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RANGE-WIDE THREATS TO A FOUNDATION TREE SPECIES FROM DISTURBANCE INTERACTIONS

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ABSTRACT

The geographic range of tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), encompasses tremendous physiographic variability, diverse plant communities, and complex disturbance regimes (e.g., development, timber harvest, and wildfire) that now also include serious threats posed by the invasive forest pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock. Knowing where these disturbance factors interact is critical for developing comprehensive strategies for conserving the abundance, structure, and function of at-risk tanoak communities. In this study, we present a rule-based spatial model of the range-wide threat to tanoak populations from four disturbance factors that were parameterized to encode their additive effects and two-way interactions. Within a GIS, we mapped threats posed by silvicultural activities; disease caused by *P. ramorum*; human development; and altered fire regimes across the geographic range of tanoak, and we integrated spatially coinciding disturbances to quantify and map the additive and interacting threats to tanoak. We classified the majority of tanoak's range at low risk (3.7 million ha) from disturbance interactions, with smaller areas at intermediate (222,795 ha), and high (10,905 ha) risk. Elevated risk levels resulted from the interaction of disease and silviculture factors over small extents in northern California and southwest Oregon that included parts of Hoopa and Yurok tribal lands. Our results illustrate tanoak populations at risk from these interacting disturbances based on one set of hypothesized relationships. The model can be extended to other species affected by these factors, used as a guide for future research, and is a point of departure for developing a comprehensive understanding of threats to tanoak populations. Identifying the geographic location of disturbance interactions and risks to foundation species such as tanoak is critical for prioritizing and targeting conservation treatments with limited resources.

Key Words: Decision support system, fire, forest ecosystems, foundation species, landscape epidemiology, *Notholithocarpus densiflorus*, sudden oak death, tree disease.

Ecological disturbance regimes play an integral role in ecosystem dynamics by altering resource availability, modifying ecosystem structures, and creating new landscape spatial patterns (e.g., Mou et al. 1993; Spies et al. 1994; Turner et al. 2003). Increasing global connectivity, population growth, and climate change are rapidly altering disturbance regimes, resulting in the emergence of novel disturbance interactions with pronounced impacts to socio-ecological systems from local to global scales (Turner 2010). Interacting disturbance regimes that alter the abundance and structure of foundation species effectively disrupt the fundamental ecosystem processes that they support and stabilize, such as clean water, decomposition, and carbon sequestration (Chapin et al. 1997; Ellison et al. 2005), which are vital for maintaining the physical, social, and economic health of human populations (Costanza et al. 1997). Recognition of the relationships and impacts of disturbance interactions by local, regional, and global stakeholders is necessary to manage for the resiliency of foundation species and their functions (Folke et al. 2004). Research explicitly addressing the effects of interacting disturbances in forest ecosystems has recently increased (e.g., Bebi et al. 2003; Buma and Wessman 2011; Metz et al. 2011), but we still understand relatively little about their impacts. The landscape heterogeneity and spatial extent over which forest disturbances occur challenges the development of ecosystem conservation strategies, presenting a pressing need to develop tools that engage and guide stakeholders in achieving conservation objectives across these broad areas.

Accessibility to and familiarity with geographic information system (GIS) technologies (e.g., GPS-enabled smartphones and online mapping) has become more widespread in recent years, increasing the potential to effectively bring stakeholders together in addressing complex conservation management problems. Spatially explicit models developed using GIS can be utilized as spatial decision support systems to identify the geographic location and potential severity of disturbance events, providing an essential tool for threat assessment and management. This adaptable framework can be applied to identify at-risk populations when the models are built using known biological relationships and sound ecological theory, even when knowledge of the precise relationships is scant. For example, Andersen et al. (2004) developed a risk model of threats to biodiversity across a large, heterogeneous landscape by examining relative risk of land use factors on several resident taxa, and Meentemeyer et al. (2004) similarly mapped the risk of establishment and spread of a forest pathogen (*Phytophthora ramorum* S. Werres, A.W.A.M. de Cock) across California. Mapping the threat to the abundance and structure of foundation species from disturbance interactions helps guide stakeholders in developing and implementing effective conservation strategies that protect vital ecosystem services.

Tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), is a foundation species threatened with functional extinction by multiple interacting disturbances throughout large portions of its range. This tree is, a dominant component of the ecosystems it inhabits (Cobb et al. this volume), has unique ecological characteristics in coastal California forests (Bergemann and Garbelotto 2006; Wright and Dodd this volume), and as the lone representative of its genus it is a significant contributor to regional as well as global biodiversity. This shade-tolerant tree can form multistoried forest canopies with other dominant overstory species, providing important stand structure for wildlife, such as the spotted owl (*Strix occidentalis*; LaHaye et al. 1997; North et al. 1999). Tanoak acorns are a traditionally important nutrition source for Native Americans, and the trees were a principal source of bark-extracted tannins until the advent of chemical tanning compounds in the 1950's (Bowcutt 2011). Since the collapse of the tanoak bark market, perspective on this species has shifted from an important forest commodity to an impediment to production of more valuable timber species, such as redwood, *Sequoia sempervirens* (Lamb. ex D. Don) Endl., and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Since the 1950's, most applied forest research on tanoak has focused on techniques to reduce competition with timber species, primarily through herbicide applications to reduce tanoak prevalence and biomass in forests managed for timber production (Harrington and Tappeiner 2009; Bowcutt 2011). In the last ten years, *Phytophthora ramorum*, and the resulting disease sudden oak death, has emerged as a major cause of tanoak mortality in central coastal California, and increasingly in northern coastal California and southwest Oregon (Rizzo et al. 2005; Meentemeyer et al. 2008; Václavík et al. 2010). *Phytophthora ramorum* has a large array of hosts, but susceptibility, impacts of infection on host health, and the competency of hosts to transmit infection varies dramatically over the 137 regulated native and exotic host species (APHIS 2012).

Silviculture, disease, development, and altered fire regimes are arguably the major disturbances threatening the abundance, function, and persistence of tanoak throughout its range. Silvicultural practices have explicitly suppressed tanoak to promote the growth of conifer species; human population expansion has resulted in conversion of forested land to development; and fire regimes have been altered from historic baselines (Havlina et al. 2010). In addition to these disturbances, tanoak is being severely impacted by *P. ramorum* on local to regional scales (Meentemeyer et al. 2008; Meentemeyer et al. 2011; Cobb et al. 2012b). Tanoak readily supports sporulation of *P. ramorum* and can be rapidly killed following infection by this pathogen (Hansen et al. 2008). Several other common native species also support sporulation, but do not die following infection, most notably California bay laurel, *Umbellularia californica* (Hook. & Arn.) Nutt. (DiLeo et al. 2009). Thus, the distribution of bay laurel and tanoak strongly influences the risk of pathogen establishment and disease emergence (Meentemeyer et al. 2004; Davidson et al. 2008; Cobb et al. 2010). The geographic variation and extent of each of these disturbances present major challenges to the conservation of tanoak ecosystems.

We present a spatially explicit model to quantify and map the area threatened by these four disturbances and their interactions across the geographic range of tanoak. This hypothesis-based modeling approach is readily integrated with adaptive management strategies. Thus, as knowledge of the system grows, the parameters of our model can be adjusted in accordance with evolving goals and the efficacy of treatments.

Geographic Range

The geographic range of tanoak stretches contiguously along the Pacific coast from a four-county area in southwestern Oregon in the north, to Monterey County, CA, in the south, with disjunct populations occurring in the Sierra Nevada foothills to the east. Our analysis excluded an isolated population occurring near Santa Barbara, CA (Tappeiner et al. 1990), because the data we used for tanoak abundance and area estimates (Lamsal et al. 2011) were incomplete in this region. Tanoak's geographic range possesses tremendous physiographic variability and complex disturbance regimes, and is broadly characterized by a Mediterranean-type

TABLE 1. THE WEIGHTS ASSIGNED TO INDIVIDUAL DISTURBANCE FACTORS AND THE INTERACTIONS IN THE INITIAL MODEL BASED ON OUR INTERPRETATIONS OF RELEVANT LITERATURE AND EXPERT OBSERVATIONS. Each disturbance factor was first standardized to a 0–3 ranking so that assigned weights used in the modeling calculations reflect their relative importance as a threat to tanoak.

Disturbance	Weights
silviculture	30
disease	25
development	10
fire	5
Interaction	**Interaction weight**
disease x fire	2
disease x silviculture	2
disease x development	1
fire x development	1
development x silviculture	1
fire x silviculture	1

climate with cool, wet winters and warm, dry summers. Tanoak occurs from sea level to roughly 2190 m, with greater abundance in forests on the leeward side of the Coast Range (Lamsal et al. 2011).

Model Development

We developed a rule-based spatial model to quantify and map the relative threat to tanoak populations from four disturbance factors occurring throughout tanoak's geographic range. This heuristic approach is akin to a mental shortcut, where empirically undefined relationships can be hypothesized and examined. In order to parameterize the relative threat to tanoak from each disturbance factor, we classified the threat level of each factor at a particular location into an integer ranking system from zero to three, with zero representing no threat and three representing high threat. At each location, we assigned each factor a low (1), intermediate (2), or high (3) threat ranking by breaking the range of values greater than zero into three equal intervals. We also assigned a weight value to each ranked disturbance factor indicating its relative importance as a threat to tanoak (Table 1). We based these weight values on our interpretations of published research and expert knowledge evaluating the impacts of each disturbance to tanoak. They can be altered within the modeling framework to explore other hypotheses of the impacts to tanoak from these disturbances. We calculated multiplicative two-way disturbance interactions for each location, assigning an additional exponential term to weight the interaction that we hypothesized as representing the greatest threat to tanoak (Table 1). For each location, we then selected the highest-valued interaction for inclusion in the final threat calculation to visualize and highlight areas with the most at-risk populations for the set of hypotheses (i.e., weights) being examined.

