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Impact of sudden oak death on tree mortality in the Big Sur ecoregion of California

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Abstract The Big Sur ecoregion in coastal California is a botanically and ecologically diverse area that has recently experienced substantial mortality of oak (*Quercus* spp.) and tanoak (*Lithocarpus densiflorus*) trees due to the emerging forest disease sudden oak death, caused by the invasive pathogen *Phytophthora ramorum.* In response to the urgent need to examine environmental impacts and create management response strategies, we quantified the impact of *P. ramorum* invasion on tree mortality across the Big Sur ecoregion using high-resolution aircraft imagery and field data. Using the imagery, we mapped all detectable oak and tanoak trees possibly killed by *P. ramorum* infection within redwood-tanoak forests and mixed oak woodlands. To validate and improve our remote assessment, we quantified the number, size, and infection status of host trees in 77 field plots (0.25 ha). The field data showed that our remote assessment underestimated mortality due to the occurrence of dead trees in the forest understory. For each forest type, we developed regression models that adjusted our remote assessments of tree mortality in relation to field observations of mortality and local habitat variables. The models significantly improved remote assessment of oak mortality, but relationships were stronger for mixed oak woodlands ($r^2 = 0.77$) than redwood-tanoak forests ($r^2 = 0.66$). Using the field data, we also modeled the amount of dead tree basal area (m^2) in relation to the density of mapped dead trees in mixed oak woodlands ($r^2 = 0.73$) and redwood-tanoak forests ($r^2 = 0.54$). Application of the regression models in a GIS estimated 235,678 standing dead trees in 2005 and 12,650 m^2 of tree basal area removed from the ecoregion, with 63% of mortality occurring in redwood-tanoak forests and 37% in mixed oak woodlands. Integration of the remote assessment with population estimates of host abundance, obtained from an independent network of 175 field plots (0.05 ha each), indicated similar prevalence of mortality in redwood-tanoak forests (20.0%) and mixed oak woodlands (20.5%) at this time. This is the first study to quantify a realistic number of dead trees impacted by *P. ramorum* over a defined ecological region. Ecosystem impacts of such widespread mortality will likely be significant.

Keywords Big Sur · Emerging infectious disease · Forest disease · Invasive species · Landscape epidemiology · *Phytophthora ramorum* · Plant-pathogen · Tree mortality · Remote sensing

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Introduction

Infectious diseases can substantially impact the biodiversity, structure, and function of plant communities (Gilbert 2002; Burdon et al. 2006). In particular, diseases caused by exotic plant pathogens may cause extensive mortality due to the low natural resistance of native host populations to infection and lack of natural enemies (Yang et al. 1991; Mack et al. 2000; Parker and Gilbert 2004). Chestnut blight, white pine blister rust, and jarrah dieback are well-known diseases that illustrate impacts invasive pathogens can have on natural communities through the loss of dominant tree species (Anagnostakis 1987; Weste and Marks 1987; Tomback and Kendall 2001).

One of the most significant emerging forest diseases is sudden oak death, caused by the invasive pathogen *Phytophthora ramorum*. This lethal canker disease was first associated with mortality of tanoak (*Lithocarpus densiflorus*) and oak (*Quercus* spp.) in the San Francisco Bay region of California during the mid 1990s (Rizzo et al. 2002). *P. ramorum* is now known to infect over 45 genera of plants, including ferns, gymnosperms, monocots, and dicots (Rizzo et al. 2005). The pathogen is thought to have been introduced into California and Oregon forests via infected nursery stock (Ivors et al. 2006; Prospero et al. 2007). Although *P. ramorum* is found in nurseries in both North America and Europe, the original geographic source of the pathogen is unknown. North American and European isolates of *P. ramorum* represent distinct populations that differ in a number of genetic markers including different mating types (A1 in Europe, A2 in North America) (Rizzo et al. 2005; Ivors et al. 2006). Exchange of nursery stock between Europe and North America does not appear to be the original source of the pathogen in California and Oregon forests, although continued trade of infected material does remain a threat (Rizzo et al. 2005; Ivors et al. 2006; Prospero et al. 2007).

Following the introduction of *P. ramorum*, sudden oak death has reached epidemic levels in many coastal forests of California, killing large, but unknown numbers of oak and tanoak trees (Fig. 1, Rizzo et al. 2005). The geographic range of the disease in natural ecosystems currently extends over 750 km from a southern extent in coastal forests of Big Sur, California, to an isolated northern outbreak in Oregon (Meentemeyer et al. 2008a). Several field-based and modeling studies indicate that sudden oak death poses a substantial threat to numerous forest ecosystems (e.g., Meentemeyer et al. 2004; Maloney et al. 2005; Barrett et al. 2006; Monahan and Koenig 2006).

Fig. 1 Example of extensive tanoak mortality due to sudden oak death. This color photograph of the Partington Canyon area was taken from a helicopter in August, 2005 (photo by D.M. Rizzo)

Widespread mortality of oak and tanoak trees will likely reduce wildlife habitat and food resources, raise the risk of forest fires, increase water runoff and soil erosion, and alter the composition and structure of natural plant, microbial, and aquatic communities (Rizzo et al. 2005). Possible movement of the pathogen through the nursery trade to potentially susceptible forests in eastern North America and other regions around the world has resulted in extensive quarantines of the pathogen (Rizzo et al. 2005).

