



Forest landscape patterns shaped by interactions between wildfire and sudden oak death disease

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ABSTRACT

Forest ecosystems are increasingly affected by a range of tree mortality events, which may permanently alter forest functional traits and disrupt their ecosystem services. While individual forest disturbances are well studied, interactions between multiple disturbances and changes of spatial patterns of forested landscapes are rarely quantified. In this study, we aim to analyze the role of wildfire in the Big Sur ecoregion of California on the spread of *Phytophthora ramorum*, an invasive pathogen which causes sudden oak death, the most important driver of mortality across 1000 km of coastal, fire-prone mixed conifer, evergreen hardwood, and woodlands. We investigated two questions specific to the impacts of these disturbances at the landscape scale: (i) did rates of *P. ramorum* caused tree mortality change after wildfire? (ii) Following the wildfire, to what degree did the continued disease-driven mortality alter forest distribution? To answer these questions, we analyzed remote-sensing-derived products of post-fire burn severity and maps of disease-driven tree mortality. Quantification of burn severity and post fire disease mortality for the burned and unburned areas provided reference conditions for statistical hypothesis tests. The results from statistical and three landscape pattern analyses (area, shape, and isolation) suggest a significant role of wildfire in the reemergence of this invasive pathogen. First, rates of disease caused mortality after wildfire was negatively associated with burn severity suggesting some fire-driven containment of disease during post-fire forest recovery. Second, disease was positively correlated with the distance to fire boundary in unburned areas suggesting the effects of fire on disease extended into unburned areas while attenuating with distance from the burn. Lastly, wildfire reduced area, edge density and isolation of healthy tree patches and these effects did not recover to pre-fire levels for any of the three metrics after eight years of vegetation recovery. Given the widespread prevalence of disease-driven mortality, the importance and frequency of fire, as well as the naturalization of *Phytophthora ramorum* across a broad geographic area, these fire-disease interactions have potential to shape forest structure and disease dynamics across millions of acres of forested wildlands in California and Oregon.

1. Introduction

Recent decades have witnessed a range of forest disturbances occurring at a rate and intensity unprecedented across spatial and temporal scales (Asner, 2013; Buma and Wessman, 2011; Hislop et al., 2020). Understanding forest responses to disturbances that occur over large spatial extents is pivotal to the short-/long-term projection of

ecosystem dynamics, promoting informed decisions in sustainable forest resources management (Buma and Wessman, 2011; Daniel et al., 2017). Over the past decades, there has been a significant increase of studies aiming to understand the effects of individual disturbances, such as disease- or insect-caused tree mortality (Andrus, et al., 2020; Janousek et al., 2019; Václavík and Meentemeyer, 2012), wildfire (He et al., 2019a; Hood et al., 2018; Yin et al., 2020), and drought (Allen et al.

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2015; Hartmann et al. 2015). More recently, a growing number of studies have confirmed a novel trend of increasing intensities and frequencies of forest disturbances, which may interact with each other and jointly affect forest landscape dynamics in complex and unpredictable manners (Jenkins et al., 2014; Rijal et al., 2020; Simler et al., 2018; Turner, 2010).

To reduce forest vulnerability and improve best management practices, researchers have begun to examine how major disturbances interact and subsequently change tree mortality and their regeneration patterns, with an emphasis on two disturbance types – wildfire and disease/insect outbreak (Johnstone et al., 2016; Kane et al., 2017; Simler et al., 2018; Simler-Williamson et al., 2019). One important research question that has yet to be fully answered is whether and how wildfire changes the spatial spread of forest disease or insect attack (Metz et al., 2011, 2013). Depending on its severity, wildfire directly damages or removes the disease-/insect-infected host trees, which can slow pathogen or insect spread by reducing local and landscape-scale inoculum or populations (Beh et al., 2012, 2014). Conversely, fire often causes vascular tissue damage and recent studies of damaging insects in the western United States have also shown that fire-stressed trees are more susceptible to attack than unburned counterparts, irrespective of pre-fire health (Jenkins et al., 2014; Powell et al., 2012). The ubiquity of fire in western North America has resulted in a woody flora that is highly adaptive to a range of fire regimes, thus tree populations are adapted to rapidly recover from fire which in turn can restore or enhance pathogen or insect host populations (White et al. 1996). For example, Beh et al. (2012) found that although the occurrence of the forest disease sudden oak death was reduced by wildfire, the disease-causing pathogen persisted in soil and unburned vegetation which in turn drove pathogen reemergence during canopy recovery that occurs following fire in many Mediterranean forests of California. Similarly, Davis et al. (2012) discovered that the thick bark of pine trees can protect bark beetles during wildfire and these refugial populations can contribute to post-fire insect outbreak. Deleterious disturbance interactions raise the specter of lost forest resilience, for example by limiting the abundance and distribution of trees and valued forest woody species. Extending our understanding of disturbance interactions to include factors such as landscape connectivity and dominant species composition could have important practical management implications (Loehman et al., 2017; Sánchez-Pinillos et al., 2019). Compounding or non-linear disturbance interactions create futures with high uncertainties in terms of forest structure and function during forest recovery (Coates et al., 2016; Johnstone et al., 2016; Kane et al., 2017). In light of this, there is a clear need to move beyond the strong, but preliminary knowledge about the effects of wildfire on disease or insect outbreak, with testable, predictive general theory and rich empirical field datasets.

Remote sensing offers a feasible solution to efficiently and repetitively monitor the impacts of forest disturbances in a synoptic view (Chen and Meentemeyer, 2016; Keeley, 2009; Hatala et al., 2010). Remote sensing is especially suitable for understanding the spatially explicit patterns of forest mortality and disturbance progression (Chen et al., 2017; Huang et al., 2019). The estimation of disease- or insect-caused tree mortality using remotely sensed data makes use of the spectral responses of damaged trees, such as altered spectral and spatial characteristics, which are distinct from their healthy counterparts (Keeley, 2009; Lentile et al., 2006; Rabaglia et al., 2019; Wulder et al., 2006). Forest disease or insect outbreak occurs in distinct temporal patterns ranging from periods of relatively discrete and intense spread on time scales of days or weeks to mortality from chronic stresses spanning years to decades that emerge from steady organism invasion or mortality emergence. Punctuated mortality events are common for environmentally sensitive biological drivers such as bark beetles and some foliar pathogens (Fei et al., 2019; Preisler et al., 2017). Many invasive pathogens and insects are associated with progressively worsening impacts that broadly follow patterns and dynamics of invasion