The equation used to calculate potential threat to tanoak from these disturbance factors is the sum of the products of each factor's rank and importance weight, plus the highest valued interaction at each mapped location (grid cell):

$$P_j = \sum_i^n W_i R_{ij} + [W_i^a R_{ij}^a \times W_i^b R_{ij}^b]^y \qquad (1)$$

where P is the calculated risk for a grid cell in the model output, W_i is the weight of the ith disturbance factor, R_{ij} is the rank value of the ith factor at location j, and y is the weight assigned to the interaction of two factors. The interaction weight (y) is determined by which pair of weighted factors, $W_i^a R_{ij}^a$ and $W_i^b R_{ij}^b$, occur together at a given location (Table 1). The superscripts of these parameters (a and b) ensure that a factor is never multiplied by itself. We developed maps of each disturbance factor and overlaid them with a tanoak abundance surface (Lamsal et al. 2011). We then applied the interaction model (Eq. 1) in a GIS environment to generate a map of at-risk tanoak populations from these interacting disturbances across the geographic range. We classified the model output into a 1–3 threat-level ranking by breaking the calculated values at equal intervals. Similar to the individual factors, we qualitatively labeled the threat levels as 'Low' (1), 'Intermediate' (2), and 'High' (3). The lack of zero values in the final map output demonstrates that at least one factor was present at every estimated tanoak location.

Quantifying Number of Tanoak at Risk

We quantified the area and number of tanoak trees in each threat category by intersecting the output of equation 1 with maps of tanoak density produced by Lamsal et al. (2011). These data were further organized by county to aid to regional decision making. We then multiplied the county-level tanoak areas (hectares) in each threat level by the average number of tanoak per hectare in each county derived from data provided by Lamsal et al. (2011). This produced the estimated number of tanoak in each threat category for each county in the study system. We report on a limited number of areas in this paper, with more detailed county summaries available from the authors.

Disturbance Factors

Silviculture

Beginning in the early to mid-20th century, silviculture in Oregon and California strongly favored softwood conifer species at the expense of hardwood species, especially tanoak (Bowcutt 2011). Most notable are broad-scale applications of herbicide to reduce tanoak competition with timber species in these forests. Tanoak vigorously sprouts following cutting and can reduce the growth of planted or naturally regenerating conifers (Harrington and Tappeiner 1997; Lorimer et al. 2009). Herbicide applications are effective in reducing tanoak cover and increasing the growth and dominance of coniferous timber species (Tappeiner et al. 1987; Harrington and Tappeiner 2009). When applied as a broadcast spray from aircraft, or at very high efficiencies by ground crews, it is reasonable to expect these practices would result in functional extinction of tanoak at local scales. For these reasons, the silviculture risk factor received a weight of 30, the highest weight (Table 1).

We developed the silviculture risk factor layer using Forest Inventory and Analysis (FIA) (USDA 2008) data for plots in California and Oregon where tanoak was reported (n = 565). FIA surveys record evidence of silvicultural treatments that affect areas of one acre or more; however, they do not specify herbicide application. We assumed the following about these data: 1. silviculture activities included suppression of undesirable species, i.e., tanoak, 2. a greater number of treatments is equivalent to greater threat to tanoak populations, and 3. recent treatments were more efficient and effective, whereas older treatments may have been overcome by recolonization from tanoak in adjacent stands (Tappeiner and McDonald 1984). We used all recorded treatment types with the exception of "Firewood or local use cut," which we interpreted as unlikely to target tanoak (or any species) for removal or suppression. We ranked locations according to the number of recorded treatments weighted by the timing of those treatments. We used 20-year intervals to capture increased activity surrounding timber harvests as well as related treatments during intervening years. This process assigned the highest risk from silviculture to locations where treatments were both persistent and more recent. We used these scores to create a map of silviculture intensity with values ranging from 0–10, which we reclassified into 0–3 rankings by splitting non-zero values at equal intervals.

Disease

Phytophthora ramorum is an unprecedented pathogen in terms of its capacity to impact the abundance, structure, and function of tanoak communities. The mortality rate of *P. ramorum* infected trees (especially tanoak but also *Quercus* species) increases with tree size (Ramage et al. 2011; Cobb et al. 2012b), leading to rapid declines in tanoak biomass, dominance, and ecological function. We assigned the disease factor a weight of 25, slightly lower than silviculture because its impact on tanoak is slower, more heterogeneous, and highly dependent on other landscape and vegetation characteristics (Haas et al. 2011). For the disease disturbance factor, we used two previously developed maps detailing the risk of *P. ramorum* establishment and spread for Oregon (Václavík et al. 2010) and California (Meentemeyer et al. 2004). These studies used heuristic models incorporating host indices and climate factors derived from known infestations to characterize disease risk throughout each landscape. We created a mosaic of these independent risk layers with values ranging from 0–100, and reclassified this map along equal intervals into 0–3 rankings.

Development

Development impacts tanoak abundance, function, and persistence through conversion of forests to developed landscapes characterized by mixtures of impervious surfaces, soil, and vegetation (including forest remnants, planted lawns, shrubs, and trees). In addition to this direct impact, development also increases human activity in extant wildland areas. We interpreted the direct threat to tanoak from development to be relatively less than from disease and silviculture factors, but greater than from fire and assigned it a weight of 10 (Table 1). To estimate tanoak area at risk from development, we produced a development density layer for the geographic range using 2006 data from the National Land Cover Database (NLCD) (Fry et al. 2011).

The NLCD classification system breaks its level 1 "Developed" class into four sub-categories based on a ratio of human-made impervious surfaces to vegetation present within 30 m × 30 m pixels as mapped from Landsat Enhanced Thematic Mapper (ETM+) imagery. Thus, as the relative proportion of impervious surfaces increases, the development "intensity" increases from a "developed low intensity" to "developed high intensity" category. We reclassified the NLCD low to high development intensity categories into our ranking system so that one, two, and three represented low, moderate, and high respectively, with the assumption that higher development intensity presents a greater threat to tanoak. We reclassified all remaining undeveloped NLCD classes to zero. We resampled this layer to 100 m × 100 m cells to match the smallest grain size of other spatial data being utilized. We then generated a development density surface by summing all rank values (0–3) within a 500 m radius (i.e., 1 km × 1 km rectangular neighborhood) of each grid cell location. This process effectively spreads some development risk into adjacent undeveloped areas. We then reclassified the resulting development density map (values ranging from 0–75) into our common 0–3 ranking system using equal intervals.

Fire

Tanoak is a species well adapted to survive and recover from fire. Mature trees have thick, fire resistant bark, and it vigorously regenerates from basal sprouts following mortality of the above ground portion of the tree (Tappeiner et al. 1990). These characteristics enable tanoak to persist and often thrive in a wide range of fire regimes, including areas of low fire frequency (Hunter 1997), albeit with varying functional roles. We hypothesized that fire regimes altered from historic baselines as well as increases in potential fire severity from higher fuel loads result in greater threat to tanoak populations. Thus, we developed the fire disturbance factor to incorporate departure from historic fire regimes and potential fire severity. We represented departure from historic fire regimes using Fire Regime and Condition Class (FRCC) layers created for Oregon (USDA 2010) and California (CDF 2003). FRCC is an interagency, standardized tool for determining the degree of departure from reference condition vegetation, fuels, and disturbance regimes (Havlina et al. 2010). FRCC layers consist of ranked categories that quantify the difference between current vegetation conditions and fire frequency from historic reference conditions. Three ordinal categories rank the degree of departure from reference conditions in addition to a 'not applicable' category based on land cover type. We represented potential fire severity using fuel risk layers developed for Oregon (ODF 2006) and California (CDF 2005). The fuel risk layers were similarly categorized with three ordinal rankings of fuel risk and one indicating 'not applicable' due to land cover type. We recoded these existing categories of the fire regime departure and fuel risk layers to the 0–3 ranking scheme. We then summed the two layers and reclassified the resulting values (ranging from 0–6) to the 0–3 rankings. Given tanoak adaptations to fire and its occurrence and persistence under a variety of fire regimes, we assigned the fire factor the lowest weight of 5 (Table 1).

Disturbance Interactions

We calculated two-way multiplicative interactions for all possible disturbance pairs at a given location weighted by the assigned exponent (y, Eq. 1). In locations where more than two factors overlapped, we selected only the highest-ranking interaction for calculating the threat value at that location. Using this approach, we assumed that one set of disturbance interactions is the dominant threat to tanoak at a given location for the set of hypotheses (i.e., factor and interaction weights) being examined. Below, we describe our reasoning behind the weights assigned to each interaction parameter in our initial model (Table 1).

Disease x Fire

We assigned the disease-fire interaction a weight of two, reflecting our hypothesis that the threat to tanoak increases where these factors coincide. Importantly, *P. ramorum* has been shown to decrease average tanoak size (Davis et al. 2010; Cobb et al. 2012b), and tree size is closely associated with the likelihood of post-fire tree survival (Hengst and Dawson 1994; Kobziar et al. 2006). This disease also increases fuel loads (Valachovic et al. 2011; Cobb et al. 2012a), which are associated with increased soil damage following fire (Metz et al. 2011). Thus, we hypothesize that tanoak in disease-impacted areas are more susceptible to fire-caused mortality, and that dead material from disease would increase fire severity (particularly ground fire), further impacting tanoak recovery. Notably, slower or reduced tanoak recovery would decrease sources of *P. ramorum* inoculum.