While our understanding of the biology of *P. ramorum* and its mechanisms for dispersal is increasing (Garbelotto et al. 2003a; Davidson et al. 2005; Condeso and Meentemeyer 2007; Fichtner et al. 2007; Meentemeyer et al. 2008b), there has been no large-scale quantification of sudden oak death mortality across a region or across the pathogen's geographic range. Plot-based and remote sensing assessments have observed variable mortality levels (Kelly and Meentemeyer 2002; Swiecki and Bernhardt 2002; Maloney et al. 2005), but regional scaling of mortality figures has not occurred due to the non-random distribution of field observations and the thus far patchy nature of the disease. Forest inventory analysis (FIA) plots have been useful for estimating pathogen-related tree mortality in other forested regions. However, relatively few FIA plots are established in coastal California forests (Barrett et al. 2006).

A quantitative assessment of sudden oak death mortality is important from a number of perspectives. An appropriate response to such a widespread invasive pathogen would require large amounts of personnel and funding resources. Are the current and potential impacts great enough to justify such a response? Second, where are forests most impacted? Quantifiable mortality data are also greatly needed to encourage allocation of resources to early detection and monitoring in uninfected regions.

One of the areas most heavily impacted by sudden oak death is the Big Sur ecoregion on the central coast of California (Rizzo and Garbelotto 2003) (Fig. 2). First observed in 1995, sudden oak death has now spread through many drainages of coast redwood-tanoak forest (*Sequoia sempervirens–L. densiflorus*) with over 60% mortality of tanoak in some stands (Maloney et al. 2005) (Fig. 1). Coast live oak (*Quercus agrifolia*) and Shreve's oak (*Q. parvula* var. *shrevei*) have also experienced high levels of mortality in Big Sur, but limited access has hindered examinations of *P. ramorum* impacts in mixed oak woodlands (Rizzo et al. 2005). Extensive tree mortality in Big Sur is especially concerning because it is one of the most botanically and ecologically diverse regions of California, recognized as a global biodiversity hotspot, and thus a high priority for conservation (Myers et al. 2000). In addition, the ecoregion represents the southern edge of *P. ramorum*'s current geographic range in California, which may continue to expand southward over time (Meentemeyer et al. 2004).

Information on the current extent and level of tree mortality in the Big Sur ecoregion are critically needed to manage further disease spread, identify sites for experimental treatments, and minimize the impacts of tree mortality on biodiversity, nutrient cycling, and fire risk. In this study we assess the current spatial distribution and magnitude of sudden oak death mortality across this unique and valuable region using high resolution imagery in conjunction with field data on oak mortality and forest structure. Specifically, we examine (1) the number of dead trees and prevalence of mortality in the Big Sur attributed to *P. ramorum*; (2) subsequent losses of tree basal area in the ecoregion, and (3) the distribution of disease severity by host forest type (redwood-tanoak forest vs. mixed oak woodland).

Materials and methods

Study system

We established a 79,356 ha study area within the Big Sur ecoregion, extending 100 km along the Pacific slope of the Santa Lucia Range, from Point Lobos south to Salmon Creek, CA (Fig. 2). The topography of the region is highly dissected by steep slopes and drainages with elevations ranging from sea level to 1571 m within 5 km of the coast. The environmentally complex region supports a diversity of plant communities (Henson and Usner 1996). Upper elevation slopes and rocky ridges are typified by mixed coniferous forests composed primarily of ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyii*), coulter pine (*P. coulteri*), and Santa Lucia Fir (*Abies bracteata*). Chaparral shrubland and annual grassland often dominate dry south-facing slopes and ridges at mid elevations.

