

The key host for an invasive forest pathogen also facilitates the pathogen's survival of wildfire in California forests

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Summary

- The first wildfires in sudden oak death-impacted forests occurred in 2008 in the Big Sur region of California, creating the rare opportunity to study the interaction between an invasive forest pathogen and a historically recurring disturbance.
- To determine whether and how the sudden oak death pathogen, *Phytophthora ramorum*, survived the wildfires, we completed intensive vegetation-based surveys in forest plots that were known to be infested before the wildfires. We then used 24 plot-based variables as predictors of *P. ramorum* recovery following the wildfires.
- The likelihood of recovering *P. ramorum* from burned plots was lower than in unburned plots both 1 and 2 yr following the fires. Post-fire recovery of *P. ramorum* in burned plots was positively correlated with the number of pre-fire symptomatic California bay laurel (*Umbellularia californica*), the key sporulating host for this pathogen, and negatively correlated with post-fire bay laurel mortality levels.
- Patchy burn patterns that left green, *P. ramorum*-infected bay laurel amidst the charred landscape may have allowed these trees to serve as inoculum reservoirs that could lead to the infection of newly sprouting vegetation, further highlighting the importance of bay laurel in the sudden oak death disease cycle.

Introduction

Disturbance is a key component of many forest ecosystems (Pickett & White, 1985). However, in addition to natural disturbances (e.g. wildfire), many forests are now being transformed by accelerated climate change, biological invasions and habitat change (Turner, 2010). As these novel disturbances proliferate, more long-term effects and qualitative changes to forest ecosystems are expected (Lovett *et al.*, 2006; Turner, 2010). Novel disturbances may interact with historically recurring disturbances in unknown ways with the potential to alter landscape structure and function (Buma & Wessman, 2011). In spite of these consequences, changing and interacting disturbance regimes have received little attention relative to other drivers of ecosystem change (Turner, 2010).

Interactions between invasive forest pests and wildfire are currently of great relevance in the USA. From 1990 to 2006, there was a nearly three-fold increase in the detection rate of established 'high impact' forest pathogens and insects (those species of regulatory significance or that have caused notable damage to forest trees) compared with the previous 130 yr (Aukema *et al.*, 2010). In addition, the frequency of large wildfires in the western USA has increased significantly since the mid-1980s, together with warming temperatures and lengthened fire seasons (Westerling *et al.*, 2006). Although there is a growing body of literature on interactions between forest insects and wildfire (e.g. McCullough *et al.*, 1998; Parker *et al.*, 2006; Jenkins *et al.*, 2008), there have been few studies on the interactions between forest pathogens and

fire. Those that do exist have focused primarily on native pathogens and the use of prescribed burning in managed forest systems. Examples include the burning of longleaf pine (*Pinus palustris*) seedlings in the southern USA to reduce brown spot needle blight (causal agent *Mycosphaerella dearnessii*), and the stimulation of conifer root rot infections by *Rhizina undulata* following fires or brush burning (Ahlgren, 1974; Hardison, 1976; Parmeter, 1977). However, research on the interactions between non-native pathogens and wildfires is extremely limited. Given that exotic pathogens have not co-evolved with their new hosts or the local disturbance regimes, these types of interactions may be some of the most unpredictable.

Coastal forests of California are part of a Mediterranean ecosystem that includes wildfire as a natural component of its disturbance regime. These forests are now coping with a new disturbance: *Phytophthora ramorum*, the introduced pathogen that causes sudden oak death (SOD), has killed millions of tanoaks (*Notholithocarpus densiflorus*) and oaks (*Quercus* spp.) (Rizzo *et al.*, 2002, 2005; Meentemeyer *et al.*, 2011). Symptoms of SOD were first noted in the San Francisco Bay area in the mid-1990s, but *P. ramorum* has since spread over a 700-km range from central California to southwestern Oregon (Rizzo *et al.*, 2002, 2005). Within *P. ramorum*-infested areas of coastal California, the historical role of wildfire is not well characterized and appears to be highly variable across different regions and forest types (Davis & Borchert, 2006; Van de Water & Safford, 2011). In the current era of fire suppression and management, however, fire frequencies and

sizes are actually increasing in some areas near the limits of *P. ramorum*'s current range in California (Moritz & Odion, 2005; Davis & Borchert, 2006; Stuart & Stephens, 2006). As the native range of *P. ramorum* remains uncertain (Goss *et al.*, 2009), it is unknown whether this pathogen may have evolved with wildfire.

Wildfire and *P. ramorum* may interact directly or indirectly. Wildfire could directly eliminate the pathogen from burned areas. In contrast, each disturbance may change the forest structure in ways that influence indirectly the frequency, prevalence or severity of the other disturbance. Selective host mortality by *P. ramorum* may affect the accumulation of woody fuels and fire severity (Metz *et al.*, 2011; Valachovic *et al.*, 2011), whereas differential susceptibility to fire among important host species (Fites-Kaufman *et al.*, 2006) has feedbacks for disease prevalence.