Disease x Silviculture

We assigned the interaction of disease and silviculture factors a weight of two. This hypothesis is supported by research demonstrating the effectiveness of herbicide applications in causing tanoak mortality and reducing tanoak dominance (Tappeiner et al. 1987; Harrington and Tappeiner 2009), and the broad patterns of tanoak mortality (Meentemeyer et al. 2008) and reduced average tree size in disease impacted forests (Cobb et al. 2012b). In stands where these disturbances coincide, they have the potential to permanently remove large, mature tanoak trees. More broadly, actions such as salvage harvesting can increase the decline of dominant tree species already impacted by landscape level outbreaks of insects or pathogens (Kizlinski et al. 2002; Foster and Orwig 2006; Freinkel 2007). Tanoak generally has little or a restricted specialty market value, and so salvage harvesting is unlikely to occur for this species. However, herbicide use has a similar effect on tanoak populations except that it may be more efficient in reducing tanoak biomass (Tappeiner and McDonald 1984). Forestry practices may also decrease local tanoak populations to levels where *P. ramorum* is unable to invade stands, but these stands would likely be devoid of ecological functions unique to tanoak (Cobb et al. 2012b; Wright and Dodd this volume).

Development x Fire

This term aims to characterize the threat to tanoak from increased fire frequency related to development density. Syphard et al. (2007) showed that fire incidence is greatest at the wildland-urban interface; however, we did not have explicit evidence for this relationship within the geographic range of tanoak. It is also likely that these fires would be aggressively combated resulting in smaller fires with shorter burn times compared to more remote areas. Thus, we assigned the interaction of these factors a weight of one (Table 1).

Development x Disease

This term represents risk to tanoak based on the relationship between higher development density and increasing likelihood of disease introduction events. While development alone has no direct physical impact in this case, Cushman and Meentemeyer (2008) showed an increased probability of *P. ramorum* occurrence in forests near higher population densities, suggesting that roads, larger populations, urban and suburban landscaping, and heavier use of wildland recreation areas provide additional spatial pathways for pathogen movement and introductions. However, we did not interpret this relationship as producing a significant impact relative to other interactions and so assigned it a weight of one.

Development x Silviculture

Silviculture and development require infrastructure (e.g., roads) for transportation and accessibility. This infrastructure enables further silviculture, recreation, and development activities. We hypothesized that this interaction would nominally increase the threat to tanoak and so assigned it a weight of one.

Fire x Silviculture

While silviculture reduces average tree size and therefore predisposes individual stems to fire-caused mortality, we also hypothesize that it reduces the risk of wildfire ignition and may reduce potential severity. Additionally, tanoak adaptations producing robust sprouting and growth following fire or timber harvest allow for an increased likelihood of tanoak persistence when these factors interact, though most mature trees may be removed. According to these postulations, we assigned this interaction a weight of one.

Sensitivity Analysis

We tested model sensitivity to interaction parameters by varying interaction weights in a series of model runs. We ran the model with all