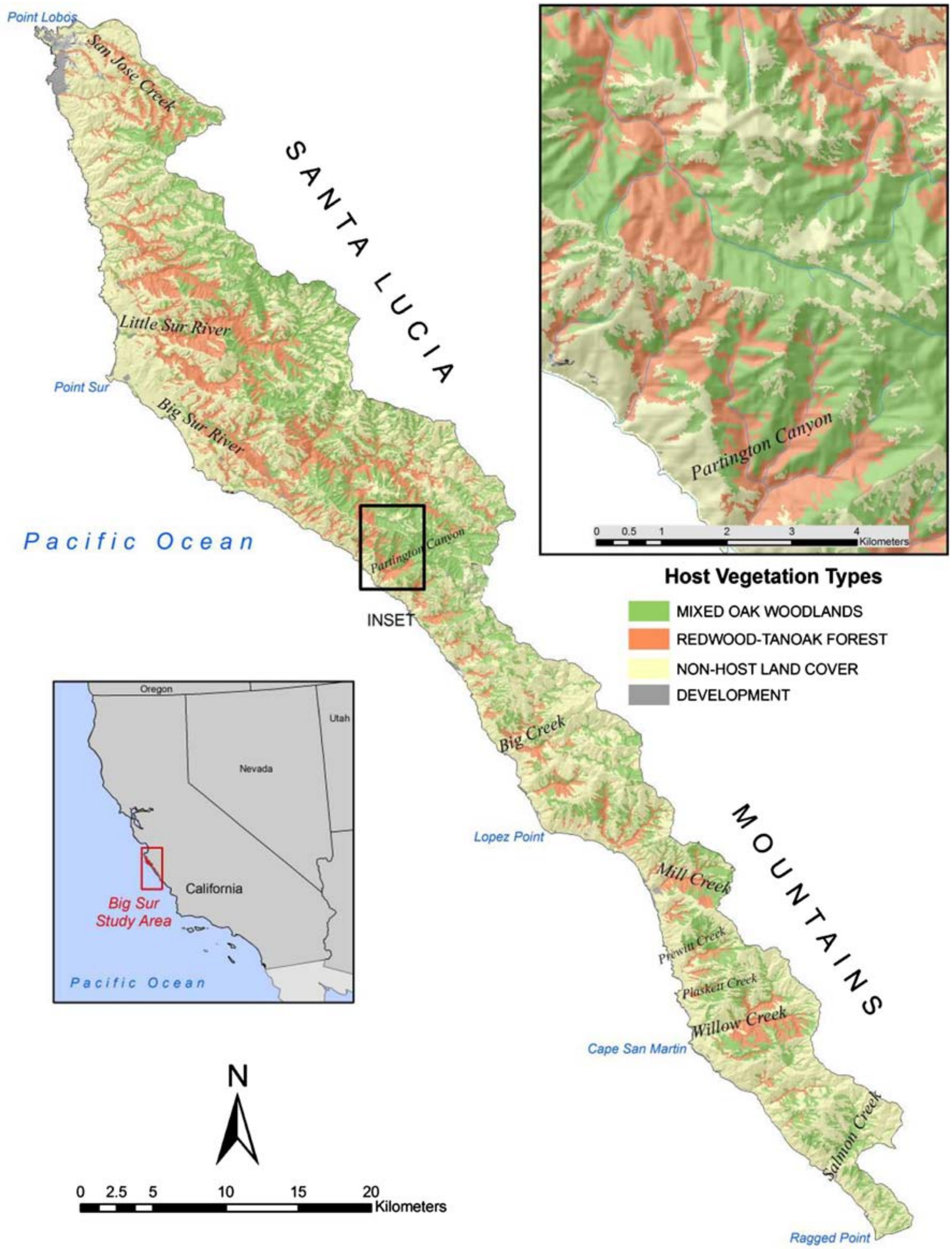

Fig. 2 Big Sur ecoregion (79,356 ha) extends 100 km along the Pacific slope of the Santa Lucia range, from Point Lobos to Ragged Point, CA. A shaded relief map of host and non-host vegetation types were developed using object-based classification and manual editing of high resolution aerial imagery shown in Fig. 3

Table 1 Total area, patch number, and mean patch size of host and non-host vegetation types in the 79,356 ha Big Sur ecoregion. Vegetation was mapped from high resolution color imagery as shown in Fig. 1

Land cover type	Area (ha)	% of total	No. of patches	Mean patch size (ha)
Host vegetation				
Mixed oak woodland	18,875.3	24	792	23.8
Redwood-tanoak forest	13,386.1	17	274	48.9
Non-host land cover				
Montane coniferous forest	3,542.5	4	113	31.3
Shrub and grassland[a]	42,709.7	54	509	83.9
Development	843.2	1	97	8.7

Notes: [a] Includes coastal sage scrub, chaparral shrubland, and annual grassland

Mixed oak woodland consisting of coast live oak, Shreve's oak, bay laurel (*Umbellularia californica*), and madrone (*Arbutus menziesii*) occur on moister slopes, giving way to riparian corridors of redwood-tanoak forest at lower elevations. Low elevation south- and west-facing slopes support drought deciduous coastal sage scrub vegetation (Borchert et al. 2004). The plant communities composing primary habitat for *P. ramorum* in this region are mixed oak woodland and redwood-tanoak forests (Maloney et al. 2005).

Host vegetation and oak mortality mapping

Complete cloudless aerial photography of the study area was digitally captured in red, green, and blue bands at a 0.33 m spatial resolution on April 19, April 25, and May 12, 2005 (AirPhoto USA). The imagery was collected during late spring to avoid mistaking winter and summer deciduous leaf drop for *P. ramorum* caused tree mortality (Kelly and Meentemeyer 2002). A total of 118 image frames were acquired and geo-rectified with an average positional error of less than 1 m.

Using this imagery, we first mapped the distribution of two vegetation communities known to contain host tree species of *P. ramorum* (redwood-tanoak forest and mixed oak woodland) and several non-host habitats based on vegetation descriptions in the Manual of California Vegetation (Table 1, Sawyer and Keeler-Wolf 1997). The plant communities were mapped in three stages. Imagery was first processed using image segmentation, an object-based classification method which iteratively grouped pixels into spectrally homogenous patches of vegetation (minimum area = 1.0 ha), using a region-growing segmentation algorithm (Espindola et al. 2006). Object-based classification is especially useful for generalizing spectral information in high resolution imagery while maintaining its spatial detail (Luscier et al. 2006; Yu et al. 2006). We next used supervised classification to assign a cover type label to each patch, based on spectral signatures of 400 photo-interpreted polygons of vegetation cover (Jensen 1996). Finally, we manually edited boundaries and land-cover type label of each patch as needed using on-screen digitizing tools in a geographic information system (GIS). For redwood-tanoak forest and mixed oak woodland, we calculated total number and area of patches and measured the size of each patch using ArcGIS 9.1 software (ESRI).

Using the imagery a single photo interpreter manually digitized point locations of every dead tree within each of the two host vegetation communities (Fig. 3). The spectral signature of sudden oak death mortality is distinct in high resolution imagery due to the characteristic "freeze-dried" appearance of foliage of dead trees and those that have cast foliage (Kelly and Meentemeyer 2002). Trees with partially dead or fading crowns were not included in the assessment. Care was also taken to distinguish tree mortality associated with sudden oak death from other types of physical disturbances, such as fire and slope instability. To prepare for remote assessment of mortality, the photo interpreter interviewed local land managers, made numerous field assessments across the study region, and extensively examined local fire history data (Fire Resource and Assessment Program[1]). The final

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[1] Fire Resource and Assessment Program. 2003. Available from The California Department of Forestry and Fire Protection's Fire and Resource Assessment Program, Sacramento, California. http://frap.cdf.ca.gov/

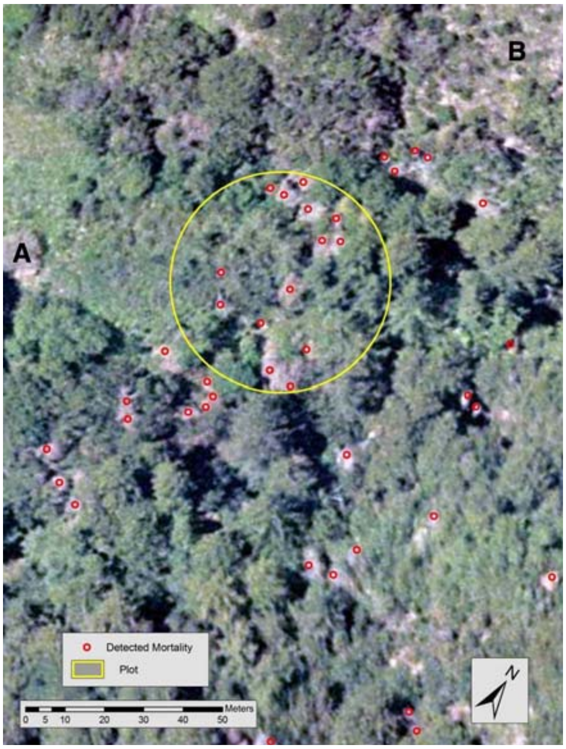

Fig. 3 An example of sudden oak death mortality mapping in a redwood-tanoak forest located within a mosaic of heterogeneous land cover. Hollow red points mark individual locations of tree mortality due to Sudden Oak Death. Photo-interpretation excluded non-subject signatures of mortality, such as chaparral (Point A) and bare earth (Point B). The yellow circle represents the size of a 0.25 ha field plot used to assess remote estimates of mortality. For this plot, we detected 14 dead trees in redwood-tanoak forest while 44 dead trees were field detected. The difference is due to trees growing in the understory of redwood tree canopies

map of dead tree point locations was generalized to a 50 × 50 m grid (0.25 ha) to provide a spatially-explicit estimate of mortality density.

Field survey of host population and mortality levels

To evaluate and improve our remote assessment of mortality, we surveyed 77 field plots (50 × 50 m, 0.25 ha) for evidence of sudden oak death mortality across a range of mortality levels in the region's two primary host vegetation types (redwood-tanoak forest and mixed oak woodland). This plot size was adopted to maximize spatial overlap between the field plot censuses and corresponding area in the imagery, yet permit sufficient plot replication across the study region. Within each plot, we visually assessed all standing dead host trees (*Q. agrifolia, Q. parvula* var. *shrevei*, *Q. kellogii, L. densiflorus*) for typical symptoms of infection by *P. ramorum*, primarily ''bleeding'' lesions (dark red exudates and discoloration of bark surface) and the presence of secondary organisms typically associated with sudden oak death (bark beetles, ambrosia beetles, *Hypoxylon thouarsianum*) (Davidson et al. 2003). Other causes of tree death, such as past wildfire, physical disturbance and canker rots, were observed but not included in the analysis of dead trees (Swiecki and Bernhardt 2002; Garbelotto et al. 2003a). Living host trees that exhibited symptoms of *P. ramorum* infection were not included in our assessment of sudden oak death mortality. For each host species we measured diameter at breast height (DBH) and basal area (m^2) of all dead trees ≥6 cm DBH, and tallied trees by the determined cause of death. All plots classified as symptomatic fell within drainages identified by Maloney et al. (2005) as *P. ramorum*-positive through laboratory examination.

Additional data on host population levels were collected to estimate prevalence of mortality due to *P. ramorum* across the ecoregion (Wickland et al. 2007). An independent network of 175 plots (0.05 ha) was established to measure variability in the number and DBH of host trees (dead and alive) that exist in the Big Sur ecoregion (Wickland et al. 2007). These plots were randomly located across a broad range of ecological conditions stratified by host vegetation type (redwood-tanoak and mixed oak), elevation, latitude, and fire history. All stems ≥1 cm DBH were recorded and tallied by species, but only stems greater than or equal to 6 cm were analyzed for consistency with the 77 0.25 ha plots. Plot locations of both datasets were mapped using survey-grade GPS receivers and differentially corrected with a horizontal accuracy of less than 1 m (Trimble Navigation Limited, California, USA).

Landscape context variables

For each field plot, we also derived several GIS-based variables to examine relationships between oak mortality and underlying landscape factors, which may influence local habitat conditions and bias in our remote assessments: elevation, solar illumination (SI), topographic moisture index (TMI), distance to coast, and latitude. SI was derived for time of imagery collection (April 21) by calculating the cosine of solar illumination angle on slope equation (Dubayah 1994) across a 30 m USGS digital elevation model (DEM). TMI characterized effects of local topography on soil moisture, computed as the natural log of the ratio between upslope drainage area and the slope gradient of a given grid cell in the DEM (Beven and Kirkby 1979; Moore et al. 1991).

