

Interacting disturbances: wildfire severity affected by stage of forest disease invasion

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Abstract. Sudden oak death (SOD) is an emerging forest disease causing extensive tree mortality in coastal California forests. Recent California wildfires provided an opportunity to test a major assumption underlying discussions of SOD and land management: SOD mortality will increase fire severity. We examined prefire fuels from host species in a forest monitoring plot network in Big Sur, California (USA), to understand the interactions between disease-caused mortality and wildfire severity during the 2008 Basin Complex wildfire. Detailed measurements of standing dead woody stems and downed woody debris 1–2 years prior to the Basin fire provided a rare picture of the increased fuels attributable to SOD mortality. Despite great differences in host fuel abundance, we found no significant difference in burn severity between infested and uninfested plots. Instead, the relationship between SOD and fire reflected the changing nature of the disease impacts over time. Increased SOD mortality contributed to overstory burn severity only in areas where the pathogen had recently invaded. Where longer-term disease establishment allowed dead material to fall and accumulate, increasing log volumes led to increased substrate burn severity. These patterns help inform forest management decisions regarding fire, both in Big Sur and in other areas of California as the pathogen continues to expand throughout coastal forests.

Key words: *Big Sur; coast live oak; emerging infectious disease; generalist forest pathogen; Phytophthora ramorum; tanoak.*

INTRODUCTION

Altered forest fire regimes and disturbances caused by biological invasions are major challenges facing forest scientists, managers, and policy makers. The interaction between fire and emerging forest pathogens and insects is of particular concern. Widespread tree mortality associated with biotic disturbances, has raised concerns about increased fuel loads and, therefore, increased fire hazard and burn severity in forests (e.g., Dale et al. 2001, Lundquist 2007). Higher severity fires can, in turn, affect forest composition and successional dynamics, increase forest susceptibility to other insects or disease, and lead to expensive firefighting operations to protect neighboring communities and public lands (Sugihara et al. 2006).

The link between a major forest disturbance and fire hazard is not as straightforward as equating an increase in dead trees with more severe fires. The agents of tree

mortality may behave in very different ways, and large-scale disturbance events occur on a continuum from acute, instantaneous events to chronic, progressive stressors. For example, windstorms or hurricanes can lead to tree mortality over large areas in a single day while bark beetles or forest pathogens can cause similar levels of mortality over longer time periods (Hansen and Goheen 2000). Interactions between pathogen- and insect-associated tree mortality and fire severity are not always clear (e.g., see reviews in Parker et al. 2006, Jenkins et al. 2008). The impact of tree mortality on subsequent fire risk will depend on a range of factors, especially the timing of mortality in respect to the seasonality of fire risk.

Understanding the interactions between fire and other disturbances is complicated by the difficulty in obtaining detailed prefire field sampling of stand conditions to estimate fuel inputs from a major disturbance because the location and timing of future wildfires are unknown. Few studies of post-wildfire ecological effects in forests are based on both pre- and postfire data. To date, most studies of fire severity employ modeling techniques to

Manuscript received 26 February 2010; revised 6 July 2010; accepted 4 August 2010; final version received 26 August 2010.
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predict potential fire behavior in forests with high levels of tree mortality or attempt to infer prefire conditions based solely on postfire examination of the landscape (Schmoldt et al. 1999, Jenkins et al. 2008).

The emerging infectious forest disease sudden oak death (SOD), caused by the generalist pathogen *Phytophthora ramorum*, is an example of a destructive biological invasion that has resulted in extensive tree mortality in coastal California forests (Rizzo et al. 2005). Particularly alarming to land managers and stakeholders at all levels are the increased fuel loads of host species in SOD-impacted forests and the potential for this disturbance to intensify wildfires. Forests where the pathogen is well established hold an abundance of downed woody debris or standing dead tree snags. Our monitoring of disease impacts throughout central and northern California indicates dead biomass can be orders of magnitude higher in infested sites than in uninfested sites (Maloney et al. 2005; D. M. Rizzo, unpublished data).