The summer of 2008 brought the first wildfires to occur in known *P. ramorum*-infested forests in California, with the largest fire burning in the Big Sur region (Monterey County) (Metz *et al.*, 2011). More than 100 000 ha were burned in Big Sur, including large portions of our long-term forest plot network established to study feedbacks between *P. ramorum*, its various hosts and the physical environment (Haas *et al.*, 2011; Metz *et al.*, 2011, 2012). Big Sur is one of the most ecologically diverse areas in California, and its forests are among the earliest infested and most impacted by SOD (Mascheretti *et al.*, 2008; Meentemeyer *et al.*, 2008). Tanoak mortality in some forest stands exceeds 60% and, across the Big Sur ecoregion, *P. ramorum* has killed hundreds of thousands of host trees (Maloney *et al.*, 2005; Meentemeyer *et al.*, 2008).

In this study, we capitalize on the natural experiment presented by the 2008 fires to examine the direct and indirect impacts of wildfire on the persistence of *P. ramorum* in Big Sur. Specifically, we address three questions: first, did the 2008 wildfires eradicate *P. ramorum* from areas known to have been infested before the fires? Second, if the wildfires did not eradicate the pathogen, under what conditions was *P. ramorum* able to persist in forest stands despite fire? And third, what are the likely reservoirs for pathogen persistence and re-invasion? We hypothesized that the detection of *P. ramorum* in the burned landscape would be negatively affected by high burn severities, and influenced by forest type and prevalence of host species. The results of this study provide much needed information on the poorly understood, but increasingly important, topic of interacting disturbances.

Materials and Methods

Study system

Phytophthora ramorum Werres, De Cock, & Man in't Veld is a generalist, oomycete pathogen capable of infecting over 45 genera of plants, including coniferous trees, shrubs, herbaceous plants and ferns (Rizzo *et al.*, 2005). Although *P. ramorum* infection on most hosts is manifested in non-lethal foliar or twig infections, the pathogen can kill susceptible oaks and tanoak through the formation of trunk cankers that lead to cambium death and xylem plugging (Rizzo *et al.*, 2005; Parke *et al.*, 2007). The death of *P. ramorum*-infected trees may be hastened by opportunistic wood-

boring beetles and wood-rotting fungi (Rizzo *et al.*, 2002; McPherson *et al.*, 2010).

In California, *P. ramorum* is associated with coastal mixed-evergreen and redwood forest types (Rizzo *et al.*, 2005). In both forest types, California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) and tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon, & Oh, syn. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) are the most epidemiologically important hosts (Davidson *et al.*, 2005, 2008). Leaves of bay laurel support non-lethal infections and abundant pathogen sporulation. Tanoak twigs also support *P. ramorum* sporulation, although not at the level of bay laurel. By contrast, the infection of tanoak and *Quercus* spp. stems may be lethal, but the pathogen does not sporulate from these infections (Davidson *et al.*, 2005, 2008). Although wind- and rain-driven *P. ramorum* spore dispersal from bay laurel leaves is the predominant mechanism for disease spread in both forest types, bay laurel leaves in redwood forests display greater pathogen survival rates and thus greater inoculum and infection levels (Davidson *et al.*, 2011).

The Big Sur ecoregion is situated on the western flank of the Santa Lucia Mountains and is defined by a rugged landscape crisscrossed by numerous steep slopes and drainages (Fig. 1). Elevation ranges from sea level to 1571 m within 5 km of the coast, facilitating a wide diversity of climatic zones and plant communities (Davis & Borchert, 2006; Meentemeyer *et al.*, 2008; Davis *et al.*, 2010). Redwood forests are generally located in ravines and river valleys at low elevations, whereas mixed-evergreen forests are predominantly located on moist slopes in lower montane zones and higher elevations; both forest types are dominated by fire-tolerant species (Maloney *et al.*, 2005; Meentemeyer *et al.*, 2008; Davis *et al.*, 2010; Metz *et al.*, 2011). Although the region's fire regime is not well characterized, it is thought that the fire return interval ranges from 5 to 75 yr, with an average return of 24 yr, and that the mixed-evergreen forests in the region experience a mixed-severity fire regime (Davis & Borchert, 2006; Davis *et al.*, 2010). During the 2008 fire season, there were two wildfires in Big Sur: the Basin Complex Fire, which burned > 95 000 ha in June and July, and the Chalk Fire, which burned an additional 6400 ha in September (USDA Forest Service, 2008).

In 2006–2007, we established a network of 280 plots throughout the Big Sur ecoregion; 121 of these plots were located within the perimeter of the Basin Complex and Chalk Fires. The plots are 500 m² and distributed in a stratified-random design across redwood and mixed-evergreen forest types, as well as in areas with and without *P. ramorum* (Haas *et al.*, 2011; Metz *et al.*, 2012). Within each plot, we originally measured all stems ≥ 1 cm diameter at breast height (dbh), confirmed the presence of the pathogen or other pests, estimated cover class by species and measured the cylindrical volume of logs ≥ 20 cm (Metz *et al.*, 2011). Burn severity was quantified in 61 plots immediately following containment of the Basin Complex Fire (Metz *et al.*, 2011) using the Composite Burn Index (Key & Benson, 2006). In the summer of 2009, all stems ≥ 1 cm dbh were again surveyed for survival and health, and the live and dead basal areas of each host were calculated using size measurements from plot establishment (Metz *et al.*, 2012).

