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Resiliency or restoration: management of sudden oak death before and after outbreak

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Abstract

Forests at risk to diseases caused by invasive *Phytophthora* pathogens can be grouped into two broad classes: those already invaded by the focal pathogen where disease has emerged or those at significant risk of invasion and subsequent emergence of disease. This dichotomy represents distinct management scenarios – treating after or before disease emerges – with a set of epidemiological, ecological, and practical management characteristics that determine optimal actions and associated costs. Here we present the initial outcomes from two management experiments aimed at restoring forest structure or protecting against changes to forest structure following invasion of *Phytophthora ramorum,* the cause of sudden oak death (SOD). We conducted a stand-level restoration experiment on Mount Tamalpais (Marin County, CA) at three sites where the disease has killed most overstory tanoak and dramatically increased understory vegetation density and fuels. A separate experiment in an uninvaded, at risk forest was conducted near Lacks Creek, in Humboldt County. This treatment is an attempt to increase forest resiliency to catastrophic loss of tanoak, increased fuels associated with tree mortality, and densification of the understory that are expected to accompany disease in these stands within the coming decade. Restoration experiments employed two types of mastication of understory vegetation and hand-crew thinning with pile burning; resiliency experiments employed hand crews. Treatments were compared to a set of reference conditions representing overly dense stands where intervention is needed and extensively managed stands that serve as management targets. Both restoration and resiliency treatments greatly reduced density of key sporulation supporting hosts with modest-to-minimal effects on stand basal area. Prior land use, especially past harvesting, was a primary factor determining treatment costs and potential disease impacts in treated vs untreated stands. Although both restoration and resiliency management strategies are likely to reduce disease impacts, treatment costs vary substantially and will greatly influence when and where each approach is optimal.

Introduction

Several biological characteristics of forest pathogens can interact to cause destructive and persistent diseases. Pathogen destructiveness is often a function of virulence, here defined in the evolutionary sense: the ability to infect and negatively impact host physiological or reproductive function (Desprez-Loustau et al. 2016). Invasion, infection, or pathogen growth – each a scale-dependent process – can determine pathogen impacts such as loss of growth and mortality. In contrast, persistence can result from a combination of factors including survival as a saprotroph, a broad host range (generalism) combined with tolerance (host amelioration of negative impacts) in some hosts (Best et al. 2014), and/or formation of long-lived survival structures (Smith et al. 2006). Disease destructiveness and persistence may interact in evolutionary and ecologically complex ways such as diseases that are persistent but not destructive, destructive but not persistent, and most consequentially, destructive and persistent disease. The latter category includes some of the most problematic non-native and invasive forest pathogens: *Phytophthora cinnamomi* Rands (jarrah dieback and many other diseases), *Phytophthora ramorum* Werres, de Cock & Man in't Veld (sudden oak death), and *Cryphonectria parasitica* (Murrill) M.E. Barr (chestnut blight). Destructive and persistent forest diseases – especially those which can rapidly invade host populations – are some of the most difficult to prepare for or control because many of the characteristics which render a pathogen persistent complicate eradication (Mbah and Gilligan 2010, Filipe et al. 2012, Cobb et al. 2013b). Although challenging, these disease characteristics should not be misconstrued as cause for dismissal of timely, active and focused management actions. Many forest resources with economic, cultural, or ecological value may be protected – or future disease impacts significantly reduced – through actions founded on an understanding of the underlying factors that drive disease.

A broad host range in combination with host tolerance to infection can complicate management prescriptions and detection efforts, particularly when a host supports cryptic or innocuous infections on leaves or roots. The large number of individual leaves and roots as well as the distribution of infections in difficult-to-observe locations such as below ground or in the canopy, render perfect detection unrealistic more often than not. However, early detection and removal of inoculum sources in isolated locations can significantly slow disease progression (Hansen et al. 2008, Cobb et al. 2013b, Cunniffe et al. 2016). Further, invasion and disease emergence rates are influenced by stand host composition and densities, suggesting that proactive management aimed at reducing invasion rate and potential disease impacts in high risk areas could be a cost-efficient way to lessen future impacts. Here, we refer to this strategy as "resiliency management". Broadly, this strategy recognizes that many *Phytophthora* pathogens are persistent within sites and aims to alter environmental conditions or host densities/composition in ways that slow pathogen spread and disease emergence. Given that these actions are very likely to result in some alteration of stand structure and composition, informed actions would take into account additional management goals such as fuels reduction, timber growth, or other objectives.

