



Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Spatial estimation of the density and carbon content of host populations for *Phytophthora ramorum* in California and Oregon

Sanjay Lamsal^a, Richard C. Cobb^b, J. Hall Cushman^c, Qingmin Meng^{a,1}, David M. Rizzo^b, Ross K. Meentemeyer^{a,*}

^a Department of Geography and Earth Sciences, University of North Carolina, Charlotte, NC 28223, USA

^b Department of Plant Pathology, University of California, Davis, CA 95616, USA

^c Department of Biology, Sonoma State University, Rohnert Park, CA 95404, USA

ARTICLE INFO

Article history:

Received 18 February 2011

Received in revised form 17 May 2011

Accepted 21 May 2011

Available online xxxx

Keywords:

Forest inventory

Landscape epidemiology

Tree mortality

Biomass

Forest carbon

Species distribution model

ABSTRACT

Outbreak of the emerging infectious disease sudden oak death continues to threaten California and Oregon forests following introduction of the exotic plant pathogen *Phytophthora ramorum*. Identifying areas at risk and forecasting changes in forest carbon following disease outbreak requires an understanding of the geographical distribution of host populations, which is unknown. In this study, we quantify and map the population density and carbon contents of five key host species for *P. ramorum* in California and Oregon, including four hosts killed by the pathogen (*Notholithocarpus densiflorus*, *Quercus agrifolia*, *Quercus kelloggii* and *Quercus chrysolepis*) and the foliar host *Umbellularia californica* which supports high sporulation rates. We integrate multiple sources of vegetation data, assembled from sparsely distributed (regional-scale) forest inventory and analysis (FIA) plots and more densely distributed (landscape-scale) plots for monitoring sudden oak death, and develop spatial prediction models based on correlation with environmental variables and spatial dependencies in host abundance. We estimate that 1.8 billion *N. densiflorus* trees (68 Tg C) and 2.6 billion *Quercus* host trees (227 Tg C) occur across 3.9 and 17.7 million ha of their respective habitat. A total of 436 million *U. californica* trees (14 Tg C) occur across 4.2 million ha which frequently overlap with *Quercus* and *N. densiflorus* host populations. Combination of landscape-scale data with FIA data resulted in more accurate estimation of host populations and their carbon contents. Forests of northern California and southwest Oregon have the highest concentration of the most susceptible hosts along with climatic conditions that favor pathogen spread. This study represents the first spatially-explicit estimate of *P. ramorum* host populations and their carbon contents which exceed previously published estimates. Our results will inform landscape- to regional-scale models of disease dynamics and guide management decisions regarding ecosystem impacts including risk of C release following widespread tree mortality.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Northern hemisphere forests are significant global sinks of atmospheric greenhouse gasses, particularly CO₂ (Houghton, 1999; Goodale et al., 2002), and key in global to regional efforts to reduce atmospheric CO₂ concentration such as the Kyoto Protocol and AB32 – a legislative effort to reduce CO₂ emissions in the state of California (Hanemann, 2007). Nations with large forested landmasses in the northern hemisphere such as Canada and Russia rely on their considerable forest carbon sinks to fulfill carbon emission commitments, but recent works have shown that the expected

carbon sequestration can be threatened by regional scale disturbances including insect and pathogen outbreak (Breshears and Allen, 2002; Kurz et al., 2008b). The importance of insect- and pathogen-related disturbances in regulating forest carbon sequestration is likely to increase over the next century due to the potential impacts of climate change on the severity and frequency of outbreaks (Bergot et al., 2004) and the acceleration of exotic insect and pathogen introduction resulting from global trade (Brasier, 2008).

Pioneering work including Odum (1969) and Likens et al. (1970) spawned a rich body of research focusing on forest disturbances and their consequences for nutrient cycling. Until recently, insect and pathogen outbreaks have received substantially less study compared to disturbances such as fire and forest harvest (Castello et al., 1995; Hunter et al., 2001; Ellison et al., 2005). Lovett et al. (2006) suggested a general framework for predicting impacts of

* Corresponding author. Tel.: +1 704 687 5944.

E-mail address: rkmeente@unc.edu (R.K. Meentemeyer).

¹ Current address: Department of Geography and Planning, University at Albany, Albany, NY 12222, USA.

emerging outbreaks where host characteristics such as phytosociology, degree of local dominance, and insect or pathogen–host interaction are crucial to the dynamics of outbreak. These expectations are supported by theoretical models focusing on spatial distribution of host species and pathogen epidemiology (Holt and Boulinier, 2005). Recent work demonstrating the sensitivity of forest carbon sequestration to insect and pathogen outbreak (Kurz et al., 2008a,b; Albani et al., 2010) illustrates the increasing importance of understanding how outbreak alters landscapes and consequently landscape to regional carbon dynamics.

The emerging infectious disease sudden oak death, caused by the exotic plant pathogen *Phytophthora ramorum*, is an example of a destructive biological invasion that threatens regional-scale mortality of several ecologically important tree species including tanoak (*Notholithocarpus densiflorus*), California black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*), coast live oak (*Quercus agrifolia*) and Shreve's oak (*Quercus parvula* var. *shrevei*) in western north American forests. The range of host plants used by *P. ramorum* is broad, with over a 100 known host species from disparate plant taxa including herbaceous species and overstory trees (Rizzo et al., 2005). However, the pathogen's ability to cause disease and sporulate from infected hosts is highly variable. Infection of oaks can cause mortality, but sporulation is very rare on oak species and thus the genus appears to act as a dead-end host (Davidson et al., 2005). Tanoak has suffered the greatest local- and landscape-level decline due to an apparent lack of host resistance and sporulation on leaf and twig infections which are sufficient to cause disease locally and spread the pathogen regionally (Rizzo et al., 2005; Davidson et al., 2008; Meentemeyer et al., 2008a). In contrast, infection of California bay laurel (*Umbellularia californica*) results in prolific sporulation during warm spring rain events, but has no documented deleterious impacts on this host at the physiological or population level (Davidson et al., 2008; DiLeo et al., 2009; Cobb et al., 2010). Thus, knowing the distribution of bay laurel is also critical to determining *P. ramorum* spread and tree mortality, especially within oak communities (Meentemeyer et al., 2008b; Brown and Allen-Diaz, 2009).

Regional spread risk models predict that *P. ramorum* could undergo considerable range expansion over the next 20 years due to high host contagion and suitable weather conditions in California and Oregon (Meentemeyer et al., 2008a, 2011; Václavík et al., 2010). However, our ability to forecast large-scale impacts of disease on declines in tree diversity and forest carbon pools has been impeded by a lack of spatially-explicit data on the density and carbon content of *P. ramorum* host populations. To date, landscape- to regional-scale models of disease risk have relied on remotely sensed maps of host distribution in the form of unitless indices of host presence and abundance (e.g. Meentemeyer et al., 2004; Václavík et al., 2010) or as vegetation community types (e.g. Meentemeyer et al., 2008c) rather than field-based measurements of stem density and size. A quantitative assessment of *P. ramorum* host populations is also needed to guide forest management and policy decisions. For example, is the number and carbon content of host trees in California and Oregon large enough to justify deployment of regional-scale control strategies, which are expensive and challenging to implement? Geographically speaking, where are the forests with the greatest host densities and carbon contents?

In this study, we quantify and map the spatial distribution of tree populations and carbon contents of five key host species of *P. ramorum* (tanoak, coast live oak, canyon live oak, California black oak and bay laurel) in California and Oregon forests. We integrated vegetation data from sparsely distributed regional-extent forest inventory and analyses (FIA) plots (Barrett et al., 2006) and densely distributed landscape-extent plots designed to monitor the spread of *P. ramorum* at local to landscape scales (Meentemeyer et al.,

2008a, 2008b; Cobb et al., 2010). We examine the hypothesis that vegetation data assembled in densely distributed plots are critical to improve spatial prediction of host communities due to the highly heterogeneous nature of these vegetative communities (Davis et al., 2010). An understanding of the distribution of host species for sudden oak death is needed to prioritize regional-scale strategies for prevention and control of disease as well as provide data for large-scale models of disease spread and ecosystem impacts.

