Mapping the risk of establishment and spread of sudden oak death in California

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Abstract

Sudden oak death, caused by the recently described pathogen *Phytophthora ramorum*, is an emerging forest disease that has reached epidemic levels in coastal forests of central California. We present a rule-based model of *P. ramorum* establishment and spread risk in California plant communities. The model, which is being used as a management tool to target threatened forests for early-detection monitoring and protection, incorporates the effects of spatial and temporal variability of multiple variables on pathogen persistence. Model predictions are based on current knowledge of host susceptibility, pathogen reproduction, and pathogen transmission with particular regard to host species distribution and climate suitability. Maps of host species distributions and monthly weather conditions were spatially analyzed in a GIS and parameterized to encode the magnitude and direction of each variable's effect on disease establishment and spread. Spread risk predictions were computed for each month of the pathogen's general reproductive season and averaged to generate a cumulative risk map (Fig. 6a and b). The model identifies an alarming number of uninfected forest ecosystems in California at considerable risk of infection by *Phytophthora ramorum*. This includes, in particular, a broad band of high risk north of Sonoma County to the Oregon border, a narrow band of high risk south of central Monterey County south to central San Luis Obispo County, and scattered areas of moderate and high risk in the Sierra Nevada foothills in Butte and Yuba counties. Model performance was evaluated by comparing spread risk predictions to field observations of disease presence and absence. Model predictions of spread risk were consistent with disease severity observed in the field, with modeled risk significantly higher at currently infested locations than at uninfested locations ($P < 0.01$, $n = 323$). Based on what is known about the ecology and epidemiology of sudden oak death, this model provides a simple and effective management tool for identifying emergent infections before they become established.
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1. Introduction

Invasive organisms are increasingly recognized as major agents of environmental change (Vitousek et al.,

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Fig. 1. Current distribution of confirmed cases of *P. ramorum* in California, based on field samples analyzed by the California Department of Food and Agriculture and geographic data maintained and distributed by the California Oak Mortality Taskforce.

1996; Mooney and Hobbs, 2000). One type of invasion that is occurring with growing regularity involves plant pathogens that either are non-native or are native but have recently expanded their geographical range (Baskin, 2002; Campbell and Schlarbaum, 2002). By killing host species that play key roles in plant communities, invasive plant pathogens can dramatically alter forest community structure and genetic diversity of host populations (Thrall and Burdon, 1999). Chest-nut blight (*Cryphonectria parasitica*) and Dutch elm disease (*Ophiostoma ulmi*) in North America and jarrah dieback (*Phytophthora cinnamomi*) in western Australia are well known examples of these effects (Anagnostakis, 1987; Brasier, 2001; Weste and Marks, 1987).

"Sudden oak death" is an emerging forest disease that has reached epidemic levels in coastal forests of central California (Fig. 1; see review by

Table 1

Known hosts infected by *P. ramorum* (compiled from Rizzo et al., 2002a, 2002b) in forests of California and Oregon

Quercus agrifolia	*Rubus spectabilis*
Quercus kelloggi	*Aesculus californica*
Quercus parvula var. *shrevei*	*Rhamnus californica*
Quercus chrysolepis	*Rhamnus purshiana*
Lithocarpus densiflorus	*Corylus cornuta*
Arbutus menzeisii	*Lonicera hispidula*
Vaccinium ovatum	*Viburnum* spp.[c]
Arctostaphylos spp.[a]	*Toxicodendron diversilobum*
Rhododendron spp.[b]	*Trientalis latifolia*
Umbellularia californica	*Sequoia sempervirens*
Acer macrophyllum	*Pseudotsuga menziesii*
Heteromeles arbutifolia	

[a] Probably multiple species infected. Known definitively from *A. manzanita*.

[b] Multiple species infected including *R. macrophyllum* and *R. catawbiense*.

[c] Multiple species infected including *V. bodnantense*, *V. fragans*, *V. plicatum*, and *V. tinus*; this host is only known from Europe.

Rizzo and Garbelotto, 2003). The disease is caused by the recently discovered pathogen, *Phytophthora ramorum*, first isolated from rhododendron (*Rhododendron* spp.) and viburnum (*Viburnum* spp.) in Europe (Werres et al., 2001; Rizzo et al., 2002a). To date, 23 plant species from 12 families have been confirmed as potential hosts in forests of California and Oregon (Rizzo et al., 2002a, 2002b; Table 1). Among these different host species, *P. ramorum* causes two forms of disease: lethal branch or stem infections, and nonlethal foliar and twig infections (Rizzo and Garbelotto, 2003; Fig. 2).

The lethal form of the disease kills several ecologically important trees, including tanoak (*Lithocarpus densiflora*), coast live oak (*Quercus agrifolia*), California black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*) and Shreve's oak (*Quercus parvula* var. *shrevei*) (Rizzo et al., 2002a). Except for tanoak, these oak species appear to be epidemiological dead-ends or "terminal hosts." That is, the pathogen's dispersal spores (sporangia and chlamydospores) have never been found on the bark or foliage of these species when infected (Davidson et al., 2002). Also, spatial patterns of oak mortality do not suggest tree-to-tree transmission between terminal hosts (Kelly and Meentemeyer, 2002). In contrast, *P. ramorum* is abundant on the foliage and branches of a variety of tree and shrub species without lethal

consequences. This second form of infection may allow *P. ramorum* to sustain its population indefinitely in infested forests and appears to play a critical role in disease spread (Rizzo and Garbelotto, 2003; Garbelotto et al., 2003). The potential for these "foliar hosts" to readily support *P. ramorum* growth and the pathogen's ability to disperse aerially (Davidson et al., 2002) in conjunction with the broad geographic range of its host species (Rizzo et al., 2002b) makes this emerging disease a serious threat to many forest ecosystems (Rizzo and Garbelotto, 2003).

In response to this threat, the state governments of California and Oregon as well as the federal government have assembled independent task forces to devise strategies for management and prevention of further spread. In California, the disease may be too widespread to broadly apply control methods such as the chemical compounds currently being used to protect high-value, individual trees (Garbelotto et al., 2002). Physical eradication, like that used to remove an isolated cluster of infested forest in southwestern Oregon (Goheen et al., 2002a, 2002b), would also be infeasible for such a large disease area (Rizzo and Garbelotto, 2003). For this reason, California has established an extensive monitoring program focused on the early detection of pathogen activity at isolated locations, where it may be possible to apply chemical treatments or attempt eradication. The monitoring program uses a range of approaches, including aerial surveys to detect dead terminal hosts (Kelly and Meentemeyer, 2002), repeat field sampling at numerous sites, regular inspection of commercial nurseries, and stream water sampling of potentially infested watersheds (Tjosvold et al., unpublished data). Regardless of the approach, the considerable cost of monitoring necessitates careful targeting and prioritization of these early-detection efforts. This presents a significant challenge given the extensive size (408,512 km^2), diversity of host species and environmental variability of the state of California. It is therefore essential to understand when and where the risk of establishment of *P. ramorum* is elevated in order to effectively monitor the disease and manage threatened forests.

We present a rule-based model of sudden oak death disease establishment and spread risk in California plant communities. This model, which is already being used to target early-detection monitoring and

Fig. 2. Types of disease caused by *P. ramorum*: lethal stem infections and non-lethal foliar infections. Photos courtesy of Sonoma State Unversity Sudden Oak Death Research Project.

predict oak and tanoak mortality, incorporates the effects of spatial and temporal variability of multiple variables on establishment and spread risk. Model predictions are based on current knowledge of host susceptibility, pathogen reproduction, and pathogen transmission with particular regard to host species distribution and climate suitability. Maps of host species distributions and monthly weather conditions were spatially analyzed in a GIS and ranked in accordance to each variable's epidemiological significance. Spread risk predictions were computed for each month of the pathogen's general reproductive season (December–May) and summarized as a cumulative, 6-month average risk index. Model performance was evaluated by comparing spread risk predictions to field observations of disease presence and absence.

2. Methods

Five predictor variables were mapped in a GIS to generate a model of *P. ramorum* establishment and spread risk, based on the combined effects of spatial variation in host species and environmental conditions. The variables include a host species index and four temperature and moisture variables.

2.1. Developing the database

2.1.1. Host species data
The CALVEG dataset (USDA Forest Service RSL 2003: USDA, 2003) is the base data from which we inferred the distribution and abundance of host species for *P. ramorum*. The dataset is organized in a GIS

vector format with 68 subregions that make up eight ecological provinces. For analysis, we combined the 68 subregions into eight province maps after removing subregion boundaries and overlapping sliver polygons.