(Cunniffe et al., 2016; Fei et al., 2019). Invasive species often remain in a non-equilibrium state with their host populations for decades which complicates and may confound estimates of their ultimate impacts (Cobb et al., 2020; Meentemeyer et al., 2012). Satellite image time series has recently gained popularity to quantify spatiotemporal trajectories of infestations at the landscape level and help surmount some of these problems (e.g., Coops et al., 2010; Meigs et al., 2015). Insect or pathogen emergence that occurs over decades will also co-occur and likely interact with other landscape-level processes, particularly fire. Fire is the most widespread and ecologically important disturbance factor shaping the forests of western North America and is most likely to interact with emerging biologically driven mortality in ways that influence the dynamics of each event. Fire effects on forests (i.e., burn severity) are typically mapped through comparing the pre- and post-fire spectral responses from burned trees. Both statistical (e.g., linear regression and random forests; Hultquist et al., 2014) and physical models (e.g., radiative transfer model by integrating PROSPECT and GeoSail; De Santis et al., 2009) are viable solutions to burn severity estimation which could accelerate quantification of disturbance interactions or provide advanced warning of their threats to forest resilience.

The main goal of this study is to analyze the role of wildfire on pathogen spread and subsequent disease-driven tree mortality in post-fire conditions, that is, the reemergence of forest disease after a major landscape-level disturbance. We address this goal in the Big Sur, California ecoregion where the invasive pathogen *Phytophthora ramorum* and the subsequent disease sudden oak death (SOD) have impacted about 80 million trees (Cobb et al., 2020). *Phytophthora ramorum* causes substantial mortality of oak (primarily *Quercus agrifolia* – coast live oak) and tanoak (*Notholithocarpus densiflorus*) while infecting several hundred other native and ornamental species (Rizzo et al., 2005). The Big Sur region has experienced major wildfire events in 2008 and 2016, which overlap with extensive areas of disease emergence since the 1990s. A combination of disease and fire monitoring, as well as remote sensing products associated with both disturbances creates an opportunity to improve understanding the role of wildfire on disease spread and the interaction of the two disturbances on landscape vegetation structure. Specially, we asked: (i) did rates of sudden oak death tree mortality change after wildfire? (ii) Following the wildfire, to what degree did continued disease-driven mortality alter forest distribution and the structure of forest distribution including forest patch size, edge density, and isolation?

2. Materials and methods

2.1. Study area

The study area (centered at 36°16' N, 121°44' W) is within the Big Sur ecoregion on the western flank of Santa Lucia Mountain of California, a total area of 80,000 ha (Fig. 1a). The area has a Mediterranean-type climate, experiencing two main seasons – a cool winter when most precipitation occurs (November–April) and a relatively hot seasonal summer dry period (May–October). The study area landscape is rugged, dissected by steep slopes and drainages with elevations ranging from sea level to 1571 m within 5 km of the coast (Meentemeyer et al., 2008b). This environmentally complex region supports a diversity of plant communities, where environmental conditions (temperature, precipitation, frost occurrence, and soil variation) creates a broad set of plant communities including forests with variable dominance and distribution of tree species. For our questions, we focus on two widespread forest types in the study region which also encompass the majority of sudden oak death impacts: (i) coastal redwood (*Sequoia sempervirens*) forests; and (ii) mixed oak woodland consisting of coast live oak (*Quercus agrifolia*), Shreve's oak (*Q. parvula*), bay laurel (*Umbellularia californica*), and Pacific madrone (*Arbutus menziesii*). Variability of dominant species occurs within these forest classifications, primarily driven by topographic variation in moisture and elevation.