Statistical analysis and spatial modeling of oak mortality

We first used paired comparison *t*-tests to examine differences between remotely assessed and field assessed measurements of mortality density within seventy-seven 0.25 ha plots. We also determined which landscape variables were associated with field assessed mortality levels using best-fit multiple regression. Nine plots that were determined to be asymptomatic and outside areas known to be infested (Maloney et al. 2005) were removed from analyses. The density and basal area of mortality variables were square-root transformed to make data conform to assumptions of parametric analysis. Square-root transformations conformed to linearity and normality assumptions better than log-transformations. Next, for each host forest type, we conducted multiple regression analyses to examine relationships between our remote and field assessments of tree mortality density, while accounting for possible contributions of five landscape variables (elevation, SI, TMI, latitude, distance to coast). We identified variables to include in the regression models using a best-fit model approach with the Akaike Information Criterion (AIC) as the criterion for model fit. Second order interactions among predictor variables were also tested. The two resulting predictive equations of tree mortality in each host forest type were applied in the GIS to each 0.25 ha grid cell.

The imagery did not enable us to remotely map tree basal area lost to sudden oak death disease. As an alternative, we quantified for each host forest type the relationship between basal area of dead trees and the density of dead trees observed in a plot. We next estimated the basal area of mortality across the study area, based on the relationship between the total basal area of dead trees and the regression adjusted density of dead trees described above. To derive this relationship, we used multiple regression to predict dead basal area as a function of dead tree density. The resulting models of dead basal area were applied to each grid cell's adjusted number of dead trees to calculate a region-wide estimate of dead basal area in each host forest type.

Finally, we determined the prevalence of sudden oak death tree mortality in each of the two host vegetation types (redwood-tanoak and mixed oak) by comparing the total number of remotely assessed dead trees to an independent estimate of the total population of host trees (alive and dead). To estimate the total number of host trees in the ecoregion we calculated the average density of host trees in each host vegetation type using data from the network of 175 field plots (0.05 ha each). We then scaled the density values to the area of a 0.25 ha grid cell in the GIS and summed them across all grid cells within each of the two host vegetation types. Prevalence of tree mortality was simply calculated as the ratio of remotely assessed dead trees to the estimated population of host trees.

Results

Host vegetation mapping

The combination of automated image processing and manual editing produced a spatially detailed map of the two forest habitats important to *P. ramorum* (Fig. 2). Host vegetation occurred in 41% of the study area (Table 1). Vegetation types were correctly classified in 64 of 77 plots (83% accuracy). Redwood-tanoak forest was mapped with zero omission error but it incorrectly included 12 mixed-oak woodland plots and one plot of non-host vegetation (28% commission error). Mixed-oak woodland was incorrectly mapped as redwood-tanoak in 12 plots (29% omission error), but had zero commission error.

Host-environment–mortality relationships

Host forest types of our plots differed with respect to two of five environmental variables. Redwood-tanoak forests occurred at significantly lower elevations ($\bar{x} = 254 \pm 40.1$ m) than mixed oak woodland ($\bar{x} = 455 \pm 34.6$ m; $F_{1,66} = 14.4$, $P = 0.0003$) and TMI was 15% greater in redwood-tanoak forests than in mixed-oak woodlands ($F_{1,66} = 4.64$, $P = 0.035$). Host vegetation types did not differ with respect to potential solar insolation, latitude, or distance to coast ($P > 0.05$). For both vegetation types, multiple regressions showed that mortality density was negatively related to TMI (redwood-tanoak, $F_{1,26} = 5.2$, $P = 0.032$; mixed oak woodland, $F_{1,36} = 4.6$, $P = 0.039$). However, SI was positively related to mortality in redwood-tanoak forest ($F_{1,26} = 5.3$, $P = 0.029$) and negatively related to mortality in mixed oak woodland ($F_{1,36} = 4.1$, $P = 0.05$).

Quantification of tree mortality

Sudden oak death mortality was observed in 76% of the 0.25 ha field validation plots (52 of 68 field plots; 29 of 39 mixed-oak woodland plots and 23 of 29 redwood-tanoak plots). Our remote mapping assessment failed to detect the presence of mortality in 24% of plots (6 of 39 mixed oak plots, 9 of 29 redwood-tanoak plots). In contrast, our remote assessment made commission errors at only two plots (i.e. mapping mortality where there is none). Paired comparisons *t*-tests showed that remote assessment significantly underestimated mortality (redwood-tanoak forest $t = 5.81$, d$f = 28$, $P < 0.0001$; mixed-oak woodland $t = 4.93$, d$f = 38$, $P < 0.0001$; Fig. 4).

The multiple regression models adjusted the remotely assessed number of dead trees based on the actual number of dead trees (Fig. 5). For redwood-tanoak forests, no landscape variables were significantly related to number dead, but for mixed-oak woodlands, elevation and an interaction term were significant factors in the model (Table 2). None of the other landscape variables (latitude, potential solar insolation, topographic moisture index, and distance to coast) were significant ($P > 0.05$). The regression coefficient for the relationship between remotely assessed and actual number of dead trees was 8% greater for mixed-oak woodlands than for redwood-tanoak forest (Table 2, Fig. 5). Both the field and remotely assessed number of dead trees were significantly related to basal area (Table 2, Fig. 6), but the regression coefficient was greater in mixed-oak woodlands than in redwood-tanoak forests. None of the landscape variables or interaction terms affected the magnitude of the relationship significantly.

