VEGETATION DISTRIBUTION, DYNAMICS AND IMPACTS BY *PHYTOPHTHORA RAMORUM* IN REDWOOD-TANOAK FORESTS IN CALIFORNIA

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Pathogen epidemiology, community ecology of host species, and land use history all play major roles in the current distribution of *P. ramorum* and the extent of damage this pathogen has caused in California forests (Rizzo et al. 2005; Meentemeyer et al. 2008b). Research on the community ecology and the interaction of community composition and disease intensity will help enable synthesis of management actions at the stand level and reduce rates of infection, mortality, and fuel accumulation. Disease and mortality of tanoak (*Lithocarpus densiflorus*) are patchy across California landscapes, and causative mechanisms for these patterns likely operate at different spatial and temporal scales. Theoretical and empirical models that reflect the interdependences of vegetation and pathogen ecology are important to identify high-risk stands and developing management practices to reduce disease impacts.

In this study, we assess the ecological characteristics of redwood forests to understand impacts by *P. ramorum* on redwood-tanoak forests in California. Since 2002, we have monitored the survival of 5769 trees in the central and southern parts of the distribution of redwood forests (Maloney et al. 2005). Using this dataset, we have asked the following questions: How does variation of host community structure affect the frequency of infection and mortality due to *P. ramorum*? What are the ecological relationships which structure these vegetation types? We address these questions by examining relationships between species biomass and edaphic factors. We then use preexisting host community structure to explore extent of *P. ramorum* infection and resulting mortality across the main area of infestation.

METHODS

The study was conducted within a network of 120 500m^2 circular plots covering redwood forests within Sonoma, Marin, Santa Cruz, and Monterey counties (Maloney et al. 2005). A total of 5,769 trees ≥ 1 cm DBH were surveyed in 2002 and 2007. Every tree species within a plot was measured for diameter at breast height and given a crown vigor rating. Basal area for each species was calculated at the plot level and reported in square meters per 1/20 ha. Susceptible host trees included coast redwood (*Sequoia sempervirens*), tanoak, California bay laurel (*Umbellularia californica*), douglas fir (*Pseudotsuga menziesii*), big leaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*), coast live oak (*Quercus agrifolia*), and California black oak (*Quercus kelloggii*). Tissue symptomatic of *P. ramorum* infection was collected from each tree; in the lab, pieces of collected leaf and bark tissue were placed in Petri dishes containing pimaricin-ampicillin-rifampicin-Pentachloronitrobenzene agar (PARP), a selective medium for *Phytophthora* spp. (Davidson et al. 2003). In 2003, one soil sample was collected within each plot to evaluate soil texture and chemical properties. Soil analysis was conducted with standard methods for soil analysis at the University of California Davis ANR Analytical Laboratory. Plot location was recorded using a global positioning system (GPS)
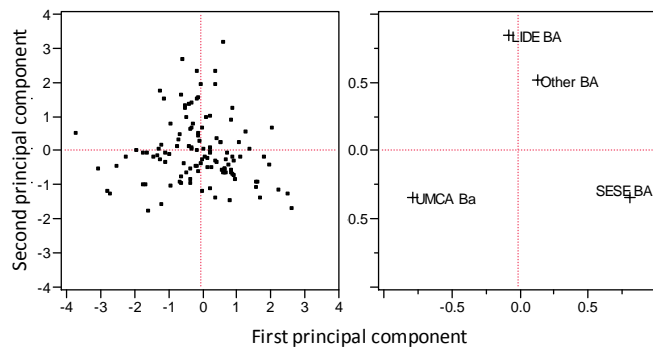
device (GARMIN, Olathe, KS, USA); plot locations were used to derive edaphic variables including topographic moisture index (TMI), elevation, and percent maximum solar radiation input. Principal component analysis (PCA) was conducted to assess multivariate correlation patterns of tree distributions with environmental variables.

Sites were divided into central (Sonoma and Marin counties) and southern (Santa Cruz and Monterey counties) redwood forest sub regions (Sawyer et. al. 2000). Principle components for vegetation were calculated using correlations of plot level basal area. Three tree species including redwood, tanoak, and bay laurel accounted for 90% (±14% standard deviation) of the total basal area within the plot network. Host community structure was analyzed by including estimated basal area of tanoak, bay laurel, and redwood with all other species collapsed into a general category of other species (including black oak, coast live oak, douglas fir, maple, and madrone). These categories reflect a general continuum of susceptibility weighted by the biomass of individual species.

