Landscape Connectivity Influences the Establishment of *Phytophthora ramorum*[1]

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Abstract

As the emergence of invasive pathogens and their impacts on ecological communities increases, so has the interest in understanding how landscape pattern (in other words the configuration and composition of suitable habitat) affects their establishment and spread. Plant pathogen invasions are inherently spatial, but few studies have demonstrated the role of landscape pattern on disease dynamics. In this study, we investigated two hypotheses: Does the spatial pattern of host habitat predict *Phytophthora ramorum* disease severity, and is this relationship scale-dependent?

To examine this question, we first mapped the spatial distribution of suitable habitat for *P. ramorum* in a 20.25 km^2 region on Sonoma Mountain (Sonoma County, California, U.S.) using ADAR multi-spectral imagery. We calculated three simple metrics of landscape pattern that described the size, shape, and connectivity of host woodland using Fragstats 3.3; these were woodland area, perimeter/area ratio and patch cohesion. To examine the spatial scale at which *P. ramorum* responds to landscape pattern, each metric was computed using a multi-scale nested approach. The metrics of area, shape and connectivity were calculated for nested landscapes of increasing size surrounding each sample plot. Each nested landscape was delineated by a circular boundary centered on the plot, with increasing radii of 50 m increments from 50 to 500 m. In the field, we established 86 field plots (15 m by 15 m) within habitat patches according to a random-stratified criterion defined by woodland patch size and distance to a forest-grassland boundary. For each plot, we quantified *P. ramorum* disease severity by counting the number of symptomatic leaves on each bay laurel stem greater than 2 cm diameter at breast height (DBH, defined at 1.4 m) for 90 sec. We confirmed the presence of *P. ramorum* in the symptomatic leaves by culturing a sample of leaves from each of plot using standard PARP methods. To control for the influence of local (within-plot) conditions in the analysis, we also measured the following variables within each of the field plots: abundance of bay laurel (*Umbellularia californica*), canopy cover, distance to forest edge and elevation.

The response of cumulative symptomatic leaf count per plot to the pattern of host woodland (area, perimeter/area ratio and patch cohesion) was examined using multiple regression, testing all possible subsets of predictors and identifying the best model using the Akaike Information Citerion (AIC). Standard beta coefficients were used to assess the relative importance of each of the significant predictors in the regression model. Potentially influential plot-level variables were controlled for by including the aforementioned measures of bay laurel abundance, plot canopy cover, distance to forest edge and elevation.

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Phytophthora ramorum disease severity was greatest in plots surrounded by a high proportion of contiguous forest, after accounting for plot-level variables of host abundance, elevation, canopy cover and microclimate. The explanatory power of the model increased with increasing scale up to 200 m. The effect of surrounding woodland area increased from 50 to 200 m scales, with the strongest effect at 200 m. The effect of bay abundance within each plot was fairly consistent across all scales. The effect of canopy cover over plots was highest at small scales, and decreased at larger scales. The effect of plot elevation became significant at the 50 m scale and remained fairly consistent. Mean perimeter-area ratio of host woodland within each nested landscape did not predict leaf count at any scale. Patch cohesion was highly correlated with woodland area at all scales (Pearson's r ranging from 0.77 to 0.92, $p<0.0001$) and was omitted from these models because when evaluated as an alternative variable, woodland area consistently explained more variance in leaf count across all spatial scales.

In summary, both landscape-scale configuration and local composition of host habitat are related to the severity of this destructive forest disease. Determining the spatial scale of a species' response to habitat is critical for understanding movement ranges and dispersal of invasive organisms such as *P. ramorum*. Increased disease severity within contiguous woodlands may have a considerable impact on the composition of such woodlands, with cascading effects on the population dynamics of both host and pathogen.

Key words: Scale, landscape pathology, connectivity, fragmentation.