The 'Vegetation Alliance' is the principle attribute that the CALVEG classification system uses to describe plant community composition and structure. The alliance describes the dominant type of vegetation within a minimum mapping unit of at least one hectare. Areas that contain a mix of conifer and hardwood types always emphasize the conifer type in the alliance description, but a 'Secondary Alliance' attribute describes the hardwood vegetation type. We use both alliance descriptions to calculate the host index described below.

CALVEG Alliance names can be readily accessed as a digital attribute in a GIS, but species-level information, needed for mapping host species distributions, is organized as a manual. The manual qualitatively describes the relative abundance of species associates in each of California's 512 Alliances. Because the same alliance names are often used in more than one ecological province, unique descriptions are given for each province. The example below describes the California Bay Alliance in the Central Coast and Montane province:

California Bay (*Umbellularia californica*) occurs in canyons, shaded slopes and moist sites in chaparral and woodland communities throughout much of California. It occasionally forms scattered small stands as a tree in more protected environments and in a more shrub-like form in exposed places and in the chaparral. It has been mapped in the South Coastal Santa Lucia Ranges (Coast Section), where it is more common in the elevation range 1000–1600 ft (305–488 m) on north-facing, medium to high gradient slopes. It also occurs in the Interior Santa Lucia Range (Ranges Section), occurring mainly on north and east facing slopes on similar gradients below 2000 ft (610 m). Coast Live Oak (*Quercus agrifolia*) is the most frequent hardwood associate, with Chamise (*Adenostoma fasciculatum*), species of Ceanothus, shrub Canyon Live (*Q. chrysolepis*) and shrub Interior Live (*Q. wislizenii*) Oaks the more common shrub associates in this Alliance. It is found adjacent to the Coast Live Oak, Mixed Hardwoods and Annual Grass—Forb Alliances.

The manual uses keywords and phrases to qualitatively describe a species' abundance in an Alliance. We scored keywords and phrases from 1 to 10, lowest to highest abundance, in order to map the abundance and diversity of host species in each alliance (Table 2). These data were then joined to the Vegetation Alliance polygons in the GIS and converted to a grid-cell format at a grain size of 30 m × 30 m. This grain size preserves the spatial integrity of the vegetation

Table 2
Keywords and phrases used in CALVEG Alliance descriptions and corresponding abundance scores, ranked 1–10 from lowest to highest abundance

Abundance description	Abundance score
Alliance type species	10
Most common associate(s); most important associate(s); indicator(s)	7
Prominent; important	7
Often associated; often present; often occurs; often includes	5
Occurs; also occurs; occurs with; includes; supports; occupies	5
Common associate; common; commonly occurs	5
Typical associate; typical	5
Associate; associated	5
Sometimes; some associated; associated in some areas or ecozones	3
Likely to be present; likely	3
Mixes with	3
May be present; may be associated; may include; may occupy; may occur	2
Occasional associate; occasional; may be occasionally present	2
Minor associate; sparsely but commonly present	2
May include or may occasionally be present in some areas or Ecozones	1
May include or may be present, but rare or infrequent, or minor amount	1

data, which is mapped from 30 m Landsat TM satellite imagery.

The CALVEG dataset is complete for most of the host species' ranges, but is incomplete in parts of the South Sierra and Central Coast, most of the Central Valley, and all of the South Interior Ecoregion. Vegetation data from the California GAP Analysis Project (Davis et al., 1998) are used in regions where CALVEG is incomplete and cross-walked to match the CALVEG classification system. In the GAP data, community-level vegetation is principally described according to the California Natural Diversity Database (CNDDB) or ''Holland'' system, using a considerably larger minimum mapping unit (100 ha). Each polygon in the GAP data contains up to three plant community types along with the area covered by each type, which are not spatially delineated and are intended for characterizing regional biodiversity at mapping scales smaller than 1:100,000 (Davis et al., 1995).

2.1.2. Temperature and moisture

The climate data used in our model include 30-year monthly averages (1961–1990) of precipitation, minimum and maximum temperature, and relative humidity (Fig. 3) produced from the model parameter-elevation regression on independent slopes model (PRISM; Daly et al., 1994, 2001). PRISM uses a large number of observations from weather base stations in conjunction with digital terrain data and other environmental factors to spatially interpolate climatic variability across a landscape. Grain size of each grid cell is approximately 2 km × 2 km. The PRISM methodology assumes elevation is the most important factor controlling landscape patterns of temperature and moisture, and uses linear regression to estimate climate variability within local topographic orientations, or facets. Other environmental factors are incorporated using differential regression weighting of the base station data points. The combined weight of a station is a function of elevation, coastal proximity, aspect, local relief, and vertical air mass layering. PRISM captures the influence of large water bodies, complex terrain, and atmospheric inversions in determining temperature and moisture, including rain shadow effects. These factors are especially important in California, where climate varies considerably over short distances.

2.2. Developing the model

A rule-based model was developed to predict the risk of *Phytophthora ramorum* establishment and spread in plant communities of California. Spatial models of this type use research data and expert input, rather than statistical inference, to determine the importance of predictor variables. In our model, each predictor variable was assigned a weight of importance, and each variable's range of values was ranked to encode the magnitude and direction of its effect on spread risk (Tables 3 and 4). The equation used to run the model is simply the sum of the product of each ranked variable and its weight of importance, divided by the sum of the weights:

$$\overline{S} = \frac{\sum_i^n W_i R_{ij}}{\sum_i^n W_i}$$

where $\overline{S}$ is the spread risk for a grid cell in the model output, W_i is the weight of the ith predictor variable, and R_{ij} is the rank for the jth value of the ith variable, the rank of j depending on the variable's value at a given grid cell. Each variable's weight and subsequent ranks were based on recent field and laboratory studies of disease symptoms on a variety of host species. Particular attention was paid to differences in a host's ability to harbor and spread the pathogen, as well as the effect of environmental factors on pathogen survival, reproduction and transmission. In this model, ''spread risk'' is defined as a location's potential to produce inoculum and further disperse the disease to additional individual plants and locations. This model concentrates on ''natural'' forms of spread and does not take into account, long distance human-mediated spread (e.g., on ornamental plants).

Table 3
Importance weights (W) assigned to predictor variables in the *P. ramorum* spread risk model, ranked 1–6 from lowest to highest importance

Variable	Weight
Host species index	6
Precipitation	2
Maximum temperature	2
Relative humidity	1
Minimum temperature	1

Table 4
Range of values for predictor variables and assigned ranks (R) in the *P. ramorum* spread risk model, ranked 0–5 from least to most suitable for spread of the pathogen

Rank	Host species index	Precipitation (mm)	Average maximum T (°C)	RH (%)	Avgerage minimum T (°C)
5	80–100	>125	18–22	>80	–
4	60–80	100–125	17–18; 22–23	75–80	–
3	40–60	75–100	16–17; 23–24	70–75	–
2	20–40	50–75	15–16; 24–25	65–70	–
1	0–20	25–50	14–15; 25–26	60–65	>0
0	–	<25	<14; >26	<60	<0

Risk predictions were computed for each month from December to May, the general reproductive season of the pathogen, and scaled 0–100, from lowest to highest risk. Finally, the six monthly maps were averaged to produce a cumulative spread risk index over the general reproductive season. The cumulative risk index was simplified into five risk levels for straightforward use in management: 81–100 (very high risk), 61–80 (high risk), 41–60 (moderate risk), 21–40 (low risk), 1–20 (very low risk).

2.2.1. Scoring the host index

Each host species is scored from 0 to 10 based on its potential to produce inoculum (Table 5). The host index is calculated in the GIS by summing the products of each host's potential spread score and its abundance score for a given vegetation polygon (Table 6; Fig. 4). The range of values (0–123) is linearly rescaled from 0 to 5, low to high spread potential, to rank (R) the variable (Table 4). This variable is assigned an importance weight (W) of 6, the highest possible weight (Table 3).