In 2008, major wildfires occurred for the first time in forests affected by SOD. The largest fire, the Basin Complex, ignited from a dry lightning storm in late June and burned over 95 000 ha in the Big Sur region along the central coast (USDA Forest Service 2008). The forests of Big Sur are among the most impacted by *P. ramorum*, with 100% of tanoaks in some stands infested by the pathogen and hundreds of thousands of dead host trees across the region (Maloney et al. 2005, Meentemeyer et al. 2008). Media reports and anecdotal accounts from firefighters linked the intensity of the fire and difficulty of firefighting operations to increased fuels from SOD (Lee et al. 2010).

The detailed measurements of all dead woody stems and downed woody debris in our monitoring network provided a valuable picture of the increased fuel loads attributable to SOD mortality one to two years prior to the Basin fire. Big Sur is one of the earliest sites of *P. ramorum* emergence in California (Mascheretti et al. 2008). Over time, the pathogen has spread throughout substantial portions of the region, creating a diversity of SOD impacts across Big Sur's heterogeneous landscapes (Fig. 1; Meentemeyer et al. 2008). Importantly, the recruitment of fuels as a result of SOD mortality occurs over a longer time period than the "sudden" nature of the disease's name would indicate (McPherson et al. 2005, Rizzo et al. 2005). Once infected, trees may take years to die, and may retain their dead leaves in the canopy for one to two years, leading to a canopy filled with extremely dry fine fuels (McPherson et al. 2005, Kuljian and Varner 2010). Dead trees begin to lose branches, fragment and fall to the ground over a period of several years. The quality and abundance of fuels will vary greatly among these stages of disease progression (Appendix A: Fig. A1; Kuljian and Varner 2010), with accompanying variation in the potential for the fuels to increase the ignition, spread or severity of surface or crown fires in the forest. Regions in Big Sur vary greatly

in their time since infection, and therefore also differ in the stage of disease progression and the amount of tree mortality.

We have an extensive network of forest monitoring plots in Big Sur (Meentemeyer et al. 2008). This large-scale and long-term project to track the impacts of the disease provided a rare opportunity to utilize pre- and post-fire empirical data to understand the ecological impacts on the forest of these two important disturbance agents, an exotic pathogen and wildfire. Specifically, we examined a major assumption underlying discussion of SOD in the context of land management and fire control, namely, that the mortality from SOD will worsen the impact of fire. We used prefire data on tree mortality and pathogen distribution and postfire surveys of burn severity to ask: (1) Did prefire fuel loads vary among areas that differ in pathogen presence or impacts? (2) Was burn severity higher in areas that had previously experienced higher SOD mortality? (3) Does the stage of disease progression influence burn severity because of changes in fuels through time? Understanding the potential relationship between disease impacts and fire severity is an important component of management decisions for coastal California forests throughout the pathogen's range.

METHODS

Study system

Phytophthora ramorum infects over 45 plant genera, but mortality is concentrated in tanoak (*Lithocarpus densiflorus*, recently attributed to a new genus as *Notholithocarpus densiflorus*) and several oak species (*Quercus* spp.). These host species are an important part of the coast redwood and mixed evergreen forests that occur in large areas along California's coast and along the wildland-urban interface (Rizzo and Garbelotto 2003). Since the mid-1990s, *P. ramorum* has killed potentially millions of trees throughout its current range from southern Oregon to the Big Sur coast in central California (Rizzo et al. 2005). Widespread tree mortality from SOD is expected to impact many aspects of forest structure and functioning, including regeneration, nutrient cycling and species diversity (Rizzo and Garbelotto 2003, Waring and O'Hara 2008).

We established a network of 280 long-term monitoring plots in Big Sur in 2006 and 2007 to understand changes in forest communities and the physical environment as a consequence of pathogen establishment and host mortality (Fig. 1). The plots were distributed in a stratified-random manner across the region in two forest types (redwood-tanoak or mixed evergreen) and in areas with and without the pathogen. In each circular 500-m² plot, we quantified disease incidence, levels of tree mortality, amount of coarse woody debris and various other biological and physical characteristics of the forest. The study area, plot network, plot selection and monitoring data are described in greater detail in Appendix B.