2. Materials and methods

2.1. Study system

Our study focused on the geographic range of five key *P. ramorum* host species in California and Oregon (Fig. 1) including three hosts that develop lethal stem cankers (coast live oak, California black oak, and canyon live oak), bay laurel which develops sporulation-supporting leaf infections, and tanoak which develops both lethal stem cankers and sporulation-supporting leaf infections. For simplicity, we term all four hosts that develop stem cankers 'canker hosts' and bay laurel as a 'foliar host'; however, from an epidemiological perspective both bay laurel and tanoak spread the pathogen, while the canker hosts are dead ends for transmission (Davidson et al., 2005). Together these species cover a broad region of tremendous physiographic variability with diverse soil conditions and complex disturbance regimes (Ohmann et al., 2007). Forested landscapes containing *P. ramorum* hosts occur from sea level to 3862 m in elevation. The region has Mediterranean-type climatic conditions with cool wet-winters and warm dry summers that exhibit substantial variability in average annual precipitation (17–458 cm) and average temperature (minimum = −5.7 to 12.7 °C;

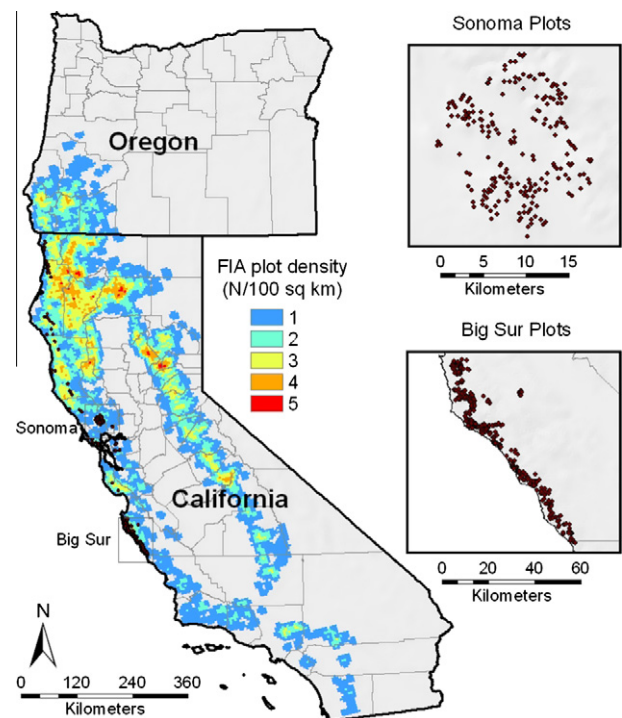


Fig. 1. Geographic range of *Phytophthora ramorum* host species and the spatial distribution of field plots used in this study. Forest inventory analysis (FIA) plots are depicted as the number of plots per 100 sq km which contain one of the five host species mapped by this study. FIA plots are sparsely distributed in many coastal forests where hosts of *P. ramorum* are known to be abundant. The inset shows the distribution of spatially intensive monitoring plots designed to monitor the spread of *P. ramorum* in Sonoma County and the Big Sur region.

maximum = 5.1 to 29.8 °C) depending on elevation, latitude, and proximity to the coast (Daly et al., 2001).

Host species distribution in California and Oregon is spatially variable and highly heterogeneous at local scales. Bay laurel is a common component of redwood, oak, and mixed evergreen forests in coastal habitats from San Diego County, California to Currie County, Oregon. Tanoak has coastal populations from Santa Barbara County, California to southwestern Oregon with a disjunct population in the northern foothills of the Sierra Nevada. Tanoak reaches its greatest density and contagion in Del Norte and Humboldt Counties in California and is a major contributor to risk of *P. ramorum* establishment and disease impacts in these regions (Meentemeyer et al., 2004; Rizzo et al., 2005). Both bay laurel and tanoak tend to be more abundant within the coastal fog belt although bay laurel often also occurs in dryer, hotter inland forests. Oak communities contain several susceptible species of oaks which vary in their susceptibility to infection and subsequent impact by *P. ramorum* (Dodd et al., 2005; McPherson et al., 2010). Coast live oak and California black oak have a high degree of overlap with bay laurel which has resulted in considerable decline of these two species in infected regions (Kelly and Meentemeyer, 2002; Rizzo et al., 2005; Brown and Allen-Diaz, 2009). Shreve's oak (*Q. parvula* var. *shrevei*) is a recently recognized species that appears to be more common in coastal California forests than previously reported. This species is closely related to coast live oak and California black oak, and shares the evergreen habit with coast live oak (Dodd and Kashani, 2003). *P. ramorum* has previously been recorded as primarily infecting the foliage and small twigs of understory canyon live oak (Murphy and Rizzo, 2003) but recently *P. ramorum* was found to cause cankers on the boles of large overstory trees in central California (Swiecki and Aram, unpublished). Therefore, we have included it in the present study as a canker host.

2.2. Datasets

2.2.1. Forest inventory and analysis field plots

We used vegetation data assembled in the FIA plots to estimate distribution and abundance of the five host species across their geographic range. This extensive national plot network, with approximately one plot per 2400 ha, is designed to monitor the status and trends of forested ecosystems across the US (Smith, 2002; Barrett et al., 2006; Fried and Zhou, 2008). We extracted information on the density and size of host trees surveyed in California and Oregon between 2001 and 2007 (Fig. 1). For geospatial modeling, we used exact co-ordinates of plot locations and not the more commonly available “fuzzed and swapped” co-ordinates. In addition to providing rigorously collected data on species composition and structure, FIA data provide estimates of above-ground dry biomass of each tree (DRYBIOT); tree carbon content was taken as half of dry biomass (Deusen, 2010). For plots that had one of the five *P. ramorum* hosts ($n = 8138$), we expanded individual tree and its carbon content to plot level using the expansion factor – trees per acre (TPA), which is a conversion factor that scales each tree within a plot to a per-acre basis (USDAFS, 2008). Finally, we converted the number of trees and carbon contents within each plot to a per hectare basis.

2.2.2. Sudden oak death plot network

We compiled data from three separate plot networks that were established between 2001 and 2007 to monitor the spread and impacts of sudden oak death at local to landscape scales in northern and central California (Fig. 1; Maloney et al., 2005; Murphy and Rizzo, 2006; Cushman and Meentemeyer, 2008; Meentemeyer et al., 2008a,b; Cobb et al., 2010; Metz et al., 2011). These plot networks consist of 280 plots in the Big Sur ecoregion (plot size = 500 m²), 202 plots in Sonoma County (225 m²), and 515

plots across coastal regions of north-central California (500 m²). Shreve's oak appears not to have been recorded in FIA plots, including areas where it is fairly common. This is most likely due to the difficulty of distinguishing this species from coast live oak. Therefore, we assume that the coast live oak numbers reported by FIA also include Shreve's oak. Because of this, we have treated coast live oak and Shreve's oak as a single host in our plot network in order to be consistent with the FIA data. In each of these 997 plots, all stems ≥ 1 cm were measured for diameter at breast height (1.3 m; dbh), identified to species, and symptoms of *P. ramorum* infection recorded. For each plot we estimated the above-ground biomass of individual trees greater than 2.5 cm dbh using generalized allometric equations developed by Jenkins et al. (2003). These generalized equations provide biomass estimations suitable for regional-to continental-scale applications but may be less accurate compared to more locally calibrated equations. For example, Jenkins et al. (2004) report equations specific for several common oak species which often have higher wood specific gravity than assumed by the general equations (Jenkins et al., 2003). Our approach may underestimate biomass of the focal species by a factor that scales linearly with the actual specific gravity for a respective species (Cobb, 2010) but result in conservative estimates of host biomass and carbon content. Finally, we extrapolated tree density and carbon content for each host species to per ha basis.