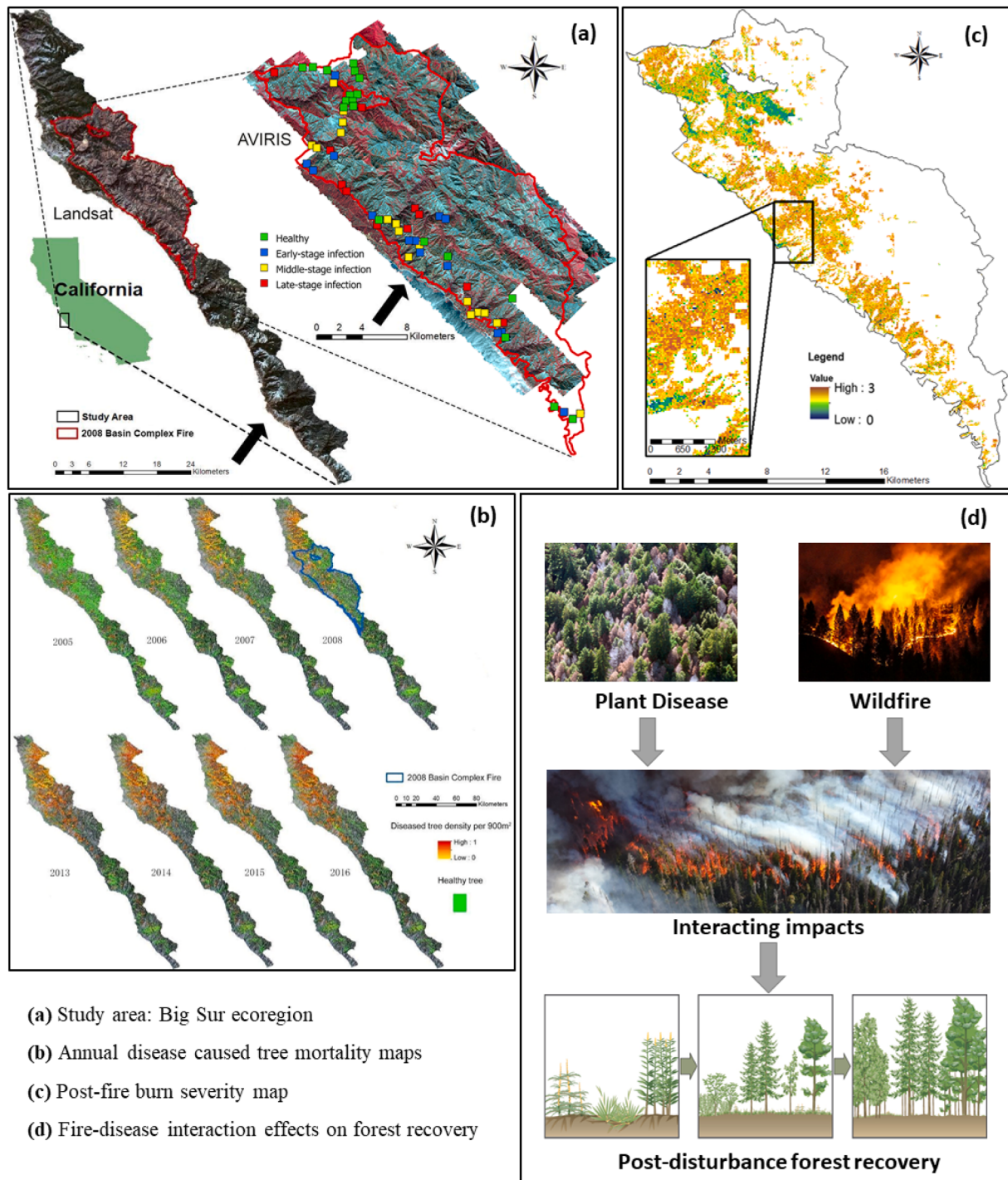


Fig. 1. (a) Illustrates the study area located in the Big Sur ecoregion on the western flank of the Santa Lucia Mountains in California. The extent of the 2008 Basin Complex Fire in the region is outlined in red. The Landsat TM imagery was from a color composite using bands 3 (red), 2 (green), and 1 (blue). The AVIRIS (Airborne Visible InfraRed Imaging Spectrometer) image is from a color composite using bands 51 (NIR), 33 (Red), and 22 (Green); (b) shows the annual maps of tree mortality caused by sudden oak death from 2005 to 2016, which is a series of mapped products by He et al. (2019b); (c) shows the burn severity map with GeoCBI showing the severity of burn from low (0) to high (3), which is a product by He et al. (2019a); (d) represents the core study in this paper that investigating the fire-disease interaction effects on forest recovery. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the study area, pathogen transmission is supported by prolific twig and leaf infections on tanoak and prolific leaf infections on California bay laurel (*Umbellularia californica*) with both species accounting for substantial-to-dominant components of the forest canopy in redwood and mixed evergreen forest types. Both species contribute to local and landscape-level spread due to their abundance at both scales, although infections on bay laurel support an order of magnitude greater

sporulation in California forests (Cobb et al., 2012; Davidson et al., 2008, 2011). However, mortality and transmission are disconnected when viewed across species. Most importantly, coast live oak and tanoak develop infections on the bole which interferes with hydrological function and leads to mortality in 2–8 years of infection (Chen et al., 2015; Cobb et al., 2012; McPherson et al., 2010). Although coast live oak suffers frequent mortality, this species does not transmit the pathogen

while tanoak both transmits and suffers mortality, and bay laurel does not suffer mortality following infection. These epidemiological differences drive much of the variation in transmission, pathogen refugia in the landscape, and patterns of mortality (Rizzo et al. 2005; Cobb et al. 2020).

To understand the response of native forest to the invasion of *Phytophthora ramorum*, we established a network of 280 long-term SOD monitoring plots (500 m² each) in 2006 and 2007 which include a full census of all stems greater than 1 cm diameter at breast height (1.3 m height; dbh). The plots were distributed in a stratified-random manner among two dominant tree types (i.e., redwood and mixed-evergreen) within our study area. We utilized a Panasonic SXBlue real-time differential GPS (Genex, Montreal) to record the plot positions, within an average of 1 m or less. In 2008, a major wildfire – the Basin Complex Fire – was ignited from a dry lightning storm in late June and burned over 28,383 ha of federal, state, and private lands in the Big Sur region that largely overlap with the forests most severely impacted by sudden oak death. A total of 61 plots were revisited immediately following the containment of the fire in September and October 2008 to assess fire severity; these included 42 plots that had been affected by *P. ramorum* and 19 had not. Burn severity for each plot was measured using the Composite Burn Index (CBI; Key and Benson, 2005), a scale ranging from 0.00 to 3.00 used to quantify the damage.

2.2. Time series of forest disease maps

The spatiotemporal dataset of disease-caused tree mortality was mapped at the 30 m resolution from a novel algorithm integrating remote sensing and species distribution modeling since 2005, until the next major wildfire (Soberanes Fire) impacted the region in 2016 (He et al., 2019b). Specifically, (i) spectral mixture analysis (Roberts et al., 1998) was first applied to the satellite Landsat time series for extracting disease-killed host candidates featuring isolated, patchy-distribution patterns. (ii) The uncertainties in the candidates were reduced by species distribution modeling (SDM) which informed the likelihood of *P. ramorum* caused mortality at specific locations. The maps demonstrate an annual disease infection rate of 7% from 2005 to 2016, with overall mapping accuracies ranging from 76% to 83%. These data show a spatial pattern of increased disease-associated mortality from the west coast to east inland particularly in the northern portion of the study region along with considerable landscape-level heterogeneity which reflects variation in disease history and host communities (Fig. 1b). These models omit Landsat data from 2012, due to Landsat 5's mechanical failures and the Landsat 7's Scan Line Corrector (SLC) problem.

2.3. Burn severity estimation

We used data from He et al. (2019a) to map tree damage caused by the 2008 Basin Complex Fire. The map was created using a Disturbance Weighting Analysis Model (DWAM) that estimated post-fire burn severity in the forest landscape jointly affected by wildfire and sudden oak death. DWAM treats burn severity in each basic mapping unit as a linear combination of burn severity of trees affected and not affected by the disease, weighted by their areal fractions in each unit. Landsat TM and AVIRIS (Airborne Visible InfraRed Imaging Spectrometer) imagery were used to create the map at the 30 m resolution (Fig. 1c), which is consistent with that of the disease maps. While also heterogeneous in terms of severity, fire impacts occur in a contiguous area and variation is driven by burn severity as estimated by the Geometrically structured Composite Burn Index (GeoCBI), an index of impact severity which ranges between 0 and 3 (De Santis and Chuvieco, 2009). Moderate burn severity ($1.5 \leq \text{GeoCBI} < 2.5$) occurred in 63.5% of the burned area while low (<1.5) and high (>2.5) occurring in 3.7% and 32.8%, respectively (He et al. 2019a; Fig. 1c). The confluence of burn and disease severity, given the heterogeneity of both disturbances, created a constellation of disease and fire impacts that span the range of most

possible combinations of intensities for each disturbance.

2.4. Environmental factors

Three groups of environmental factors were integrated into our analysis: climatic, topographic, and factors associated with fire dynamics (see Table 1). Both climate and topography are known to affect *P. ramorum* spread and disease-driven mortality (Kelly et al., 2005; Cobb, 2010; Davidson et al., 2008). Climatic factors can be summarized in many different ways and we extracted the monthly mean precipitation and temperature from December to May because this reflects the period where pathogen sporulation and transmission occurs in natural ecosystems (Meentemeyer et al., 2008a). The climatic data are from a collection of gridded estimates (Daymet; <https://daymet.ornl.gov>) of daily weather parameters generated by interpolation and extrapolation using daily meteorological observations rendered on a continuous surface dataset available at a spatial resolution of 1 km for the Contiguous United States (Thornton et al., 2018). The complex topography in the study area required the use of the fine-resolution 10 m Digital Elevation Model (DEM) from the National Elevation Dataset (NED; <http://ned.usgs.gov/>). Elevation, topographic moisture index (TWI), and solar insolation index (SII) were generated from the DEM. Among those factors, TWI describes the effect of topography on local moisture availability, which was calculated as the natural log of the ratio between the upslope contributing drainage area and the slope gradient of the grid cell (Moore et al., 1991). Specifically, the upslope contributing drainage area is the accumulation of flow from upstream. The factor SII characterizes the potential mean solar irradiation for the rainy season (December to May) and was calculated using the cosine of illumination angle on the slope equation (Dubayah, 1994). Both TWI and SII have been shown to influence the dynamics of infection and mortality for a range of species (Cobb et al., 2020).

To further identify wildfire influences on disease spread, we extracted two fire factors that reflect the range of fire impacts on host communities. First, locally derived burn severity (i.e., GeoCBI) was assigned to trees (i.e., individual pixel) within the fire boundary. Second, the shortest Euclidean distance to the fire boundary was extracted for the trees that lie outside of the burn area (i.e., unburned trees) to better test for potential impacts of proximity to fire (heat, smoke) on the pathogen and disease dynamics.

All the factors were derived from 300 randomly sampled plots which span a range of within-plot pathogen prevalence. In total, 106 plots were within the burned area, and 194 plots were outside of the Basin Fire area (unburned). To ensure minimized spatial autocorrelation among the plots, we conducted a semivariogram analysis in the ArcGIS environment (Esri, Redlands, California, USA). The effective distance of spatial autocorrelation was found at 600 m, which was smaller than the average distance between our tested plots. We also set up a minimum distance value of 400 m between any two plot centers to further reduce

Table 1

Description of environmental factors used in statistical analysis. In total, seven factors were chosen to represent three aspects of environmental conditions, including climate, topography, and fire-related context.

Factor	Description
Climate	
• Precipitation	• Monthly mean precipitation (December to May)
• Temperature	• Monthly mean temperature (December to May)
Topography	
• Elevation	• Mean elevation
• TWI	• Mean Topographic Wetness Index
• SII	• Mean Solar Insolation Index (December to May)
Fire-related	
• Burn severity	• Mean burn severity
• Distance	• Shortest Euclidean distance to fire boundary

inferential bias.

2.5. Statistical analysis

To evaluate the significance of wildfire in changing the disease spread rate, we compared four different circumstances. Temporally, we divided the disturbance time window into two distinct periods of ecosystem dynamics: pre-fire (2005 to 2008), and post-fire (2013 to 2016). Here, we did not consider the post-fire early stage of tree recovery (2008–2013), because burned and disease-killed trees revealed high spectral similarities in remotely sensed data causing uncertainties to identify diseased trees (Chen et al., 2017). After five years of recovery (starting from 2013), fire-damaged tree crowns clearly began to re-foliate, facilitating the identification of those which were diseased-killed since the fire (Chu et al., 2017). Spatially, we divided the study area into two classes: burned (area within the fire boundary) and unburned (area outside the fire boundary). In total, the four disturbance cases included: (a) pre-fire and burned, (b) pre-fire and unburned, (c) post-fire and burned, and (d) post-fire and unburned.

We fit a multiple regression model on the data for each of the four disturbance categories with the average rate of disease spread during each of the two-time windows serving as the dependent variable and a set of independent variables specific to each model. Specifically, for the pre-fire circumstances (a and b), the independent variables were climatic (precipitation and temperature), and topographic factors (elevation, TWI, and SII). For pre-fire models, fire-related factors were, of course, omitted. For the post-fire circumstance (c), the independent variables included climatic (precipitation and temperature), topographic (elevation, TWI, and SII), and burn severity factors. For post-fire unburned stands (d), we replaced burn severity with the shortest Euclidean distance to the fire boundary. We intended to evaluate whether the proximity to wildfire may have played a role in post-fire disease progression. All models were developed at a 0.05 significance level using Akaike's information criterion (AIC) for determining the best model. The variance inflation factor (VIF) parameter was calculated for all the predictors in each model to identify multicollinearity and modify models to reduce this bias. We followed a common rule of thumb that all predictor variables with a VIF smaller than 5 were retained in our analyses (Neter et al., 1996). The development of all models was completed in the statistical environment R package (R Core Team, 2019).

2.6. Landscape pattern analysis

Forest landscapes may demonstrate a unique fragmentation pattern caused by the fire-disease disturbances. Here, we applied landscape metrics to quantify such patterns and compare the differences among the four circumstances: (a) pre-fire and burned, (b) pre-fire and unburned, (c) post-fire and burned, and (d) post-fire and unburned. While a range of metrics has been examined to assess the effects of disease/insect outbreaks on landscape change (Chen et al. 2017; Coops et al., 2010;

Gillanders et al. 2008; Lee et al., 2009), we selected and calculated four representative metrics in Fragstats (Table 2; McGarigal, 2014) with data from the annual disease maps (Fig. 1b): Class Area (CA), Number of Patches (NP), Edge Density (ED), Mean Proximity Index (PROX_MN). These metrics were chosen to represent three categories of landscape, including area (CA and NP), shape (ED), and isolation/proximity (PROX_MN), respectively. In previous studies, these metrics have been shown to be critical for understanding and analyzing the relationship between forest segmentation and biological outbreak, including bark beetles and *Phytophthora ramorum* (Lee et al., 2009; Chen et al. 2017; Coops et al., 2010).

We focused on healthy tree patches for calculating the landscape metrics, aiming to understand how disturbances have affected the spatial patterns of tree recovery. The 8-neighbor rule was chosen for patch delineation treating both cardinal and diagonal pixels/cells as adjacent neighbors. This rule has been found to generate appropriate patches in previous studies (e.g., Chen et al., 2017; Richardson and Moskal, 2011). Consistent with other considerations for the period immediately post fire, we did not calculate any metrics from 2009 to 2012 at the early stage of tree recovery in the burned area (2008–2013), because of the high uncertainties in extracting diseased trees from the burned trees (Chen et al., 2017).

3. Results

Fire-related factors (Burn Severity and Distance) demonstrated a significant contribution to disease spread as revealed in the post-fire circumstances (Table 3). Specifically, for the burned area, we found a significant ($p < 0.01$) negative correlation between the rate of disease spread and burn severity (Table 3). Outside of the fire scar, we found a significant ($p < 0.05$) positive correlation between disease spread and the distance to the fire boundary (Table 3). Apart from the wildfire, the topography related factors also significantly contributed to the disease progress, that is, moisture (TWI) was positively associated with mortality in pre-fire conditions and elevation was negatively associated with mortality in the post-fire unburned area. To further understand correlation strength, we calculated Pearson's r among all the model variables (Fig. 2). We found that moisture (Pearson: $r = 0.26$ or 0.28) was the most important variable affecting disease spread before the fire event. However, in the post-fire environment within the fire boundary, we observed a shift of critical variables to burn severity and elevation with each factor having similar effect size (Pearson: $r = -0.13$ versus -0.12). For the regions outside the fire scar, distance was found to have stronger influence than elevation (Pearson: $r = 0.22$ versus -0.18). We have also tested several other types of relationships, including the nonparametric statistic Spearman's ρ , which revealed similar findings.

Overall, the landscape metrics of unburned portions of the study area were relatively uniform from 2005 to 2016, while the patterns of the burned area were substantially different following fire (Fig. 3). Prior to

Table 2

Descriptions of the selected landscape pattern indices applied to this study. Four metrics were employed to represent three categories of landscape patterns, including shape, area and Isolation/proximity, for the statistical analysis of the forest ecological function in terms of fire-disease interaction.

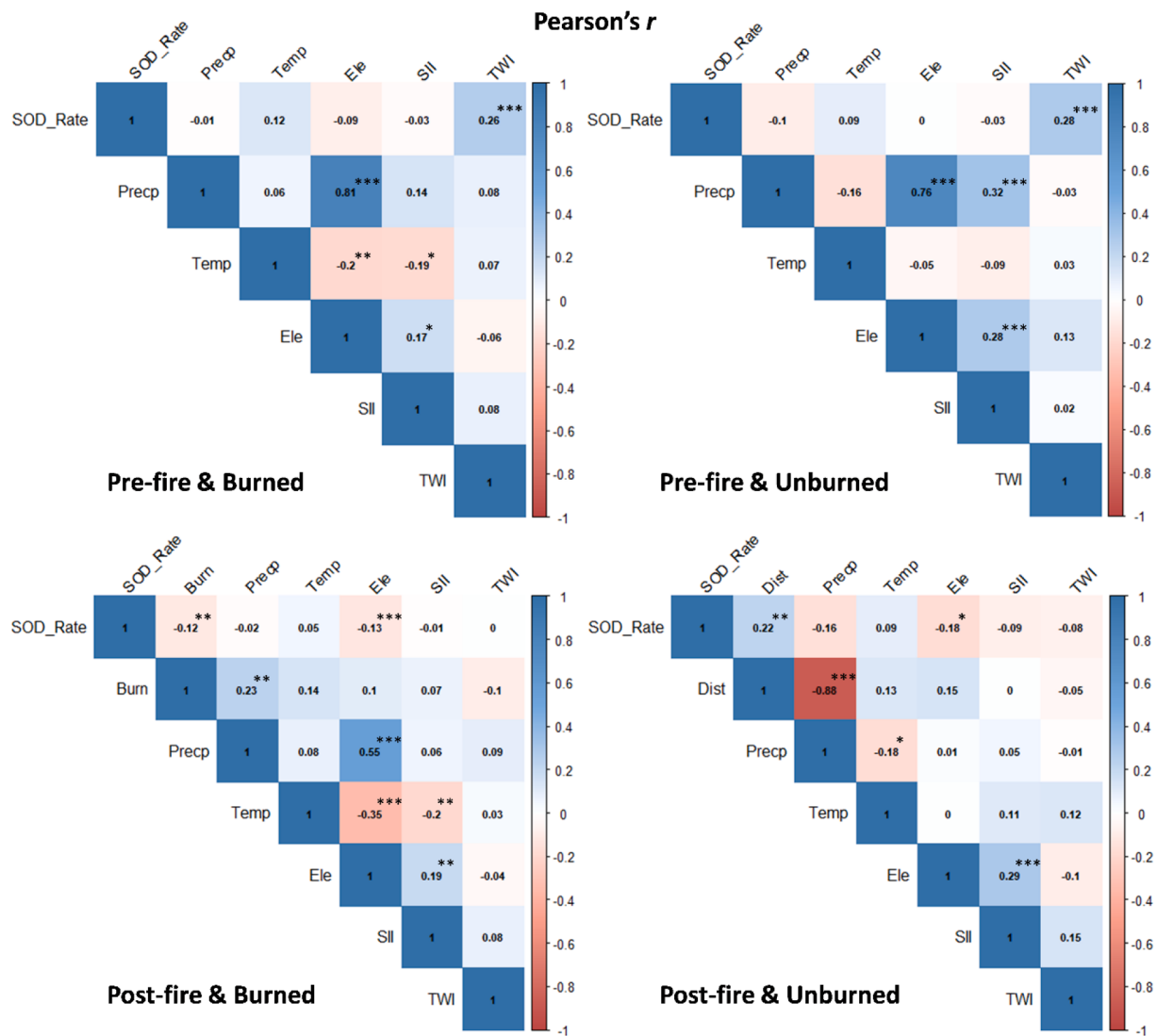
Landscape Metric	Description	Category
Class Area (CA)	Total class area (ha)	Area
Number of Patches (NP)	Total number of patches in a class	Area
Edge Density (ED)	The ratio of total edges and total area (m/ha)	Shape
Mean Proximity Index (PROX_MN)	The degree of isolation and fragmentation of the corresponding patch type	Isolation/proximity

Table 3

Multiple regression models for estimating disease-driven mortality rate for the four disturbance circumstances.