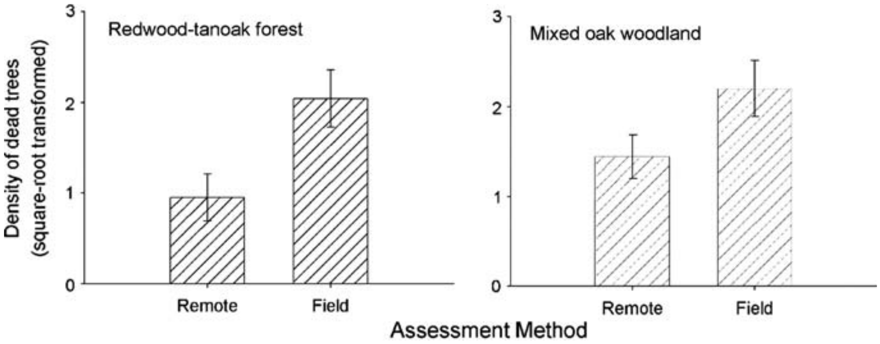

Fig. 4 Comparison of field versus remotely assessed numbers of dead trees for each vegetation type. Data shown are least square means and standard errors

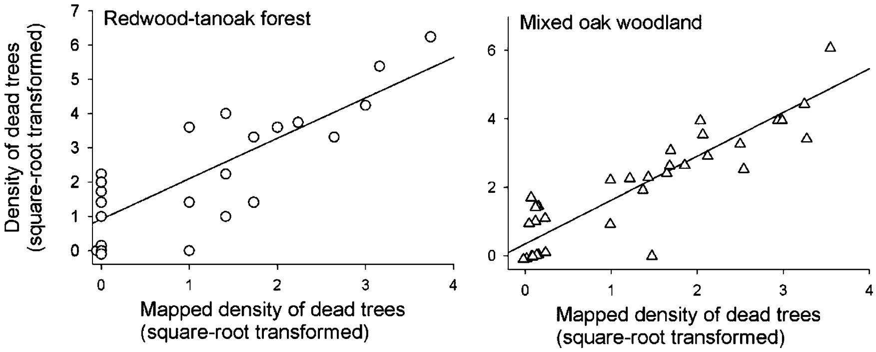

Fig. 5 Relationship between remotely mapped dead tree density and field assessed density (number of trees per 0.25 ha). Redwood-tanoak forest results based on one independent variable. Mixed oak woodland results are based on the leverage plot within the multiple regression model described in Table 2

Table 2 Regression correction models predicting tree mortality based on remotely assessed mortality. All partial regression coefficients shown were statistically significant ($P < 0.001$)

Models	N	r^2	RMSE	Model
Field assessment vs. mapped assessment of dead tree density				
Redwood-tanoak	29	0.66	1.00	$0.92 + 1.18\ md$
Mixed-oak	39	0.87	0.95	$1.38 + 1.28\ md - 0.001e - 0.001\ md \times e$
Regression adjusted mapped assessment vs. basal area				
Redwood-tanoak	29	0.54	0.29	$0.043 + 0.23\ md$
Mixed-oak	39	0.73	0.37	$-0.036 + 0.33\ md$

Notes: md = mapped density; e = elevation

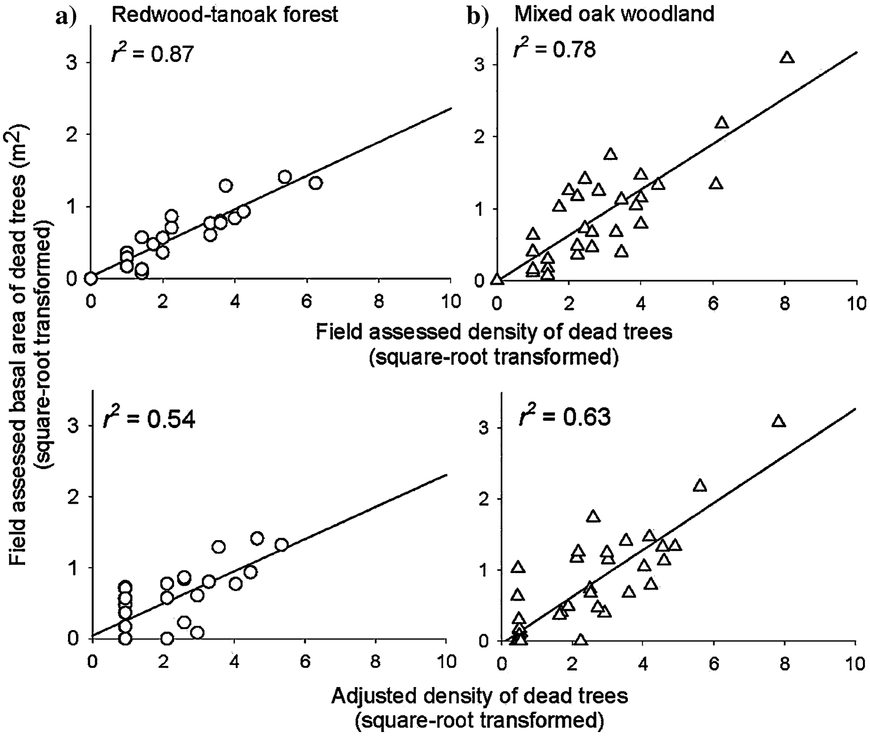

Fig. 6 Relationships between cumulative tree basal area and field assessed dead tree density (upper graphs) and adjusted dead tree density (lower graphs) by forest type: (**a**) Redwood-tanoak forest and (**b**) mixed oak woodland

Application of the density and basal area models to each 0.25 ha grid cell in the GIS produced an estimate of 235,678 dead trees and 12,653 m^2 of dead tree basal area in the study area (Fig. 7). The models estimate that 63% of the dead trees occurred in redwood-tanoak forest (148,469 trees; 8,410 m^2 basal area) and 37% occurred in mixed oak woodland (87,209 trees; 4,243 m^2 basal area).