2.3. Environmental variation

Using data assembled in plot networks described above, we assessed the influence of 12 environmental variables on the distribution of host populations and their biomass accumulation (Table 1). Within a geographic information system (GIS), we calculated four topographical variables: elevation, slope gradient, topographic moisture index (TMI) and potential solar insolation (PSI). Elevation of each plot was estimated with a 100 m digital elevation model (DEM) that was resampled (via cubic convolution) from the 30 m USGS National Elevation Dataset DEM. Using the DEM, we calculated TMI as the natural log of the ratio between upslope drainage area and local slope gradient (Moore et al., 1991) and PSI as the mean potential solar insolation at the spring equinox using the cosine of illumination on slope algorithm (Dubayah, 1994). We used the 100 m DEM resolution to match the size of the 1 ha standardized plot measurements.

We described regional climatic variation in precipitation, minimum temperature, and maximum temperature (800 m resolution) based on 30-year average annual values (1971–2000) from the topoclimate model PRISM (Daly et al., 2001). We also mapped latitude and proximity to the Pacific Ocean to provide additional insight into geographical and physiographical effects on climate. Variation in soil properties was assessed at the soil sub-order level

Table 1

Ecological and physiographic variables used to characterize environmental regimes and develop predictive models of *P. ramorum* host populations and biomass.

Variables	Data source
Soil orders, sub-orders and drainage classes	Soil survey staff, Natural Resources Conservation Service, United States Department of Agriculture
Elevation (meter), slope (%), topographic moisture index (TMI) and solar radiation intensity (SRI)	United States Geological Survey, National Elevation Dataset
Temperature (°C) and precipitation (mm)	PRISM Daly et al. (2001)
Normalized difference vegetation index (NDVI)	LandSat TM imagery
Distance to coast and latitude (m)	County boundary map for California and Oregon

using Soil Survey Geographic (SSURGO) database (<http://soildatamart.nrcs.usda.gov>). Finally, we computed the normalized difference vegetation index (NDVI) using Landsat TM satellite imagery to account for landscape variation in land cover. NDVI is a key remote sensing predictor of forest inventory variables especially biomass and carbon (e.g. Goward et al., 1985; Meng et al., 2009). Sixty Landsat images, acquired in summer 2006, were preprocessed to remove atmosphere and cloud effects and mosaicked to cover the study extent.

2.4. Geo-spatial modeling

For each host species, we performed a sequence of statistical and spatial analyses to (i) delineate their geographical range, (ii) assess spatial dependence and autocorrelation structure in host density and carbon content, and (iii) develop spatial prediction models, based on a combination of statistical and geospatial modeling approaches (Fig. 2).

2.4.1. Geographic range definition

To avoid over prediction of host populations, we first identified Level III ecoregions (Omernik, 1987), defined as areas of general similarity in ecosystems and in the type, quality, and quantity of environmental resources, which contained host species in the widely distributed FIA plot data (Fig. 1). We used all FIA plots within these regions (host-present and -absent plots) to map the probability of host species-presence using probability kriging, a geostatistical method that uses binary data to map the probability of occurrence (Webster and Oliver, 2007). For each species, we classified the resultant probability surface into host species-present or -absent based on probability threshold values of commission and omission errors (Freeman and Moisen, 2008). To select the optimal probability threshold, we used the criteria of maximum sum threshold (MST), which is a sum of the sensitivity (the ratio of correctly predicted presences to their total) and specificity (the ratio of correctly predicted absences to their total) (Jiménez-Valverde and Lobo, 2007). For all species, this approach yielded a probability of 0.70 as optimal threshold and each cell with $p > 0.70$ was classified as containing the respective host. To avoid omitting disjunct host-present plots that fell below the MST threshold, we delineated buffer regions around isolated plot locations with buffer radius equal to the spatial autocorrelation range (described below), and included these areas as part of each species' geographical range and resultant spatial prediction boundary.

2.4.2. Assessment of spatial autocorrelation structure

We performed semivariance analyses and developed omnidirectional semivariogram models of spatial autocorrelation in tree density and carbon contents of each species (Webster and Oliver,

2007). In order to assess differences in the spatial autocorrelation structures based on the FIA and sudden oak death plot data, we computed two sets of semivariograms for each species using (i) the FIA data, and (ii) the combined data from FIA and sudden oak death plots. Lag spacing for the analyses was chosen to ensure that at least 25 sample pairs contributed to semivariance estimation for all lag intervals.

2.4.3. Spatial prediction modeling

We used the combined dataset of FIA and sudden oak death plots to assess the performance of three modeling methods to estimate host densities and their carbon contents within the study region: (1) traditional univariate ordinary kriging, (2) non-spatial multivariable regression, and (3) and the hybrid approach known as regression kriging (Hengl et al., 2004; Vanwalleghe and Meentemeyer, 2009). Ordinary kriging uses a semivariogram model to derive linear predictions at unsampled locations (Webster and Oliver, 2007). Non-spatial multiple regression integrates environmental covariates (Table 1) into a Poisson multivariable regression with log link function for tree density and multiple linear regression for carbon contents (Lehmann et al., 2003). Our regression kriging models combine deterministic variation through regression with environmental variables and spatially autocorrelated variation through geostatistical kriging of regression residuals (Hengl et al., 2004). Regression kriging assumes that prediction of a variable $\hat{Z}(x_i)$ at an unvisited location (x_i) is an additive function of variables describing spatial and environmental variation:

$$\hat{Z}(x_i) = m(x_i) + \varepsilon(x_i) + \varepsilon'$$

where, $m(x_i)$ is a structural component that can have a constant mean or exhibit a trend, $\varepsilon(x_i)$ is the random but spatially autocorrelated variation, and ε' is the spatially uncorrelated residual error term. We modeled the structural component of variation using regression (described above) and the spatially autocorrelated component through semivariance analysis and ordinary kriging. We randomly split the data into model building (85%) and validation (15%) datasets to perform independent assessment of model prediction quality across the three approaches.

2.4.4. Model performance and application

The performance of each model was evaluated using three error metrics: (i) the coefficient of determination (r^2) as a measure of overall variation explained by the model, (ii) the mean error as a measure of directional bias where positive and negative values indicate over- and under-prediction, respectively, and (iii) the root mean squared error (RMSE) as a measure of overall prediction quality based on differences between true and predicted values. For each host species, we used the best performing model to devel-

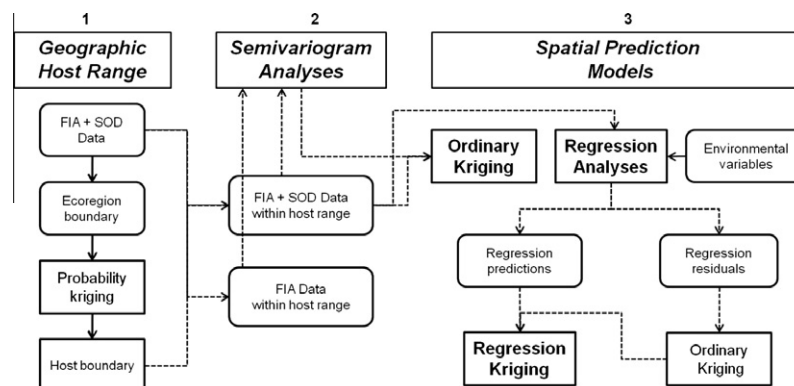


Fig. 2. Summary of statistical and spatial data analyses used to delineate the geographic range of *P. ramorum* host species, and build spatial prediction models for their tree density and carbon mass.

op spatially-explicit estimates and maps of tree density and carbon contents. Finally, the 100 m cell values in each map were summed by host species for California, Oregon, and the relevant ecoregions (Omernik, 1987).

