Forest Succession Following Wildfire and Sudden Oak Death Epidemic[1]

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Introduction

The Big Sur region of central California is a rugged, fire-prone area that has been severely affected by *Phytophthora ramorum*. Meentemeyer et al. (2008) estimated that over 200,000 oaks and tanoaks had been killed by *P. ramorum* across the Big Sur ecoregion by 2005. In June of 2008, a complex of lightning-initiated fires burned over 95,000 ha in Big Sur, including 43 percent of our long-term network of disease monitoring plots. Here we compile data collected in these plots before the fire in 2006 and 2007 (Metz et al. 2011), with 3 consecutive years of data following the fire (2009 through 2011).

Metz et al. (2011) demonstrated that fire severity was greater in areas recently invaded by *P. ramorum*. We further demonstrate how fire and *P. ramorum* have interacted to affect tree mortality and regeneration, and document the first stages of forest succession. The asymmetric impacts of these two disturbances across species may create significant conservation and management challenges in years to come (Metz et al. 2011).

Methods

During 2006 and 2007, we established 280 plots (each 500 m^2) to assess the ecological effects of *P. ramorum* across the Big Sur region (Metz et al. 2012). We then examined 42 plots that burned in the summer of 2008 and were re-surveyed once in 2009 and again between 2010 and 2011. Twenty plots were in redwood-tanoak forest, while 22 plots were in mixed-evergreen forest. About half of the plots (23) yielded positive culture results for *P. ramorum* at the time of establishment. This resulted in a fairly balanced study design in which disease, fire, and disease-fire interactions could be studied in natural ecosystems.

During a plot census, we recorded size and health for all stems with at least 1 cm diameter at breast height (DBH), and cultured symptomatic tissue to survey for *P. ramorum* infection. All tissue samples that were not positive in culture were genetically sequenced to screen for *P. ramorum*. We compared live and dead basal area, new stem recruitment, and plot-level *P. ramorum* infestation status among dominant tree species for all 3 survey years.

Results

Post-Fire Mortality

Grouping all host and non-host species together, live basal area was greater in uninfested plots across all years (MANOVA, P=0.0339, N=42). Regardless of infestation status, there was significant

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mortality in burned plots following the fires (P<0.0001). Total mortality was primarily driven by fire, with no discernible effect of *P. ramorum* infestation on mortality in burned plots (P=0.7152). A significant amount of standing dead basal area had fallen by our 2010/2011 sampling season, but *P. ramorum* infestation was not a significant driver of the recruitment of logs from snags (standing dead trees).

An analysis of tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh) alone yielded similar results. However, no significant difference in live tanoak basal area was observed between infested and uninfested plots (MANOVA, P=0.1299, N=42). Infestation status did not have a significant effect on the amount of standing dead tanoak overall, though a trend toward higher amounts in infested plots is suggested by the data (MANOVA, P=0.0862). Furthermore, mortality during the 2008 fires did not vary between infested and uninfested plots, but the rate of snag fall was significantly greater in infested plots (MANOVA, P=0.0376).

Post-Fire Recruitment

We analyzed the effect of *P. ramorum* infestation on the recruitment of new stems for each host species independently. New stem recruitment encompasses all stems which grew into our 1 cm minimum DBH criterion since the fire. While some of these new stems represent recruitment from saplings, most are basal sprouts from previously existing trees. For each species, we co-varied pre-fire live basal area with its corresponding density of new stems and compared them by infestation status using a GLM with a Poisson distribution.

The density of new stems was greater in 2010-2011 than in 2009 for all species, regardless of plot infestation status. All species with the exception of California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) have higher densities of newly recruited stems in uninfested plots. However, much of this difference is due to the co-linearity of tree species and pathogen distribution. In fact, *P. ramorum* infestation did not significantly affect stem recruitment for tanoak (P=0.3333, N=32). For oak (*Quercus* spp.), new stem density was higher in uninfested plots independent of initial basal area, but oak recruitment only occurred in ten plots, and was highly variable (P<0.0001, N=24).

Bay laurel had significantly higher recruitment density in infested plots, independent of pre-fire live basal area (P<0.0001, N=25). This relationship was particularly strong compared with the other species examined. The data for redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) are more difficult to interpret. When we do not include pre-fire live basal area in our analysis, it appears as though new stem density is slightly higher in uninfested plots (P=0.0020, N=20). However, when initial live basal area is included as a factor, new stem density is higher in infested plots (P<0.0001). A more sophisticated analysis is needed to further separate the effects of species occurrence and pathogen impacts.

Conclusions

The collective effects of *P. ramorum* and wildfire have reduced live tree basal area across all species, but especially in oaks and tanoaks. It may be necessary to incorporate more sophisticated analyses and yet unexamined variables to conclusively explain the impact of *P. ramorum* infestation on mortality in burned plots. Plot-level infestation status may not be an adequate predictor of disease impacts due to heterogeneity in pathogen arrival date and disease severity (Metz et al. 2011). Furthermore, it may be inherently difficult to separate the effects of fire and *P. ramorum* because the reduction of live host material due to fire may temporarily diminish pathogen effects on live basal area (Beh 2011).

Higher fall rates of dead tanoak in infested plots may lead to increased woody debris accumulation and greater fire severity in the future (Metz et al. 2011). The prolific sprouting of bay laurel in infested plots suggests it will have greater importance in the future, which may increase the long-term persistence of *P. ramorum* and increase its potential impacts.

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