Many forest pathogens are also remarkable for their realized impacts after disease emergence. The previously listed examples of non-native pathogens demonstrate a clear and alarming power to transform species distribution and ecosystems including region-scale host tree decline or loss and a reduction of stand-level carbon sequestration. For example, chestnut blight has caused a continental-scale loss of a previously common overstory tree; this disease transformed forest structure, composition, and eliminated a highly valuable timber species (Paillet 2003). *Phytophthora cinnamomi* has altered species composition and resulted in ecosystem transformation on multiple continents (Shearer et al. 2007, Corcobado et al. 2014). *Phytophthora ramorum* is notable for both direct disease impacts (Meentemeyer et al. 2011) as well as the degree that sudden oak death changes fire intensity, fire related mortality, reduces carbon sequestration and shifts forest structure and composition at the landscape-scale (Metz et al. 2012, 2013, Cobb et al. 2013a). The extent of stands with severe disease impacts indicates the need for development of "restoration management" – treatments to restore ecosystem functions lost due to disease and to break epidemiological feedback that maintains dense, contiguous fuels and restricts recruitment of resilent species such as redwood.

Our goal here is to describe, compare, and evaluate resiliency and restoration management actions using sudden oak death/*Phytophthora ramorum* as our focal disease. Sudden oak death has been an exceptionally destructive invasive disease in California and Oregon coastal forests where it kills trees at landscape and regional scales in multiple forest types (Meentemeyer et al. 2008, Cobb et al. 2012b, Metz et al. 2012). Tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. Oh) and several coastal red oak species (primarily coast live oak, *Quercus agrifolia* Née) can be killed in as little as two years following bole infection (Cobb et al. 2012b). Mortality rates accelerate with increasing tree size, which compounds disease impacts including fuels accumulation and loss of living biomass (Cobb et al. 2012a, 2012b). Sudden oak death is likely to impact an order of magnitude more individual trees and acres of forest land in CA and OR in the coming decades. These potential impacts stem from high levels of host biomass and density as well as a conducive environment for the pathogen in regions where there is currently only limited invasion (Lamsal et al. 2011, Meentemeyer et al. 2011). Furthermore, a collection of case studies and modeling studies illustrates the difficulty and likely impossibility of eradication at regional and landscape scales (Hansen et al. 2008, Filipe et al. 2012, Valachovic et al. 2013a, Cunniffe et al. 2016). *Phytophthora ramorum* is a management challenge in both impacted and at risk stands as these conditions are abundant in CA and OR. Furthermore, *P. ramorum*'s rapid invasion rate, substantial ecological impacts, and broad host range place it squarely within the category of persistent and destructive forest diseases for which it is most important to understand and devise responses.

Forest disease management does not occur in a vacuum and managers are often confronted with concurrent issues and concerns including wildfire, insect outbreak, and soil erosion. Historical logging and past disturbances also alter forest structure, resources, and disturbance dynamics (Hirt 1996, Colombaroli and Gavin 2010, Trumbore et al. 2015) often creating a spate of management challenges related to forest health and timber production. Further, the need for forest management investment is occurring in the context of inadequate agency budgets to address these challenges (MacCleery 2008) meaning that management will be most effective it achieves multiple aims. What are the management goals in the absence of disease? In California and similar ecological-sociological environments, where management priorities are often directed at reducing potential wildfire impacts, maintaining water quality and quantity, protecting or enhancing biodiversity, and improving access to public lands, these issues must be balanced against or articulated with, actions aimed at disease.

Historically harvest has occurred extensively throughout the distribution of redwood forests as well as much of the Klamath mountains (Hirt 1996, Lorimer et al. 2009). Rapid and prolific tanoak resprouting in response to harvesting can lead to long-term shifts in stand structure, including shifting stands from dominance by high economic value conifers to tanoak (Harrington and Tappeiner 2009). Extensive harvesting in the last century occurred in the context of broad-scale fire suppression contributing to increased fire intensity due to increased forest density and fuels (Colombaroli and Gavin 2010). All of these land use and land management changes favor dominance of tanoak, particularly in northern coastal California where the greatest density and biomass of tanoak occur (Lamsal et al. 2011). Tanoak is a relatively low-timber value species (Harrington and Tappeiner 2009). Increased tanoak and other hardwood species dominance along with land management policy changes and depletion of high value old-growth timber stocks has contributed to mill closures and a decline in the importance of timber management in many areas (Hirt 1996, MacCleery 2008, Bowcutt 2011). Changes in demand and policy, as well as technological innovations that increase hardwood timber value could increase future timber management within the region.