Two PCA analyses were conducted. The first used only vegetation structure (four categories) to examine multivariate associations in host community structure. A second PCA analysis included edaphic variables and vegetation structure in order to elucidate environmental controls on host community composition. Eigenvalues for the first five principal components were used to examine associations between vegetation and edaphic factors. Effects of host community composition on intensity of Sudden Oak Death was examined with multiple linear regression (MLR) using vegetation structure as independent variables and amount of tanoak and bay laurel, and tanoak mortality as dependent variables (Maloney et al. 2005). Independent and dependent variables were square root transformed prior to analysis.

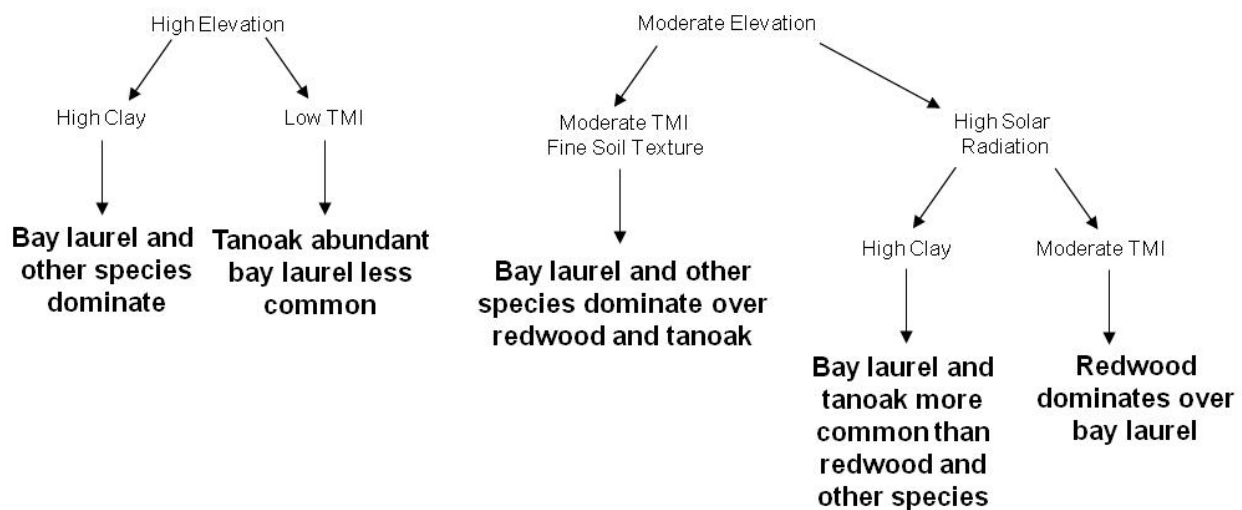## Community composition and disease impacts

Results from PCA analysis indicate strong negative correlations among bay laurel, tanoak, and redwood when considered at the redwood forest community level (Fig 1). The first and second principle components accounted for 62% of the variation in vegetation structure and suggest segregation of host species within redwood forest types. Redwood and bay laurel basal area were negatively correlated and both species showed less pronounced

Figure 1. Score (left) and loadings (right) plots from a PCA analysis on correlations among tanoak (LIDE), bay laurel (UMCA), redwood (SESE), and all other species (Other) basal area from 120 plots in redwood forests. This analysis illustrates variation in host community structure and suggests that edaphic and/or competitive interactions are important in structure host populations.

negative correlation with tanoak. All other species were positively correlated with tanoak basal area suggesting that stands with greater tanoak dominance have higher overstory tree diversity compared to redwood stands dominated by redwood or bay laurel at the plot level. The large amount of spread in the data and lack of obvious plot clustering suggests that segregation of host species occurs along gradients within redwood forests.

Central Redwood Forest Subregion A.

High Elevation
→ High Clay → **Bay laurel and other species dominate**
→ Low TMI → **Tanoak abundant bay laurel less common**

Moderate Elevation
→ Moderate TMI Fine Soil Texture → **Bay laurel and other species dominate over redwood and tanoak**
→ High Solar Radiation
  → High Clay → **Bay laurel and tanoak more common than redwood and other species**
  → Moderate TMI → **Redwood dominates over bay laurel**

Southern Redwood Forest Subregion B.