3. Results

3.1. Plot-level tree density and carbon

The combined FIA and sudden oak death plots showed that carbon content of the five host species differed significantly ($p < 0.001$). Average tree carbon content was 539 kg for coast live oak, 282 kg for California black oak, 180 kg for canyon live oak, 166 kg for tanoak, and 120 kg for bay laurel. Within the geographic range, the five host species were present in approximately half of the combined FIA and sudden oak death plots. Average tree density in the plots ranged from 60 trees ha^{-1} for coast live oak to a maximum of 316 trees ha^{-1} for tanoak, and average plot carbon varied from 4.4 Mg carbon ha^{-1} for bay laurel to 21.6 Mg carbon ha^{-1} for coast live oak (Table 2). Correlation analyses showed that plot level tree density explained only 18%, 13%, 10%, 15% and 8% of their carbon content for tanoak, coast live oak, California black oak, canyon live oak and bay laurel, respectively.

3.2. Spatial autocorrelation

Both the FIA only and FIA–sudden oak death combined datasets exhibited significant spatial autocorrelation in host density and carbon contents. The FIA data revealed autocorrelation structure at spatial scales of 2 km and above, while the combined dataset revealed autocorrelation structure at spatial scales of 200 m and above (Table 3; Fig. 3). Across all five species, semivariograms developed using the combined dataset exhibited lower RMSE compared to semivariograms developed using FIA data only. For exam-

ple, semivariograms for tanoak based on the FIA versus the combined data resulted in a RMSE of 5918 and 4147 for tree density, and 34.0 and 31.7 for carbon contents, respectively. Using the combined dataset from coarse and fine scale sampling consistently produced models with the lowest RMSE and showed spatial autocorrelation of tree density and carbon stocks occur at finer scales than suggested by the FIA data alone.

3.3. Spatial prediction models

Among hosts, the ordinary kriging models explained 7–48% and 10–36% of the variance in host density and carbon content, respectively, while Poisson and linear regression models explained 6–25% and 9–21% of the variance in these parameters respectively (Table 5). Among the 10 regression models (host density and carbon for five species), NDVI was a significant predictor in nine models, followed by topographic moisture index (8), soil order and maximum temperature (6), annual precipitation (4), and distance to coast, precipitation and elevation (3) (Table 4). While the performance of ordinary kriging models versus regression models varied by species (Table 5), regression kriging models performed better than either approach for all five species explaining 35–59% and 22–45% of the variance in tree density and carbon content, respectively.

3.4. Regional estimation of host population density and carbon contents

Application of regression kriging models in a GIS produced predictive maps of host population density and carbon contents (ha^{-1}) across the geographic host range of each species (Fig. 4). Host-present areas varied from 3.6 million ha for coast live oak to 7.5 million ha for canyon live oak (Table 6), and exhibited strong south to north and west to east trends. Tanoaks and coast live oaks were present along coastal forests, while California black oaks and canyon live oaks were more common in drier sites which occur more frequently with distance from the coast. Tanoak increased in tree density and carbon from south to north with the highest densities and carbon contents in the Klamath Mountains and Coast Range ecoregion of northern California and southeast Oregon (Fig. 4). Coast live oak and bay laurel had higher densities and carbon contents in central coastal California. The maximum carbon contents at the plot level differed among host species: 169 Mg ha^{-1} in tanoak, 142 Mg ha^{-1} in coast live oak, 102 Mg ha^{-1} in canyon live oak, 63 Mg ha^{-1} in California black oak, and 76 Mg ha^{-1} in bay laurel. Similarly, host distribution and concentration including tree density and carbon masses differed among host species (Fig. 5; Table 7). Tanoak had the largest number of cells with population density greater than 1000 trees ha^{-1} , followed by canyon live oak, bay laurel, California black oak and coast live oak (Fig. 5a). Tanoak and coast live oak also had the greatest local average carbon contents as indicated by the number of cells with carbon >50 Mg ha^{-1} (Fig. 4). Modeled host population density and carbon contents

Table 2

Number of plots from the combined sudden oak death and FIA plot networks with the average number of trees, and average carbon amounts calculated from this dataset.

Species	Number of plots ^a	Number of trees (ha^{-1}) ^b	Carbon content (Mg ha^{-1}) ^b
Tanoak	1851 (996)	316 (627)	15.5 (30.3)
Coast live oak	1198 (684)	60 (132)	21.6 (34.6)
Canyon live oak	2601 (1013)	168 (479)	9.0 (21.9)
California black oak	2181 (1022)	81 (269)	7.4 (15.6)
Bay Laurel	1658 (960)	171 (364)	4.4 (10.1)

^a Number of plots include both host-present and -absent plots, and values in parentheses indicate the number of host-present plots.

^b Values in parentheses are one standard deviation of the mean. Both mean and standard deviation are based on total number of plots (host-present and -absent plots).

Table 3

Semivariogram parameters used to model spatial autocorrelation of tree density and carbon based on the combined FIA–sudden oak death dataset.

Host species	Number of trees (ha^{-1})				Carbon (Mg ha^{-1})			
	Model ^a	Nugget	Sill	Range (m)	Model	Nugget	Sill	Range (m)
Tanoak	Exp	0.91	8.05	6377	Exp	0.79	2.62	5850
Coast live oak	Exp	0.87	4.60	5760	Exp	1.10	3.06	9200
Canyon live oak	Sph	0.93	7.19	27,910	Sph	0.46	2.09	26,100
California black oak	Exp	2.05	5.10	17,828	Sph	1.18	1.72	5507
Bay laurel	Sph	2.34	5.07	5320	Exp	0.61	1.24	4000

Notes: All semivariograms are computed in natural log scale.

^a Indicates model structure as Exp = exponential, and Sph = spherical.

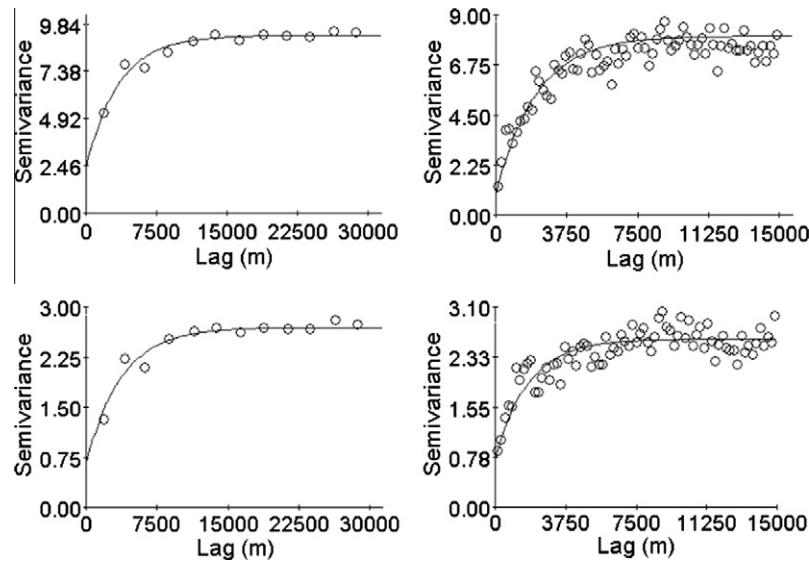


Fig. 3. Spatial dependencies of tanoak density (a and b) and carbon content (c and d). Figures are semivariograms for the univariate spatial model when only spatially extensive (FIA) data are included (a and c) and spatially extensive and intensive data are combined (b and d).

Table 5

Error statistics for spatial prediction models from model validation (see text). The model with the lowest RMSE is in bold. Error statistics are abbreviated as RMSE: root mean squared error, and ME: mean error.