Bay laurel (*Umbellularia californica*) was assigned the highest potential spread score (10) among the hosts because foliar infections on this species provide an important source of readily spread inoculum in the form of sporangia, zoospores, and chlamydospores (Davidson et al., 2002; Garbelotto et al., 2003; Rizzo and Garbelotto, 2003; Fig. 2). The presence of bay laurel trees in a forest stand is significantly correlated with *P. ramorum* infection on oak (Kelly and Meentemeyer, 2002; Swiecki and Bernhardt, 2002). Tanoak (*Lithocarpus densiflorus*) and *Rhododendron* species are scored moderately high (5) because they are also susceptible to foliar and branch infection and play an important role in the epidemiology of the disease, but probably to a lesser extent than bay laurel. *Rhododen-*

dron is a key host at infected sites in Oregon (Goheen et al., 2002a), and it is widely distributed in the understory of mixed evergreen and conifer forests of coastal northern California. Tanoak is associated with high levels of leaf and stem infections in Redwood and mixed evergreen forests of the central coast (Maloney et al., 2002; Rizzo et al., 2002a), and the tree is widely distributed throughout coastal northern California. It is also found in scattered locations in the Sierra Nevada foothills. Redwood (*Sequoia sempervirens*) was assigned a score of 3 as it supports limited foliar infection and production of inoculum from its leaves (Maloney et al., 2002). The remaining hosts that acquire foliar infections were assigned a score of 1 (Table 5). Disease symptoms are typically much less

Table 5
Scores assigned to host species, ranked from 1 to 10 from lowest to highest potential to spread inoculum of *P. ramorum*

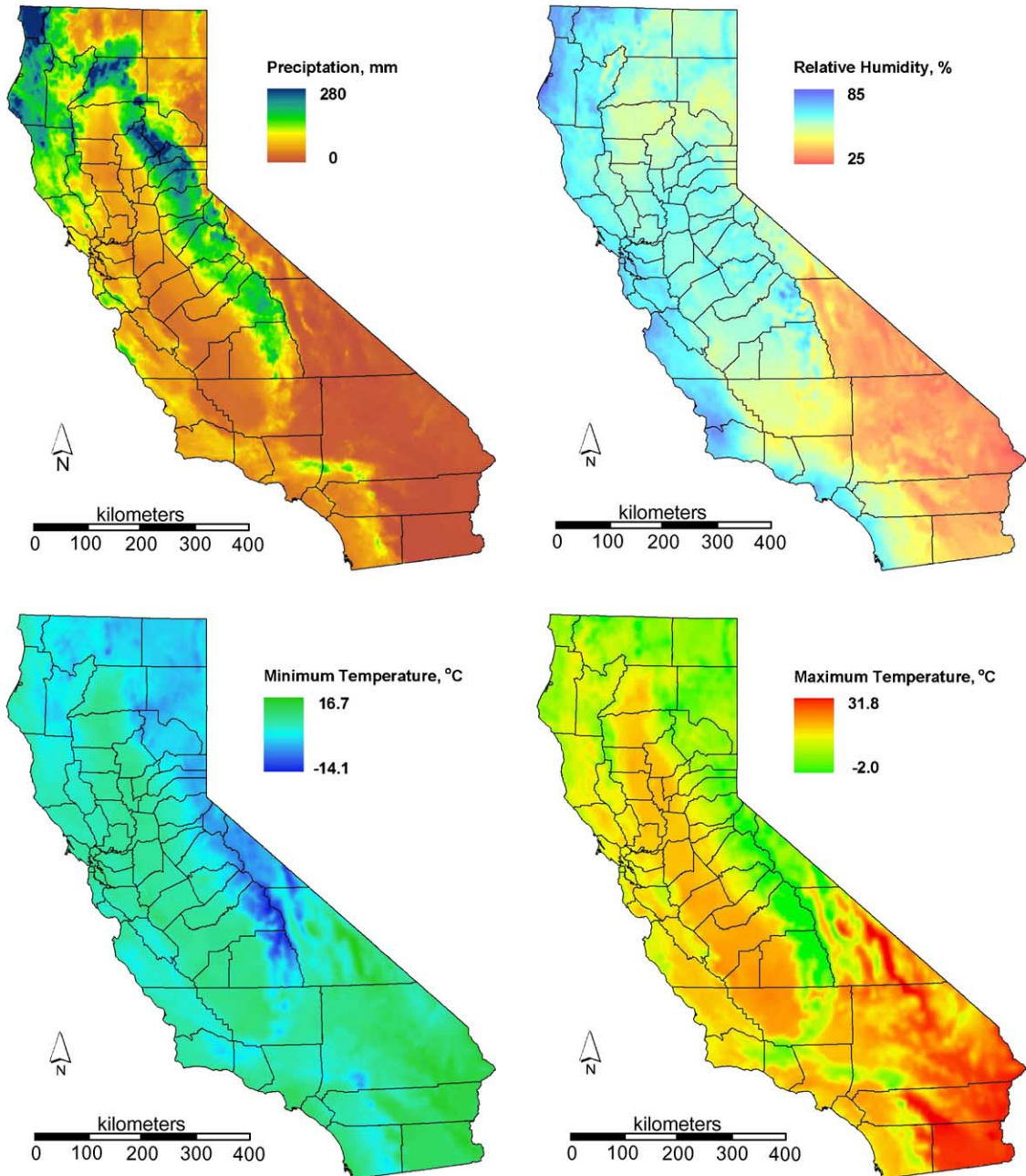| Host score	Scientific name	Common name
10	*Umbellularia californica*	California Bay
5	*Lithocarpus densiflorus*	Tanoak
5	*Rhododendron macrophyllum*	Coast Rhododendron
5	*Rhododendron occidentale*	Western Azalea
5	*Rhododendron* spp.	Rhododendron species
3	*Sequoia sempervirens*	Redwood
1	*Acer macrophyllum*	Bigleaf Maple
1	*Aesculus californica*	California Buckeye
1	*Arctostaphylos manzanita*	Common Manzanita
1	*Arbutus menziesii*	Madrone
1	*Heteromeles arbutifolia*	Toyon
1	*Lonicera hispidula*	California Honeysuckle
1	*Pseudotsuga menziesii*	Douglas fir
1	*Rhamnus californica*	California Coffeeberry
1	*Vaccinium ovatum*	California Huckleberry
0	*Quercus agrifolia*	Coast Live Oak
0	*Quercus chrysolepis*	Canyon Live Oak
0	*Quercus kelloggii*	Black Oak
0	*Quercus parvula* var. *shrevei*	Shreve Oak

Fig. 3. Climate variables for April: 30 year averages (1961–1990) of precipitation, relative percent humidity, minimum temperature, and maximum temperature.

severe on these hosts and are sometimes absent altogether even when they co-occur with other infected individuals (Davidson et al., 2002). The potential for sporulation on these hosts is not well characterized.

The oak species, *Quercus agrifolia*, *Quercus chrysolepis*, *Quercus kellogii*, and *Quercus parvula* var. *shrevei*, were assigned a spread potential score of zero because their stem infections appear to be epidemio-
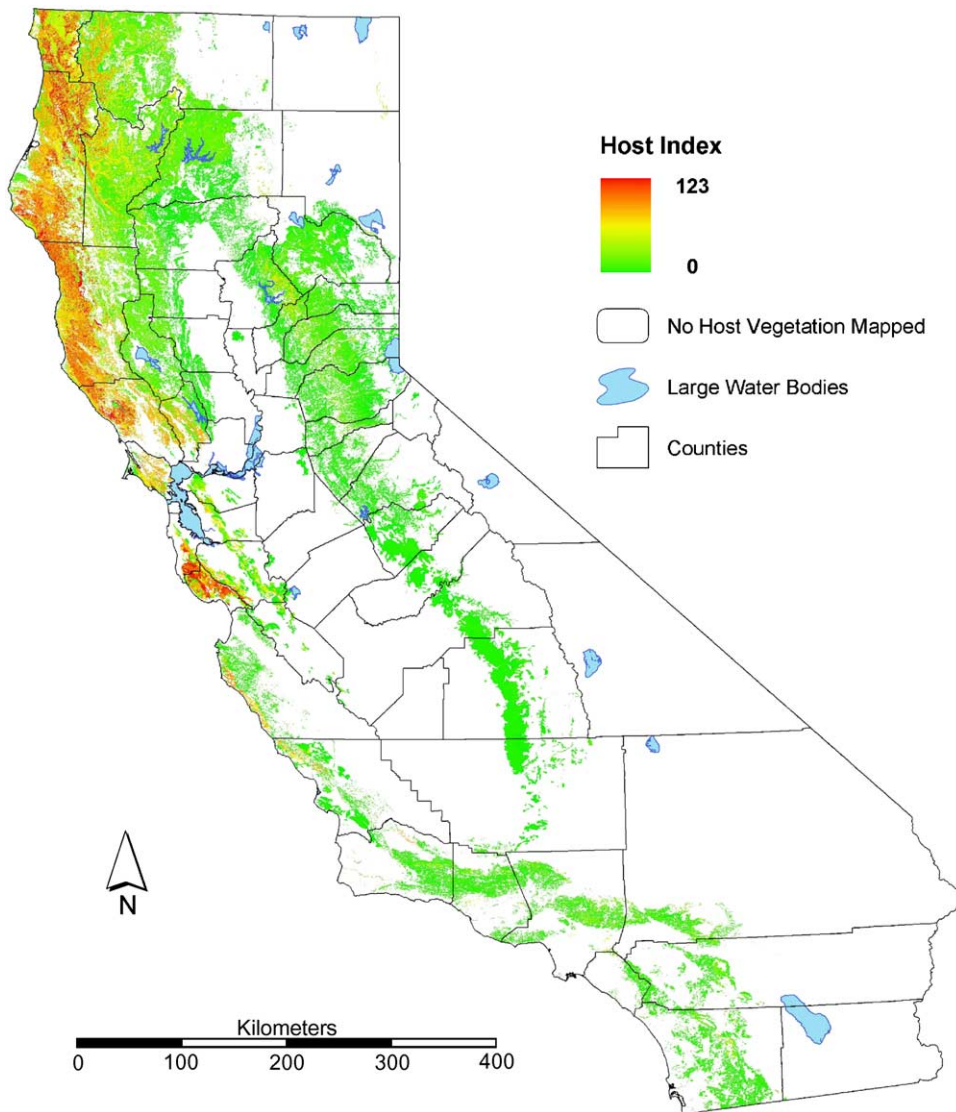
Fig. 4. Host species index; values range from 0 to 123, from lowest to highest potential of CALVEG Alliances to host and spread *P. ramorum*.

logical dead-ends (Davidson et al., 2002; Garbelotto et al., 2003).

2.2.2. Scoring temperature and moisture

Growth of *P. ramorum* is greatest at mild temperatures between 18 and 22 °C (Werres et al., 2001; Garbelotto et al., 2003). Recent laboratory tests show bay leaf infection rates of 92% at 18 °C, but only 50% at a colder temperature of 12 °C and 37% at a hotter temperature of 30 °C (Garbelotto, unpublished data).

For each month (December–May), we assigned average maximum temperatures between 18 and 22 °C the highest rank of 5. Temperatures outside of this range were assigned progressively lower ranks (Table 4). Less is known about the effect of minimum temperature on infection rates in the field, but it is clear that *P. ramorum* growth is best at mild temperatures (Rizzo and Garbelotto, 2003). As such, we assigned sites that experience average monthly minimum temperatures below 0 °C a rank of zero and a rank of 1 is given to

Table 6
Host index for CALVEG Alliances in the North Coast and Montane Ecoregion (highest 20 scores)

CALVEG Alliance	Host species index	acma	aeca	arma	arme	hear	lide	lohi	psme	rhca	rhma	rhoc	rhod spp.	sese	umca	vaov
Tanoak (Madrone)	123	5 × 1			7 × 1		10 × 5		5 × 1				1 × 5		5 × 10	1 × 1
California Bay	103		3 × 1												10 × 10	
Redwood	85						5 × 5		5 × 1		5 × 5			10 × 3		
Sitka spruce–redwood	85				5 × 1		5 × 5				5 × 5			10 × 3		
Mixed hardwoods	80		7 × 1		3 × 1										7 × 10	
Redwood–Douglas fir	70				5 × 1		5 × 5		10 × 1					10 × 3		
Pacific Douglas fir	62	1 × 1			2 × 1		7 × 5	2 × 1	10 × 1						1 × 10	2 × 1
Northern coast mixed shrub	60									5 × 1					5 × 10	5 × 1
Ultramafic mixed conifer	49				1 × 1		3 × 5		5 × 1	3 × 1		3 × 5			1 × 10	
Grand fir	45						5 × 5		5 × 1					5 × 3		
Port Orford Cedar	43						3 × 5		3 × 1		3 × 5	2 × 5				
Upper Montane mixed shrub	35						7 × 5									
Douglas fir–Grand fir	35						5 × 5		10 × 1							
Bishop Pine	35				5 × 1				5 × 1	5 × 1				5 × 3		5 × 1
Salal-CA Huckleberry	32										5 × 5					7 × 1
California Buckeye	30		10 × 1												2 × 10	
Interior Live Oak	27		2 × 1							5 × 1					2 × 10	
Tree Chinquapin	27						5 × 5		2 × 1							
Mendocino Manzanita	25								5 × 1					5 × 3		5 × 1
Douglas fir–White fir	25	5 × 1					2 × 5		10 × 1							

The host index value is the product of each host's spread potential score and abundance score, summed for all hosts in the alliance. acma: *Acer macrophyllum*, aeca: *Aesculus californica*, arma: *Arctostaphylos manzanita*, arme: *Arbutus menziesii*, hear: *Heteromeles arbutifolia*, lide: *Lithocarpus densiflorus*, lohi: *Lonicera hispidula*, psme: *Pseudotsuga menziesii*, rhca: *Rhamnus californica*, rhma: *Rhododendron macrophyllum*, rhoc: *Rhododendron occidentale*, rhod spp.: *Rhododendron* spp., sese: *Sequoia sempervirens*, umca: *Umbellularia californica*, vaov: *Vaccinium ovatum*.

sites with a minimum temperature above freezing (Table 4). The maximum and minimum temperature variables were given importance weights (W) of 2 and 1, respectively (Table 3).

Free water must also exist on plant surfaces for a minimum of 6–12 consecutive hours for significant infection to occur (Garbelotto et al., 2003). This moisture may come from multiple forms, such as rain, fog, or dew (Davidson et al., 2002). For each month (December–May), we assigned monthly rainfall amounts above 125 mm the highest rank of 5, with lower ranks assigned to progressively lower rainfall amounts (Table 4). A rank of 5 was assigned to sites that experience relative humidity conditions greater than 80%, with progressively lower ranks assigned to lower humidity levels (Table 4). Rainfall and relative humidity were given importance weights (W) of 2 and 1, respectively (Table 3). Fig. 5 illustrates the combined effect of climate averaged over all 6 months, based on the weights and ranks assigned to each climate variable.
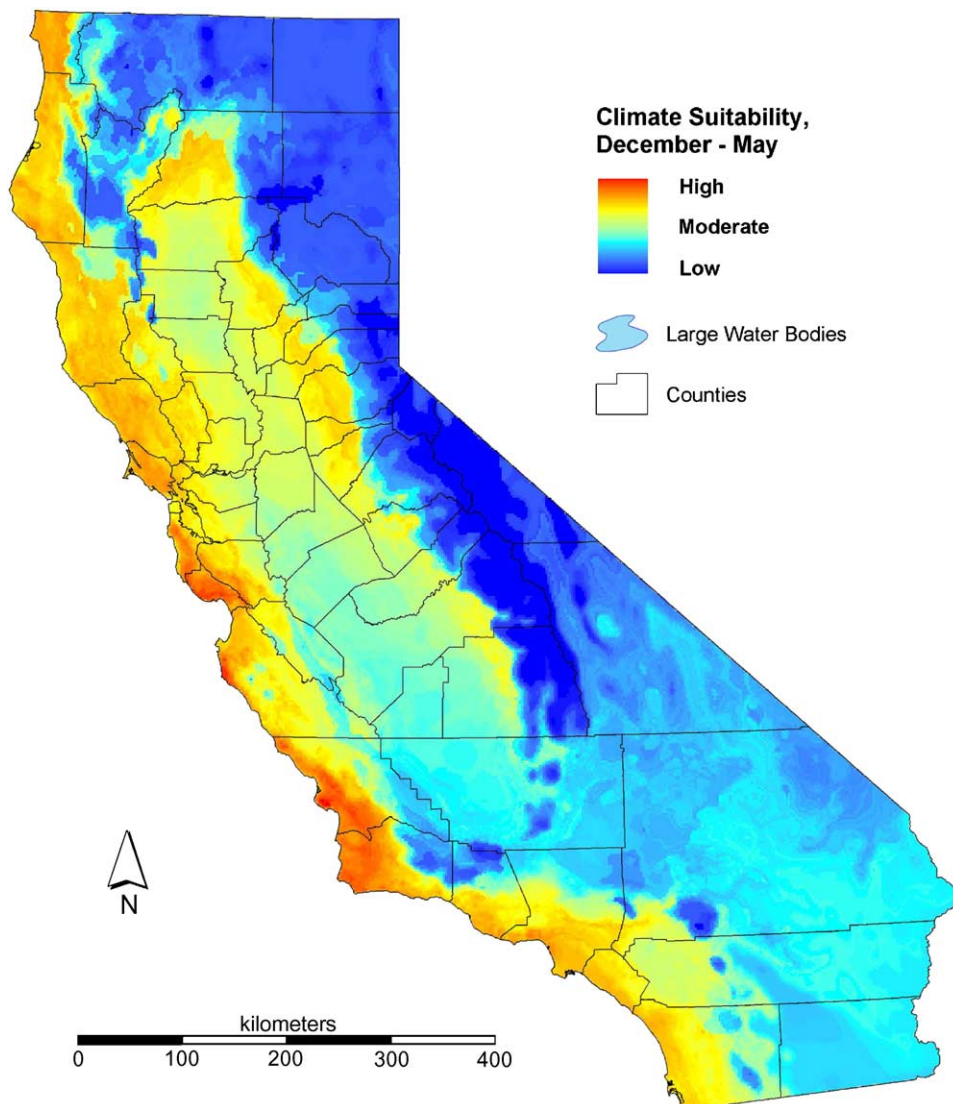

Fig. 5. Six-month average (December–May) climate suitability index, based on weights and ranks assigned to each input climate variable.

2.3. Evaluating the model

The model was evaluated by examining the degree of correspondence between the predicted risk of establishment and 323 field observations of *P. ramorum* occurrence. The 323 observations were compiled from two datasets. In the first dataset, we sampled 130 sites in 39 public land units in 15 counties along the Coast Ranges from Del Norte and Siskiyou counties at the Oregon border south to Santa Barbara County. Plot locations were randomly generated in a GIS and located in the field using the Global Positioning System (GPS) in conjunction with digital aerial photography. Restricting sampling to public land avoided substantial costs involved with seeking permission to access private property. At each plot, two transects (50 m × 10 m) were established running perpendicular to each other from the plot center. The first transect runs in the upslope direction from plot center and the other runs along a bearing 90° clockwise from the first across the slope. Along each transect, samples were collected from all host individuals showing potential disease symptoms from *P. ramorum*. Leaf and woody samples collected in infested counties were sealed in the field, stored in ice, and promptly sent to the California Department of Food and Agriculture for lab analysis of *P. ramorum* presence/absence. Samples collected in uninfested counties were sent to the University of California, Davis. The second dataset includes 183 locations of *P. ramorum* presence discovered by land managers, arborists, and researchers (Fig. 1). This dataset is maintained and updated by the California Oak Mortality Task Force and is verified by California Department of Food and Agriculture.

We compiled the two datasets and used a *T*-test to examine the degree to which predicted risk of establishment (0–100) differs between currently infected and uninfected sites. We also qualitatively examined the distribution of infected sites versus uninfected sites at each risk level.

3. Results

3.1. Geographic patterns

The model predicts spatial and temporal variability of *P. ramorum* establishment and spread risk, based on the combined influence of host species abundance and four temperature and moisture climate variables. Risk is mapped for each month of the pathogen's general reproductive period (December–May) and averaged to generate a cumulative spread risk map (Fig. 6). County divisions are used to report geographic patterns of spread risk, rather than ecological regions, because California and other federal agencies (e.g., APHIS) use the infection status of counties to regulate the movement of host plant material outside an infected area. Geographic patterns of cumulative risk of establishment and spread are summarized below for each risk level.

3.1.1. Very high risk

Nine hundred thirty-seven kilometer square (0.2%) of California's 408,512 km^2 of land area was mapped very high risk for *Phytophthora ramorum* (Fig. 6; Table 7). Very high risk habitats occur in coastal environments within 50 km from the Pacific Ocean. They are concentrated in the northern Coast Range Mountains from Del Norte County extending south into northern Humboldt County, southwestern Humboldt County extending into northwestern Mendocino County, northwestern Sonoma County near Cazadero, and in the Santa Cruz Mountains in San Mateo and Santa Cruz counties. Very high risk habitats generally occur in relatively small areas (mean = 0.2 km^2; Table 8) nested within larger areas mapped high risk (mean = 0.5 km^2). The largest contiguous area of very high risk encompasses 105 km^2 in Santa Cruz and San Mateo counties (Table 8). Humboldt County has the most area mapped very high risk (209.3 km^2; 2.3% of county; Table 7) and Santa Cruz County has the greatest amount as a percent of county area (186.3 km^2; 16.1% of county; Table 7).

Sites mapped as very high risk occur where very high host index values (Fig. 4) coincide with highly suitable climate conditions from December to May (Fig. 5). Precipitation and humidity are generally higher in these coastal environments than at more inland locations and the marine influence moderates winter low and late-spring high temperatures (Fig. 3). Tanoak and redwood generally dominate very high risk forests north of San Francisco. California bay laurel is also common in these forests, along with a diverse assemblage of other foliar hosts. North of Mendocino County, the common occurrence of rho-
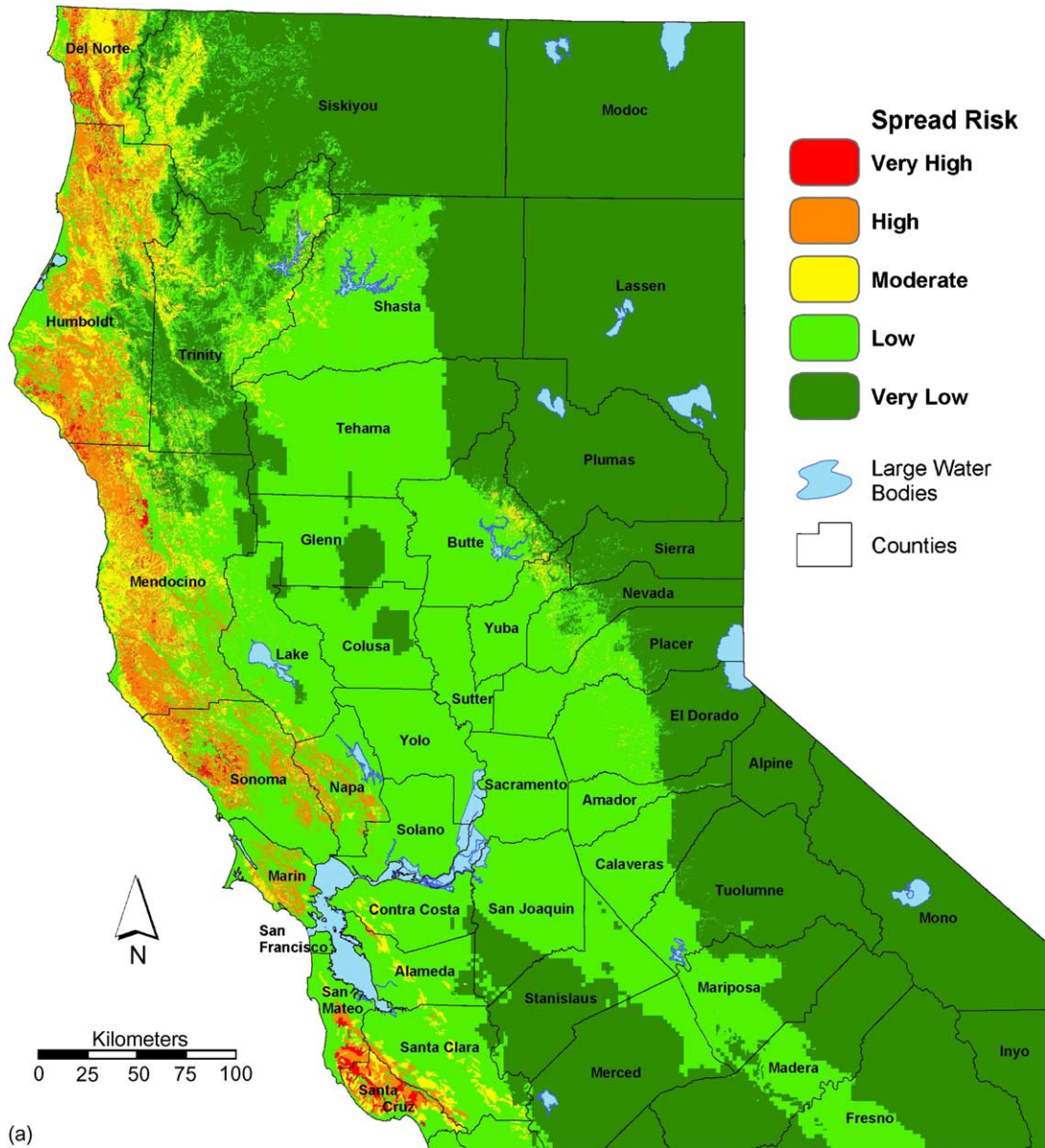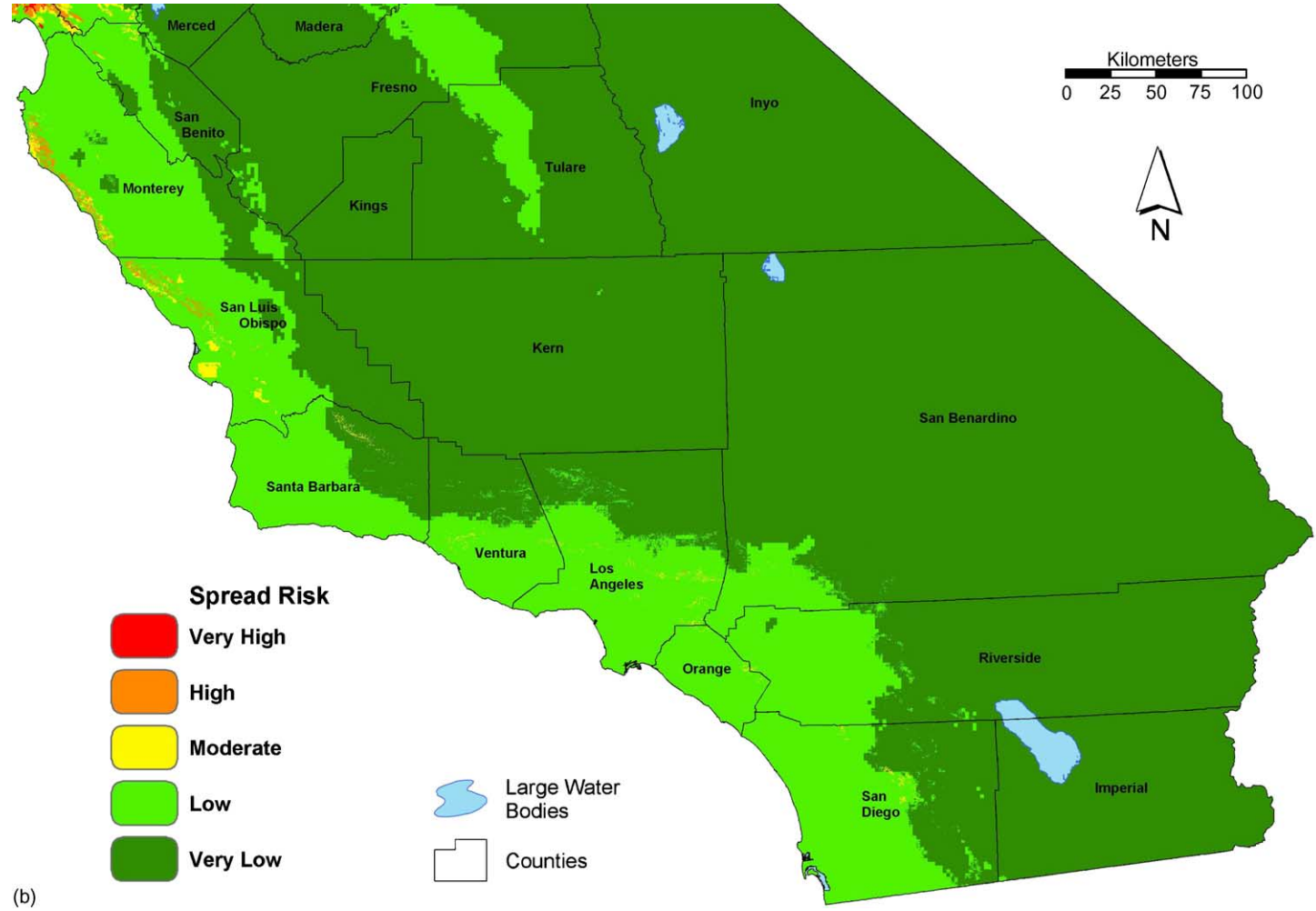
Fig. 6. Six-month average (December–May) predicted spread risk map for *P. ramorum*: (a) northern California; (b) central and southern California.