The emergence of sudden oak death in forests with substantial tanoak results in changes in forest structure that pose multiple resource problems. *Phytophthora ramorum* kills tanoak by infecting the bole and eventually disrupting vascular function (Parke et al. 2007). These infections kill the above ground portion of trees, but basal sprouting from these individuals can be so extensive as to create a new forest structure where understory tanoak densities are very high with interspersed overstory trees, such as redwood (*Sequoia sempervirens* (D. Don) Endl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), that do not suffer mortality following infection (Cobb et al. 2012b, Metz et al. 2012). In stands dominated by tanoak, infection can result in substantial amounts of dead fuels in the canopy and on the soil surface (Valachovic et al. 2011, Cobb et al. 2012a). An increase in canopy fuels is positively associated with greater fire intensity (Metz et al. 2011) while increased fuels at the soil surface can decrease tree survival, soil nutrients, and soil carbon during wildfire (Metz et al. 2013, Cobb et al. 2016). The persistence of *P. ramorum* at the forest level is maintained either in California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) or in resprouting tanoak which facilitates rapid pathogen population reestablishment after events that are unfavorable to the pathogen such as fire or drought (Beh et al. 2012, Eyre et al. 2013). These disease-caused changes in forest structure also result in reduced rates of nitrogen transfer to the forest floor, reduced carbon storage, and increased carbon efflux from some soil carbon pools (Cobb et al. 2013a, Cobb and Rizzo 2016). High densities of understory tanoak inhibit establishment of Douglas-fir (*Pseudotsuga menziesii*) (Harrington and Tappeiner 2009) suggesting the cycle of tanoak mortality and dense basal sprouting could limit conifer reestablishment in the overstory. These factors suggest intervention is needed to restore fire safe conditions as well as ecosystem functions compromised by disease.

Both pre- and post-*P. ramorum* invasion tanoak forests are problematic in California and Oregon. Here we contrast the pre- and post-treatment conditions for restoration- and resiliency-focused management actions aimed at sudden oak death. The effects of treatments on stand structure were compared to a set of reference conditions that span best- and worst-case scenarios for management. We then forecast expected treatment benefits using a field parameterized epidemiological model and discuss these expected disease benefits in light of treatment effects on fuels, above ground carbon, and forest structure.

Study sites and methods

Restoration management

We conducted a full-factorial replicated restoration management experiment on lands managed by the Marin Municipal Water District (MMWD), a public utility established in 1912. The MMWD was one of the first wildland areas to be invaded by *P. ramorum* (circa 1995) and is valuable for understanding the longer-term consequences of sudden oak death in Douglas-fir-tanoak and redwood forests, two of the most commonly impacted coast range forest types. The water district lands are centered on Mount Tamalpais, a prominent peak north of San Francisco, which provides drinking water for approximately 186,000 people in Marin County and is a recreation resource for millions of people in the greater San Francisco Bay Area. The water district manages approximately 8755 ha (21,635 ac) of land, several reservoirs, and water treatment and conveyance infrastructure. Wildlands managed by the MMWD include grassland, chaparral, and forested ecosystems including redwood, Douglas fir-tanoak, and a variety of mixed-evergreen hardwood forests, many of which include a significant California bay laurel component. Here we focus on forest communities that include tanoak, as these are the most severely disease-transformed forests in the region. *Phytophthora ramorum* challenges two central responsibilities of the MMWD: to provide: 1) high quality and reliable drinking water and 2) fire prevention in the form of fuels management.

Figure 1. *Phytophthora* restoration management on Mount Tamalpais (Marin County, CA). (A) Dense resprouting of tanoak has developed over the ~20 years since disease emergence. Resprouting tanoak maintains the pathogen and perpetuates a low statured stand. (B) Thinning and pile-burning and mastication were applied to intervene in this cycle. (C) Treated (foreground) and untreated conditions. Panel B photo credit E. Gunnison.

We conducted restoration experiments in redwood-tanoak and Douglas fir-tanoak forests impacted by *P. ramorum* (Figure 1). Heavily disease-impacted areas were identified with at least 2 ha (~5 ac) of suitable forest for restoration. Criteria included slopes flat enough to use heavy machinery, extensive tanoak mortality, and no risk of impacting species of concern. This resulted in treatments at three locations: Bolinas Ridge, a 6 ha (~15 ac), heavily impacted redwood forest; Laurel Dell, a 4 ha, heavily impacted Douglas fir-tanoak forest; and San Geronimo Ridge, a 2 ha, heavily impacted Douglas fir-tanoak forest. This design provided ~6 ha of treated area in each forest type and also met our criteria of applying uniform treatment in 0.405 ha square units (1 ac). Within each site, five non-overlapping 0.405 ha blocks were identified and randomly assigned to one of several treatments. In redwood forests, we applied two types of mechanical understory mastication with or without follow-up removal of resprouting by tanoak and other species. Mastication was conducted with an excavator with a masticating head or a skid-steer with a masticating-head forestry attachment. Mastication was applied in two ways: solely with heavy machinery or in conjunction with hand-crews who concentrated materials in a centralized location for later mastication by a skid-steer. Half of the treated plots were then randomly assigned for hand-crew stump sprout removal one year later (results not shown). Within each treatment block, one plot was left as an untreated reference. In both types of mastication, trees up to 5cm dbh were masticated into 3-8 cm length fragments. Mastication also typically pushed over dead standing trees up to ~20 cm dbh and ground them in place; sound dead standing trees were generally left in place. In the Douglas-fir-tanoak sites, treatments consisted of mastication with a skid-steer or traditional hand-crew piling with or without pile burning. Mastication treatments were analogous in redwood forests, while hand-crew work allowed cutting of trees up to 25 cm dbh. In this study, we examine only the three treatments with the greatest potential to result in initial differences in stand density and basal area: 1) mastication with heavy machinery only (mast), 2) an alternative mastication treatment that employed machinery and hand crews (alt mast), and 3) hand crew-only treatments which placed cut materials in piles (pile).

Figure 2. *Phytophthora* resiliency management. (A) Inadequate silvicultural investments can lead to high fuels and dense host conditions (Friday Ridge, Humboldt Co., CA). (B) Stand treatments to reduce host density, fuels, and increase the prevalence of non-host species is a common approach to proactive management (Lacks Creek, CA). (C) Deliberate hardwood silviculture is highly valuable for demonstrating desired stand conditions for many agencies such as lower fuels as well as fewer large tanoak and conifers. Panel C shows an example from the Yurok Indian Reservation (Humboldt, Co.) where a legacy of intentional cutting and repeated use of fire has created resilient conditions at the stand level.

Resiliency management

A single forest-level experiment was applied on the Lacks Creek Management Unit, a 1,820 ha multi-use landholding (~4,500 ac) near the community of Redwood Valley (Humboldt County, CA) managed by the Bureau of Land Management (BLM), where cutting of redwood and Douglas-fir has occurred across most of the area. Although management could favor timber growth and harvest, on this property most management actions focus on habitat conservation/restoration, enhancing public access, and fuels management (Raoush 2010). In 2010, *P. ramorum* was identified as the cause of tanoak mortality in the nearby rural community of Redwood Valley, which triggered an attempt to eradicate a geographically isolated outbreak (Valachovic et al. 2013b). Similar to several other attempts to eradicate *P. ramorum* from wildlands, eradication treatments greatly reduced pathogen populations and appeared to slow pathogen spread, but did not achieve eradication, and the pathogen remains poised to invade the abundant surrounding tanoak populations. Past conifer harvest in the Lacks Creek area increased tanoak densities in parts of the study area (Figure 2) creating a need to protect stands against the substantial impacts observed at sites similar to our MMWD study area.

The BLM identified a continuous ~60 ha area with a relatively high density of tanoak and located close to known wildland infections (within ~200 m). This area had also been identified as potentially benefiting from thinning treatments to restructure species composition and reduce fuels. Species composition is variable across the study site with pockets of relatively dense tanoak or Douglas-fir. Scattered California bay laurel was also located throughout the treatment area, primarily in drainages. Treatments were conducted solely with hand crews with a tree removal limit of ~40cm dbh. Tree removals were restricted to significant *P. ramorum* hosts (tanoak and California bay laurel) but in practice removed trees were almost exclusively tanoak. By design this created thinning levels which are highly variable across the treatment area and primarily dependent on pre-treatment tanoak density. Removed tanoak were piled for later burning; thinning levels aimed to retain a closed overstory canopy to limit post-treatment resprouting. No herbicides – for example to reduce stump sprouting – were applied during these treatments.

We employed two different reference conditions to compare and evaluate treatment effects. Two untreated stands adjacent to the Lacks Creek treatment were identified and measured to provide long-term experimental controls. However, the high degree of variation in tanoak density in the broader landscape and the need to identify restoration targets led us to establish a second set of reference measurements in stands that reflected these conditions. To compare stand treatments vs potential long-term management targets, we measured plots (N = 10) in actively managed tanoak stands on the nearby Hoopa and Yurok reservations where tanoak thinning and burning treatments have been applied over the last several decades. An additional set of reference measurements were established in plots in high-density tanoak stands on Friday Ridge (Willow Creek, CA; N = 8), a previously clear-cut site which reflects the frequent high-density tanoak conditions that develop following Douglas-fir harvesting (Figure 2).

Field measurements

A common set of measurements was conducted at all of the sites. Study plots were randomly located within sites with a minimum distance of 100-200 m between plots. Each plot was circular and 500 m^2, within which each tree was mapped and every stem $\geq$ 1cm dbh measured for diameter, identified to species, and given a health rating. Symptoms of *P. ramorum* infection were recorded when present and occasionally returned to the laboratory for isolation on a *Phytophthora* selective media (see Davidson et al. 2005) to confirm if infection had occurred (primarily in the uninvaded resiliency study sites). Plots were established and measured prior to treatment application; a follow-up survey occurred for each experiment within 6 months post treatment to quantify changes in forest structure and host composition. Each plot was also assessed for pre- and post-treatment fuel levels, coarse woody debris, and soil carbon and nutrient pools (data not shown). The restoration treatments (Mount Tamalpais) included 30 individual 0.405 ha blocks and six control plots (one per five-plot block). The resiliency study included 10 study plots in the treated area, two reference plots in adjacent stands, eight reference study plots at the high tanoak density Friday Ridge reference site, and an additional 10 reference study plots in actively managed stands on Hoopa and Yurok lands (30 total). The resiliency experiment study plots were overlaid with a variable radius plot (basal area factor 5) to facilitate comparisons to the Friday Ridge study site where study plots were 201 m^2 and Hoopa and Yurok plots where only variable radius plots were conducted at five locations within a 2 ha study plot.