Low Elevation
→ Low Clay → **Redwood dominant over other species**
→ High Silt → **Bay laurel more common than tanoak**

Moderate Elevation
→ High TMI → **Tanoak more common than bay laurel**
→ Low Solar Radiation
  → High Clay → **Bay and tanoak dominate over other species**
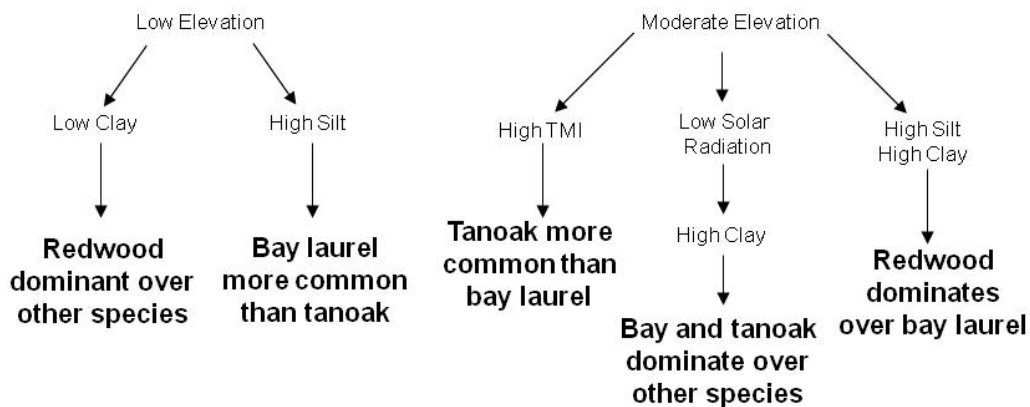→ High Silt High Clay → **Redwood dominates over bay laurel**

Figure 2. Edaphic dependencies of species dominance in central and southern redwood study sites. Edaphic-species relationships are based on dominant eigenvalues from a PCA analysis of vegetation abundances and edaphic factors including soil texture, elevation, and topographic moisture index (TMI).

Results from our second PCA analysis suggest that stand level vegetation structure in redwood forests is related to edaphic factors but the relative importance of edaphic drivers differ between sub regions (Fig 2A and B). Overall, edaphic factors and competition were important in determining species biomass at the plot level in both regions. For the central redwood forest sub-region, all species out-compete coast redwood at relatively higher elevation sites with edaphic factors determining the abundance of alternative dominant species. Bay laurel and other species occurred at greater basal area in sites with higher soil clay content. At these sites, tanoak was more abundant where TMI values were lower suggesting that tanoak may out-compete bay laurel in relatively drier high elevation sites. Low resource sites are known to support high species richness in Coastal scrub ecosystems (Moody and Meentemeyer 2001). Figure 1 shows strong tanoak association with all other overstory species that commonly occur in our plots. This pattern may reflect resource poor growing conditions in these plots and suggests that tanoak is

adapted to more resource poor conditions compared to redwood and bay laurel. Tanoak and other species were associated with fine texture soils at middle elevation and moderate moisture sites. Within these middle elevation areas, in which solar radiation output was high, tanoak and bay dominated over redwood and other species where there was relatively more clay in the soil (Fig 2A). In the southern redwood forest sub region bay laurel was dominant at low elevation, high solar radiation sites that were relatively wet and comprised of fine textured soils. At moderate elevations, redwood dominated bay laurel on fine textured soils. Redwood was dominant over other species at lower elevation sites that had soils with less clay content. In this subregion, bay laurel and tanoak were more dominant over other species in sites with relatively lower solar radiation and high soil clay content (Fig 2B).