Species	Model ^a	Number of trees (ha ⁻¹)			Carbon (Mg ha ⁻¹)		
		RMSE	ME	<i>r</i> ²	RMSE	ME	<i>r</i> ²
Tanoak	R	553.0	−24.4	0.25	28.6	1.0	0.21
	OK	590.8	−226.8	0.26	33.3	−31.2	0.11
	RK	473.4	44.3	0.54	25.3	0.0	0.37
Coast Live Oak	R	117.1	−5.5	0.17	38.7	−2.9	0.11
	OK	131.9	−32.8	0.07	30.5	−7.7	0.12
	RK	84.8	−0.4	0.59	23.1	2.7	0.22
Canyon Live Oak	R	504.6	−9.2	0.06	21.8	−0.8	0.09
	OK	494.1	−138.9	0.16	21.8	−5.8	0.10
	RK	405.0	42.2	0.49	18.3	1.0	0.38
California black oak	R	381.7	−19.8	0.09	15.2	−0.3	0.07
	OK	333.6	−78.9	0.48	14.7	−4.7	0.25
	RK	262.8	−7.1	0.54	12.5	0.4	0.40
Bay laurel	R	343.2	19.2	0.09	9.8	0.0	0.09
	OK	121.7	−16.7	0.18	4.2	1.5	0.36
	RK	81.0	0.1	0.35	3.2	−0.1	0.45

^a Models are abbreviated as R: regression; OK: ordinary kriging, and RK: regression kriging.

varied by ecoregion and state reflecting geographical differences in host distribution (Fig. 4; Table 7).

4. Discussion

Sudden oak death has emerged as a major forest disease that has affected millions of trees in California and Oregon (Rizzo et al., 2005; Meentemeyer et al., 2008c). A number of recent studies have shown the impact of this disease on mortality of oak and tanoak populations at spatial scales ranging from local (e.g., Brown and Allen-Diaz, 2009; McPherson et al., 2010; Cobb et al., 2010; Ramage and O'Hara, 2010) to regional (Meentemeyer et al., 2008c; Davis et al., 2010) scales. Our study developed the first regional estimate and distribution map of *P. ramorum* host populations and their carbon contents in western US forests. This information is a prerequisite for future studies that aim to predict where in the landscape and to what extent this disease will impact ecosystem function and community structure. The results from our study should be combined with regional scale analyses of disease risk

(c.f. Meentemeyer et al., 2004, 2008a; Václavík et al., 2010) to assess the potential ecological impacts of sudden oak death. Host populations and their carbon contents are likely to shift with mortality and release of co-occurring trees via apparent competition. For sudden oak death, apparent competition is likely to increase the prevalence of bay laurel in mixed evergreen forests, and redwood and bay laurel in coast redwood forests (Brown and Allen-Diaz, 2009; Cobb et al., 2010).

Our results show that forests with higher host population density and carbon content occur in regions shown to have high risk for *P. ramorum* establishment (Meentemeyer et al., 2004, 2008a). Although tanoak accounts for less carbon than the oak species that we describe here, tanoak has the greatest potential for carbon release into the atmosphere due to its locally high biomass and overlap with environmental conditions that are highly conducive to sudden oak death outbreak (Meentemeyer et al., 2008b, 2011). Unlike coast live oak that has a genetic basis for resistance to *P. ramorum* infection (Dodd et al., 2005), tanoak appears to have limited host resistance and unlike the oak species, tanoak leaf and twig infections support sporulation at levels adequate for forest disease

Table 4

Non-spatial Poisson multivariable regression equations for number of trees and their carbon content.

Species	Number of trees (ha ⁻¹)	r ²	Carbon (Mg ha ⁻¹)	r ²
Tanoak	$-4.03 + 0.005^*P + 0.18^*T - 0.0036^*D + 7.44^*NDVI + SO$	0.25	$-76.03 + 0.007^*P + 2.61^*T - 0.99^*TMI + 75.5^*NDVI - 0.094^*D + SO$	0.21
Coast live oak	$6.18 - 0.001^*P - 0.09^*TMI - 1.87^*NDVI + SO$	0.17	$50.78 - 0.028^*P - 1.27^*TMI + 0.041^*S_Mar + SO$	0.11
Canyon live oak	$-2.72 + 0.23^*T + 0.02^*TMI + 1.38^*NDVI + 0.001^*E + 0.002^*S_Mar$	0.06	$-76.24 + 2.5^*T + 0.98^*TMI + 21.73^*NDVI + 0.01^*E + 0.03^*S_Mar$	0.09
California black oak	$2.60 - 0.12^*TMI + 2.43^*NDVI$	0.09	$-46.20 + 1.84^*T + 26.19^*NDVI + 0.007^*E$	0.07
Bay laurel	$-23.73 - 24.83^*NDVI + 21.90^*T + 11.03^*TMI + SO$	0.09	$15.78 - 0.03^*D - 13.5^*NDVI + SO$	0.09

Notes: r²: coefficient of variation. Abbreviation for predictor variables are D: distance to coast (in km); E: elevation (in m); NDVI: normalized difference vegetation index, P: normal Annual precipitation (in mm), S_Mar: solar radiation intensity for the month of March; SO: suborder effects; T: normal annual maximum temperature (in °C); TMI: topographic moisture index. Suborders effects are categorical variables.

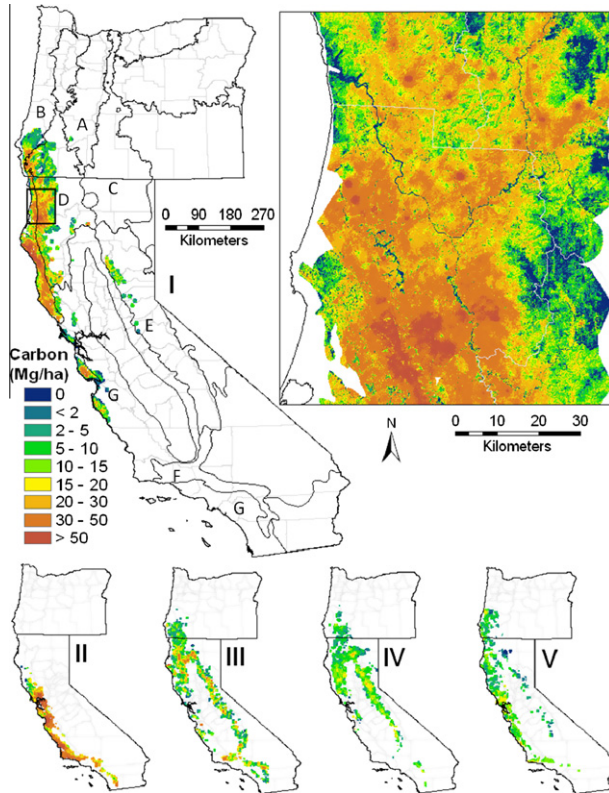


Fig. 4. Spatial prediction maps of carbon contents in major *P. ramorum* host species: I – tanoak, II – coast live oak, III – canyon live oak, IV – California black oak, and V – bay laurel. The inset shows tanoak carbon content in northern California. Ecoregions in tanoak map (I) are abbreviated as: A – Cascades, B – Coast Range, C – Eastern Cascades Slopes and Foothills, D – Klamath Mountains, E – Sierra Nevada, F – Southern California Mountains, and G – California Chaparral and Oak Woodlands. Areas in white are outside the geographic range of host species.

outbreak. Tree mortality has a dual effect on carbon stored within forest ecosystems: (i) transfer of carbon from living biomass to dead biomass, thus increasing forest carbon losses by decay of dead trees, and (ii) reduced net primary productivity and carbon

sequestration by growing trees (Kurz et al., 2008b; Cobb, 2010). Thus, extensive sudden oak death has the potential to compromise the role of these forests in mitigating regional or national goals of CO₂ emissions.