Integration of the 175 plots (0.05 ha) with the remote assessment of absolute tree mortality showed that mixed oak woodlands had a greater total number of host trees (≥6 cm DBH) with a greater mean population density than redwood-tanoak forests (Table 3). However, the proportion of hosts trees killed by sudden oak death was similar in each of the two host vegetation types (Table 3). We were not able to distinguish the difference between dead coast live oak, Shreve's oak and black oak within mixed oak woodlands via remote sensing, and thus cannot quantify species level mortality estimates within *Quercus*.

Current mortality in the study area is concentrated in the northern portion of the ecoregion (Fig. 7). The drainages experiencing highest mean densities of mortality in redwood-tanoak forest were Partington Canyon (mean = 31 dead trees per ha), Bixby Creek

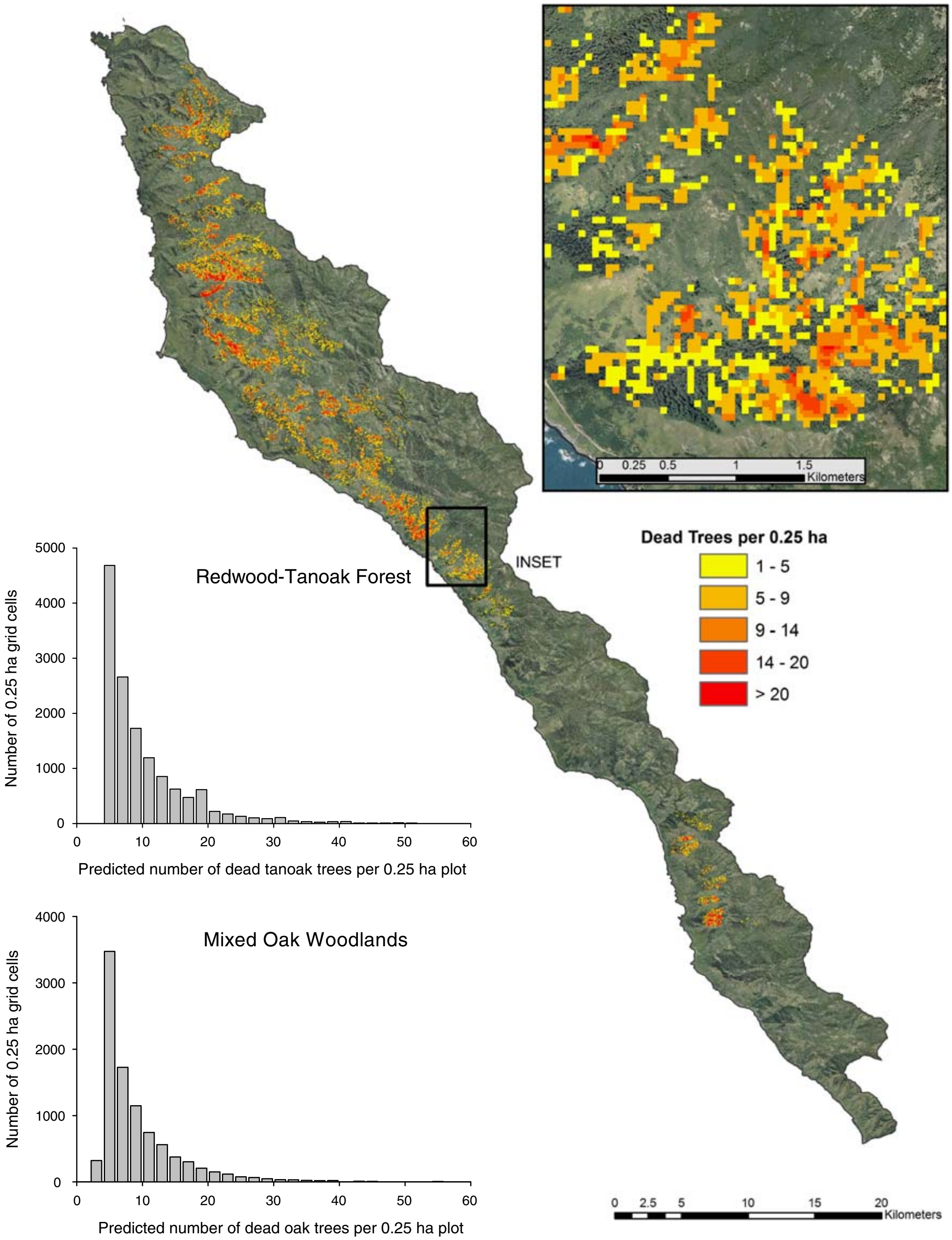

Fig. 7 Spatial distribution of the estimated density of sudden oak death tree mortality based on the redwood-tanoak forest and mixed oak woodland correction models described in Table 3. The inset map illustrates a magnified view of the 0.25 ha grid cell mortality estimates overlaying the digital color imagery. Histograms indicate number of 0.25 ha cells as a function of density of dead trees in each host forest type

Table 3 Estimated number, basal area, and prevalence of dead host trees within the ecoregion's two primary host vegetation types

	Redwood-tanoak	Mixed oak
Area of impacted host vegetation (ha)[a]	4,870	1,446
Mean population density (host trees/ha)	152.3 ± 21.43 S_E	294.1 ± 23.25 S_E
Estimated population of host trees in impacted areas	741,863	425,250
Estimated population of host trees in the ecoregion	2,039,134	5,550,891
Cumulative number of dead trees	148,469	87,209
Mean number of dead trees per grid cell[a]	9.50	9.18
Proportion host trees dead	0.200	0.205
Cumulative basal area (m^2) of dead trees	8,410	4,243
Mean cumulative basal area (m^2) of dead trees per grid cell[a]	0.54	0.46

[a] Based on grid cells with at least 1 dead tree mapped as sudden oak death

Redwood-tanoak forest and mixed oak woodland

(28 ha^{-1}) and the south fork of the Little Sur River (27 ha^{-1}). The highest mean densities of mortality in mixed oak woodlands occur along moderate elevation slopes of Granite Canyon (19 ha^{-1}) and Sycamore Canyon (15 ha^{-1}) drainages. No mortality was detected in Big Creek, Vincente Creek, and Salmon Creek canyons, despite the existence of susceptible host habitat (Fig. 7). Relatively small amounts of mortality were detected in remote areas of several canyons previously thought to be uninfected, including Willow Creek (<1 ha^{-1}), Prewitt Creek (10 ha^{-1}), and Mill Creek (4 ha^{-1}) (Fig. 7).