Host community structure was an important factor influencing the intensity of disease impacts in coastal California redwood forests. Amount of bay laurel infected basal area was best described as a simple linear function of bay laurel basal area (Table 1). Very little residual variation occurred in this model (r^2_{adj} = 0.82) suggesting that additional factors such as host and pathogen genetic structure did not dominate bay laurel infection dynamics within our study sites. Tanoak infection levels were linear functions of tanoak and bay laurel basal area (Table 1) but had considerably more residual variation compared to bay laurel. This difference in model performance may reflect greater sensitivity to historical, host genetic, and pathogen genetic effects but the overall slower rate of tanoak infection compared to bay laurel likely accentuates these effects. Consequently, our understanding of *P. ramorum* infection will be improved with better understanding of pathogen invasion dynamics including the effects of tanoak and pathogen genetics. Tanoak mortality was also a linear function of tanoak and bay laurel basal area (Table 1). The overall dependency of tanoak infection and mortality on tanoak and bay laurel basal area reflects transmission dynamics of *P. ramorum*. Bay laurel produces substantially higher inoculum levels compared to tanoak; therefore,

Table 1. Results from multiple regression modeling of vegetation structure on infection and mortality caused by *P. ramorum*. Standardized regression coefficients are reported when the effects of a vegetation factor were significant at the p ≤ 0.05 level. Degrees of freedom for calculation of statistical effects (DF) and adjusted r square values are listed at the bottom of the table for each analysis.

Dependent variable	Bay laurel infection	Tanoak infection	Tanoak mortality
Independent variables			
LIDE BA	NS	0.73	0.75
UMCA BA	0.95	0.18	0.29
SESE BA	NS	NS	NS
Other species BA	NS	NS	NS
DF	119	119	119
Model r^2_{adj}	0.88	0.51	0.60

higher levels of infected bay laurel basal area should increase tanoak infection levels at the stand level (Davidson et al. in press; Rizzo et al. 2005). High inoculum is likely to increase rate of secondary infection and increase the frequency of tanoak mortality (Gilligan 2006). Inoculum loads have been recovered from rainwater in significantly larger proportions under bay laurel canopies compared to mixed canopies at Jack London State Park (Davidson et al. in press). Assuming a linear relationship between infected basal area of inoculum supporting species and stand level inoculums load, we would expect to find the overall linear relationships between amount of infection and mortality present in our dataset (cf Table 1). In our system of study plots, highest inoculum pressures likely occur in stands with high bay laurel basal area; however, Sudden Oak Death impacts are likely highest in stands at the edaphic and competitive interface

between bay laurel and tanoak as these stands will have the highest inoculums loads on tanoak and the most frequent opportunities for secondary infection.

Implications for stand level management

Understanding the biology and ecology of *Phytophthora ramorum* as well as the ecology of the forests it invades are necessary for managing Sudden Oak Death on a landscape level (Rizzo et al 2005). This study assesses host distribution and community structure of redwood forests invaded by *P. ramorum* from a comprehensive data set comprising of nearly six thousand trees. Edaphic factors in conjunction with historical disturbance are likely major drivers of current species distribution and abundance in these forests (Foster 1988; Meentemeyer et al. 2008b). Compounded with the fact that host community composition is heterogeneous within the central and southern distributions of the redwood forest type in coastal California, management actions may be targeted differently depending on forest composition.

The finding that *P. ramorum* most readily establishes in stands with more tanoak and laurel bay basal area follows predictions based on ecological niche modeling and community level investigations of pathogen establishment (Davison et al. 2003; Maloney et al. 2005; Rizzo et al. 2005; Meentemeyer et al. 2008a). These data also demonstrate that community level vegetation manipulation may be risky at sites where edaphic factors enhance the dominance of sporulation supporting species. For example, results from PCA suggest that bay laurel removal efforts would be most successful in sites where tanoak has a competitive advantage over bay: drier sites at higher elevations in the central sub region and wetter sites at moderate elevations within forests of the southern redwood sub region. These efforts should be avoided in the south where soil silt content is relatively high at lower elevations and in the central region at mid-elevations where soils are fine textured at moderate moisture levels because of likely reestablishment of bay laurel and consequently *P. ramorum* over a decadal time scale. Areas in which bay and tanoak coexist and dominate over redwood and other species may require further study to identify the outcome of stand manipulation. Pruning lower branches of bay laurel and thinning of understory tanoak may be effective in reducing infection due to an overall higher susceptibility of these individuals. Pruning may be most effective at moderate elevation sites where the soil clay content is high for both regions and solar radiation is low in the southern region. Because tanoak supports pathogen sporulation, thinning of tanoak in the understory would be prudent in any case to decrease *P. ramorum* dispersal. Future research efforts will use pre-disease vegetation structure to make predictions of future forest structure and improve disease and forest management strategies.

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