildfire in a semi-urban national park. *Fremontia* 42:14–18.
- Hemstrom, M. A., and J. F. Franklin. 1982. Fire and Other Disturbances of the Forests in Mount Rainier National Park. *Quaternary Research* 18:32–51.
- Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271:81–90.
- Hoffman, C. M., P. Morgan, W. Mell, R. Parsons, E. Strand, and S. Cook. 2013. Surface Fire Intensity Influences Simulated Crown Fire Behavior in Lodgepole Pine Forests with Recent Mountain Pine Beetle-Caused Tree Mortality. *Forest Science* 59:390–399.
- Hoffman, C., P. Morgan, W. Mell, R. Parsons, E. K. Strand, and S. Cook. 2012. Numerical Simulation of Crown Fire Hazard Immediately after Bark Beetle-Caused Mortality in Lodgepole Pine Forests. *Forest Science* 58:178–188.
- Holzman, B. A., and K. Folger. 2005. Post-fire vegetation response in the bishop pine forest at Point Reyes National Seashore. *Vision fire, lessons learned from the October*:49–57.
- Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254:16–34.
- Jenkins, M. J., J. B. Runyon, C. J. Fettig, W. G. Page, and B. J. Bentz. 2014. Interactions among the Mountain Pine Beetle, Fires, and Fuels. *Forest Science* 60:489–501.

- Jolly, W. M., R. A. Parsons, A. M. Hadlow, G. M. Cohn, S. S. McAllister, J. B. Popp, R. M. Hubbard, and J. F. Negrón. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management* 269:52–59.
- Jones, G. A., and W. Russell. 2015. Approximation of Fire-Return Intervals with Point Samples in the Southern Range of the Coast Redwood Forest, California, USA. *Fire Ecology* 11:80–94.
- Keeley, J. E. 2002. Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography* 29:303–320.
- Keeley, J. E. 2005. Fire history of the San Francisco East Bay region and implications for landscape patterns. *International Journal of Wildland Fire* 14:285–296.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116.
- Keeley, J. E., G. Ne'eman, and C. J. Fotheringham. 1999. Immaturity risk in a fire-dependent pine. *Journal of Mediterranean Ecology* 1:8.
- Keeley, J. E., and A. D. Syphard. 2018. Historical patterns of wildfire ignition sources in California ecosystems. *International Journal of Wildland Fire* 27:781–799.
- Kennedy, P. G., and K. G. Peay. 2007. Different soil moisture conditions change the outcome of the ectomycorrhizal symbiosis between *Rhizopogon* species and *Pinus muricata*. *Plant and Soil* 291:155–165.
- Klutsch, J. G., M. A. Battaglia, D. R. West, S. L. Costello, and J. F. Negrón. 2011. Evaluating Potential Fire Behavior in Lodgepole Pine-Dominated Forests after a Mountain Pine Beetle Epidemic in North-Central Colorado. *Western Journal of Applied Forestry* 26:101–109.
- Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, and R. Caissie. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management* 258:641–649.
- Kulakowski, D., and D. Jarvis. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. *Forest Ecology and Management* 262:1686–1696.
- Kulakowski, D., and T. T. Veblen. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88:759–769.
- Lee, Christopher A.; Voelker, Steve; Angwin, Peter A. 2019. Chapter 8 - Investigating causes of bishop pine decline on California's north coast. (Project WC-B-16-02). In: Potter, Kevin M.; Conkling, Barbara L., eds. *Forest health monitoring: national status, trends, and analysis 2018*. Gen. Tech. Rep. SRS-239. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 145-153.
- Linhart, Y. B. 1978. Maintenance of Variation in Cone Morphology in California Closed-Cone Pines: The Roles of Fire, Squirrels and Seed Output. *The Southwestern Naturalist* 23:29.
- Martínez-Álvarez P., R. A. Fernández-González, A. V. Sanz-Ros, V. Pando V, and J. J. Diez. 2016. Two fungal endophytes reduce the severity of pitch canker disease in *Pinus radiata* seedlings. *Biological Control* 94:1–10.
- McCune, B. 1988. Ecological Diversity in North American Pines. *American Journal of Botany* 75:353–368.

- Meddens, A. J., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22:1876–1891.
- Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? *Environmental Research Letters* 11:045008.
- Millar, C. I. 1983. A steep cline in *Pinus muricata*. *Evolution* 37(2): 311-319.
- Millar, C. I., 1986a. Bishop pine (*Pinus muricata*) of inland Marin County, California. *Madrono* 33(2): 123-129.
- Millar, C. I., 1986b. The Californian closed cone pines (subsection *Oocarpae* Little and Critchfield): a taxonomic history and review. *Taxon* 35(4): 657-670.
- Moriarty, K., A. S. Cheng, C. M. Hoffman, S. P. Cottrell, and M. E. Alexander. 2019. Firefighter Observations of “Surprising” Fire Behavior in Mountain Pine Beetle-Attacked Lodgepole Pine Forests. *Fire* 2:34.
- Ornduff, R. 1998. Three years after the Vision Fire in Point Reyes. *Fremontia* 26: 26–27.
- Ornduff, R. and V. Norris. 1997. Rebirth of a Bishop Pine Forest: First Year after the Mount Vision Fire. *Fremontia* 25(3): 22-28.
- Ostojia, S. M., and R. C. Klinger. 1999. The relationship of bishop pine cone morphology to serotiny on Santa Cruz Island, California. Page 5 D. R. Brown, K. L. Mitchell, and H.W. Chaney (eds.), *Proceedings of the 5th Channel Islands Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Page, W. G., M. E. Alexander, and M. J. Jenkins. 2013. Wildfire’s resistance to control in mountain pine beetle-attacked lodgepole pine forests. *The Forestry Chronicle* 89:783–794.
- Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010. Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology* 91:3631–3640.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58:501–517.
- Redmond, M. D., F. Forcella, and N. N. Barger. 2012. Declines in pinyon pine cone production associated with regional warming. *Ecosphere* 3:art120.
- Reynolds, G., T. Gordon, and N. McRoberts. 2016. Quantifying the Impacts of Systemic Acquired Resistance to Pitch Canker on Monterey Pine Growth Rate and Hyperspectral Reflectance. *Forests* 7:20.
- Romme, W. H. 1982. Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park. *Ecological Monographs* 52:199–221.
- Schmale, D. G., and T. R. Gordon. 2003. Variation in susceptibility to pitch canker disease, caused by *Fusarium circinatum*, in native stands of *Pinus muricata*. *Plant Pathology* 52:720–725.
- Schoennagel, T., T. T. Veblen, J. F. Negrón, and J. M. Smith. 2012. Effects of Mountain Pine Beetle on Fuels and Expected Fire Behavior in Lodgepole Pine Forests, Colorado, USA. *PLoS ONE* 7:e30002.
- Sharpe, M., and S. R. Ryu. 2015. The moisture content and opening of serotinous cones from lodgepole pine killed by the mountain pine beetle. *The Forestry Chronicle* 91:260–265.

- Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs* 81:3–24.
- Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters* 21: 243-252.
- Storer A.J., T. R. Gordon, D. L. Wood, and P. Bonello. 1997. Pitch canker disease of pines: current and future impacts. *Journal of Forestry* 95:21—26.
- Storer A. J., D. L. Wood, and T. R. Gordon. 2004. Twig beetles, *Pityophthorus* spp. (Coleoptera: Scolytidae), as vectors of the pitch canker pathogen in California. *Canadian Entomologist* 136:685—693.
- Stuart, J. D., and J. O. Sawyer. 2001. *Trees and Shrubs of California*. Berkeley, CA: University of California Press.
- Stuart, J. D., and S. L. Stephens. 2006. North Coast Bioregion. in *Fire in California's Ecosystems*, ed. Sugihara, N. G., J. W. Van Wagendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, pp. 147-169. Berkeley, CA: University of California Press.
- Sugnet, P. W. 1985. Fire history and post-fire stand dynamics of Inverness bishop pine populations. M.S. Thesis, University of California, Berkeley, Berkeley, CA.
- Swain, D. L., D. E. Horton, D. Singh, and N. S. Diffenbaugh. 2016. Trends in atmospheric patterns conducive to seasonal precipitation and temperature extremes in California. *Science Advances* 2:e1501344.
- Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. *Nature Climate Change* 8:427–433.
- Swett, C. L., and T. R. Gordon. 2017. Exposure to a pine pathogen enhances growth and disease resistance in *Pinus radiata* seedlings. *Forest Pathology* 47:e12298.
- Talucci, A. C., and M. A. Krawchuk. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. *Ecosphere* 10:e02744.
- Talucci, A. C., K. P. Lertzman, and M. A. Krawchuk. 2019. Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreak and wildfire in British Columbia. *Forest Ecology and Management* 451:117500.
- Teste, F. P., V. J. Lieffers, and S. M. Landhausser. 2011. Viability of forest floor and canopy seed banks in *Pinus contorta* var. *latifolia* (Pinaceae) forests after a mountain pine beetle outbreak. *American Journal of Botany* 98:630–637.
- Turner, M. G., K. H. Braziunas, W. D. Hansen, and B. J. Harvey. 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences*:201902841.
- Walter, H. S., T. Brennan, and C. Albrecht. 2005. *Fire Management in Some California Ecosystems: A Cautionary Note*. Page 5. USDA Forest Service Gen. Tech. Rep., USDA Forest Service.
- Watt, L. A. 2002. The Trouble with Preservation, or, Getting Back to the Wrong Term for Wilderness Protection: A Case Study at Point Reyes National Seashore. *Yearbook of the Association of Pacific Coast Geographers* 64:55–72.
- Wikler, K., and T. R. Gordon. 2000. An initial assessment of genetic relationships among populations of *Fusarium circinatum* in different parts of the world. *Canadian Journal of Botany* 78:709-717.

- Wikler, K., A. J. Storer, W. Newman, T. R. Gordon, and D. L. Wood. 2003. The dynamics of an introduced pathogen in a native Monterey pine (*Pinus radiata*) forest. *Forest Ecology and Management* 179:209–221.
- Williams, A. P., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam, S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and N. G. McDowell. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3:292–297.
- Williams, A. P., R. Seager, J. T. Abatzoglou, B. I. Cook, J. E. Smerdon, and E. R. Cook. 2015. Contribution of anthropogenic warming to California drought during 2012–2014. *Geophysical Research Letters* 42:6819–6828.
- Wingfield, M. J., A. Hammerbacher, R. J. Ganley, E. T. Steenkamp, T. R. Gordon, B. D. Wingfield, and T. A. Coutinho. 2008. Pitch canker caused by *Fusarium circinatum* – a growing threat to pine plantations and forests worldwide. *Australasian Plant Pathology* 37:319.
- Woolley, T., D. C. Shaw, L. T. Hollingsworth, M. C. Agne, S. Fitzgerald, A. Eglitis, and L. Kurth. 2019. Beyond red crowns: complex changes in surface and crown fuels and their interactions 32 years following mountain pine beetle epidemics in south-central Oregon, USA. *Fire Ecology* 15:4.