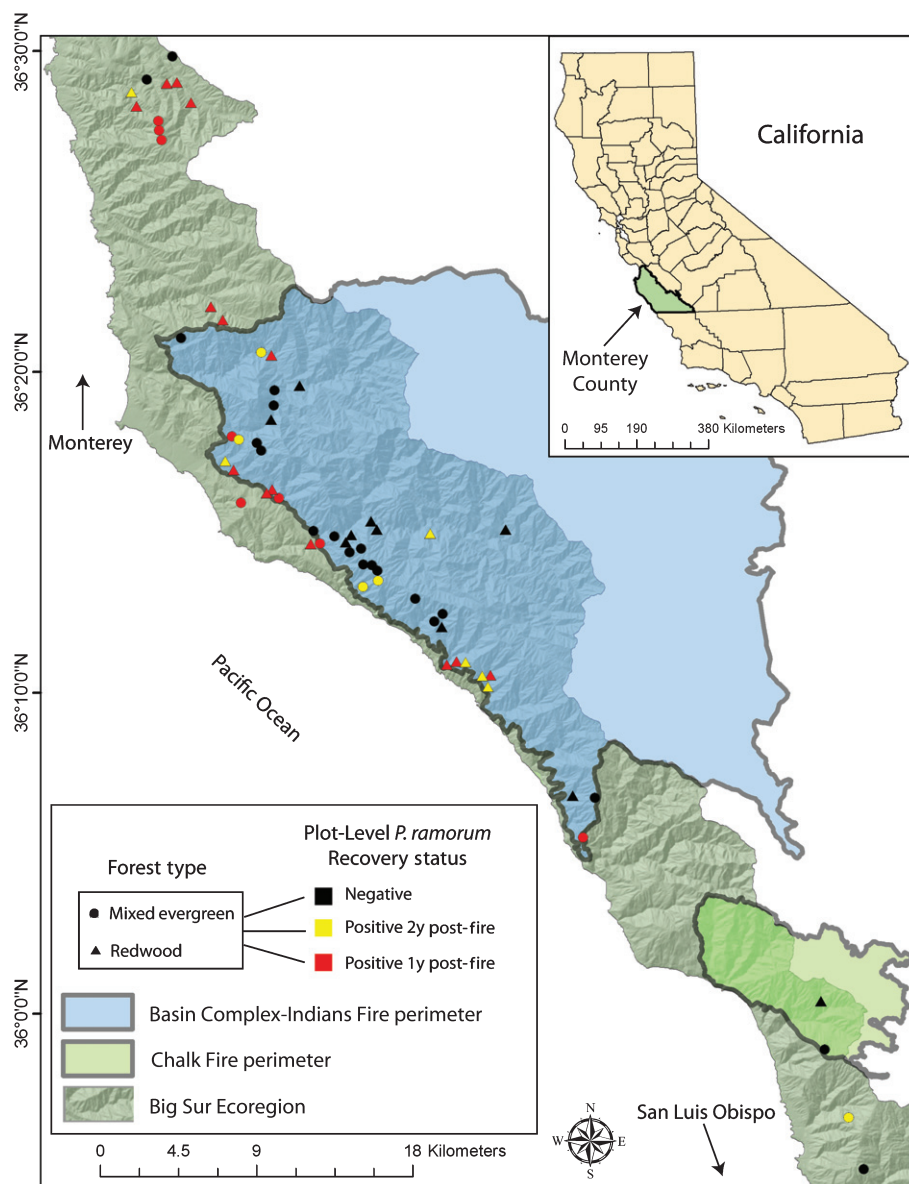


Fig. 1 Location of study area ('Big Sur Ecoregion'), plots, and Basin Complex and Chalk Fire perimeters in the Big Sur region, Monterey County, CA, USA. All plots were known to be infested with *Phytophthora ramorum* before the fires. The results of the 2009 and 2010 *P. ramorum* survey (referred to as 'Plot-Level *P. ramorum* Recovery Status') are indicated for each plot by the symbol color (circles and triangles are plots in mixed-evergreen and redwood forest types, respectively).

To understand the interactions between wildfire and *P. ramorum*, we chose to focus on 63 plots that were known to contain *P. ramorum*-infested trees at the time of plot establishment. Of these plots, 45 were located within the areas burned in the 2008 wildfires (24 mixed-evergreen and 21 redwood) and 18 were outside of the fire perimeters (nine in each forest type) (Fig. 1). We used the stand composition and disease impact data from 2006 to 2007 to characterize the pre-fire conditions of the plots, and the post-fire burn severity measurements (conducted in 37 of our burned plots) and basal area calculations to determine the impacts of the wildfires on the plots (Metz *et al.*, 2011). We used these data to examine whether *P. ramorum* persistence in host vegetation was related to pre-fire host density and disease prevalence, burn severity

and post-fire host mortality, and/or topographic features in the plot (Supporting Information Table S1).