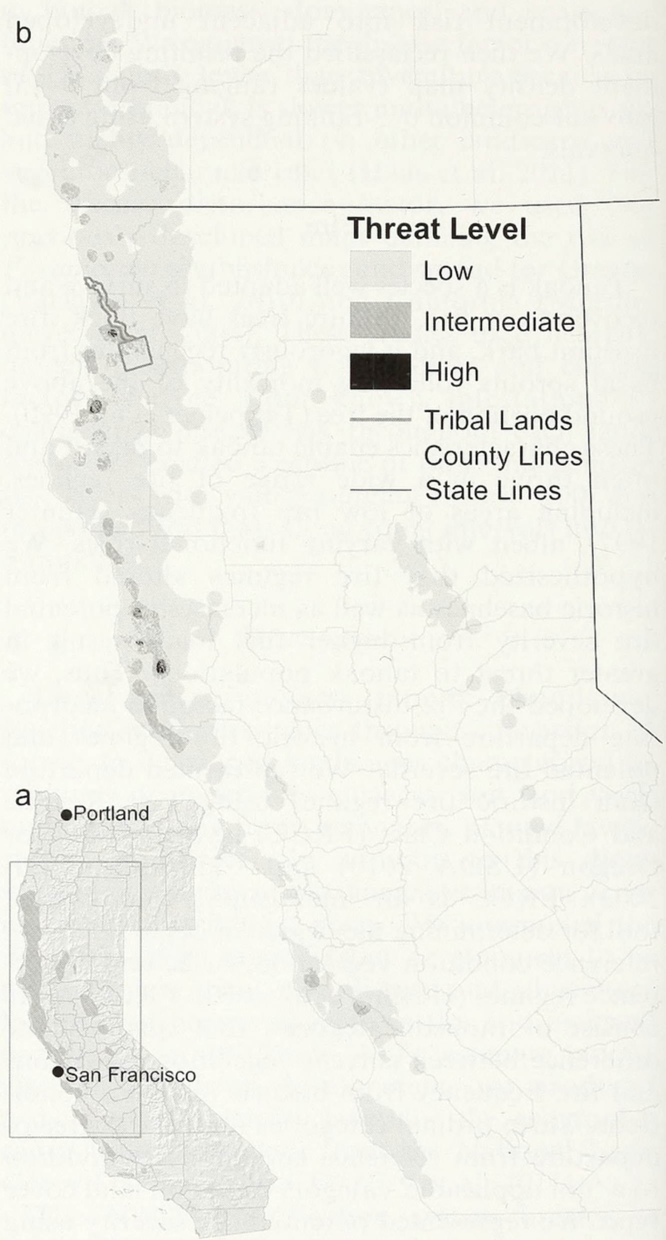

FIG. 1. The spatial distribution of (a) tanoak and (b) threats from weighted interacting disturbances (see Table 1) across tanoak's geographic range. Tanoak range adapted from Tappeiner (1990). Tanoak populations facing elevated threats were concentrated in Humboldt and Mendocino Counties, and partially located on Hoopa and Yurok tribal lands.

interaction weights set to zero, which produced threat values for only the additive part of the model. While this sums the weighted rank values occurring at each location it does not provide insight into local factor interactions. We then ran the model with all the interaction weights set to one (equally weighted) and used multiple iterations to examine how results changed when each interaction term was assigned a weight of two while holding all other factors at one. These tests produced no zero values, indicating that at least one factor was present at each location in our map of tanoak distribution (Lamsal et al. 2011). Using equal intervals, we reclassified the resulting

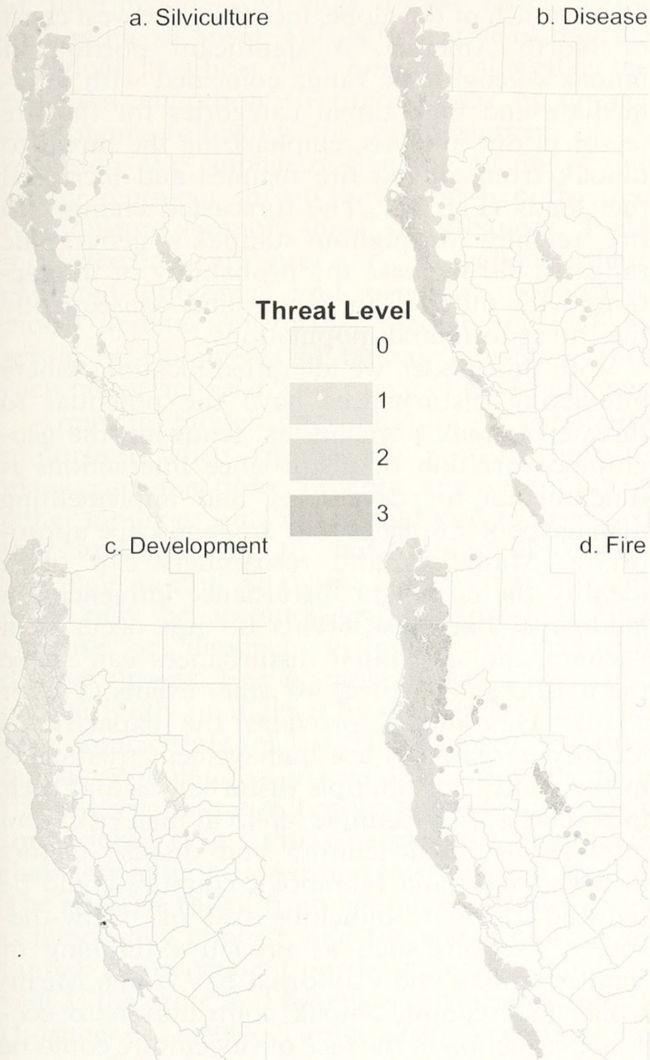

FIG. 2. Four disturbance factors overlaid on estimated tanoak area. Each map shows the classified threat level to tanoak from each disturbance factor across tanoak's geographic range, ranked zero to three ('none', 'low', 'intermediate', and 'high', respectively).

range of values from each model run into low (1), intermediate (2), and high (3) threat levels.

Results

Risk from Disturbance Interactions

Across its geographic range tanoak predominantly faces low to intermediate threats from disturbance interactions, with smaller areas at high risk. The weights listed in Table 1 resulted in a threat map (Fig. 1) with 10,905 hectares (<1%) of estimated tanoak area at high risk, 222,795 ha (5.6% of estimated tanoak area) at intermediate risk, and over 3.7 million ha (94% of estimated tanoak area) at low risk from disturbance interactions. Elevated fire and silviculture risk factors overlap in the Sierra Nevada, whereas disease risk was low throughout much of this region (Fig. 2a, b, d). The influence of development on disturbance interaction risk was observed primarily in the San Francisco Bay Area, where it coincided with low values for other disturbance factors (Fig. 2c). Tanoak faces intermediate and/or high threats from disturbance interactions in 20 of the 30 counties within its geographic range. Using this model formulation, areas classified as intermediate and high threat occurred predominantly where disease and silviculture factors overlapped (Figs. 1 and 2a, 2b). The intermediate and high categories covered 233,700 ha containing an estimated 134.4 million tanoak, with 108.9 million (81%) of these trees located in Humboldt and Mendocino counties, CA. Some of the elevated threat categories are located in areas where tanoak has high cultural importance, including on Hoopa and Yurok tribal lands (Fig. 1).

Sensitivity analysis of the interaction weights demonstrated general robustness of the total amount of tanoak area classified into low and intermediate threat levels, with these two categories accounting for 91% to 99% of the total tanoak range across model runs with different interaction weights. With interaction weights all held at zero (the sum of weighted factors only), nine percent of tanoak area was at high risk, 73% at intermediate risk, and 18% at low risk. With all interaction weights set to one (the sum of the weighted factors plus the highest valued interaction at each location), six percent of tanoak area was at high risk, 24% at intermediate risk, and 70% at low risk. Results from these analyses, respectively, highlight areas where overlapping disturbance factors accumulate and where higher weighted factors coincide. In sensitivity analyses with each interaction weight increased to two while holding others constant at one, we found the disease-silviculture interaction produced the same result as the weighting scheme of the initial model (Table 1). The fire-silviculture interaction resulted in values similar to those produced by our initial model parameters: 6419 ha (<1%) at high risk, 222,790 ha (5.6%) at intermediate risk, and 3.7 million ha (94%) at low risk. Most significantly, the disease-fire interaction was most sensitive to changes in the interaction weight parameter and resulted in five percent of tanoak area at high risk, 31% at intermediate risk, and 64% at low risk. Development impacts on risk were generally small and consistently resulted in >99% of tanoak area in the low threat category. Of the three disturbance interactions that included development, the disease-development interaction resulted in the greatest area in intermediate (9990 ha) and high (1593 ha) threat levels.

Discussion

Mapping the geographic distribution of disturbance factors that threaten foundation species is essential for understanding and managing population and ecosystem impacts (Holdenreider et al. 2004; Ellison et al. 2005). Since many landscapes are influenced by multiple disturbances, spatially explicit tools identifying areas at risk from disturbance interactions are critical to conservation of threatened populations. These tools can be used for prioritizing limited resources for efficient and effective conservation of at-risk species.

Since European settlement, harvesting of tanoak bark, and the subsequent increasing application of herbicides by industrial forestry interests to favor more marketable conifer species (Bowcutt 2011), undoubtedly altered the structure and function of tanoak forests. Coinciding with these processes was an increasing human population resulting in development of forest and wildlands, and alteration of fire regimes to favor conifer species that were valued over tanoak in post-1950 timber markets. Remarkably, tanoak has shown substantial resilience under these adverse conditions, but the introduction of *P. ramorum* into tanoak ecosystems presents a new and significant threat to this species. Although diseases can increase extinction risk (Smith et al. 2006), it is unlikely that tanoak could be eliminated by this pathogen alone. Species extinction most often occurs when multiple stressors coincide to reduce at-risk populations to unsustainable levels (de Castro and Bolker 2005; Smith et al. 2006). Analogously, disturbance interactions, especially novel ones such as those resulting from impacts of an emergent pathogen like *P. ramorum* (e.g., Metz et al. 2011), may increase the likelihood of stand-level tanoak extirpation. Thus, the functional extinction of tanoak due to the removal of all or most large trees over broad areas may be more likely to occur where disturbances interact (cf., American chestnut blight, Paillet 2002; jarrah dieback, Podger 1972).

Cobb et al. (2012b, this volume) indicated that significantly more *P. ramorum*-caused tanoak mortality is likely to occur over the coming decades. This is largely due to the epidemiological role of tanoak in driving pathogen spread and disease emergence, and the high abundance of tanoak in climates favorable to *P. ramorum* (Meentemeyer et al. 2011). Annual variability of temperature and precipitation significantly impact the likelihood of pathogen establishment and spread (Rizzo et al. 2005; Davidson et al. 2011), which was reflected in the observed difference in risk of disease establishment between coastal and inland landscapes (Fig. 2b; Meentemeyer et al. 2004; Václavík et al. 2010).

Global to regional climatic changes are forecasted to influence fire incidence, and changes in fire frequency and intensity could affect tanoak resilience. Moritz et al. (2012) projected significant increases of fire frequency in the near future across much of the globe, including the west coast of North America. A significant portion of tanoak's geographic range coincided with intermediate and high threat categories for the fire factor in our analysis, emphasizing the threat to tanoak from altered fire regimes and increased fuel loads (Fig. 2d). The forecasted changes to fire regimes throughout tanoak's geographic range would increase the probability of interactions with other disturbances and consequently the threat to tanoak populations.