Model application

We applied the SODDr (Sudden Oak Death Dynamics in R) model to estimate potential treatment benefits following restoration and resiliency experiments. The SODDr model is a dynamic, multi-species, size-structured, and spatially explicit, susceptible-infective (SI) host-pathogen model of SOD dynamics, parameterized based on a 6-year dataset of SOD spread (infection and mortality) in redwood forests (see Cobb et al. 2012b, 2013b). The current iteration of the model is implemented in R and available at https://github.com/noamross/SODDr.

We calculated median stand densities for each treatment type for both restoration and resiliency treatments and parameterized the SODDr model with the respective proportions of tanoak, California bay laurel, and other species – primarily redwood and Douglas-fir – that have a minimal epidemiological role, so call 'non-competent' species. Proportional species composition was calculated using the species densities within each treatment, rather than average density across all treatments, since the highly disparate tanoak densities across treatments would likely bias model results towards slow pathogen spread and limited or no disease emergence in treated stands. This could bias the model results toward excessively rapid pathogen spread. Therefore, we restrict our model interpretations to relative differences in disease dynamics between treated and untreated conditions. Although SODDr is a size-specific model, we employ a single uniform size class for the purposes of this study to facilitate comparisons across sites.

Results

Restoration treatments

Each restoration treatment type resulted in a dramatic reduction of stem density (Figure 3). Although there were clear differences in pre-treatment stand densities among treatment types – particularly the hand-crew treatment area had lower initial stem densities (Figure 3 A&B; "pre-pile") – each treatment type resulted in post-treatment stem densities which did not statistically differ. In contrast, stand basal area was not significantly different between pre- and post-treatment measurements (Figure 3) and reflects the relatively low contribution of tanoak resprouts to total stand basal area. This was true for all treatment types and is demonstrated in Figure 3 which contrasts basal area and stem densities for standard mastication ("mast"), mastication with joint machinery and hand crews ("alt mast"), or hand crew treatments ("pile"). Specifically, mastication, alt mastication, and pile treatments reduced density by 96.3, 83.1, and 90.7%, respectively. In contrast, basal area was reduced by 7.9, 14.1, and 3.7% for the same treatments. Treatments dramatically reduced the stem density of tanoak while having little effect on density of other species, which reflects the dominance of tanoak in small size classes that developed in the 20 years of disease progression at Mount Tamalpais.

Model projections suggest dramatic increases in tanoak survival following restoration treatments (Figure 4). Differences between treatment types are difficult to discern in Figure 4 because post-treatment tanoak densities were similar (and very low). Forecasted disease dynamics for pre-treatment stand conditions (untreated stands), showed more variation than treated stands and reflects variation in tanoak densities prior to treatment in our study sites. However, rapid and extensive mortality was common among untreated stand conditions in the model which agrees with observations from the field plots that *P. ramorum* transforms stand structure to a dense understory with scattered less susceptible trees such as redwood or Douglas-fir in the overstory.

