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Apparent competition among host species and feedbacks on disease severity in the sudden oak death pathosystem

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Background/Question/Methods
Selective infection and mortality by generalist pathogens holds the potential to shift competitive interactions and radically transform community structure. *Phytophthora ramorum*, the causative agent of sudden oak death, has a broad host range but is highly virulent to only a few species. In California redwood forests, susceptibility to foliar *P. ramorum* infection varies from high in California bay laurel (*Umbellularia californica*) to low in redwood (*Sequoia sempervirens*) but neither species suffers mortality. In contrast, tanoak (*Lithocarpus densiflorus*), an important component of these forests, is highly susceptible but suffers extensive mortality due to stem cankers. We hypothesize that differing susceptibility among host species to *P. ramorum* results in apparent competition among hosts and causes feedback between removal of tanoak and disease intensification. Because high amounts of pathogen sporulation occurs on leaves of bay laurel, increased survival of this species is likely to increase disease severity in tanoak. Conversely, increased survival of redwood is likely to decrease inoculum load because redwood is much less susceptible and supports minimal sporulation. Over the course of six years, we monitored survival of 5769 trees spanning the current geographic distribution of *P. ramorum* in California to estimate effects of *P. ramorum* on competitive interactions and host survival.

Results/Conclusions
Principal components analysis showed orthogonal relationships among host species before the arrival of sudden oak death which were influenced by edaphic factors such as topographic moisture index, aspect, and soil texture. Multivariate regression analysis of stand structure showed positive relationships between the level of tanoak mortality over a 12-year period and the biomass of bay laurel and tanoak existing before the onset of the disease. Negative correlations between tanoak and bay laurel after the arrival of the disease are similar to the patterns expected if these species were competing for

resources. The difference in the patterns before and after pathogen introduction suggest that sporulation pressure is important in structuring community composition in impacted stands, and consequently that *P. ramorum* results in negative effects of bay laurel on tanoak. Logistic regression showed increased survival of infected redwood and bay laurel compared to uninfected trees in small size classes suggesting that infection may increase survival of these hosts, presumably through reduced competition for resources. These changes in community structure are likely to increase disease intensity in stands with niche structure favoring bay laurel and decrease disease intensity in those with niche structure favoring redwood.