Discussion

Information on the spatial distribution of tree diseases are needed for landscape-scale analyses of disease dynamics and impacts, and subsequent development of management actions (Holdenrieder et al. 2004). Our spatially-explicit assessment of oak mortality indicates that *Phytophthora ramorum* has substantially impacted forest ecosystems in the Big Sur region of coastal California, killing over 200,000 oak and tanoak trees with a total loss of at least 12,650 m^2 of tree basal area—20% of available host trees in the impacted forest stands. Although mortality has been observed in Big Sur since the mid 1990s (16 years ago), we have documented impacts relatively early in the epidemic. The majority of potential host habitat in the Big Sur ecoregion has yet to experience sudden oak death tree mortality. The majority of potential host habitat (80%) has yet to experience sudden oak death tree mortality.

Over the past century, a number of introduced forest pathogens have caused extensive tree mortality over wide geographic areas (Rizzo et al. 2005). In North America, Chestnut blight (causal agent *Cryphonectria parasitica*) has dramatically changed the composition of forests in the eastern United States by removing the dominant chestnut (*Castanea dentata*), while white pine blister rust (causal agent *Cronartium ribicola*) has killed many five-needled pines (*Pinus* spp.) in both eastern and western forests (Anagnostakis 2001). In Western Australian jarrah forests, *Phytophthora cinnamomi* has caused significant tree mortality over tens of thousands of hectares (Weste and Marks 1987). While the damage caused by these diseases is impressive, the extensive tree morality and subsequent ecological impacts of these important diseases occurred over many decades. For example, chestnut blight took nearly 50 years to spread throughout the geographic range of chestnut trees (Anagnostakis 2001). Therefore in the case of sudden oak death, we have begun to document tree mortality levels and potential ecological impacts at a relatively early stage in the epidemic.

Our estimates of tree mortality are likely conservative, even after field validation. We were only able to record standing-dead trees in 2005, not those that had fallen to the ground. Field studies have suggested that dead trees will only remain standing for 2–4 years following death. Sites that have been invaded by *P. ramorum* longer than 5 years often have a large number of stems that could not be measured because they had either fallen over time or were too decayed to assess symptoms of *P. ramorum* caused mortality. Thus, standing dead trees observed in the 2005 imagery and field survey likely do not represent all cumulative mortality since 1995. In addition, we were also not able to record *P. ramorum*-caused mortality of tanoak saplings and seedlings less than 6 cm DBH.

We also expected to underestimate sudden oak death mortality in the digital imagery because dead trees can be hidden in shadows of larger adjacent trees and steep terrain. Our field data on oak mortality revealed that we indeed systematically underestimated *P. ramorum*-related mortality in the aircraft imagery and overestimated mortality at higher elevations. Integration of the field and elevation data with the imagery allowed us to quantitatively correct and validate our remote assessment. With model correction, our field plot measurements showed that we were able to remotely detect the density and basal area of sudden oak death tree mortality at a relatively high accuracy ($r^2 = 0.54$–0.87). However, we were able to more accurately estimate density and basal area of mortality in mixed oak woodlands than redwood-tanoak forests. We more often missed dead tanoak than oak because it often grows beneath the canopy of large redwood trees and *P. ramorum* more aggressively attacks tanoak saplings than oak saplings in the forest understory (Rizzo et al. 2005).

The current patchiness of sudden oak death in Big Sur provides opportunities and challenges for management actions in infected and uninfected areas. Our efforts to map mortality will help prioritize areas for containment and eradication as well as identify areas at imminent risk for infection for careful monitoring. However, manager action must also be consistent with goals of regional land management, such as removing invasive species, conserving threatened species, and controlling wildfire. In addition, over 90% of the Los Padres National Forest in the Big Sur area is designated wilderness that requires special considerations prior to management. Ultimately, landscape-level management strategies for *P. ramorum* that incorporate prevention, treatment, restoration, and conservation will be the most successful. By working with both public and private partners, the pervasive conservation issues facing the Big Sur ecosystem can be addressed.

Natural ecosystems globally are being increasingly altered by the spread of emerging pathogens of plants and wildlife (Daszak 2000; Dobson and Foufopoulos 2001; Harvell et al. 2002; Anderson et al. 2004; Ehrenfeld 2005). Tree mortality of the magnitude and spatial scale identified in this study has never been quantified for sudden oak death. These results illustrate the virulence of this pathogen and emphasize the importance of managing disease spread. Further studies are needed to examine the efficacy of management strategies for application at landscape scales, such as thinning of foliar host vegetation (Rizzo et al. 2005), increasing host resistance (Garbelotto et al. 2003b), and early detection of pathogen spread (Meentemeyer et al. 2004; Murphy et al. 2005). Without management intervention, further disease spread may substantially impact the biodiversity and structure of numerous coastal California forests.

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