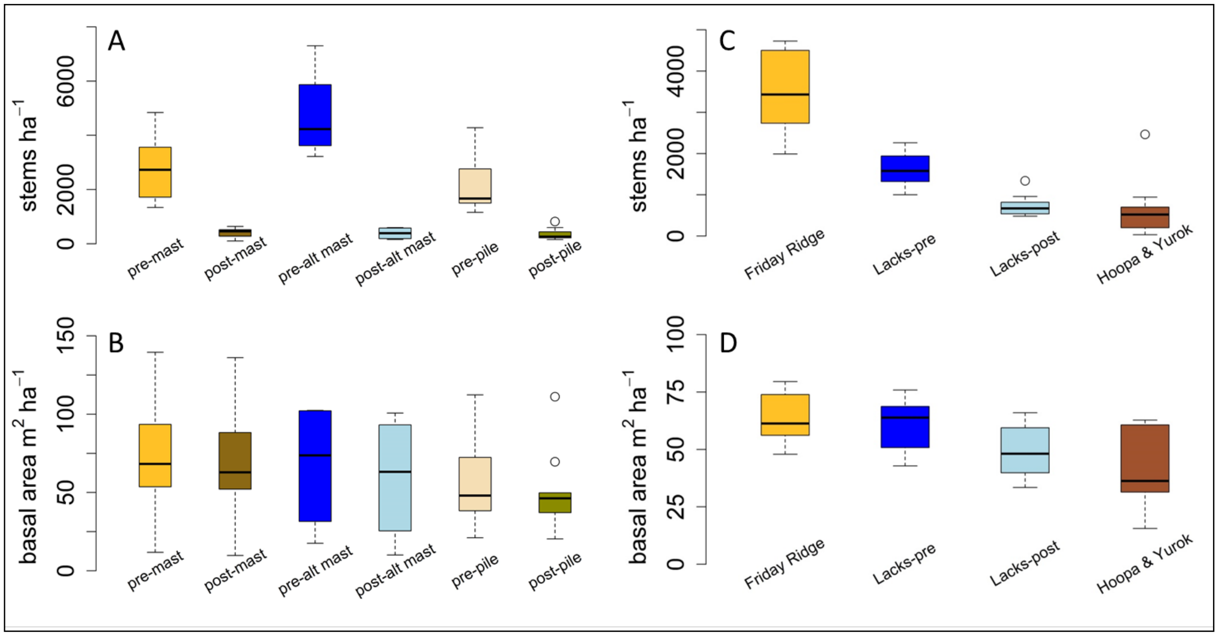

Figure 3. Comparison of *Phytophthora* restoration and resiliency treatment effects. Restoration of disease impacted forests on Mount. Tamalpais (Marin Co., CA) are shown with pre- and post- treatment changes in stem densities (A) and basal area (B). Resiliency treatments were conducted at the Lacks Creek field site ("Lacks") with the untreated Friday Ridge and treated Hoopa and Yurok sites used as reference comparisons (see text); resiliency treatment stand densities (C) and basal area (D) are presented for comparison with restoration treatment effects.

Resiliency treatments

At Lacks Creek, resiliency treatments reduced tanoak densities relative to pre-treatment conditions but not as dramatically compared to the restoration experiment (Figure 3C). Specifically, the pile-treatments at Lacks Creek resulted in a 42.4% decrease in stand density. However, basal area was reduced 24.6% in the pile treatments (Figure 3D). The differences in treatment effects reflect differences pre-treatment distribution of size between the forest conditions, disease-impacted stands have high densities of trees under 5cm dbh and hence density can be dramatically reduced with little effect on basal area. Further, in the forest conditions of the resiliency treatment sties much of the tanoak component is present in the overstory, including in the high-density Friday Ridge study site. Given that these treatments could remove tanoak up to ~40 cm dbh, some loss of basal area is unsurprising. Basal area was similar but density differed by an order of magnitude between the post-clear cut Friday Ridge site and the tribal plots where a range of fuels, prescribed burning, and other tanoak-focused silviculture has been applied. Tribal plots have been managed for specific tanoak resources, often provisioned by large trees; thus the differences in structure (Figure 3) reflect the dominance of smaller diameter overstory trees at Friday Ridge (< 40cm dbh) and larger tanoak (>50cm dbh) trees on many of the tribal plots. Lacks Creek post treatment densities and basal area were 19.5 and 75.4% of the same stand parameters at the post-clear cut Friday Ridge study site but were 128.3 and 132.6% compared to the Hoopa/Yurok study plots. Multiple stand treatments have been necessary to create the structure found on our Hoopa/Yurok study plots and a long-term commitment to management at Lack Creek or in forest conditions similar to our Friday Ridge site will be needed to create a similar structure. In addition to changes in density and basal area, the Lacks Creek experimental treatment removed all bay laurel individuals which should have a substantial benefit in terms of pathogen invasion rate.

Model projections suggest a clear benefit of thinning treatments in terms of reduced mortality rates in addition to a delay of tanoak demographic decline (Figure 4). However, the model results show tanoak populations were still in decline in the resiliency scenario at the end of the 100-year simulation suggesting these treatments will slow rather than arrest disease progression over the longer term. A comparison of the reference sites suggests a tanoak density threshold in the model where feedback between tanoak populations and the *P. ramorum* pathogen results in a stable tanoak population. It must be noted that the model is not direct evidence that these thresholds exist in nature and the reference sites have not yet been invaded by *P. ramorum*. Unlike the MMWD restoration experiments, these model results cannot yet be validated from field data, as long-term measurements of post-treatment dynamics are not yet available.