Our analyses show that integrating sparsely collected data (e.g. FIA) with more densely collected plot-network data can improve characterization of spatial variability of host density and carbon at regional scales compared to using coarse-scale data only (Fig. 3). FIA data estimated spatial autocorrelation structure at distances greater than 2 km, which greatly exceeds the <200 m distance where most *P. ramorum* dispersal occurs (Rizzo et al., 2005; Hansen et al., 2008; Mascheretti et al., 2008). Thus, intensive sampling of vegetation data is critical for spatial characterization and prediction of host communities (Latimer et al., 2006). Efforts to describe *P. ramorum* host populations and their carbon contents in other regions (e.g. eastern US and Europe) should, at a minimum, assess the scale of spatial dependence for pathogen and host populations in order to understand the need for spatially intensive sampling.

The non-spatial regression models had relatively poor fit, which may be attributed to unaccounted spatial heterogeneity that is typical of spatial data derived from tree species distribution (Franklin and Miller, 2009) and scale dependence in vegetation–environment interactions (Reed et al., 1993). Additionally, complex disturbance regimes and forest management approaches occur across the western US (Ohmann et al., 2007) which ideally would be included in the models but it is currently not possible to reliably map these variables across such a large area. Despite relatively weak model fit, environmental correlation approaches are useful for species distribution modeling as they offer the advantages of mapping variables at finer spatial scales given the distribution of predictor variables across the landscape (Franklin, 1995; McKenzie and Ryan, 1999). Because kriging and regression methods offer distinct advantage in addressing the drivers of spatial heterogeneity, with the former focusing on spatial autocorrelation and the later focusing on correlation with environmental variables, combination of these methods can offer more accurate predictions of host tree density and their carbon contents. When regression models are weak, as in our case, substantial amounts of spatial variation remain as unexplained variance in the residuals, and as such, mapping spatially autocorrelated residuals substantially improved

Table 6Regional estimations of area containing *P. ramorum* host species focused on by this study for California (CA) and Oregon (OR).

Species	Total area (ha)	Area by state (ha)		Proportion of state area (%)	
		CA	OR	CA	OR
Tanoak	3,957,500	3,073,304	884,196	7.5	3.5
Coast live oak	3,604,566	3,604,566	NA	8.8	NA
Canyon live oak	7,536,054	6,695,313	840,741	16.3	3.3
California black oak	6,605,964	5,957,105	648,859	14.5	2.5
Bay laurel	4,192,560	3,454,732	737,828	8.4	2.9

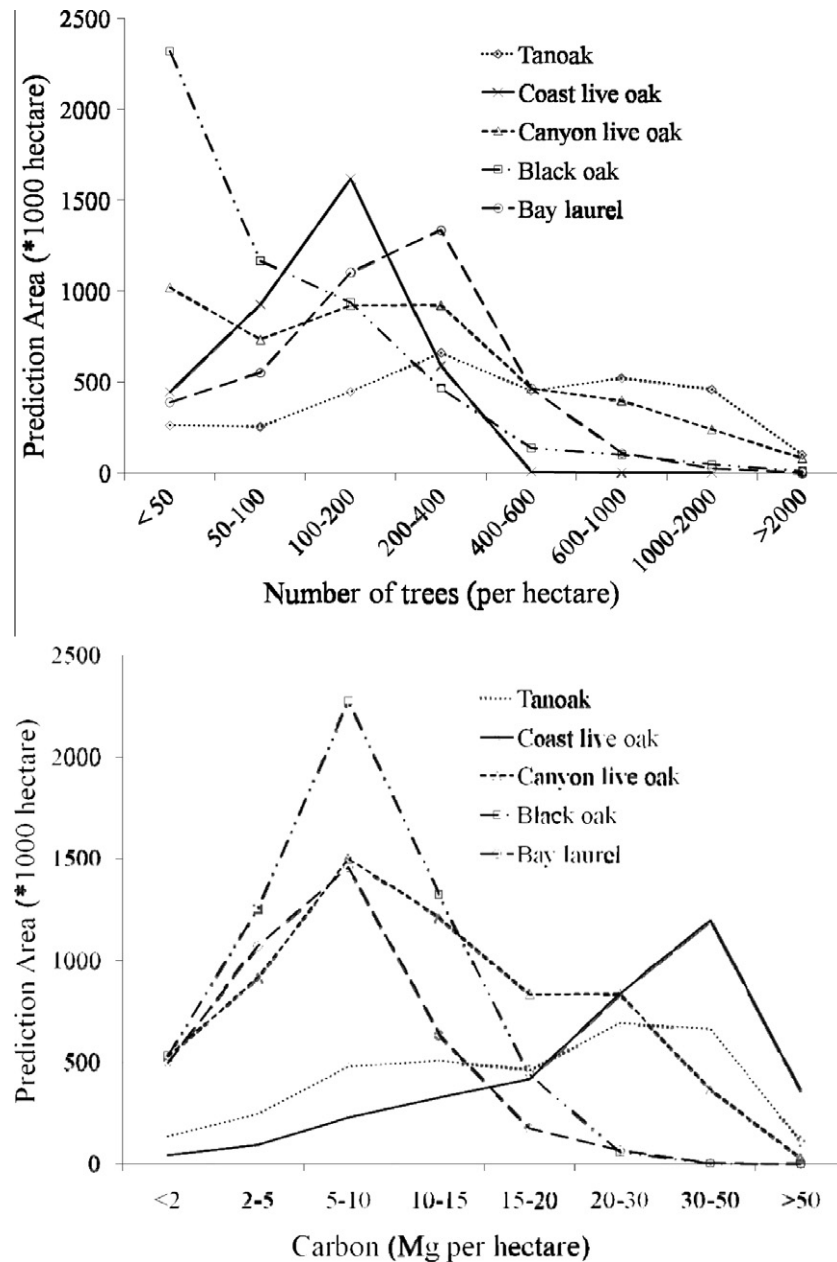


Fig. 5. Frequencies of tree densities and carbon amounts for the *P. ramorum* host species focused on by this study.

our spatial predictions. Regression kriging prediction maps show the geographic range of *P. ramorum* hosts, their spatial distribution, and carbon contents (Fig. 4). These maps should be used to guide management response to *P. ramorum* establishment by illustrating areas with high host density and host contagion. These data give insight into disease treatment costs, potential impacts, and potential spread if new infections are left unmanaged (see also Hansen et al., 2008). These maps are also a useful region-wide baseline of host populations, which are essential for future assessments of sudden oak death mortality and carbon losses. Our estimates of total host populations (Table 7) greatly exceed those reported by Barrett et al. (2006) who estimated host densities of trees greater than 5 inches in diameter (12.7 cm) for selected counties. We suggest three causes for the differences in estimates. First, trees less than 12.7 cm account for over half the stems in our fine scale plot network (data not shown). Second, our estimates are for the entire state while the Barrett et al. (2006) analysis excluded state and na-

tional parks as well as some reserve lands. Third, the FIA plot network sparsely covers the geographical areas dominated by highly susceptible *P. ramorum* hosts (Fig. 1).

In total, we estimate 4.39 billion oak and tanoak trees in California and Oregon forests with an estimated 295 Tg Carbon in their above-ground biomass. Assuming ~1 Pg of carbon in California forests (Fried and Zhou, 2008) and ~15 Pg nationally (Goodale et al., 2002), *P. ramorum* susceptible forests account for about 29% and 2.2% (respectively) of total above ground forest C. Although *P. ramorum* establishment will be limited in drier oak forests and those which lack bay laurel, landscape-scale mortality has resulted in decline of native forest that has likely reduced carbon sequestration, biodiversity, and possibly even ecosystem resilience to subsequent disturbances (Tilman, 1996; Ellison et al., 2005; Lovett et al., 2006; Kurz et al., 2008b; Meentemeyer et al., 2008c). Further, the spatial distribution of host populations and carbon contents reported in this study indicates that the ecological impact of sudden

Table 7

Estimates of *P. ramorum* host populations and total above ground carbon content by state and ecoregion. For this analysis, populations and carbon content for *Q. parvula* were lumped with coast live oak (see text).