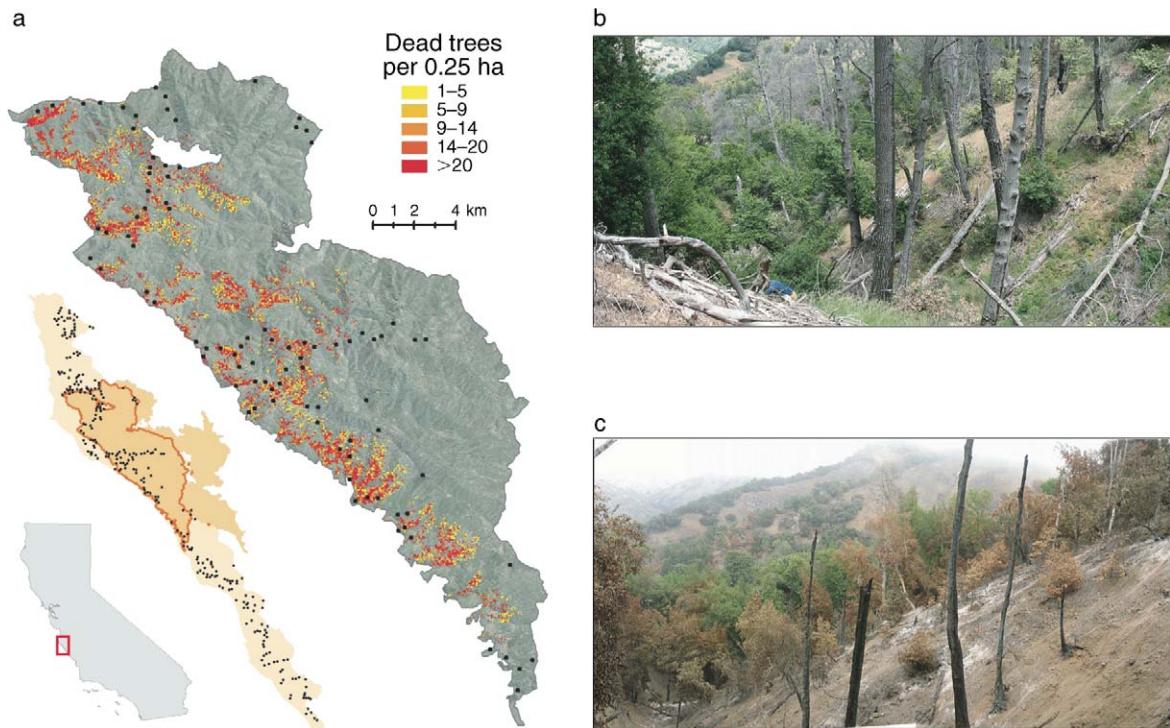


FIG. 1. (a) The estimated density of sudden oak death (SOD) tree mortality from aerial imagery (Meentemeyer et al. 2008) and spatial distribution of monitoring plots in Big Sur redwood–tanoak and mixed evergreen forests in relation to the Basin Complex fire perimeter (upper right); the entire Big Sur plot network (280 plots) in relation to the Big Sur ecoregion (pale orange) and the Basin Complex fire perimeter in red (center); and the location of Big Sur along California's coast (lower left). The fire perimeter contains 98 plots, 61 of which were surveyed for burn severity in September–October 2008 immediately following the fire. (b) A monitoring plot (BS195) from east Andrew Molera State Park in 2006 with very high tanoak mortality from SOD, resulting in high fuel volume from standing dead host trees and downed woody debris. (c) The view from the same position in plot BS195 in September 2008, following the Basin fire, showing high fire severity and fuel consumption. The before-and-after views from this plot represent the hypothesized relationship between SOD and wildfire severity.

The interval between fires in the Big Sur region is thought to range from 5 to 75 years with an average return of 24 years, but the historical fire regime for the region is not well characterized (Davis and Borchert 2006). Fires occurring in the mixed evergreen and redwood-tanoak forests of our study area are primarily surface fires and current knowledge of the fire regimes are described in greater detail in Sugihara et al. (2006). Both habitats are dominated by fire-resistant and fire-tolerant species that can produce basal resprouts following fires.