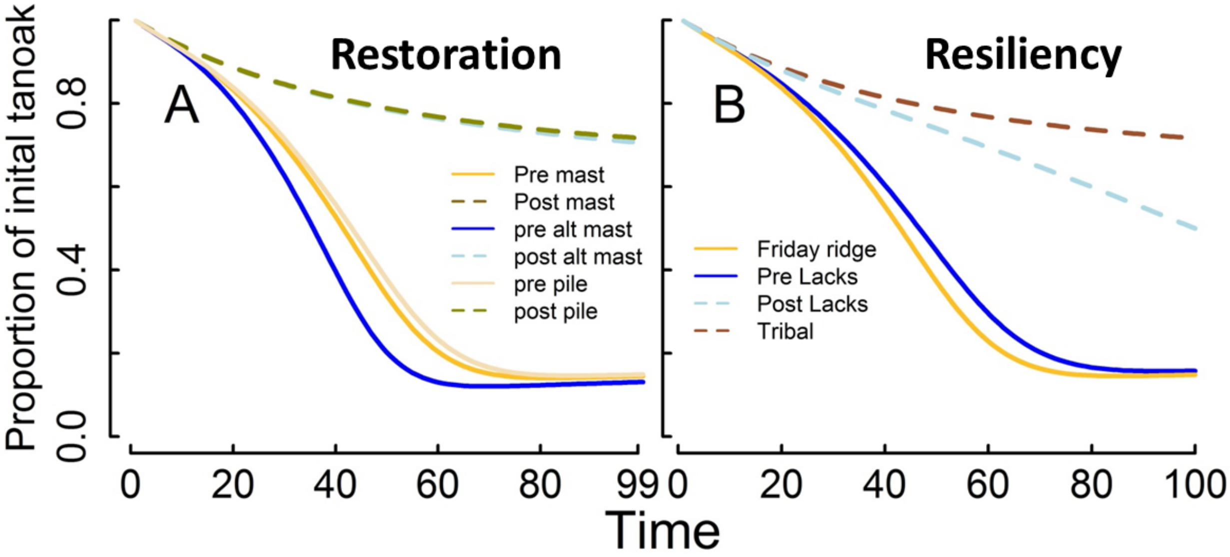

Figure 4. Effects of management actions on disease progression estimated from an epidemiological model (SODDr). For both (A) restoration and (B) resiliency treatments, pretreatment or untreated stands are shown with solid lines while treated stands are shown with dashed lines. For the post mastication treatment simulation ("Post mast" brown dashed line), results were virtually identical to the other treatments and are obscured by the other lines. In resiliency treatments the Friday ridge study site and plots on Hoopa and Yurok, "Tribal" lands are included as high tanoak density and low tanoak density silvicultural outcomes. In these simulations, a single uniform infection and mortality rate were applied to the tanoak population.

Discussion

With over a billion individual tanoak stems at risk from *P. ramorum* in California and Oregon (Lamsal et al. 2011), the scale of potential impacts from sudden oak death is daunting however, only a fraction of at-risk trees and stands have been impacted. This set of conditions creates a set of pressing management problems for Coast Range forests for the next several decades: what levels of protection can be applied to uninvaded stands while resources are also being directed towards restoring degraded disease-impacted stands? Current spread models suggest that rates of invasion will peak in the next 10-20 years (Meentemeyer et al. 2011, Cunniffe et al. 2016); given that stand-level inoculum buildup and mortality are thought to occur from several years to a decade after initial invasion, the ecological impacts of the disease will become realized over the next half-century (Cobb et al. 2012b, Filipe et al. 2012). Although invasion and disease emergence are both rapid and extensive, these model estimates suggest adequate time is available to design, test, and coordinate deployment of the most effective treatments. Currently, most stand experiments have focused on local and regional eradication efforts (Hansen et al. 2008, Valachovic et al. 2013b; Valachovic *this volume*), this study seeks to expand management experiments into a broader range of stand conditions and objectives. Our study also represents one of the first attempts to design a sudden oak death restoration treatment, specifically in stands where the disease has been present for up to two decades. These stand conditions are frequent in the San Francisco Bay Area, Big Sur, southern Humboldt County, and parts of Curry County, Oregon, suggesting the need to expand and improve restoration approaches will increase in the coming years.

Implication for forest carbon sequestration

Restoration treatments at MMWD resulted in a dramatic change in stand structure (Figure 1; Figure 3). However, for carbon sequestration goals, since basal area is conserved, treatments had a nominal effect on above ground carbon storage. The reduction of density without biomass loss also suggests these treatments will increase water outflow by decreasing transpiration at the stand-level. Treatments are likely to cause a short-term decrease in fine carbon production (leaf litter and fine root production), but this loss to ecosystem carbon input is likely to be overcome by longer-term increases in overstory tree growth and productivity (Cobb et al. 2010, 2013a). An additional immediate treatment benefit is suggested by the model results which forecast increased survivorship of scattered overstory tanoak which, despite extensive disease, still occur throughout the area (Figure 1 & 4). However, increased survival of small-diameter tanoak would be detrimental to our longer-term management goals because these individuals are likely to be reinfected and contribute to the perpetuated dominance of understory tanoak stems. In fact, treatment maintenance in the form of repeated removal of resprouts from stumps will be necessary to avoid the return of undesirable high-density understory tanoak with high infection levels. Where tanoak densities can be maintained, increased survival of overstory tanoak individuals could be important for maintenance of ectomycorrhizal fungi in these stands as well as acorn production. Tanoak is the sole acorn-producing species or ectomycorrhizal host in the redwood study sites, meaning that its complete loss would reduce biodiversity as well as remove this source of below ground carbon input. Helpfully, none of the restoration treatments produced significant differences in post- treatment tanoak basal area indicating that these treatments do not accelerate loss of overstory tanoak. Our restoration treatment experiment suggests any of the specific techniques (mechanical, hand-crew) are effective and the decision of specific treatment type can be optimized for logistical and cost constraints.