Circumstance	Independent Variable	Estimate	Standard Error	t Value
Pre-fire & Burned	Intercept	-4.6928	1.9801	-2.37*
	TWI	0.6014	0.1629	3.69***
Pre-fire & Unburned	Intercept	-7.1633	1.4831	-4.83***
	TWI	0.8136	0.2311	3.52***
Post-fire & Burned	Intercept	-8.6673	3.8866	-2.23*
	Burn Severity	-0.3456	0.1144	-3.02**
	Elevation	-0.0340	0.0121	-2.81**
Post-fire & Unburned	Intercept	-12.343	-4.1419	2.98**
	Distance	0.0036	0.0016	2.25*

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.



* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Fig. 2. Pearson's correlation coefficients in the four circumstances. SOD_Rate: rate of sudden oak death tree mortality; Precp: precipitation; Temp: temperature; Ele: elevation; SII: solar insolation index; TWI: topographic moisture index; Burn: post-fire burn severity; Dist: shortest Euclidean distance to the fire boundary.

wildfire occurrence, the calculated landscape metrics were different for the burned versus the unburned area suggesting different fragmentation patterns (Fig. 3). Specifically, the burned area demonstrated lower CA (class area) and NP (number of patches) and higher ED (edge density) than the unburned area. However, the trajectories of post-fire (2013–2016) were similar for the two areas, i.e., decreased CA, increased NP, decreased ED, and decreased PROX_MN, as compared to the pre-fire condition. For the burned area, the wildfire caused dramatic impact on forest patterns, initially reducing class area (CA), edge density (ED) and Mean Proximity Index (PROX_MN) (Fig. 3). Despite steady forest recovery, these factors did not return to the pre-fire levels by 2016, eight years following fire. We reiterate that the post-fire early stage of tree recovery (2008–2013) was not considered due to the limitation that burned and disease-killed trees revealed high spectral similarities in remotely sensed data causing uncertainties to diseased tree identification (Chen et al., 2017). However, patterns of landscape structure following this initial recovery period demonstrate clear structural differences between burned and unburned forests (healthy forest area, frequency, and proximity; Fig. 3) which may further contribute to lower disease-caused mortality in the burned area.

4. Discussion

4.1. Effects of wildfire on disease reemergence rate

Our study revealed a significant impact of wildfire on post-fire sudden oak death emergence within the burned area, specifically by reducing post-fire disease-associated tree mortality. These fire effects on disease extended into unburned areas in ways that were spatially dependent on the distance to burned areas (Fig. 4). This is consistent with the finding by Beh et al. (2012), who studied the same fire-disease disturbances and discovered a substantial decrease of *Phytophthora ramorum* prevalence in burned areas, likely an effect of removal/loss of infected host tissue within infected individuals and mortality of host trees overall. The Beh et al. (2012) analysis was based on the data acquired immediately following the wildfire and the present study demonstrates these impacts to pathogen dynamics appear to extend at least eight years post-fire in these forests, to 2016 for the Basin Fire.

The *P. ramorum* pathogen is sensitive to moisture dynamics in both space and time, generally with wetter conditions increasing between-year spread and increasing infection prevalence within or between