Ninety-eight of our monitoring plots (35% of the Big Sur network) were within the perimeter of the 2008 Basin Complex fire (Fig. 1; see also Plate 1). In September and October 2008, immediately following containment of the fire, we revisited 61 of the plots within the fire perimeter to assess burn severity based on measurements that would disappear with the onset of California's winter rains. The analyses that follow use pre- and postfire conditions of these 61 plots to examine the potential relationship between disease-caused tree mortality and burn severity. These sites include 30 mixed evergreen plots (nine uninfested, 21 infested) and 31 redwood-tanoak plots (10 uninfested, 21 infested).

Assessing fuel abundance and burn severity

In each surveyed plot, every standing stem ≥ 1 cm dbh (diameter at breast height, 1.3 m) was identified to species, and measured for dbh to obtain basal area. Dead stems were classified according to an estimated time since death based on the presence or absence of leaves and fine twigs or the fracturing and falling of major crown branches. Downed logs ≥ 20 cm in diameter were identified to species and their length and diameter measured to estimate a cylindrical volume. Fuels of this size generally fall into the 1000-hour or larger category, and, therefore, our data describe only the larger, coarse fuel portion of total fuel availability (see Appendix B for further discussion).

We used prefire measures of standing dead basal area and downed log volume for *P. ramorum* hosts that may be killed by the pathogen (i.e., tanoak, coast live oak [*Quercus agrifolia*], and Shreve's oak [*Quercus parvula* var. *shrevei*]) to quantify changes in fuels caused by SOD and address our research questions. Because burn severity is also due to the presence of fuels unrelated to SOD, we calculated the prefire basal area and downed log volume for other tree species that are not killed by *P.*

ramorum (this includes both non-hosts and host plants that are not killed but may play a role in some part of the pathogen's epidemiology, together called "non-hosts" hereafter). Because live material is also part of the fuel complex, we examined whether the basal area of host and non-host species or the coverage of shrubs differed between infested and uninfested areas.

Plot-level postfire severity was rated using the composite burn index (CBI), a continuous variable averaged across the impacts to five forest strata (substrate, herbs, shrubs, intermediate trees, and dominant trees), with several characteristics of each layer rated from zero to three and averaged (Key and Benson 2006). We also quantified soil and tree severity using indicators such as the depth of deposited ash or the height of tree crown scorching; these were measured at eight random locations in each plot and averaged across sampling locations for estimates of plot-level means and variability (see Appendix B for further description of these measurements).

Analyses

We compared prefire fuels (standing dead basal area or downed log volume) for host species between infested and uninfested areas in the full network of plots using one-sided Mann-Whitney U tests, hypothesizing that host fuel loads were higher in plots where *P. ramorum* was present. We used two-sided tests to compare other aspects of the fuel complex (e.g., non-host species, host species not killed by the pathogen, or live material) to examine whether potential SOD-caused differences in fuels were not confounded with other variables.

We assessed the relationship between burn severity and SOD impacts in several ways. First, we used one-sided Mann-Whitney U tests in each forest type to compare CBI between infested and uninfested plots, hypothesizing that burn severity was greater where SOD was present. Second, we examined whether CBI increased with increasing basal area of standing dead host trees (or greater SOD mortality) across all plots using linear regression. We used CBI as our general indicator of fire severity for these two analyses because it was significantly correlated with each tree and soil severity metric we measured in more detail within the plots (all $r > 0.42$, $P < 0.001$). Third, we used the detailed tree and soil severity data to ordinate the plots using nonmetric multidimensional scaling (NMDS). We then used multi-response permutation procedure (MRPP) to ask whether uninfested plots differed from infested plots when burn severity was examined using these multiple quantitative measures, or whether forest types differed in fire severity characteristics.

Finally, we examined the range of variation among infested plots in the proportion of new host mortality (as quantified in 2006–2007 during plot establishment), which we considered a proxy for recency of pathogen establishment, and the variation in host log abundance, which we considered an indication of longer-term

establishment and progression of the disease (see Appendix B for further discussion of inferring disease progression from fuel type). We separately analyzed the relationship of CBI to standing dead basal area in 27 infested plots that contained recent SOD mortality and compared the relationship to that found in the remaining 15 infested plots with older mortality and 19 uninfested plots. We also examined whether greater host log abundance increased impacts to the substrate layer portion of the CBI (litter, duff, underlying mineral soils and small woody fuels) in infested plots with accumulated host logs using linear regression; as above, the same relationship was examined in the remaining uninfested plots or infested plots without host logs.