Post-fire *P. ramorum* survey

The 63 focal plots that were known to have been infested with *P. ramorum* before the 2008 wildfires were surveyed for the pathogen in 2009 and 2010, 1 and 2 yr post-fire, respectively. In 2009, we sampled vegetation exhibiting *P. ramorum* symptoms in all 63 plots and, in a subset of plots, leaves (including asymptomatic leaves) from bay laurel that were known to be positive for *P. ramorum* before the fires. Based on our findings that *P. ramorum* was not recovered from any asymptomatic pre-fire-infested bay

laurel, we classified plots lacking symptoms in 2009 as '*P. ramorum* negative' and plots with *P. ramorum* recovery from at least one tree in 2009 as '*P. ramorum* positive'. In 2010, to understand how pathogen persistence may have changed with increasing time since wildfire, the survey focused on the 36 burned and five unburned plots that were *P. ramorum* negative in 2009. In these plots, we sampled symptomatic trees as well as pre-fire *P. ramorum*-positive or symptomatic trees. As a control, we also re-surveyed 11 plots (six burned and five unburned) that were *P. ramorum* positive in 2009 by sampling from specific trees from which the pathogen was isolated in 2009. Based on our findings that all of the re-surveyed control plots remained *P. ramorum* positive in 2010, we classified plots that were *P. ramorum* positive in 2009, but not re-surveyed in 2010, as also *P. ramorum* positive in 2010.

Nearly all vegetation sampled for *P. ramorum* was from bay laurel and tanoak, the two most prevalent and epidemiologically important hosts in our plots. Occasional samples were also taken from known host species California coffeeberry (*Rhamnus californica*), canyon live oak (*Quercus chrysolepis*), coast live oak (*Quercus agrifolia*), evergreen huckleberry (*Vaccinium ovatum*), redwood (*Sequoia sempervirens*), Shreve oak (*Quercus parvula* var. *shrevei*) and toyon (*Heteromeles arbutifolia*). Because all of these evergreen species sprout prolifically following injury or fire, many samples collected from burned plots originated from post-fire regenerative growth, including leaves and twigs from basal and epicormic sprouts. In the event that we sampled from a tree containing both post-fire growth and pre-fire crown growth, we were careful to keep samples from these different sources separated. All plant materials collected during the surveys were processed using standardized isolation techniques for the culture of *P. ramorum* (Davidson *et al.*, 2003); small sections of leaf, twig or cambial tissues from the margins of symptomatic lesions and cankers were excised with scalpels or hole-punchers and embedded in PARP (cornmeal agar with pimarin, ampicillin, rifampicin and pentachloronitrobenzene), a *Phytophthora*-selective medium (Erwin & Ribeiro, 1996). *Phytophthora ramorum* was identified on the basis of its characteristic morphology of large chlamydospores (Werres *et al.*, 2001). *Phytophthora pseudosyringae* and *P. nemorosa*, two other species that share similar ranges and hosts with *P. ramorum* (Wickland *et al.*, 2008), were noted from isolations in the 2010 survey.

Statistical analyses

We examined the conditions under which *P. ramorum* persisted in host vegetation following the 2008 wildfires in three analyses. First, we compared the frequencies of pathogen detection in burned and unburned plots using a Pearson chi-squared test with a Yates' continuity correction. Second, we ran a set of multiple logistic regression models using the results from all 63 plots with pathogen recovery (yes or no) in each year as the dependent variable and burn status, forest type, pre-fire host abundance (total (live + dead) basal area of bay laurel and tanoak), pre-fire disease prevalence (the number of symptomatic bay laurel and tanoak) and post-fire host mortality (the proportion of bay laurel and tanoak basal area that died between 2006 and 2009) as independent variables. The

strength of each model's predictive power was assessed using the area under the receiver operating characteristic curve (AUC value), which estimates the probability that the predictions and the outcomes are concordant (Kutner, 2005). Third, we used all 24 continuous plot variables listed in Table S1 in a two-dimensional non-metric multidimensional scaling (NMDS) ordination with Bray–Curtis dissimilarities to compare the characteristics of *P. ramorum*-positive and *P. ramorum*-negative plots. We used a multi-response permutation procedure (MRPP) to determine whether *P. ramorum*-positive and *P. ramorum*-negative plots differed significantly from one another in their plot characteristics (groups were plots that were positive in both 2009/2010, plots that were negative in 2009 and positive in 2010, and plots that were always negative). The eight burned plots lacking post-fire burn severity measurements from 2008 were omitted from the ordination.

All analyses were performed with the statistical programming language R (R Development Core Team, 2009). The ordinations were performed using the *metaMDS* routine in the R package *vegan* (Oksanen *et al.*, 2010).