dodendron also contributes to very high risk levels in these forests. South of San Francisco in the Santa Cruz Mountains in the Central Coast region, very high risk sites generally occur in upland forests dominated by redwood with an abundance of understory bay laurel and tanoak.

3.1.2. High risk

Nine thousand three hundred sixty-eight kilometer square (2.3%) of the state is mapped high risk (Fig. 6; Table 7). High risk areas form a nearly contiguous band through the coastal counties from the Oregon border to northwestern San Luis Obispo County. North

Spread Risk

- Very High
- High
- Moderate
- Low
- Very Low

Large Water Bodies

Counties

(b)

Fig. 6. (Continued).

Table 7
Land area of each spread risk level in California counties, in square kilometers and in percent of total county area

County	Area (km²)	Very high risk		High risk		Moderate risk		Low risk		Very low risk	
		km²	Percentage	km²	Percentage	km²	Percentage	km²	Percentage	km²	Percentage
Alameda	1905	0.0	0.0	11.9	0.6	119.9	6.3	1617.7	84.9	155.2	8.1
Alpine	1925	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1924.9	100.0
Amador	1565	0.0	0.0	0.0	0.0	4.0	0.3	1169.2	74.7	391.6	25.0
Butte	4344	0.0	0.0	5.3	0.1	135.7	3.1	3320.2	76.4	882.5	20.3
Calaveras	2685	0.0	0.0	0.0	0.0	0.0	0.0	1953.1	72.7	732.3	27.3
Colusa	2995	0.0	0.0	0.0	0.0	0.2	0.0	2515.2	84.0	479.1	16.0
Contra Costa	1938	0.0	0.0	8.2	0.4	77.7	4.0	1766.9	91.2	85.3	4.4
Del Norte	2627	188.4	7.2	690.4	26.3	977.0	37.2	572.0	21.8	199.5	7.6
El Dorado	4639	0.0	0.0	0.0	0.0	35.1	0.8	2316.2	49.9	2287.8	49.3
Fresno	15585	0.0	0.0	0.0	0.0	0.0	0.0	2283.3	14.7	13301.7	85.3
Glen	3437	0.0	0.0	0.0	0.0	0.2	0.0	2692.8	78.3	744.4	21.7
Humboldt	9287	209.3	2.3	3193.8	34.4	2370.0	25.5	2626.4	28.3	887.9	9.6
Imperial	11608	0.0	0.0	0.0	0.0	0.0	0.0	10.4	0.1	11597.3	99.9
Inyo	26488	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26488.2	100.0
Kern	21138	0.0	0.0	0.0	0.0	0.0	0.0	4.7	0.0	21133.3	100.0
Kings	3604	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3603.9	100.0
Lake	3443	0.0	0.0	50.2	1.5	102.3	3.0	3115.6	90.5	175.3	5.1
Lassen	12225	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12225.3	100.0
Los Angeles	10241	0.0	0.0	2.5	0.0	62.1	0.6	5802.3	56.7	4374.5	42.7
Madera	5577	0.0	0.0	0.0	0.0	0.0	0.0	1140.8	20.5	4436.1	79.5
Marin	1356	0.0	0.0	336.4	24.8	110.6	8.2	909.4	67.0	0.0	0.0
Mariposa	3788	0.0	0.0	0.0	0.0	0.0	0.0	1978.1	52.2	1810.3	47.8
Mendocino	9100	151.3	1.7	2431.6	26.7	2073.5	22.8	3476.3	38.2	966.8	10.6
Merced	5107	0.0	0.0	0.0	0.0	0.0	0.0	922.0	18.1	4185.0	81.9
Modoc	10886	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10886.5	100.0
Mono	8111	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8111.3	100.0
Monterey	8584	0.1	0.0	170.0	2.0	122.7	1.4	7029.4	81.9	1262.0	14.7
Napa	2042	0.0	0.0	400.3	19.6	94.1	4.6	1547.2	75.8	0.0	0.0
Nevada	2524	0.0	0.0	0.2	0.0	35.7	1.4	1080.7	42.8	1407.2	55.8
Orange	2070	0.0	0.0	0.0	0.0	12.2	0.6	2057.6	99.4	0.0	0.0
Placer	3885	0.0	0.0	0.0	0.0	36.7	0.9	1922.0	49.5	1926.5	49.6
Plumas	6769	0.0	0.0	0.0	0.0	0.4	0.0	23.9	0.4	6744.7	99.6
Riverside	18915	0.0	0.0	0.0	0.0	4.7	0.0	4634.5	24.5	14276.2	75.5
Sacramento	2578	0.0	0.0	0.0	0.0	0.0	0.0	2578.3	100.0	0.0	0.0
San Benito	3602	0.0	0.0	1.7	0.0	25.7	0.7	1580.9	43.9	1993.6	55.3
San Bernardino	52073	0.0	0.0	0.2	0.0	8.0	0.0	1986.2	3.8	50078.7	96.2
San Diego	10965	0.0	0.0	0.0	0.0	34.7	0.3	6587.6	60.1	4342.7	39.6
San Francisco	122	0.0	0.0	0.0	0.0	0.0	0.0	121.6	100.0	0.0	0.0
San Joaquin	3694	0.0	0.0	0.0	0.0	0.0	0.0	2873.4	77.8	820.6	22.2
San Luis Obispo	8598	0.0	0.0	102.2	1.2	225.2	2.6	4891.3	56.9	3379.1	39.3
San Mateo	1176	85.7	7.3	170.8	14.5	82.1	7.0	837.2	71.2	0.0	0.0
Santa Barbara	6616	0.0	0.0	1.5	0.0	29.3	0.4	4586.6	69.3	1998.9	30.2
Santa Clara	3362	0.1	0.0	145.6	4.3	384.2	11.4	2585.6	76.9	246.8	7.3
Santa Cruz	1158	186.3	16.1	361.3	31.2	256.1	22.1	354.4	30.6	0.0	0.0
Shasta	9964	0.6	0.0	0.6	0.0	263.1	2.6	5416.6	54.4	4283.6	43.0
Sierra	2492	0.0	0.0	0.2	0.0	1.9	0.1	45.6	1.8	2443.8	98.1
Siskiyou	16440	0.0	0.0	10.4	0.1	778.3	4.7	1460.8	8.9	14190.1	86.3
Solano	2192	0.0	0.0	9.3	0.4	3.5	0.2	2179.1	99.4	0.0	0.0
Sonoma	4117	115.1	2.8	1223.3	29.7	347.2	8.4	2431.6	59.1	0.0	0.0
Stanislaus	3923	0.0	0.0	0.0	0.0	0.0	0.0	1531.6	39.0	2391.4	61.0
Sutter	1577	0.0	0.0	0.0	0.0	0.0	0.0	1576.8	100.0	0.0	0.0
Tehama	7672	0.0	0.0	0.3	0.0	53.4	0.7	5764.2	75.1	1853.8	24.2

Table 7 (*Continued*)

County	Area (km^2)	Very high risk		High risk		Moderate risk		Low risk		Very low risk	
		km^2	Percentage	km^2	Percentage	km^2	Percentage	km^2	Percentage	km^2	Percentage
Trinity	8307	0.0	0.0	36.2	0.4	943.3	11.4	3159.2	38.0	4168.8	50.2
Tulare	12533	0.0	0.0	0.0	0.0	0.0	0.0	1623.3	13.0	10909.3	87.0
Tuolumne	5891	0.0	0.0	0.0	0.0	0.0	0.0	950.6	16.1	4940.1	83.9
Ventura	4749	0.0	0.0	0.0	0.0	20.6	0.4	2603.1	54.8	2125.2	44.8
Yolo	2649	0.0	0.0	0.0	0.0	0.0	0.0	2648.9	100.0	0.0	0.0
Yuba	1667	0.0	0.0	3.0	0.2	79.7	4.8	1449.2	86.9	134.8	8.1
Total state	408512	936.9	0.2	9368	2.3	9912	2.4	120312	29.5	267984	65.6

of San Francisco, high risk habitat extends up to 60 km inland in Sonoma and Napa counties north to the Oregon border. South of San Francisco, high risk areas occur in a narrow strip within about 15 km from the coast from central San Luis Obispo County to central Monterey County. The strip broadens to about 30 km from the coast in Santa Cruz, Santa Clara, and San Mateo Counties. Large areas of low risk interrupt this band at the border of Sonoma and Marin Counties, between Marin and central San Mateo Counties, and in the Monterey Bay area in northern Monterey County. The largest contiguous area of high risk encompasses 1532 km^2 in Humboldt and Mendocino Counties (Table 8). Humboldt County has both the most total area mapped as high risk (3193.8 km^2) and the most area mapped as high risk as a percent of county area (34.4%; Table 7).

High risk habitats occur where moderately high host index values (Fig. 4) correspond with moderately to highly suitable climatic conditions from December to May (Fig. 5). High risk habitats are typically mixed hardwood and mixed evergreen forests including abundant bay laurel, tanoak, rhododendron and/or redwood. Douglas fir and oak species often dominate these communities. Eight-nine percent of all high risk

Table 8
Statewide statistics for area mapped in the five predicted spread risk levels

Risk	Area (km^2)			
	Maximum	Minimum	Mean	S.D.
Very high	105	0.01	0.2	1.8
High	1532	0.01	0.5	16.4
Moderate	542	0.01	0.3	4.8
Low	111330	0.01	3.8	618.6
Very low	260168	0.01	25.6	2543.4

habitats occur in the Coast Ranges north of San Francisco with another 10% in the central coast region between San Francisco and northwestern San Luis Obispo County. Small areas of high risk also occur within larger areas of moderate risk in the Sierra Nevada foothills in Butte (5.3 km^2) and Yuba (3.0 km^2; Table 7) Counties. High risk habitats in this region are often dominated by black oak with co-occurring species of tanoak, bay laurel, and madrone. In southern California, a few high risk habitats also occur in the Santa Ynez Mountains in Santa Barbara County (1.5 km^2) and in the San Gabriel Mountains in Los Angeles County (2.5 km^2; Table 7). These locations occur in small patches (<32 ha) dominated by bay laurel in north-facing canyons with moderate to high climate suitability (Fig. 5).

3.1.3. Moderate risk

Nine thousand nine hundred twelve kilometer square (2.4%) of the state is mapped moderate risk (Fig. 6; Table 7). Humboldt County has the most area mapped moderate risk (2370.0 km^2) and Del Norte County has the most area as a percent of county area (37.2%). Moderate risk habitats are generally smaller in area (mean = 0.3 km^2) than high risk habitats (Table 8). In the Coast Ranges, moderate risk habitats are interspersed with the coastal band of high and very high risk habitats, occurring where host index values are lower (Fig. 4) and/or climate is less suitable (Fig. 5). In the Coast Ranges north of San Francisco, moderate risk extends up to 150 km inland in western Siskiyou County (778.3 km^2; 4.7%), Trinity County (943.3 km^2; 11.4%), western Shasta County (263.1 km^2; 2.6%), northwestern Tehama County (53.4 km^2; 0.7%), Lake County (102.3 km^2; 3.0%), and Napa County (94.1 km^2; 4.6%; Table 7). South of

San Francisco, moderate risk extends up to 75 km inland in the counties of Contra Costa (77.7 km^2; 4.0%), Alameda (119.9 km^2; 6.3%), Santa Clara (384.2 km^2; 11.4%), and northern San Benito (25.7 km^2; 0.7%; Table 7).

Other places of moderate risk are scattered across the state in smaller areas with moderate to high climate suitability (Fig. 5) and moderately abundant host vegetation. This includes mixed forests in the Sierra Nevada foothills in Butte (135.7 km^2; 3.1%), Yuba (79.7 km^2; 4.8%), and Nevada (35.7 km^2; 1.4%) counties with some tanoak, bay laurel, Douglas fir, and madrone; mixed forests in Placer (36.7 km^2; 0.9%) and El Dorado (35.1 km^2; 0.8%) counties with some bay laurel, big leaf maple, and Douglas fir; mixed evergreen forests with moderately abundant bay laurel and/or tanoak in north-facing canyons in the Sierra Madre in northern Santa Barbara County (29.3 km^2; 0.4%); and mixed evergreen forests with moderately abundant bay laurel in the San Gabriel Mountains in Los Angeles County (62.1 km^2; 0.6%) and in the Peninsular Ranges in Orange (12.2 km^2; 0.6%), Riverside (4.7 km^2; 0.02%), and San Diego (34.7 km^2; 0.3%) counties (Table 7; Fig. 6).

3.1.4. Low risk

A 120,312 km^2 (29.5%) of the state is mapped low risk (Fig. 6; Table 7). Low risk areas are frequently interspersed with high risk habitats in the Coast Ranges from the Oregon border south to northern San Luis Obispo County. Most low risk habitats have suitable climate in this area (Fig. 5), but few or no foliar host species are mapped (Fig. 4) due to the presence of coastal scrub, chaparral, grassland, or urban development. Low risk habitats are generally larger in area (mean = 3.8 km^2) than higher risk habitats (Table 8). A large zone of low risk occurs within 100 km of the southern coast from Santa Barbara County south to San Diego County (Fig. 6). Climate in this zone is moderately to highly suitable (Fig. 5), but few to no hosts are mapped. Other significant areas of low risk exist inland in the northern Central Valley from Shasta County to Sacramento County, in the eastern Coast Ranges from southwestern Shasta County south to San Luis Obispo County, and the southern Sierra Nevada foothills from San Joaquin County south to Tulare County (Fig. 6). These three regions have moderate climate suitability from

December to March (Fig. 5), but generally little or no foliar hosts (Fig. 4).

3.1.5. Very low risk

A 267,984 km^2 (65.6%) of the state is mapped very low risk (Fig. 6; Table 7). Very low risk habitats typically occur at cold, high elevation locations or hot, dry inland locations (Figs. 3 and 5), and generally encompass considerably more area (mean = 25.6 km^2; maximum = 260,168 km^2) than the other risk levels (Table 8). Cold, higher elevation areas (>1200 m) primarily occur in the Sierra Nevada from Plumas County south to Kern County, the Modoc Plateau including Modoc and Lassen counties, the Cascades including eastern Siskiyou and Shasta counties, the Klamath including western Siskiyou County and Trinity County, and the northern Coast Range from Del Norte County south to northeastern Lake County. Hot, dry inland areas mapped very low risk occur in the southern Central Valley from San Joaquin County south to Kern County and in deserts in southeastern California primarily including Inyo, San Bernardino, Riverside, San Diego, and Imperial counties. There are no foliar host species mapped in 91% of the very low risk areas, with the exception of a few species (e.g., Douglas fir, shrub from of tanoak) mapped in cold, higher elevation inland locations (Fig. 4). The following seven counties were mapped entirely very low risk (100%): Alpine, Inyo, Kern, Kings, Lassen, Modoc, Mono (Table 7).

3.2. Model evaluation

P. ramorum was found in only 9 of the 130 randomly located field plots surveyed in the Coast Ranges during summer 2003, making a total of 192 infected locations and 121 locations that *P. ramorum* was not detected (Table 9). A *T*-test showed that modeled risk (0–100) is significantly higher at currently infested locations ($n = 192$) than at currently uninfested locations ($P < 0.01$). Most of the 192 infected locations were mapped high risk (59%), followed by low risk (21%), moderate risk (15%), very high risk (4%), and very low risk (0%; Table 9). Most of the 121 locations that *P. ramorum* was not detected were mapped low risk (34%), followed by moderate risk (25%), high risk (21%), very low risk (18%), and very high risk (2%; Table 9).

Table 9
Model evaluation: distribution of field sites with *P. ramorum* detected versus not detected by predicted spread risk level

Risk class	*P. ramorum*	
	Detected, $n = 192$ (%)	Not detected, $n = 121$ (%)
Very high	8 (4.2)	2 (1.7)
High	114 (59.4)	26 (21.4)
Moderate	29 (15.1)	30 (24.8)
Low	41 (21.3)	41 (33.9)
Very low	0 (0.0)	22 (18.2)

4. Discussion

Phytophthora ramorum is currently established in coastal forests over a distance of 750 km although the greatest area of establishment covers about 450 km (Fig. 1). The risk of continued spread and establishment of *P. ramorum* in California reflects spatial variability in climate and host vegetation. The model described here matches field-based observations of disease incidence. However, *P. ramorum* was not detected at 48% of field samples mapped moderate risk or higher. This result suggests that there is a large amount of currently uninfested area in California facing substantial infection risk based on our model criteria. This includes, in particular, the broad band of high risk north of Sonoma County to the Oregon border, the narrow band of high risk south of central Monterey County south to central San Luis Obispo County, and scattered areas of moderate and high risk in the Sierra Nevada foothills in Butte and Yuba counties (Fig. 6).

The data show that 21% of the locations where *P. ramorum* is currently present are mapped low risk. This type of under-prediction occurs in three situations. First, digital *ortho*-rectified air photos indicate that small patches of host vegetation sometimes occur, but are mapped as non-host vegetation like grassland, developed, and chaparral, because the patch area of host vegetation is smaller than the minimum mapping unit of CalVeg (1 ha) and Gap (100 ha) data. Thus, the disease can occur at a finer scale than the model's input variables. There are likely also cases where the vegetation data is incorrectly mapped from satellite imagery. We are currently using 9117 USDA Federal Inventory Analysis (FIA) plots of plant community structure to examine the accuracy and effectiveness of the CalVeg and Gap datasets for mapping the distribu-

tion and abundance of *P. ramorum* host species. A third source of error may be related to GPS accuracy. Many of the *P. ramorum* detected locations in the dataset maintained by the California Oak Mortality Task Force were collected using recreational-grade GPS receivers with substantial potential for locational error. We have observed that this error causes some locations to not overlay precisely with the correct grid cells in the spread risk map.

Sudden oak death is an emerging forest disease with only a limited understanding of the processes that may contribute to disease establishment and spread. The model presented here examines the likelihood that a site is invaded, *P. ramorum* is established and subsequently the site serves as a source of inoculum for further invasion in the local area or via long-distance dispersal. A site with few, or no, foliar hosts would have low "spread risk" because it is less likely to serve as a source of inoculum for further spread. However, such a site (e.g., oak only) may still be invaded and the pathogen established for a short period of time. Long-term establishment of a *P. ramorum* population requires the disease to be transmitted to at least one other susceptible individual.

There are multiple spread pathways for *P. ramorum*. Natural spread is most likely over relatively short distances via rainsplash or wind-driven rain from inoculum produced on foliage of infected plants (Davidson et al., 2002). It is possible that longer dispersal distances may also be achieved during rare storm events. Other potential dispersal pathways for natural spread of *P. ramorum* have been identified, but their epidemiological importance is unknown at this time. *P. ramorum* can be recovered during the rainy season from soil (Davidson et al., 2002) and it is possible that a variety of animals (e.g., deer) may disperse spores through movement of soil-borne propagules. In addition, *P. ramorum* is commonly recovered from streams that may also serve for long distance dispersal.

Humans probably have a considerable influence on the long-distance spread of *P. ramorum*. Movement of ornamental plants such as rhododendron, camellia, and viburnum is the most likely source of long distance spread. Spread of *P. ramorum* via ornamentals has occurred in Europe and recently in the United States. Although the evidence is anecdotal, initial outbreaks of sudden oak death have been associated with plantings of ornamental rhododendron under

native vegetation (Rizzo et al., 2002a). Environmental conditions for establishment of *P. ramorum* in nurseries will be similar to that in natural plant communities; i.e., presence of susceptible hosts and suitable temperature and moisture conditions for sporulation. However, in this artificial environment the local plant community is not taken into account and the pathogen can be established in ''low risk'' areas. Recently, *P. ramorum* was found in a nursery in Stanislaus County in an area that is mapped low risk and very low risk. Other potential sources of human mediated spread of *P. ramorum* include movement of infected soil and green waste.

As research progresses, incorporation of additional factors, such as land-use history, may enhance the model's predictive power. Forest ecosystems in California have undergone substantial changes in structure and composition as a result of land-use practices, such as grazing, fire suppression, logging, and intensive agriculture. Because of these tremendous changes, and their impacts on forest health, we hypothesize that land-use history plays a critical role in determining the susceptibility of an area to the establishment of *P. ramorum.*

Differences in susceptibility to *P. ramorum* among host populations may influence establishment and spread of the pathogen across the landscape. If significant, population susceptibility could be mapped as a variable and used to improve model performance. A preliminary study by Hüberli and Garbelotto (personal communication) shows that infection rates on bay laurel leaves in controlled laboratory conditions can significantly vary among different populations across the state.

Research is also needed to determine the degree to which the spatial arrangement of host vegetation across a landscape influences establishment and spread. Like other dispersing organisms, it is likely that small stands and isolated stands of host vegetation are less likely to be colonized successfully by *P. ramorum* than those that are large or close to other stands of host vegetation.

Data on the geographic distribution of closely related *Phytophthora* species with similar habitat requirements as *P. ramorum* may provide an additional variable to help forecast the likelihood a location becomes infected in the future. For example, *Phytophthora nemorosa* is a newly discovered, probably

native species that is also associated with cankers on oaks and leaf infections on bay laurel (Hansen et al., 2003). Like *P. ramorum*, *P. nemorosa* also occurs in mixed forests in coastal environments, but has a much broader known range than *P. ramorum*, occurring from Big Sur, California to Coos Bay, Oregon. *P. nemorosa* does not seem to be as virulent as *P. ramorum*. It is typically only associated with single tree mortality of oaks and tanoak and leaf infections on bay laurel (Hansen et al., 2003).

The climate data (1961–1990 monthly averages) used in the model effectively characterizes general moisture and temperature regimes suitable for *Phytophthora ramorum*. However, the pathogen does not sporulate and spread in response to average climate. We hypothesize that *P. ramorum* likely spreads in response to specific weather events, such as heavy late-spring rain. Heavy late-spring rain that occurred during the 1998 El Nino events, in particular, may have played an influential role in determining the current distribution of *P. ramorum* in California. Work is in progress on using near real-time weather mapping to predict spatial patterns of potential pathogen activity and spread based on individual weather events, rather than average climate. Growth chamber experiments are also underway to better understand infection rates on various hosts as a function of moisture and temperature. This information will be valuable for refining the scores and weights assigned to each variable in model development. This information may also be used with spatial modeling techniques to develop a cellular automata model of disease spread through time based on statistical probabilities of dispersal and infection processes.

In conclusion, the model's predictions of spread risk are consistent with disease severity observed in the field. Based on our results, there are also an alarming number of uninfected forest ecosystems in California, which face considerable risk of infection by *Phytophthora ramorum*. It is essential that we develop effective management strategies for susceptible forests and that we prevent long distance spread of the pathogen, a threat that could drastically alter forests in California. Although much remains to be learned about the ecology and epidemiology of the sudden oak death disease (Rizzo and Garbelotto, 2003), the model presented here provides a simple, yet effective management tool to target threatened

forests for early-detection monitoring and protection. This strategy may play an especially important role in identifying isolated infections before they have established significantly.

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