RESULTS

Across our 280-plot monitoring network, standing dead basal area and downed log volume of *P. ramorum*-susceptible species were significantly higher in plots with the pathogen present than in plots without (Fig. 2, Appendix C: Table C1). There was no significant difference in the abundance of live or dead non-host species within the 61 focal plots between infested and uninfested areas (Appendix C).

Despite differences in dead woody material of SOD-associated species, we found no significant difference in burn severity between infested and uninfested plots in either forest type, whether measured by CBI (Fig. 2c; Appendix D: Fig. D1) or using multivariate metrics of soil and tree severity (Appendix D). The CBI also showed no relationship with the amount of standing dead host basal area across all 61 plots (Appendix E: Fig. E1).

We observed great variation among plots in the volume of downed host logs and the proportion of newly dead basal area (Fig. 3a, d), both measures we used as indicators of the relative time since disease establishment. Newly dead host trees were overwhelmingly found in sites where *P. ramorum* was present (27 infested plots and only two uninfested plots). Similarly, most plots containing downed host logs were in infested areas (25 infested vs. 5 uninfested plots). Fifteen infested plots had no recent standing host mortality, suggesting a longer presence of the disease (Fig. 3d) and 17 infested plots did not contain any downed host logs, indicating more recent infection and mortality (Fig. 3a).

Relationships between burn severity and fuel abundance were detected when areas of recent or older SOD were examined separately. In infested plots with recent SOD mortality, where dead trees still possessed leaves and fine twigs when surveyed in 2006 and 2007, CBI increased with standing dead host basal area, although relatively little of the variance was explained ($R^2 = 0.21$, $P = 0.02$; Fig. 3e). In the remaining plots, there was no such relationship, however (Fig. 3f). Impacts to the substrate layer significantly increased with an increase in the volume of host logs ($P = 0.012$) in infested plots, but

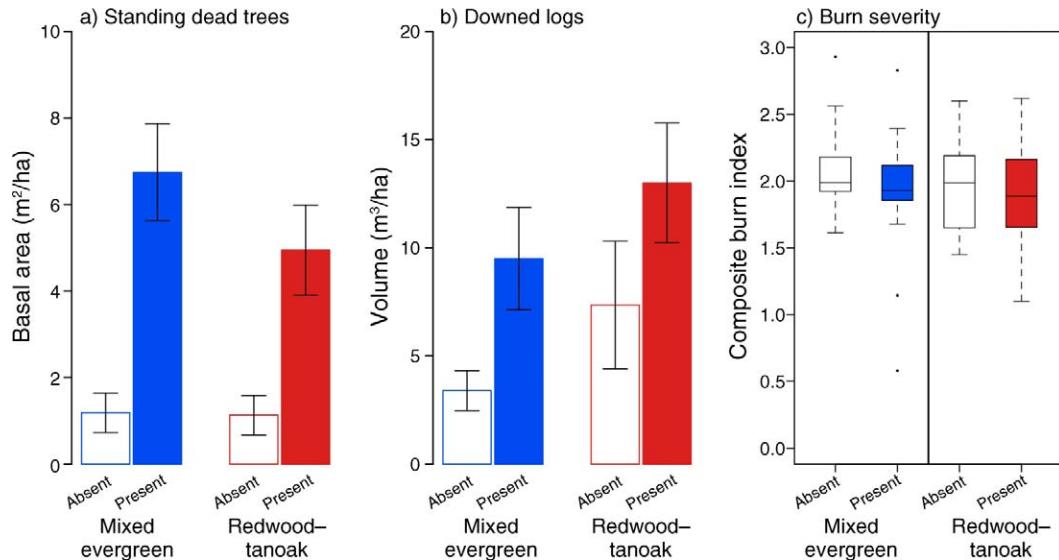


FIG. 2. The basal area of (a) standing dead trees and (b) downed woody logs of species that suffer lethal infections from *P. ramorum* are significantly greater in infested plots than uninfested plots for both forest types across the 280 plots in the Big Sur network (all $P < 0.02$). Values are means \pm SE. (c) Burn severity was not greater in infested areas compared to uninfested areas in either habitat (mixed evergreen, $U = 163$, $P = 0.11$; redwood-tanoak, $U = 31.5$, $P = 0.72$). Open bars indicate SOD absent; solid bars indicate SOD present.