Results

Conditions favoring *P. ramorum* persistence

In 2009, 1 yr post-fire, *P. ramorum* was recovered from nine burned and 13 unburned plots, and, in 2010, 2 yr post-fire, *P. ramorum* was recovered from an additional nine burned and two unburned plots. The pathogen was *not* recovered following the 2008 fires in the remaining 27 burned and three unburned plots (Fig. 1). The total number of *P. ramorum*-positive plots in the burned areas was disproportionately low both 1 and 2 yr post-fire (2009: $\chi^2 = 13.21$, $df = 1$, $P < 0.001$; 2010: $\chi^2 = 8.01$, $df = 1$, $P < 0.01$). One year following the fire, a plot's burn status and the number of pre-fire symptomatic bay laurels were important determinants of pathogen persistence (Table 1): *P. ramorum* was *c.* 29 times more likely to be recovered in unburned plots than burned plots, as well as increasingly likely to be recovered in plots with greater numbers of symptomatic bay laurel before 2008 (Table 1, Fig. 2a). Two years following the fire, forest type and post-fire bay laurel mortality were significant predictors of *P. ramorum* presence within a plot (Table 1): the pathogen was *c.* 12 times more likely to be recovered in redwood-type plots than mixed-evergreen plots, and the chances of recovering *P. ramorum* decreased with increasing basal area of post-fire dead bay laurel (Table 1, Fig. 2b).

In the NMDS ordination (stress: 9.22), there was a significant difference in means among groups despite great heterogeneity in plot characteristics within each *P. ramorum* status group (MRPP: $A = 0.0443$, $P = 0.008$; Fig. 3). The group mean of plots from which *P. ramorum* was recovered in 2009 and onwards was located in the direction of decreasing burn severity (Fig. 3). For plots that were negative in 2009 and positive in 2010, the group mean shifted in the direction of increased burn severity and post-fire bay laurel mortality compared with the 2009 *P. ramorum*-positive plots and oriented towards greater numbers of pre-fire symptomatic bay

Table 1 The estimated odds ratios and *P* values for the predictor variables in the multiple logistic regression models used to determine the influence of plot variables on *Phytophthora ramorum* presence within 63^a forest plots in the Big Sur region, Monterey County, CA, USA, 1 and 2 yr following wildfires (2009 and 2010, respectively)

Predictor variable ^b	2009		2010	
	Odds ratio	<i>P</i> value	Odds ratio	<i>P</i> value
Burn status: unburned vs burned	29.117	0.009**	5.740	0.129
Forest type: RW ^c vs ME ^d	6.418	0.134	11.682	0.038*
Pre-fire plot variables				
Total basal area, bay	2.006	0.627	6.670	0.094 [†]
Total basal area, tanoak	3.156	0.128	1.164	0.817
No. of symptomatic bays	1.237	0.008**	1.079	0.200
No. of symptomatic tanoaks	1.056	0.267	1.016	0.708
Post-fire plot variables				
Prop. dead basal area ^e , bay	0.053	0.133	0.019	0.006**
Prop. dead basal area ^e , tanoak	0.276	0.436	0.972	0.981
AUC value	0.943		0.920	

P values: [†], *P* < 0.1; *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.

^aAll plots were known to be infested with *P. ramorum* before the fires.

^bBasal area (m²) and number of symptomatic hosts are given per plot (1/20 ha).

^cRW, redwood.

^dME, mixed-evergreen.

^eProportion of basal area that died between 2006 and 2009.

laurel and higher pre-fire total bay laurel basal area. Lastly, the group mean of plots from which *P. ramorum* was not recovered either 1 or 2 yr post-fire was located in the direction of low pre-fire bay laurel basal area and symptoms, as well as increased burn severity and post-fire bay laurel mortality compared with the 2009 *P. ramorum*-positive plots.

Potential reservoirs of the pathogen

As the vast majority of samples were collected from bay laurel and tanoak, these were the host species from which we recovered *P. ramorum* most frequently, although we also occasionally recovered the pathogen from *Quercus* spp. In burned plots,

P. ramorum was recovered from bay laurel crown leaves at twice or greater the frequency as from basal sprout leaves in both 2009 and 2010 (Table 2). In unburned plots, however, *P. ramorum* isolation frequency was greatest from basal sprout leaves in both years, despite the low sample numbers of this tissue type. Interestingly, over 96% of the total *P. pseudosyringae* and *P. nemorosa* isolates recovered during our 2010 survey (*n* = 55) came from bay laurel basal sprout leaves collected in burned, mixed-evergreen plots. From tanoak, neither post-fire growth nor pre-fire crown growth yielded consistently greater recovery of *P. ramorum* (Table 2). Overall, there tended to be greater recovery of *P. ramorum* from tanoak than bay laurel, and from both of these hosts located in redwood-type plots relative to mixed-evergreen-type plots.

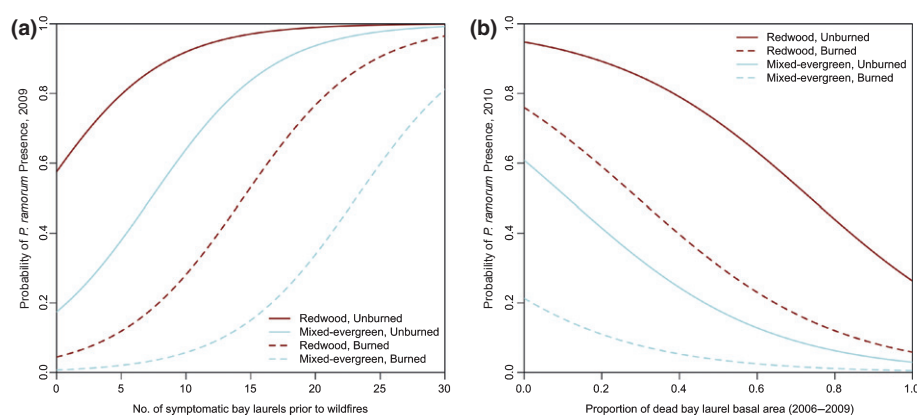


Fig. 2 Fitted probabilities for the post-fire presence of *Phytophthora ramorum* in 63 plots in the Big Sur region, Monterey County, CA, USA, known to be infested with *P. ramorum* before the fires: (a) pathogen recovery in 2009 in response to the number of symptomatic bay laurel trees before the wildfires; (b) pathogen recovery in 2010 in response to varying proportions of post-fire bay laurel mortality levels. The predicted fits are from the models presented in Table 1. Variables on the x axis were varied across the 2.5–97.5 percentile range of values observed in our plot network, whereas other model predictors were each held at their respective median value. Red and blue lines indicate redwood and mixed-evergreen forest types, respectively, with unburned and burned plots indicated with solid and dashed lines, respectively.

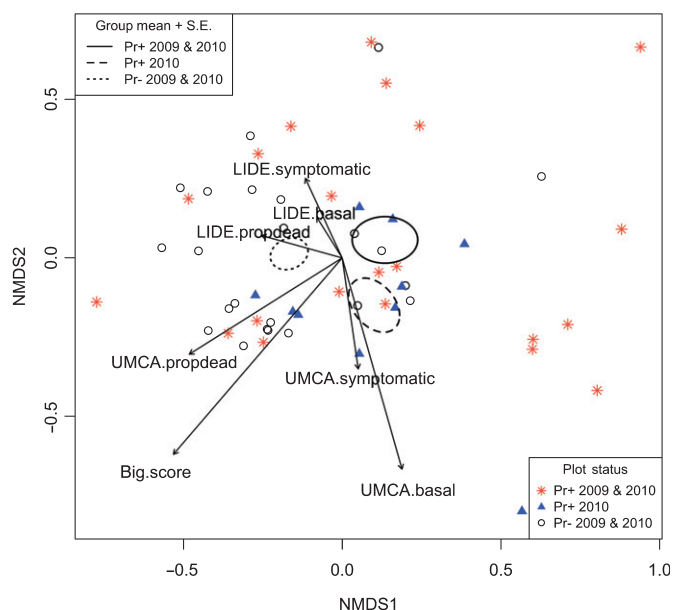


Fig. 3 Non-metric multidimensional scaling (NMDS) of plots known to be infested with *Phytophthora ramorum* before the fires using 24 continuous plot variables (see Table S1 for the complete list). The plot symbols indicate the *P. ramorum* status of each plot in the Big Sur region, Monterey County, CA, USA, both 1 and 2 yr following the fires (2009 and 2010, respectively), and the ellipses show the mean ordination location plus SE for each of the three *P. ramorum* status groups. The seven vectors overlaid on the ordination represent the six continuous predictor variables used in the logistic regression models (UMCA.basal, total pre-fire bay laurel basal area (m^2 per plot); UMCA.symptomatic, number of pre-fire symptomatic bay laurels per plot; UMCA.propdead, proportion of dead bay laurel basal area 2006–2009; LIDE.basal, total pre-fire tanoak basal area (m^2 per plot); LIDE.symptomatic, number of pre-fire symptomatic tanoaks per plot; LIDE.propdead, proportion of dead tanoak basal area 2006–2009) and an additional continuous variable to illustrate burn severity (Big.score, burn severity to dominant trees). Unburned plots were given a 'Big.score' of zero, whereas burned plots in which burn severity measurements were not made in 2008 ($n = 8$) were omitted from the ordination. The length of each vector arrow represents the strength of correlation with the ordination configuration.

In 2009, the mean *P. ramorum* isolation frequency from trees in burned plots was significantly less than that of trees in unburned plots (12% vs 39%; $t = -2.83$, $df = 26$, $P = 0.009$), but, when the isolation frequencies were compared between only those plots from which *P. ramorum* was actually recovered in 2009, there was no significant difference in isolation frequencies from trees in burned plots (62%) relative to trees in unburned plots (54%). In 2010,

there were no significant differences between the mean *P. ramorum* isolation frequencies in burned vs unburned plots. When *P. ramorum* isolation frequencies within the same plot were compared from 2009 to 2010, there were greater proportions of *P. ramorum*-positive trees in 2010 in all but one plot from which *P. ramorum* was recovered following the fires.