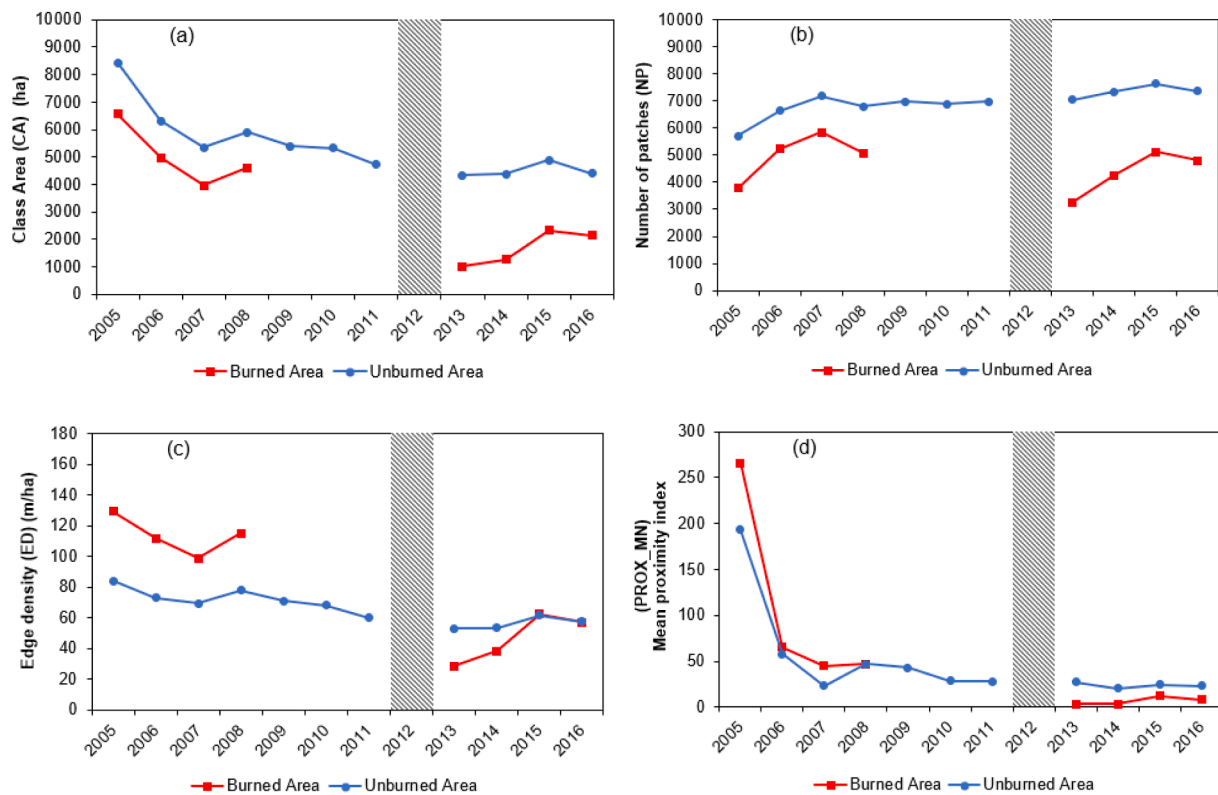


Fig. 3. Comparisons of the spatial patterns for the burned (red line) and the unburned area (blue line). The gray area means the lack of high-quality data in 2012, due to Landsat 5's mechanical failures and the Landsat 7's Scan Line Corrector (SLC) problem. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stands (Cobb et al. 2020; Condeso and Meentemeyer 2007; Davidson et al. 2005). While our study did not quantify the mechanistic drivers of pathogen survival, lower disease impacts with proximity to the Basin Fire – our empirical data demonstrate increased tree survivorship near burn boundaries – are consistent with at least two distinct ecological and/or biophysical dynamics. First, fire-impacts alter the surrounding habitat in ways that decrease pathogen spread or decrease pathogen survival, for example decreased canopy cover and associated increases in temperature or lower relative humidity. A well-developed body of previous work showing temperature and moisture (including humidity) influences on pathogen dynamics lends support to this conjecture (Davidson et al. 2005, 2008; Hansen et al. 2008; Eyre et al. 2014; Cobb et al. 2020). Typically, in wet climates with cold temperatures and dry climates with hot temperatures, *P. ramorum* was less likely to occur, demonstrating the sensitivity of pathogen growth and reproduction to temperature extremes and moisture availability (Meentemeyer et al. 2008a). Second, direct impacts of fire including heat, ash, and/or smoke could alter pathogen survival and subsequent disease impacts or re-emergence. Presumably, the mechanism driving these patterns would be magnified senescence of pathogen-infected foliage in bay laurel which has been previously demonstrated outside of burned areas (Davidson et al. 2011), although rapid pathogen population recoveries following fire or drought suggests the expected duration of these changes is unlikely to extend beyond 1–2 years post fire (Davidson et al. 2008; Beh et al. 2012; Eyre et al. 2014). Senescence of foliage in this study is equivalent to crown scorch, referring to the portion of the tree's foliage that is killed by heat transferred via convection during a fire, which would lead scorched foliage appear brownish red (Hood et al., 2018). Senescence changes analogous to bay laurel are unlikely in tanoak given infections in this species are more likely to be located in woody twig tissue which is unlikely to be senesced at the same rate. Irrespective of potential *en planta* differences in pathogen survival among host species, fire, heat or smoke impacts to pathogen survival in bay laurel alone

could be sufficient to alter landscape-level disease impacts for at least a few years given the disproportionate importance of bay laurel in driving pathogen spread and subsequent mortality in the wildland forests of this region (Cobb et al. 2020; Meentemeyer et al. 2012; Davidson et al. 2008). Distinguishing distinct drivers of post-fire changes in disease dynamics has clear management implications as changes in forest structure could be achieved through thinning interventions while there is no clear surrogate for the direct impacts of fire (heat, smoke, tissue consumption).

4.2. Effects of disturbance interaction on forest fragmentation pattern

While sudden oak death affected the burned and unburned area in a similar way prior to fire occurrence in 2008, the forest landscapes revealed different patterns of post-fire recovery after the fire event (Fig. 3). Specifically, forests in the burned area remained at the recovery stage in the 2013–2016 period, where new and healthy tree patches continued to appear in the area, with CA (class area) and NP (number of patches) values showing an upward trend. New healthy tree patches over time also likely drives the increase of edge density (ED) in the burned area. The unburned area, however, showed relatively flat trending lines for all the four metrics, suggesting that the fragmentation level of the forest has reached an equilibrium, presumably this is at least a partial reflection of disease which has been progressive over the study period. However, the reader should also remain aware that our data suggests wildfire together with sudden oak death had a long-term detrimental effect on forest recovery. Although the pre-fire edge density and proximity to edge (ED and PROX_MN values, respectively) for the burned area were consistently higher than or equal to those for the unburned area, their relationship was reversed for most of the forest recovery period even after eight years of fire occurrence (Fig. 3). While the rate of forest recovery from wildfire depends on multiple factors (e. g., the severity of the fire, plant species, site productivity, pre- and post-