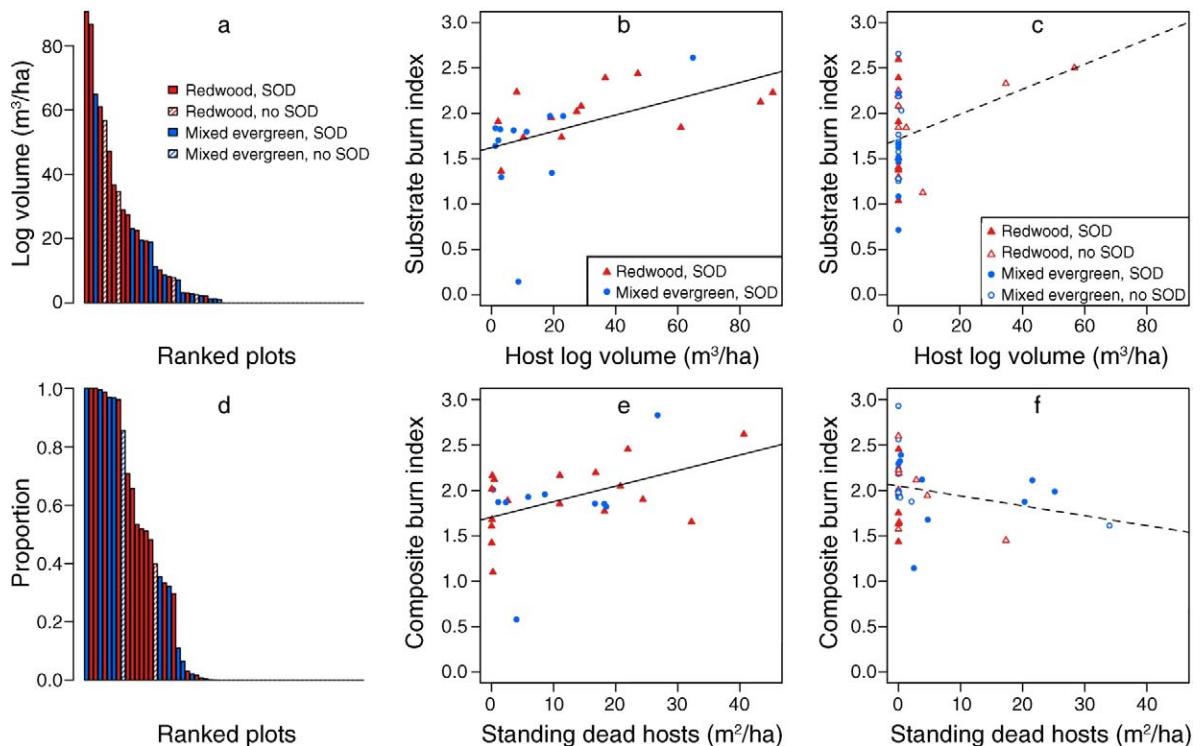


FIG. 3. Fuel availability (basal area or volume) and indices of burn severity for 61 monitoring plots in two forest types, with and without infection by *P. ramorum* (21 infested, nine uninfested mixed evergreen plots; 21 infested, 10 uninfested redwood-tanoak plots). (a) Volume of downed host logs per hectare in ranked order with the majority of logs found in infested plots, but 17 infested plots did not have downed host logs. (b) In infested plots where host logs had begun to accumulate, damage to the substrate (soil, duff, leaf litter layers) increased with increased host log volume across forest types, ($R^2 = 0.24$, $P = 0.012$). (c) In uninfested plots or infested plots that did not yet have accumulated surface fuels, the relationship between host mortality and substrate burn index was not significant and determined largely by two outlier uninfested redwood-tanoak plots with large logs. (d) The proportion of standing dead biomass in 2006 and 2007 that had recently died (i.e., retained dead leaves and fine twigs) in ranked order, with the majority of recent death occurring in infested plots, although 15 infested plots did not have recent mortality. (e) CBI increased with the basal area of standing dead host trees per hectare for infested plots with recent host mortality ($R^2 = 0.21$, $P = 0.016$), but (f) there was no such relationship in uninfested plots and infested plots with older mortality ($R^2 = 0.07$, $P = 0.14$).