With this model, we identified locations where interacting disturbances have the potential to threaten tanoak populations. Knowing the geographic variation of disturbance interactions is fundamental for developing and implementing management strategies that are landscape appropriate. Managers and researchers can often identify the dominant disturbance influencing a landscape, but these events do not occur in a vacuum and individual disturbances can shape the nature and intensity of other events (Turner 2010). This model provides the capacity to identify, target, and test management treatments in the context of multiple disturbances and their interactions. For example, areas at high risk from interactions of silviculture and disease factors in Mendocino and Humboldt counties could be reduced through judicious use of "slow-the-spread" actions such as proactive thinning of smaller tanoak and California bay laurel. Meanwhile, maintaining tanoak contribution to ecosystem function in the face of silviculture could be accomplished by retaining large tanoak in stands managed for timber. Tanoak in the Sierra Nevada is primarily threatened by fire and silviculture interactions, again suggesting that retention of large tanoak in stands managed for timber would be appropriate to enhance habitat as well as maintain tanoak resilience to fire.

Using models to guide decision-making requires recognition of model assumptions and limitations, principally that results (in this case mapped disturbance interaction threats to tanoak) are often sensitive to the values of the input parameters. The weighting of disturbances and the interactions using the initial model parameters (Table 1) resulted in a map where the interaction of silviculture and disease factors produced intermediate and high threat levels to tanoak over a relatively small portion of tanoak's geographic range (Fig. 1). This essentially shows that high intensity silviculture and disease factors are concentrated in a few smaller areas. Also, these two factors could potentially be the most addressable by management action and minor alteration to forestry practices in these areas. Our sensitivity analysis demonstrated that the model is robust with respect to parameter values for disease and fire interactions. Further, these factors resulted in the greatest total tanoak area at intermediate and high threat levels (>1.4 million ha, or 36%). This is indicative of the role of tanoak as a host of *P. ramorum* as well as the potential alteration to fire regimes in tanoak ecosystems following the establishment of *P. ramorum*. We emphasize that the results of our model represent threats based on hypothesized relationships among these disturbances. Field measurements are necessary to validate these expected outcomes and provide appropriate model updates for further predictions, such as actual measurements of tanoak mortality from each factor across a wide range of environments.

Apposite model interpretation is especially important when results are used to inform management actions, because misconception of either inputs or outcomes could lead to decisions that are contrary to stakeholder objectives. Through careful analysis, diverse management goals may be accomplished by applying more effective, or "designer" treatments to areas with distinct threats. For example, forests at low risk and currently unaffected by disturbances may be most appropriate for the establishment of refuge tanoak populations. Areas facing intermediate threat levels that also border regions with higher threat levels (Fig. 1) may be ideal for treatments that slow pathogen invasion into adjacent stands. The effective threat from interacting disturbances is temporally implicit, and the actual impacts to tanoak are dependent on the state of a stand, as well as the order and timing of disturbance events (Lorimer et al. 2009; Turner 2010). Therefore, the timing of treatments is an essential consideration. For example, fuel load reduction activities could also address disease risk by reducing densities of bay laurel and tanoak, but these treatments would be most beneficial when applied between July and the onset of winter rains to avoid introduction or spread of the *P. ramorum* pathogen (Davidson et al. 2008, 2011). Also regarding disease, management efficacy decreases with time since *P. ramorum* arrival (Filipe et al. 2012), highlighting the importance of treatments that may prevent establishment as well as rapid responses to new invasions in order to mitigate impacts (Meentemeyer et al. 2012). These actions can provide time and space needed to implement further treatments that reduce the cost of disease (and potential interactions with other disturbances) to local communities (Kovacs et al. 2011; Cobb et al. this volume). Lastly, policy changes favoring retention of high value tanoak habitat, especially in locations at high risk from disturbance interactions could be effective at reducing the rate and extent of tanoak population decline as well as maintaining biodiversity and ecosystem function.

Although the maps of areas at-risk from disturbance interactions are static, the databases used to produce them are typically dynamic as new data is acquired and analyzed over time. As new discoveries are made and our knowledge of disturbance interactions and their impacts evolves, model parameters can be updated and results tested in order to maintain reliability of recommendations. Through integration into an adaptive management framework, updates can be quickly applied, enabling new strategies to be developed and implemented in a timely and effective manner. The model framework may also be similarly applied to examine the spatial variation of threats to other species from disturbance interactions.

Conclusions

With increasingly limited resources it is important to rapidly identify target areas where management actions will have the greatest chance of achieving objectives. We propose that this model of threats to tanoak from interacting disturbances could be used as part of an adaptive management plan to bring stakeholders together in prioritizing and achieving conservation of the abundance, structure, and function of tanoak trees and ecosystems. Tanoak is by all accounts a resilient species, persisting and sometimes thriving under a variety of pressures. By applying knowledge and tools currently available, this resiliency can be enhanced, tanoak mortality may be reduced, and the vital services provided by tanoak ecosystems can be conserved for the health and prosperity of current and future generations.

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