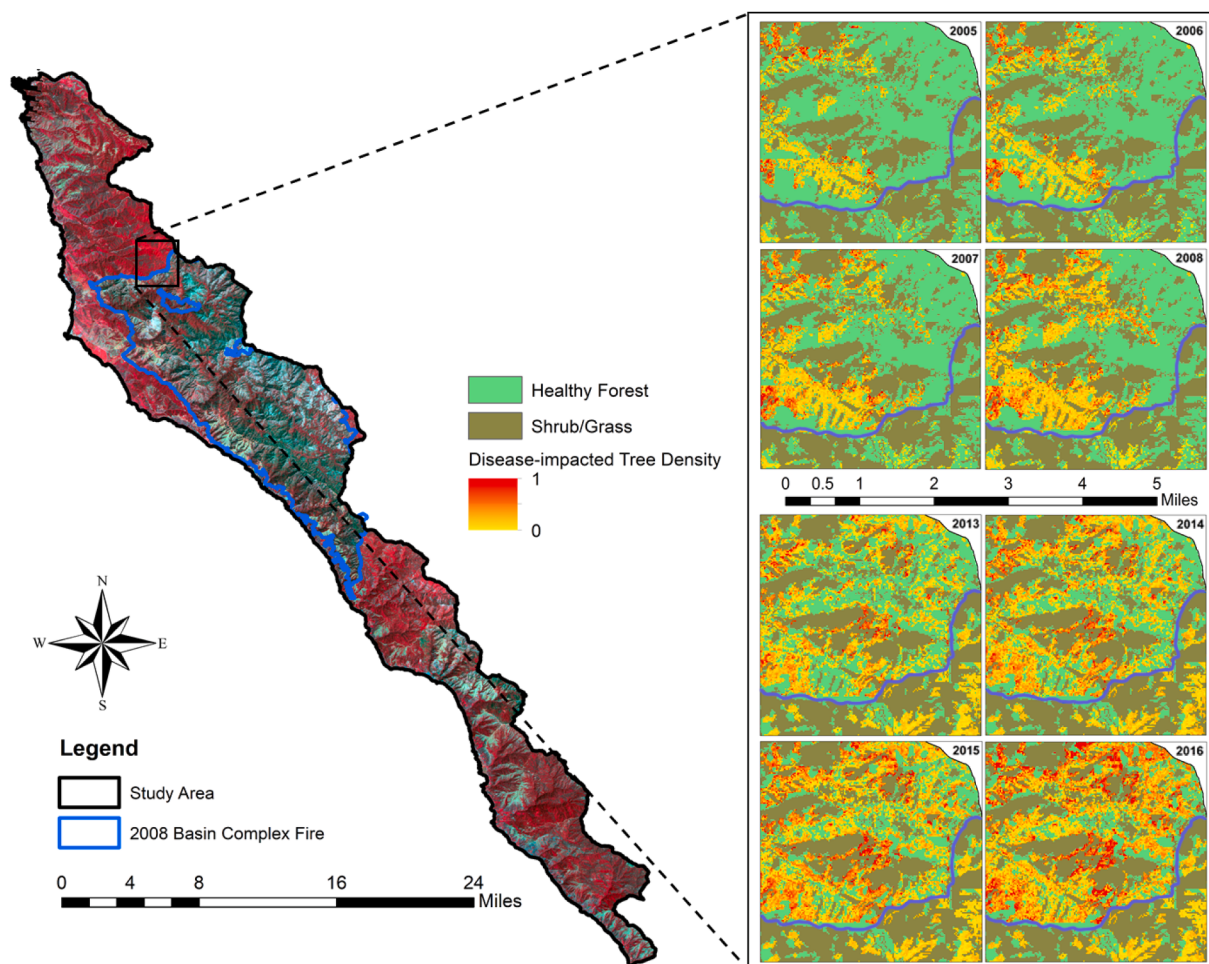


Fig. 4. A subset of the BigSur region crossing the fire boundary showing the pattern of forest change from 2005 to 2016.

fire climate), our study showed slower recovery rate (e.g., 46% of the pre-fire conditions for the healthy tree Class Area; Fig. 3a) compared to that of a forest in a similar Mediterranean climate (Viana-Soto et al., 2017) and the boreal ecoregion (Pickell et al., 2016). Collectively, fire and disease interactions in Big Sur appeared to slow forest recovery and reduce diversity of some metrics of landscape structure for at least eight years.

4.3. Other potential disease-fire interactions and broader applicability

Although significant effects of the wildfire on disease spread are apparent in our findings, caution is advised when extrapolating the conclusions to other regions. In a case study examining the interaction between bark beetle and wildfire in the Northern Rocky Mountains, Harvey et al. (2014) did not find a direct relationship between beetle outbreak and post-fire tree seedling establishment, suggesting strong resilience of the lodgepole pine (*Pinus contorta* var. *latifolia*) dominated subalpine forests to the interacting disturbances. It is likely that the post-fire disease or insect spread not only depends on the complex environmental factors (as discussed in our study), but also relies on the spatial patterns of host tree recovery (Lombardero and Ayres, 2011). Furthermore, sudden oak death was shown to increase fire-caused tree mortality, fire intensity, and ecosystem-level fire impacts (Metz et al. 2011, 2013; Cobb et al. 2016). In each case, these disease-fire impacts appeared to be driven by increased fuels associated with oak and tanoak mortality (Metz et al. 2011; Kuljian and Varner, 2010; Chen et al., 2017). Thus, it is likely that the post-fire reductions in disease-caused mortality are themselves driven at least in part by pre-fire disease dynamics given

these areas are likely to experience greater burn severity.

Our results strongly suggest that fire has significant impacts on disease dynamics during forest recovery and further that some of these patterns can be predicted with topographical data. Clearly, further evaluation of disease-fire interactions for the Basin Fire is worthwhile as it could improve management approaches for fire-prone coast range forests, for example by focusing on the substantial accumulation of disease-driven fuels in many forests (Metz et al. 2011; Cobb et al. 2012). Taken as a whole, inference from the Basin Fire and broader study of disturbance interactions demonstrates the need and potential benefit to management of tree mortality through a better understanding of disturbance interactions (Buma 2015; Johnstone et al., 2016). However, translating these basic insights into management actions will be more complex. Intense wildfires in California are major forest management, public health and safety problems. The benefits of intense fire on disease dynamics is almost certainly outweighed by the costs and risks to life, property, and natural resources that accompany these events. A key unanswered question in this system and many others is whether or not the benefits of fire on disease-caused mortality can be realized outside of destructive megafires, such as through thinning and prescribed fire. We hope this study and associated work will motivate management experiments using these approaches and applied at significant spatial scales.

5. Conclusion

This study reveals a significant impact of wildfire on the post-fire dynamics of sudden oak death and highlights the utility of remote sensing data and associated products for spatially explicit disturbance

monitoring and evaluation at the landscape scale. For the burned forest, the severity of fire exerted a significantly negative effect on disease reemergence in post-fire forest recovery. Outside the burned area, the distance to the fire boundary showed a significantly positive effect on the disease severity (tree mortality). Our findings also suggest slowed forest recovery due to the disease-fire interaction. The spatial patterns of the forest landscape (e.g., area, edge density and isolation of healthy tree patches) did not recover to the pre-fire levels after eight years of the fire event and some of these patterns may reflect pre-fire disease patterns. Our study illustrated a novel way of using remote sensing to understand disturbance interactions in coastal forest ecosystems of a much greater region covering the northern half of the California floristic province, a region spanning ~700 km and billions of individual trees susceptible to *P. ramorum*.

CRediT authorship contribution statement

Yinan He: Methodology, Data curation, Writing - original draft. **Gang Chen:** Conceptualization, Methodology, Writing - original draft, Supervision, Project administration, Funding acquisition. **Richard C. Cobb:** Writing - review & editing. **Kaiguang Zhao:** Writing - review & editing. **Ross K. Meentemeyer:** Resources, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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