PLATE 1. Landscape heterogeneity, sudden oak death mortality, and the 2008 Basin Complex Fire in Big Sur, California, USA. The photo shows a typical habitat mosaic in Big Sur, with grasslands in the foreground, coast live oak woodlands at the edge of the grassland, and redwood–tanoak forest intermixed with chaparral in the background. Tanoaks killed by sudden oak death appear light gray and are scattered across the landscape. Several plumes of smoke from the Basin Fire are visible beyond the ridge. Photo credit: K. M. Frangioso.

the relationship explained only 24% of the variation in substrate burn severity (Fig. 3b).

DISCUSSION

The Big Sur wildfire provided a unique opportunity to examine the potential for interacting effects of an exotic pathogen with wildfire, a natural disturbance in the ecosystem. Increased fuel loads from SOD mortality did not lead to increased burn severity in infested areas compared to areas without the disease, although the assumption that SOD worsened the Basin fire was widespread (Lee et al. 2010). Instead, the relationship between the two disturbances was complex and reflected the changing nature of the disease impacts over time. The great variability in SOD impacts across the region corresponds to great variability in prefire fuel structure and burn severity.

Our results indicate that the timing of fire relative to disease progression is an important predictor of burn severity in infested areas because differences among fuel types were more important indicators of damage than pathogen presence alone. Both infested and uninfested areas had high severity fires. However, SOD may initially increase burn severity because of the retention of dry, fine crown foliage and twigs in the year following tree mortality. In areas with this recent host mortality,

burn severity increased linearly with increasing standing dead host biomass, whereas no such relationship existed in plots where the pathogen had been established for longer periods of time. Over time, as the dead snags fragment and fall, surface fuels accumulate and increase potential fire severity to the understory and soil (Brown et al. 2003, Peterson et al. 2009). We found increased soil burn severity in infested plots with greater volumes of large downed host logs. In higher severity plots, the fire consumed more of the litter and duff and damaged soil to greater depths. The heat transfer to the soil causing this damage may also kill remnant tree fine or coarse roots (Swezy and Agee 1991, Varner et al. 2009), and the soil impacts will likely affect water flow and soil erosion (Wohlgenuth et al. 2006). Nevertheless, SOD mortality constitutes only part of the available fuels in these forests (Appendix C: Table C1), and we did not detect an important role for host fuel abundance in determining burn severity when analyzing across infested and uninfested plots.

The Basin fire occurred early in the 2008 fire season, following two very dry years in California and the driest spring in California history (2008; California Department of Water Resources 2010). Previous to that, wet weather in 2003–2005 spawned an increase in spore production and infection by *P. ramorum* resulting in a

spike in host mortality in subsequent years (Davidson et al. 2008). Interestingly, one of the larger, recent wildfires in Big Sur, the 1977 Marble-Cone fire, occurred three years after a major ice storm caused widespread tree mortality in the region. Two years of severe drought following the 1974 ice storm and the driest rain season on record for California (1976–1977) (California Department of Water Resources 2010) allowed the fuel to accumulate and dry before the fire occurred (Griffin 1978).