	Number of trees (millions)					Carbon (Tg)				
	Tanoak	Coast live oak	Canyon live oak	Black oak	Bay laurel	Tanoak	Coast live oak	Canyon live oak	Black oak	Bay laurel
Total	1791.3	465.7	1515.0	620.4	435.5	68.4	101.8	78.4	46.7	13.6
<i>Estimation by state</i>										
California	1412.2	465.7	1405.0	570.9	394.5	58.7	101.8	74.0	43.9	12.0
Oregon	379.1	0.0	110.0	49.5	41.0	9.7	0.0	4.4	2.8	1.6
<i>Estimation by ecoregion^a</i>										
A	0.3	0.0	1.3	3.3	0.0	0.1	0.0	0.1	0.3	0.0
B	863.8	18.2	31.3	4.5	83.9	34.1	4.6	3.8	1.2	4.2
C	0.0	0.0	0.1	37.0	0.0	0.0	0.0	0.0	1.5	0.0
D	814.1	0.7	604.5	240.5	77.3	29.0	0.1	32.1	16.5	2.2
E	55.0	0.0	266.9	230.1	29.5	2.0	0.0	17.4	17.7	0.3
F	0.0	53.7	336.6	17.0	23.0	0.0	11.1	12.0	1.0	0.4
G	58.1	393.1	274.4	87.9	221.7	3.2	86.0	13.0	8.5	6.5

^a Abbreviation for ecoregion are A: cascades; B: coast range; C: eastern cascades SLOPES and foothills; D: Klamath mountains; E: Sierra Nevada; F: southern California mountains; G: California chaparral and oak woodlands.

oak death in California and Oregon forests will worsen because of the high degree of overlap with bay laurel, community, and climate conditions that favor disease emergence. Positive associations between tree size and above-ground biomass carbon are likely to compound this problem as large trees tend to have higher mortality rates following infection (McPherson et al., 2010; Cobb et al., 2010). Therefore, the greatest potential for decline in host populations and carbon release are in forests dominated by tanoaks in northern California and southwest Oregon suggesting that management aimed at reducing ecological impacts of sudden oak death should be focused in these areas.

Acknowledgements

We are deeply grateful to those who assisted with collecting field data, including J. Amaris, S. Benson, C. Boylen, T.E. Condeso, M. Cooper, D. Dann, D. DiPietro, K. Frangioso, G. Garner, A. Gauthier, E. Gordon, R. Hunter, C. Jensen, S. King, M. Kozanitas, N. MacCallum, E. McCowan, P. Maloney, M. Metz, L. Miller, S. Moyile, S. Murphy, G. Neargarder, N. Rank, H. Torpin, K. Ward, A. Wickland, and J. Zanzot. We thank S. Murphy, P. Maloney, A. Wickland, C. Jensen, K. Frangioso, M. Metz, and M. Vaclavikova for vital help with compiling the multi-dataset information. We also thank K. Waddell for collaboration with the FIA data and we thank S. Frankel at the US Forest Service and members of the Center for Applied GIScience at UNC Charlotte for their helpful comments on the manuscript. This research was supported by grants from the USDA Forest Service–Pacific Southwest Research Station, National Science Foundation Ecology of Infectious Disease program (EF-0622677), the Gordon and Betty Moore Foundation.

References

- Albani, M., Moorcroft, P.R., Ellison, A.M., Orwig, D.A., Foster, D.R., 2010. Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests. *Canadian Journal of Forest Research* 40, 119–133.
- Barrett, T.M., Gatzliis, D., Fried, J.S., Waddell, K.L., 2006. Sudden oak death in California: what is the potential? *Journal of Forestry* 104, 61–64.
- Bergot, M., Cloppet, E., Pérarnaud, V., Déqué, M., Marçais, B., Desprez-Loustau, M.-L., 2004. Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. *Global Change Biology* 10, 1552–1559.
- Brasier, C.M., 2008. The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology* 57, 792–808.
- Breshears, D.D., Allen, C.D., 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography* 11, 1–5.

- Brown, L.B., Allen-Diaz, B., 2009. Forest stand dynamics and sudden oak death: mortality in mixed evergreen forests dominated by coast live oak. *Forest Ecology and Management* 257, 1271–1280.
- Castello, J.D., Leopold, D.J., Smallidge, P.J., 1995. Pathogens, patterns and processes in forest ecosystems. *BioScience* 45 (1), 16–24.
- Cobb, R.C., 2010. Mechanisms of community change and impacts on functional processes by the generalist pathogen *Phytophthora ramorum* in California coast redwood forests. Dissertation, University of California Davis.
- Cobb, R.C., Meentemeyer, R.K., Rizzo, D.M., 2010. Apparent competition in canopy trees determined by pathogen transmission rather than susceptibility. *Ecology* 91 (2), 327–333.
- Cushman, J.H., Meentemeyer, R.K., 2008. Multi-scale patterns of human activity and the incidence of an exotic forest pathogen. *Journal of Ecology* 96, 766–776.
- Daly, C., Talyon, G.H., Gisbon, W.P., Parzybok, T.W., Johnson, G.L., Pasteris, P., 2001. High-quality spatial climate data sets for the United States and beyond. *Transactions of the American Society of Agricultural and Biological Engineers* 43, 1957–1962.
- Davidson, J.M., Wickland, A.C., Patterson, H.A., Falk, K.R., Rizzo, D.M., 2005. Transmission of *Phytophthora ramorum* in mixed-evergreen forest in California. *Phytopathology* 95, 587–596.
- Davidson, J.M., Patterson, H., Rizzo, D.M., 2008. Sources of inoculum for *Phytophthora ramorum* in a redwood forest. *Phytopathology* 98, 860–866.
- Davis, F.W., Borchert, M., Meentemeyer, R.K., Flint, A., Rizzo, D.M., 2010. Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur ecoregion; California. *Forest Ecology and Management* 259, 2342–2354.
- Deusen, P.V., 2010. Carbon sequestration potential of forest land: management for products and bioenergy versus preservation. *Biomass and Bioenergy* 34, 1694–1867.
- DiLeo, M.V., Bostock, R.M., Rizzo, D.M., 2009. *Phytophthora ramorum* does not cause physiologically significant systemic injury to California bay laurel, its primary reservoir host. *Phytopathology* 99, 1307–1311.
- Dodd, R.S., Kashani, N., 2003. Molecular differentiation and diversity among California red oaks (Fagaceae; *Quercus* section Lobatae). *Theoretical and Applied Genetics* 107, 884–892.
- Dodd, R.S., Hüberli, D., Douhovnikoff, V., Harnik, T.Y., Afzal-Rafii, Z., Garbelotto, M., 2005. Is variation in susceptibility to *Phytophthora ramorum* correlated with population genetic structure in coast live oak (*Quercus agrifolia*)? *New Phytologist* 165, 203–214.
- Dubayah, R.C., 1994. Modeling a solar radiation topoclimatology for the Rio Grande river basin. *Journal of Vegetation Science* 5, 627–640.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 9, 479–486.
- Franklin, J., 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19 (4), 474–499.
- Franklin, J., Miller, J.A., 2009. Mapping Species Distributions. Cambridge University Press, New York, NY.
- Freeman, E.A., Moisen, G.G., 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modeling* 217, 48–58.
- Fried, J.S., Zhou, X., 2008. Forest inventory-based estimation of carbon stocks and flux in California forests in 1990. United States Dept of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-750, p. 32.

- Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., Ahivdenko, A.Z., 2002. Forest carbon sinks in the northern hemisphere. *Ecological Applications* 12, 891–899.
- Goward, S.N., Tucker, C.J., Dye, D.G., 1985. North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer. *Vegetation* 64, 3–14.
- Hanemann, W.M. 2007. How California came to pass AB 32, the Global Warming Solutions Act of 2006. California Climate Change Center, University of California, Berkeley, CA. Available at <<http://www.escholarship.org/uc/item/1vb0j4d6>>.
- Hansen, E.M., Kanaskie, A., Prospero, S., McWilliams, M., Goheen, E.M., Osterbauer, N., Reaser, P., Sutton, W., 2008. Epidemiology of *Phytophthora ramorum* in Oregon tanoak forests. *Canadian Journal of Forest Research* 38, 1133–1143.
- Hengl, T., Heuvelink, G.M.B., Stein, A., 2004. A generic framework for spatial prediction of soil variables based on regression-kriging. *Geoderma* 120, 75–93.
- Holt, R.D., Boulenger, T., 2005. Ecosystems and Parasitism: The Spatial Dimension. In: Thomas, F., Renaud, F., Guégan, I.F. (Eds.), *Parasitism and Ecosystems*. Oxford University Press, Oxford, UK.
- Houghton, R.A., 1999. The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus* 51B, 298–313.
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29, 440–455.
- Jenkins, J.C., Chojnacki, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49 (1), 12–35.
- Jenkins, J.C., Chojnacki, D.C., Heath, L.S., Birdsey, R.A., 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. USDA-FS Gen Tec Report NE-319.
- Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica* 31, 361–369.
- Kelly, N.M., Meentemeyer, R.K., 2002. Landscape dynamics of the spread of sudden oak death. *Photogrammetric Engineering and Remote Sensing* 68, 1001–1010.
- Kurz, W.A.G., Stinson, G., Rampley, G.J., Dymond, C.C., Neilson, E.T., 2008a. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences USA* 105, 1551–1555.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008b. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990.
- Latimer, A.M., Wu, S., Gelfand, A.E., Silander, J.A., 2006. Building statistical models to analyze species distributions. *Ecological Applications* 16, 33–50.
- Lehmann, A., Overton, J.M., Leathwick, J.R., 2003. GRASP: generalized regression analysis and spatial prediction. *Ecological Modeling* 160, 165–183.
- Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., Pierce, R.S., 1970. Effects of forest cutting and herbicide treatments on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monograph* 40, 23–47.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience* 56, 395–405.
- Maloney, P.E., Lynch, S., Kane, S., Jensen, C.E., Rizzo, D.M., 2005. Establishment of an emerging generalist pathogen in redwood forest communities. *Journal of Ecology* 93, 899–905.
- Mascheretti, S., Croucher, P.J.P., Vettraino, A., Prospero, S., Garbelotto, M., 2008. Reconstruction of the sudden oak death epidemic in California through microsatellite analysis of the pathogen *Phytophthora ramorum*. *Molecular Ecology* 17, 2755–2768.
- McKenzie, N.J., Ryan, P.J., 1999. Spatial prediction of topsoil properties using environmental correlation. *Geoderma* 89, 67–94.
- McPherson, B.A., Mori, S.R., Wood, D.L., Kelly, M., Storer, A.J., Svihra, P., Standiford, R.B., 2010. Responses of oaks and tanoak to the sudden oak death pathogen after 8 y of monitoring in two coastal California forests. *Forest Ecology and Management* 259, 2248–2255.
- Meentemeyer, R.K., Rizzo, D.M., Walter, M., Lotz, E., 2004. Mapping the risk of establishment and spread of sudden oak death in California. *Forest Ecology and Management* 200, 195–214.
- Meentemeyer, R.K., Anacker, B.L., Walter, M., Rizzo, D.M., 2008a. Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecological Applications* 18, 377–390.
- Meentemeyer, R.K., Rank, N.E., Anacker, B.L., Rizzo, D.M., Cushman, J.H., 2008b. Influence of land-cover change on the spread of an invasive forest pathogen. *Ecological Applications* 18, 159–171.
- Meentemeyer, R.K., Rank, N.E., Shoemaker, D., Oneal, C., Rizzo, D.M., 2008c. Impacts of sudden oak death on tree mortality in the Big Sur ecoregion of California. *Biological Invasions* 10, 1243–1255.
- Meentemeyer, R.K., Cuniffe, N., Cook, A.R., Filipe, J.A.N., Hunter, R.D., Rizzo, D.M., Gilligan, C.A., 2011. Epidemiological modeling of invasion in heterogeneous landscapes: Spread of sudden oak death in California forests (1990–2030). *Ecosphere* 2(2):art17.
- Meng, Q., Cieszewski, C., Madden, M., 2009. Large area forest inventory using Landsat ETM+: a geostatistical approach. *ISPRS Journal of Photogrammetry and Remote Sensing* 64, 27–36.
- Metz, M.R., Frangioso, K.M., Meentemeyer, R.K., Rizzo, D.M., 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. *Ecological Applications* 21 (2), 313–320.
- Moore, I.D., Grayson, R.B., Ladson, A.R., 1991. Digital terrain modeling: a review of hydrological, geomorphological, and biological applications. *Hydrological Processes* 5, 3–30.
- Murphy, S.K., Rizzo, D.M., 2003. First report of *Phytophthora ramorum* on canyon live oak in California. *Plant Disease* 87, 315.
- Murphy, S.K., Rizzo, D.M., 2006. Incidence of *Phytophthora ramorum*, *P. nemorosa*, and *P. pseudosyringae* in three coastal California forest communities. Frankel S.J., Shea P.J., Haverly M.I. eds. *Proceedings of the Second Sudden Oak Death Science Symposium*. Gen. Tech. Rpt. PSW-GTR-196.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Ohmann, J.L., Gregory, M.J., Spies, T.A., 2007. Influence of environment, disturbance, and ownership on forest vegetation of coastal Oregon. *Ecological Applications* 17, 18–33.
- Omerik, J.M., 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77, 118–125.
- Ramage, B.S., O'Hara, K.L., 2010. Sudden oak death-induced tanoak mortality in coast redwood forests: current and predicted impacts to stand structure. *Forests* 1, 114–130.
- Reed, R.A., Peet, R.K., Palmer, M.W., White, P.S., 1993. Scale dependence of vegetation-environment correlations: a case study of a North Carolina piedmont vegetation. *Journal of Vegetation Science* 4, 329–340.
- Rizzo, D.M., Garbelotto, M., Hansen, E.M., 2005. *Phytophthora ramorum*: integrative research and management of an emerging pathogen in California and Oregon forests. *Annual Review of Phytopathology* 43, 309–335.
- Smith, W.B., 2002. Forest inventory and analysis: a national inventory and monitoring program. *Environmental pollution* 116, S233–S242.
- Tilman, D., 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77, 350–363.
- USDAFS (United States Department of Agriculture Forest Service). 2008. The forest inventory and analyses database: database description and users manual version 3.0. USDA Forest Service, Forest Inventory and Analysis Program.
- Václavík, T., Kanaskie, A., Hansen, E.M., Ohmann, J.L., Meentemeyer, R.K., 2010. Predicting potential and actual distribution of sudden oak death in Oregon: prioritizing landscape contexts for early detection and eradication of disease outbreaks. *Forest Ecology and Management* 260, 1026–1035.
- Vanwallendael, T., Meentemeyer, R.K., 2009. Predicting forest microclimate in heterogeneous landscapes. *Ecosystems* 12, 1158–1172.
- Webster, R., Oliver, M.A., 2007. *Geostatistics for Environmental Scientists*. John Wiley and Sons, Chichester, England.