Resilience treatments also altered stand structure with greatly reduced tanoak densities and decreased disease impacts within the model (Figure 3; Figure 4). Hand-crew pile treatments at Lacks Creek are distinguished from the restoration treatments at MMWD (Mount Tamalpais) by the larger average size of removed tanoaks at Lacks Creek. In addition to having an immediate greater impact on stand carbon, larger diameters create two challenges: fewer individual trees can be removed, and considerably more dead material is generated by the treatment (Figure 2). The scale of treating high density post-harvest tanoak stands is also apparent when contrasting stand conditions between the Friday Ridge site and the Hoopa/Yurok sites. The high densities of overstory trees at Friday Ridge cannot be easily converted to the more park-like, low density, large average tree size conditions of the tribal study plots. Efforts by Hoopa and Yurok forestry professionals and tribal members have transformed or maintained these stand conditions over tens to hundreds of years (Waterman 1920, Bowcutt 2013). But the lesson of these plots is clear: a long-term commitment to management can have a significant benefit to multiple forest management goals. Considering sudden oak death more narrowly, the potential benefits of slowed pathogen spread and reduced disease emergence through reduced tanoak densities is also strongly suggested by the SODDr model results (Figure 4). The model results are especially striking when comparing potential disease impacts between the Friday Ridge stand and the Hoopa/Yurok sites. We again emphasize that both stands are reference conditions with the former reflecting degraded stands and the latter reflecting a potential hardwood management goal. Although transforming problematic stand conditions of post-clear cut sites including Friday Ridge will almost certainly require multiple treatments and a long-term commitment, this effort has the additional benefit of addressing multiple resource problems simultaneously (e.g., increasing timber growth and carbon sequestration rates, reducing crown fuel continuity, and increasing stand diversity). Initial treatments are complicated by multiple factors, but removal of cut tanoak material is especially challenging. This material has a very low market price dictated by biomass fuel and firewood prices. Lacking incentive for material removal and cost recuperation will increase the difficulty of treating these stands and must be overcome before resiliency treatments can be applied more broadly. However, the epidemiological model results suggest that these treatments can greatly reduce potential disease-related mortality which would increase stand-level carbon sequestration.

Treatment financial costs

Treatment cost differences between restoration and resiliency treatments in our study were substantial and represent a serious caution to decisions about when and where to apply treatments. Restoration treatments in the most difficult stand conditions (high density and steep slopes) reached up to $24,710 per ha ($10,000 ac). Total costs will increase over time depending on the intensity of follow-up treatments. In contrast, the hand-crew thinning employed for resiliency treatments cost an average of $2,471per ha ($1,000 ac). Resiliency treatments initially cost less due to considerably lower pre-treatment stand densities. In some locations tanoak was a relatively minor component compared to Douglas-fir; this facilitated treatment completion even though larger diameter trees were cut into ~1m lengths and piled. Our study suggests proactive treatments may be substantially less expensive to apply. As previously noted, sudden oak death impacts are forecast to be realized over the course of the next several decades, meaning that a proactive campaign to reduce future impacts could yield longer term cost savings while also addressing the non-disease issues of overly-dense stands and fuels accumulation. In both resiliency and restoration treatments, reduced total and understory stand density is likely to result in reduced fire risk. This suggests that fuels reduction programs hold promise to reduce disease risk, particularly when they can be focused strategically to include stands with a high capacity for pathogen spread (Cobb et al. 2013b, Cunniffe et al. 2016).

Conclusions

Restoration and resiliency treatments have received less critical study compared to eradication and quarantine efforts for many forest *Phytophthora* species. Restoration and resiliency treatments appear to be useful techniques for reducing or avoiding the problematic stand conditions generated by *P. ramorum* and sudden oak death in California. This study reports the effects of disease treatments for both management scenarios in terms of changes in stand composition and structure. Treatments greatly reduced tanoak density without substantial changes in basal area, effects that reflect the extensive removal of small stems. Proof of treatment efficacy on disease dynamics is not available at the early stage of these experiments, but estimates from a dynamic epidemiological model suggest pathogen spread and subsequent mortality rates will be greatly reduced by stand treatments. These expectations need evaluation with empirical data collected through further monitoring to understand the overall efficacy of the respective treatment strategies. Both treatments hold potential to also address co-occurring management challenges including fuels accumulation, loss of biodiversity, and carbon storage. In California, rates and patterns of *P. ramorum* invasion suggest a window of several decades is available further optimize the cost-efficiency of these treatments and to apply them at a broader scale. Given the potential scale and extent of disease impacts, as well as the important ecosystem attributes represented by tanoak, a greater emphasis on development and application of these techniques is likely to yield considerable benefits to biodiversity conservation, forest carbon storage, and creation of fire-safe forests through a reduction of overall disease impacts.

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