Our prefire data allowed us to test hypotheses about fuel abundance and fire severity. These field-based findings are similar to fire modeling predictions based on bark beetle outbreaks that have resulted in high levels of tree mortality (Jenkins et al. 2008). Bark beetle activity is widely assumed to increase fire severity, but empirical data have not usually supported this assumption, and the role of tree mortality in burn severity can change greatly with time since the beetle outbreak (see, for example, reviews in Lynch et al. 2006, Parker et al. 2006). Windstorms and ice storms can also create large inputs of fuels that are heterogeneous across the landscape, but the input mainly occurs over a short time period while pathogen- or insect-caused mortality plays out over longer time scales (Foster et al. 1998). The impact to forest composition and fuel beds from these disturbances that input large amounts of dead woody material is in contrast to the effects of wildfires, where fuels are initially consumed and later augmented through subsequent tree death (Peterson et al. 2009).

Because the relationship between SOD and fire changes with the stage of the disease, the implications for management will also change as *P. ramorum* continues to invade new areas. There is a need for further research on the fine fuels contributed by SOD mortality to aid our understanding of fire behavior in SOD-impacted forests. Management efforts to mitigate fire severity should note that areas with large amounts of recent, standing SOD mortality could be the focus of efforts to reduce risk. Inputs to fire behavior models may also need to account for changes in fuel loadings that occur with the progression of the disease.

While there are valid concerns about SOD mortality and wildfire impacts based on these results, these concerns must be balanced against the fact that there remains much unexplained variation in fire severity among our research plots. The relationships we observed between SOD mortality and fire severity in infested plots do not account for the similar range of burn severities observed in uninfested areas. Fire behavior and spread depend on fuel availability, habitat characteristics and the weather conditions occurring at the time of fire (Rothermel 1983). Big Sur contains a complex mosaic of plant communities (e.g., grassland, chaparral, mixed-evergreen forest, redwood forest) and steep topography with pronounced temperature and moisture gradients from north to south or from the

coast towards inland areas. Dispersal of the pathogen is patchy, resulting in areas that have been invaded by *P. ramorum* for differing amounts of time, and SOD mortality across the landscape varies by region and forest type (Maloney et al. 2005, Meentemeyer et al. 2008). The processes that determined fire severity during the Basin fire likely occurred at multiple scales and were dependent on many landscape factors, only one of which was the SOD mortality measured at the scale of our plots.

The geographic range of *P. ramorum* continues to expand throughout coastal California forests. Wildfires remain a major part of the forest dynamics in these landscapes. Our data suggest that SOD had a significant but perhaps minor effect on fire severity, with the greatest concern in areas of recent SOD establishment. Continued study of the Big Sur system will help guide management and policy decisions regarding fire hazards of SOD in other areas of California. Long-term research will also be important for understanding how combined impacts of disease-fire interactions affect tree survival and future changes to forest structure and diversity.

ACKNOWLEDGMENTS

We thank A. Wickland, E. Paddock, K. Pietrzak, J. Vieregge, L. Waks, K. Aram, M. Beh, A. Brauer, M. Chan, R. Cobb, H. Mehl, A. Oguchi, P. Amante, S. Haas, S. Lamsal, Q. Meng, D. Shoemaker, and M. Vaclavikova for providing field and laboratory support for this research. We are grateful to H. Safford, J. Varner, and H. Kuljian for advice and discussions about this work. The manuscript benefited greatly from the comments of M. Turner and an anonymous reviewer. We thank the California State Parks, the Los Padres National Forest, the University of California Natural Reserve System, and numerous private landowners in the Big Sur area for allowing research access following the fire. This research was funded by the NSF-NIH Ecology of Infectious Diseases program EF-0622770, the USDA Forest Service Pacific Southwest Research Station, USDA Forest Service Forest Health Protection, State and Private Forestry, and the Gordon and Betty Moore Foundation.

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APPENDIX A

Fuels vary as *Phytophthora ramorum* becomes established and the disease progresses in a stand (*Ecological Archives* A021-016-A1).

APPENDIX B

Additional description of the Big Sur ecoregion, the sudden oak death monitoring network, and the post-fire survey of burn severity (*Ecological Archives* A021-016-A2).

APPENDIX C

Prefire fuel abundance in SOD-infested and uninfested plots (*Ecological Archives* A021-016-A3).

APPENDIX D

Additional metrics describing burn severity following the Basin Complex fire (*Ecological Archives* A021-016-A4).

APPENDIX E

The abundance of host species mortality does not predict burn severity (*Ecological Archives* A021-016-A5).