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# Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur region; California

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ABSTRACT

Mixed-evergreen forests of central coastal California are being severely impacted by the recently introduced plant pathogen, *Phytophthora ramorum*. We collected forest plot data using a multi-scale sampling design to characterize pre-infestation forest composition and ongoing tree mortality along environmental and time-since-fire gradients. Vegetation pattern was described using trend surface analysis, spatial autocorrelation analysis and redundancy analysis. Species-environment associations were modeled using non-parametric multiplicative regression (NPMR). Tanoak (*Lithocarpus densiflorus*) mortality was analyzed with respect to environmental and biotic factors using trend surface analysis and multivariate regression. Mixed-evergreen forest occurs throughout the Big Sur region but is most widespread in the north, on north facing slopes, at mid-elevations near the coast. Relative basal area of the dominant tree species changes fairly predictably from north to south and from coast to interior in relation to mapped patterns of precipitation, temperature factors and soil characteristics. Most dominant tree species sprout vigorously after fire. The forests experience a mixed-fire regime in this region ranging from low severity understory burns to high severity crown fires, with the latter increasing above the marine inversion layer and at more interior locations. *Ceanothus* spp. can dominate mixed-evergreen sites for several decades after severe fires. All of the dominant broadleaf evergreen tree species are hosts of *P. ramorum*, although not all will die from infection. Tanoak mortality decreases from northwest to southeast and is significantly correlated with climate, especially growing degree days and mean annual precipitation, and with basal area of the foliar host bay laurel (*Umbellularia californica*) in a 0.5–1 ha neighborhood. Adaptive management of mixed-evergreen forest to mitigate *P. ramorum* impacts in the region will need to consider large local and regional variation in forest composition and the potentially strong interactions between climate, fire, forest composition and disease severity.



## 1. Introduction

Exotic plant pathogens are important agents of forest change in many regions around the globe (Castello et al., 1995; Hall et al., 2002; Loo, 2009). The spread and consequences of these pathogens regulate and are regulated by landscape patterns in biophysical environments (White et al., 2002), forest structure and composition (Perkins and Matlack, 2002; Condeso and Meentemeyer, 2007), and disturbance processes such as fire (Holzmueller et al., 2008) and landslides (Johnson and Wilcock, 2002). For example, Perkins and Matlack (2002) demonstrated that spread of fusiform rust (causal agent *Cronartium quercuum*) is promoted by the high level of connectivity of pine plantations in the southeastern United States. Condeso and Meentemeyer (2007) found that the severity of sudden oak death (causal agent *Phytopthora ramorum*) in mixed-evergreen forests of northern California was greater in plots surrounded by a high proportion of contiguous forest. Understanding landscape patterns and controls on forest composition in relation to disease dynamics is an important component of developing management strategies to cope with forest disease outbreaks (Holdenrieder et al., 2004; Chornesky et al., 2005).

Since its discovery in the San Francisco Bay area of California in the mid-1990s, *P. ramorum*, the causal agent of the forest disease known as “Sudden Oak Death” (SOD), has killed millions of tanoaks (*Lithocarpus densiflorus*, recently attributed to a new genus *Notholithocarpus densiflorus*) and oaks (*Quercus* spp.) in the mixed broadleaf evergreen forests (“mixed-evergreen forests”) and redwood forests of coastal California (Meentemeyer et al., 2008c). *P.*

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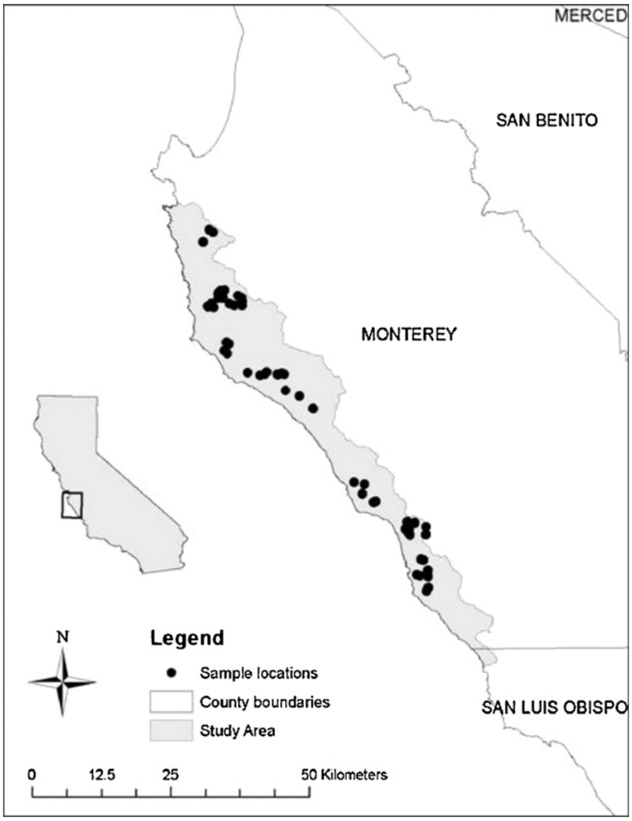


**Fig. 1.** Map of the study area (shaded) with inset showing the areas's location in California. Dots indicate sites for clustered sampling of forest structure and composition.