Discussion

The 2008 Big Sur wildfires suppressed, but did not eradicate, *P. ramorum* from vegetation in areas that were previously infested. We were able to recover *P. ramorum* 1 and 2 yr post-fire in burned plots of both forest types, and, in some cases, with no difference in frequency than in unburned plots. However, *P. ramorum* recovery 1 yr after the wildfires tended to take place in plots with the lowest burn severities, whereas pathogen recovery 2 yr post-fire occurred in plots with greater burn severities and was largely influenced by high levels of pre-fire disease prevalence and low levels of post-fire bay laurel mortality (Table 1, Figs 2, 3). In plots in which *P. ramorum* was not recovered even 2 yr post-fire, burn severities and levels of post-fire bay laurel mortality tended to be high (Table 1, Fig. 3). In summary, multiple interacting biotic and abiotic factors were responsible for the persistence of *P. ramorum* in previously infested burned plots. Just as the establishment, spread and survival of *P. ramorum* in the absence of fire is dependent on the biological and physical environment, host susceptibility and attributes of the pathogen (Rizzo *et al.*, 2005), these same types of characteristics influenced pathogen survival and re-establishment in burned forests.

Impacts of fire on *P. ramorum* and its hosts

As a result of direct lethality of fire or of fire's consumption of *P. ramorum*'s required hosts, the pathogen was detected in only one-fifth of the burned plots in the first year following wildfire. Although flame temperatures from wildfires can reach 1400°C , and temperatures in the combustion zone can reach $1000\text{--}1200^\circ\text{C}$ (DeBano *et al.*, 1998), *P. ramorum* is known to survive exposure to fairly high temperatures (Harnik *et al.*, 2004; Swain *et al.*, 2006; Tooley *et al.*, 2008), and thus it is conceivable that the pathogen could have persisted in host tissues that survived the fires. Furthermore, host tissues probably provide a level of heat protection for *P. ramorum* (Harnik *et al.*, 2004; Swain *et al.*, 2006). Smoke produced by wildfires has also been suggested as a

Table 2 Proportion of *Phytophthora ramorum*-positive samples (with the total number of samples included in parentheses) from specific host and host tissue types in the Big Sur region, Monterey County, CA, USA, 2009 and 2010

Plot type	Year	Bay laurel tissue type		Tanoak tissue type	
		Leaf, crown	Leaf, basal sprout	Twig, crown	Twig, basal sprout
Burned	2009	0.49 (65)	0.21 (113)	0.33 (18)	0.44 (52)
	2010	0.68 (22)	0.24 (202)	0.92 (12)	0.48 (145)
Unburned	2009	0.27 (75)	0.41 (22)	0.46 (76)	0.59 (64)
	2010	0.22 (36)	0.67 (3)	0.74 (46)	0.92 (26)

potential mechanism for the inhibition of fungal pathogens (Parmeter & Uhrenholdt, 1975) and *P. ramorum* (Moritz & Odion, 2005), but our recovery of the pathogen in heavily burned areas, which were surely exposed to large amounts of smoke, indicates that smoke probably has little residual effect on *P. ramorum* growth.

Fire-caused mortality of *P. ramorum* hosts, especially bay laurel, probably had the most significant impact on pathogen survival. In burned plots, foliage was dead and scorched, tree crowns were dead or dying as a result of cambial damage, and entire trees were consumed in the fires. It is unlikely that *P. ramorum* would be able to subsist in these incinerated trees, regardless of whether it survived the high temperatures of the fires. However, the pathogen was not recovered post-fire from some unburned plots that were previously known to be infested, and it was readily recovered from some plots that suffered severe fire effects. These exceptions indicate that fire, burn severity and post-fire mortality of hosts are not the only variables affecting *P. ramorum* survival in Big Sur.

Despite the reduced chance of recovering *P. ramorum* from burned plots, pathogen isolation frequency from bay laurel in unburned plots was no greater than that from burned plots in 2009, and both were lower than the detection frequencies from four California counties in 2002–2003 (42–69% per plot in pathogen-infested, unburned areas; Maloney *et al.*, 2005). The poor *P. ramorum* isolation frequency from unburned plots in 2009 was possibly a result of unfavorable conditions for growth, sporulation and infection (Garbelotto *et al.*, 2003). Rainfall levels in the central coast region were *c.* 50% of average over 2007–2009, and 2008 had the driest spring of the last 114 yr (California Department of Water Resources, 2010a). Increased pathogen isolation frequency and number of *P. ramorum*-positive plots in 2010 reflected both post-fire re-establishment of the pathogen and changing weather conditions. Water content in California's

mountain snowpack was 143% of normal at the end of April 2010 (California Department of Water Resources, 2010b), signaling an end to the 3-yr drought in the region. With the onset of conditions more conducive to *P. ramorum* growth and the increasing quantities of host tissue available for potential infection, pathogen recovery from redwood plots increased greatly in 2010.

Pathogen persistence and re-colonization

One potential survival mechanism for *P. ramorum* in areas with high burn severities could be partially a function of the wildfires themselves. Patchy burn patterns that result in 'green islands' are typical of mixed-severity fires with variable burn intensities (Fites-Kaufman *et al.*, 2006; Perry *et al.*, 2011). Even one dominantly situated *P. ramorum*-infected sporulating host could provide sufficient inoculum to re-infest post-fire re-growth in a plot (Fig. 4). Similar scenarios involving surviving dwarf mistletoe-infected pines in burned forests have resulted in dwarf mistletoe infections in newly regenerated stands (Parmeter, 1977).

In Big Sur, we observed that large numbers of pre-fire *P. ramorum*-infected bay laurel increased the likelihood of pathogen recovery post-fire, presumably because there was a greater chance that at least one of these trees would be spared the flames and serve as a refugium for the pathogen. Indeed, surveys in 2009 documented a number of surviving bay laurel 'green islands' in burned plots, which probably provided an important source of post-fire inoculum. Not only are attached bay laurel leaves thought to be the best niche for *P. ramorum* survival during adverse conditions, such as hot, dry California summers, but they also support the highest sporulation rates of forest trees in California and produce the bulk of *P. ramorum* inoculum in mixed-evergreen forests (Davidson *et al.*, 2005, 2008, 2011).

By the first summer post-fire, there was already a proliferation of new vegetative growth (mainly basal sprouts) in burned plots. Young host tissues have been shown to be more susceptible than mature host tissues to *P. ramorum* infection (Hansen *et al.*, 2005), yet we found relatively low *P. ramorum* isolation frequency from young bay laurel basal sprouts in burned plots. In contrast, the high incidence of *P. ramorum*-infected tanoak basal sprouts in burned plots in 2009 came as no surprise. The susceptibility of this type of host tissue to *P. ramorum* infection following controlled burns in Oregon was found to be so severe that the pathogen eradication protocol was amended to include the use of herbicides on tanoak sprouts following fire to help prevent the re-establishment of the pathogen in treated areas (Hansen & Sutton, 2006; Goheen *et al.*, 2009). These findings suggest that the copious tanoak basal sprouts that arise after fire are important to the re-establishment of *P. ramorum* in forest types in which this host is particularly abundant, such as redwood forests of coastal California and Douglas fir–tanoak forests of southwestern Oregon. *Phytophthora ramorum* has also been detected in soil adjacent to stumps of previously infected trees at controlled-burn eradication sites in Oregon (Goheen *et al.*, 2009), as have other forest *Phytophthora* species following prescribed fires or wildfires (see Marks *et al.*, 1975; Hardison, 1976; Betlejewski, 2009; Meadows *et al.*, 2011), but it is unclear whether *P. ramorum* soil inoculum plays an



Fig. 4 Photograph of a bay laurel tree in a 'green island' (indicated by the arrow) created by the patchy burn patterns of the 2008 wildfires in the Big Sur region. Prolific basal and epicormic sprouting can also be seen on the burned trees in this photograph.

important role in the re-establishment of this predominantly aerial, splash-dispersed pathogen.

One unexpected discovery from this study was how frequently two other non-native *Phytophthora* species, *P. pseudosyringae* and *P. nemorosa*, were isolated from bay laurel basal sprouts in burned mixed-evergreen plots. Both species are also found throughout the range of *P. ramorum* and beyond, yet neither had previously been detected in any of the plots included in this study. Given that *P. ramorum* recovery was low from bay laurel basal sprouts in burned plots, our findings suggest that *P. pseudosyringae* and *P. nemorosa* enjoyed a competitive advantage over *P. ramorum* in this particular niche. The ecology of *P. pseudosyringae* and *P. nemorosa* is deserving of more attention, especially as infrequently detected invasive species can emerge as serious pathogens under varying environmental conditions (Linzer *et al.*, 2009).

Implications for management of the pathogen

The persistence and re-establishment of *P. ramorum* in 2 yr following large-scale wildfires demonstrate that fire is not a panacea for the control of this forest pathogen. Just as controlled burns have been ineffective in the eradication of *P. ramorum* in infested forests of southwestern Oregon (Goheen *et al.*, 2009) and California (Lee, 2009), it is unlikely that fire will serve as a natural control of *P. ramorum*, except over very short time frames. Factors that aid *P. ramorum*'s persistence in burned areas are some of the same attributes that make it successful as an invasive pathogen in California's coastal forests: aerial dispersal of spores, the pathogen's ability to utilize multiple hosts in mixed-forest communities and the hosts' propensity for vegetative sprouting following disturbance. Exotic pests and pathogens, if they manage to become established in an area, usually remain as permanent components of that ecosystem (Lovett *et al.*, 2006), and this seems to be the case with *P. ramorum* in the Big Sur ecoregion.

The dynamic nature of landscapes, together with the rapid increase in biological invasions, climate shifts and human exploitation of resources, make it difficult to predict the response of an ecosystem to disturbance (Turner, 2010). In the midst of such change, the use of field-based studies is essential for a full understanding of the range of ecological impacts and feedbacks caused by disturbance. The results of this study, combined with those of Metz *et al.* (2011), reveal complexities of interacting biotic and abiotic disturbances in the heavily disease-impacted Big Sur landscape that a modeling study would be hard pressed to capture. Continued and ongoing surveys in Big Sur will provide additional information on *P. ramorum* re-establishment following fires, host mortality trends and the effects of competing *Phytophthora* species in the post-fire landscape.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1 Mean values and standard deviations for plot descriptor variables in all burned plots used in a study of the survival of *Phytophthora ramorum* following wildfires in the Big Sur region, Monterey County, CA, USA, 2009 and 2010

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