*ramorum* is now established in coastal forests from the Big Sur coast northward to southern Mendocino County; disjunct introductions have also been detected in southern Humboldt County and Curry County, Oregon.

*P. ramorum* infects at least 30 native California woody and herbaceous host species, causing non-lethal foliar and twig damage in some species (e.g., California bay laurel, *Umbellularia californica*) and lethal twig and stem cankers in others (notably some Fagaceae) (Rizzo and Garbelotto, 2003). Among canker-forming hosts, tanoak is especially susceptible to infection and subsequent mortality; basal area and tree density reductions of over 50% have been observed in monitored tanoak stands within 8 years of initial infestation (Waring and O'Hara, 2008). Annual mortality rates of 4.5–5.5% (an order of magnitude higher than background rates) have also occurred in coast live oak (*Quercus agrifolia*) populations in infested areas (Brown and Allen-Diaz, 2009). Other tree species that may be killed by *P. ramorum* in California include Shreve oak (*Q. parvula var. shrevei*), black oak (*Q. kelloggii*), canyon live oak (*Q. chrysolepis*) and madrone (*Arbutus menziesii*), all of which are important members of mixed-evergreen forest communities (Rizzo and Garbelotto, 2003). The immediate and long term impacts of *P. ramorum*-associated mortality on California mixed-evergreen forests are not well understood, in part because of the relatively short time since the pathogen was introduced, but also because of the limited ecological research on mixed-evergreen forest composition and dynamics (Rizzo and Garbelotto, 2003).

Forests in the Big Sur region (Fig. 1) are among the most impacted by *P. ramorum* (Meentemeyer et al., 2008b). Due to disease-associated tree mortality, mixed-evergreen forests here are undergoing rapid, large scale changes in overstory composition and structure that could have cascading effects on multi-scale vegetation pattern and composition, and associated ecosystem and disturbance processes. However, the ecology of coastal mixed-evergreen forests has not been well characterized (Davis and Borchert, 2006).

**Fig. 2.** Example of fine-grained vegetation on the Big Sur Coast. Mixed-evergreen forest (rough-textured patches) occurs in a patchwork with coast redwood forests, grassland, coastal scrub and chaparral. Image is oriented north-south and 5 km across.

Mixed-evergreen forest in Big Sur is patchily distributed in complex, fine-grained vegetation mosaics of coast redwood (*Sequoia sempervirens*) forest, coastal sage scrub, annual grassland and chaparral (Fig. 2). Forest composition turns over rapidly as one moves upslope and away from the coast along steep gradients in maritime influence and orographic precipitation that interact with soil topo-mosaics and fire history (Cooper, 1922; Wells, 1962; Sawyer et al., 1977; Davis and Borchert, 2006). As a result of *P. ramorum*'s rapid spread and establishment, we are currently in a narrow window of time where it is still possible to characterize pre-infestation forest composition and dynamics in relation to the spread and impacts of the disease. This information will be critical in setting priorities and goals leading to potential disease management decisions. In particular, we lack quantitative information on how host tree species' distributions vary across local-to-regional scales, the association of host species distributions with site factors and fire history, and the current scale-dependent pattern of tree mortality in relationship to forest composition and environmental factors.

We sampled mixed-evergreen forests of the Big Sur Coast, focusing on stands co-dominated by tanoak, to answer the following questions:

- How does forest composition vary across the Big Sur region in relation to location, environmental gradients and fire history?
- How does basal area of dominant tree species vary as a function of spatial scale, environmental factors and fire history?

Although our research focused on characterizing pre-infestation forest composition and dynamics, because we measured both dead and live basal area we also considered two additional questions.

- How has recent SOD-associated tree mortality affected spatial pattern and composition of mixed-evergreen forest?
- How does the current level of forest dieback – in particular the dieback of tanoak – vary as a function of relative abundance of other host tree species, climate, topography, soils and fire history?

Based on previous research, our study design and statistical analyses were guided by the following premises: