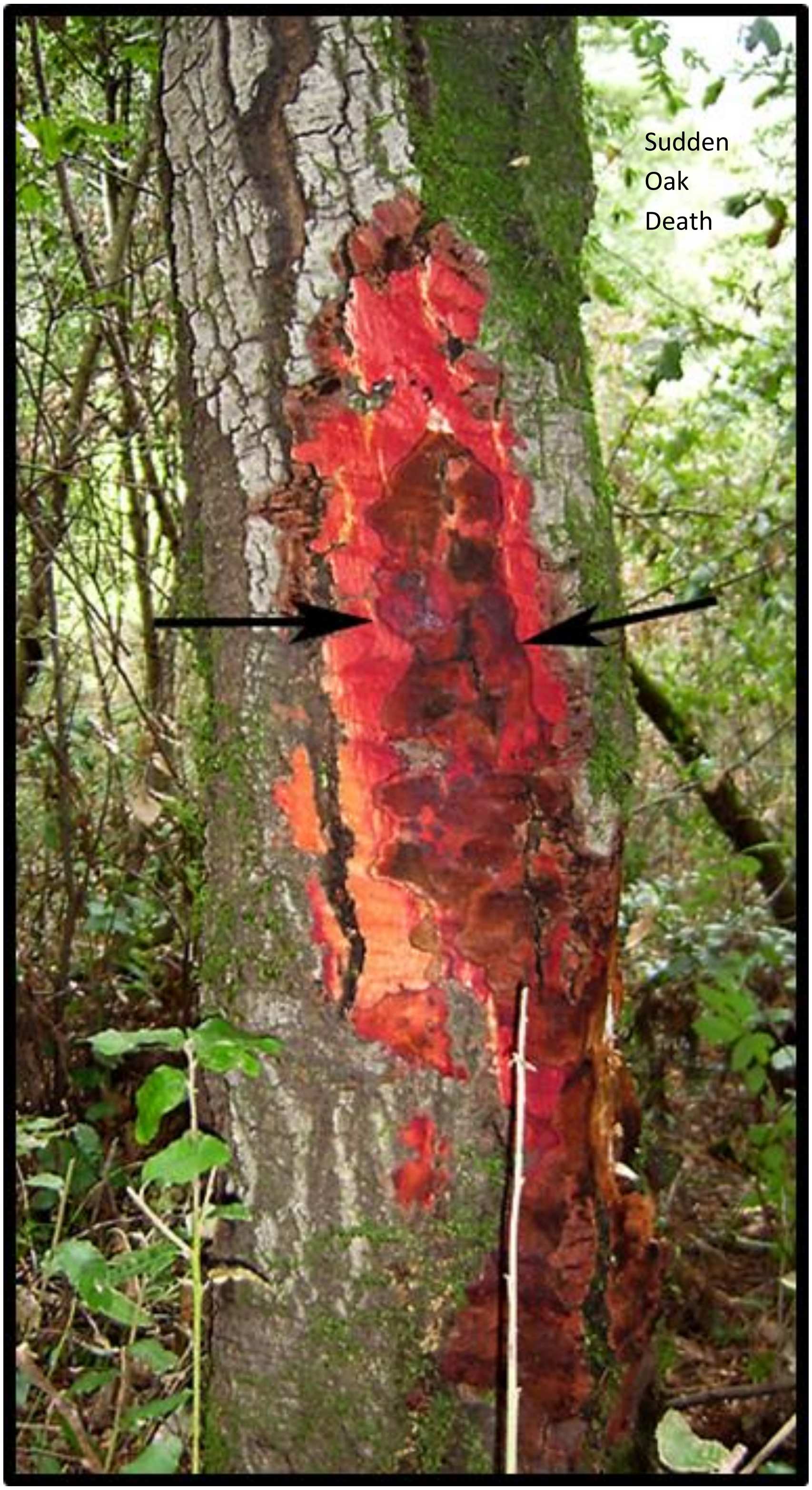
Does topography play a role in *Phytophthora ramorum* distribution?



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Introduction:

Invasive forest insects and pathogens are a significant threat to ecosystem services and functions worldwide (Liebhold et al. 1995, Vitousek et al. 1996, Vitousek et al. 1997, Simberloff 2000, Perles et al. 2010). The rate of introduced species continues to increase due to increases in global trade (Levine and D'Antonio 2003, Holmes et al. 2010). Invasive forest pests pose a serious risk to natural, agricultural and urban systems. Public awareness of ecosystem effects of invasive insects and pathogens is on the increase due to highly damaging pests like the Asian longhorned beetle, Hemlock Woolly Adelgid, emerald ash borer, and *P. ramorum* (Nowak et al. 2001, Ward et al. 2004, Anulewicz et al. 2007, Meentemeyer et al. 2008b, Cobb 2010, Cobb et al. 2012). Given these risks it is important to understand factors influencing pest and pathogen distribution across a landscape.

Phytophthora ramorum is an oomycete, a fungus like eukaryotic microorganism, which has been shown to infect 37 different species, see table 1. Disease symptoms are expressed in two forms: lethal stem cankers, *P. ramorum* (SOD), on oak species and tanoak or as non-lethal foliar infections, Ramorum Blight, in many other species. The canker hosts are epidemiological dead ends while the foliar hosts allow for the production of large amounts of inoculum. California Bay Laurel produces the most inoculum of all host species (Kelly and Meentemeyer 2002, Meentemeyer et al. 2008a, Václavík et al. 2010). The range of *P. ramorum* is from the Big Sur region of California to Southwestern Oregon (Meentemeyer et al. 2008a, Cobb et al. 2010, Václavík et al. 2010, Cobb et al. 2012), see figure 1. *P. ramorum* produces two types of spores: chlamydospores (resting spores) and zoospores, which have flagella for swimming. Spores are transmitted via rain-splash and wind driven rain, which can knock spores into watercourses where they can be transmitted great distances. People engaged in outdoor activities can also transmit the disease spores on their equipment, especially in muddy areas (Davidson et al. 2002). Due to the transmission dynamics of *P. ramorum*, complex topography is likely to play a role in *P. ramorum* distribution across the landscape.

Topography has been shown to play a significant role in the ability of other forest pests to distribute across a landscape (Royle and Lathrop 2002, Pontius et al. 2010). To date no study has examined the effects of complex topography on the distribution of *P. ramorum*. The goal of this study twofold: analyze the effects of complex topography.

Methods:

Data:

The study area was the Big Sur ecoregion in California, see figure 2. Digital elevation models (DEM) were obtained from the USGS at a 30 meter resolution for the study area (Gesch et al. 2002). First the elevation data was filled in order to remove pits from the area and ensure that all areas drained until they meet the edge. Slope was calculated in degrees for the study area. Flow Direction and Flow Accumulation were also calculated from this filled elevation DEM. Topographic Wetness Index (TWI) was calculated for each DEM using the equation $TWI = L(((FAC+1)*Cell\ Size)/Tan(slope))$, where FAC= flow accumulation and slope is converted into radians for the calculation. ArcGIS was used for all topographic calculations, see figure 3 for flow chart (Burrough and McDonnell 1998). TWI was then resampled to a 1 km resolution using inverse distance weighted kriging in order to match the rest of the data. PRISM data from 2010 was obtained for California at a 1 km by 1 km resolution and clipped to the study area (Daly et al. 2000). The daily precipitation, minimum temperature, and maximum temperature data was averaged for every month. I used FIA plot data and CALVEG data to interpolate 7 tree species, see table 2, to a 1 km by 1 km resolution in order to keep the same spatial resolution as the PRISM data. All 7 species, 3 topographic variables, and 36 climatic variable, see table 2, values were extract to the plot locations shapefile and exported into the R statistical program for analysis and model building.

Plot and tree data:

In 2006 a long term monitoring network for *P. ramorum* was established by the Meentemeyer, Rizzo, and Garbelotto labs. The network consisted of 280, 12.5 m radius plots throughout a 79,356 hectares study area within the Big Sur ecoregion. The plots were randomly located across a range of ecological conditions stratified by elevation, latitude, fire history, and forest community type (mixed evergreen and redwood forests). Additionally, the plots were located in areas with and without pathogen presence. The topography in this region is characterized by deeply dissected slopes and drainages, with elevation ranging from sea level to 1571 m within 5 km of the coast (Henson 1996). All trees ≥1 cm in diameter at breast height (dbh) and shrubs that reached an area ≥ 1 m^2. *P. Ramorum* symptoms are recorded for hosts that meet these requirements and tissue from symptomatic individuals is brought to the lab for pathogen isolation (Davidson et al. 2005). For this project the total number of infected trees as of 2010 was calculated for each plot as well as the total number of trees. Percent *P. ramorum* infected trees was then calculated for each plot. This percentage was used as the dependant variable for model construction and interpretation.

Model:

In order to determine whether complex topography plays a role in the distribution of *P. ramorum* across a landscape models were fit with all variables thought to be possible predictors of *P. ramorum*, see table 2 for a list of potential model variables. For this project a simple generalized linear model was fit with all variables, non-significant variables were removed from the model. The only individual tree variable that remained significant was the relative frequency of California bay laurel. All three topographic variables were used to check for the effect of topography on *P. ramorum*; the only significant parameter was TWI.

The final model contained 11 variables: TWI, California Bay Laurel, January and February Minimum temperature, March, August, September and December Maximum Temperature, and April, May, and July Precipitation, see table 3 The model was then tested for spatial autocorrelation using the mantel test based on Legendre and Legendre (2012). Spatial autocorrelation was not significant in this data set and was therefore not account for in the model. The final model had an AIC of 60.0051 and R^2 of 0.456, see figure 4. Raster Calculator in ArcGIS was used to make a map of percent *P. ramorum* infection using the coefficients from this model as all independent variables were derived from raster grids, see figure 5 for final map predictions.

Results:

TWI and many climatic variables proved to be significant predictors in the model, see table 3 for p values. It is not surprising that California bay laurel is a significant predictor as it is the species that produces the most spores and was rated as the most important tree species in predicting *P. ramorum* (Meentemeyer et al. 2004, Meentemeyer et al. 2008a, Václavík et al. 2010). TWI is a significant predictor of *P. ramorum* distribution but it has a small effect on the likelihood of a plot having more trees infected, for every one unit increase in TWI the number of trees infected in a plot is expected to increase by 0.008. This positive influence is probably due to *P. ramorum* having higher reproduction and higher survivability in moist areas and higher values of TWI indicate areas that are likely to be more moist (Rizzo and Garbelotto 2003). The climate variables are not surprising with the exception of maximum temp in December and minimum temperature in January and February. Other studies have showed that inoculum production begins in April and ends in September and is highly dependant on temperature and precipitation (Meentemeyer et al. 2011, Meentemeyer et al. 2012).

Conclusions:

While TWI has a significant effect on the distribution of *P. ramorum* in this study area the effect is small. This effect have been largely ignored in the current work done on *P. ramorum*. Future work could benefit from using TWI or another variable that explains topographic complexity. By incorporating some of these findings into spread models early detection of *p. ramorum* could be increased, thus preventing further spread and harm to the endemic California oak species. It is important to keep in mind that this work was done on a relatively small dataset and may not hold over the larger range of *P. ramorum*. Future work will examine the full range of *P. ramorum* in order to determine if these effects hold at larger spatial scales.

Appendix:

Table 1:
Known hosts infected by *P. ramorum* (Rizzo et al. 2002a, Rizzo et al. 2002b) in forests of California and Oregon

Quercus agrifolia	*Rubus spectabilis*
Quercus kelloggii	*Aesculus californica*
Quercus parvula var. shrevei	*Rhamnus californica*
Quercus chrysolepis	*Rhamnus purshiana*
Lithocarpus densiflorus	*Corylus cornuta*
Arbutus menzeisii	*Lonicera hispidula*
Vaccinium ovatum	*Viburnum spp.*
Arctostaphylos spp.	*Toxicodendron diversilobum*
Rhododendron spp.	*Trientalis latifolia*
Umbellularia californica	*Sequoia sempervirens*
Acer macrophyllum	*Pseudotsuga menziesii*
Heteromeles arbutifolia	

Table 2: Potential model variables including 7 host species, 3 topographic, and 36 climatic variables

RF	**Topographic**	**Climate**
California laurel	TWI	Monthly Average PPT
California live oak	Slope	Monthly Mean TMAX
California black oak	Elevation	Monthly Mean TMIN
redwood		
tanoak		
Pacific Madrone		
Douglas Fir		

Table 3: Final model parameter significance

Variable	Estimate	Pr(>|t|)
(Intercept)	2.139	0.022
TWI	0.008	0.022
TMAX3	-0.364	<0.001
TMAX8	-0.215	0.001
TMAX9	0.278	0.001
TMAX12	0.156	0.002
TMIN1	-0.318	0.048
TMIN2	0.380	0.048
PPT4	-0.004	0.044
PPT5	0.018	0.036
PPT7	-0.855	<0.001
California Bay Laurel	0.501	0.030

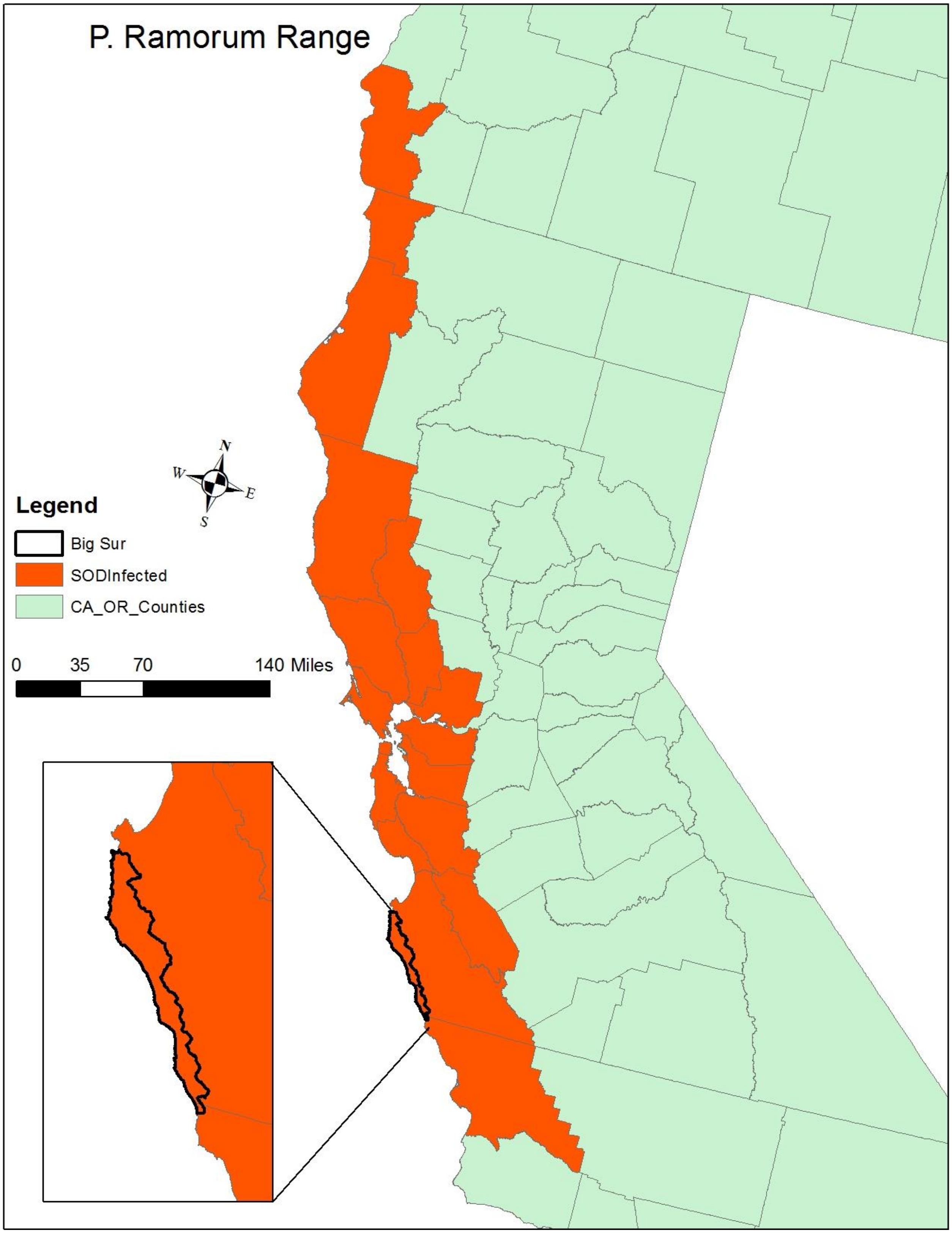

Figure 1: *P. ramorum* range

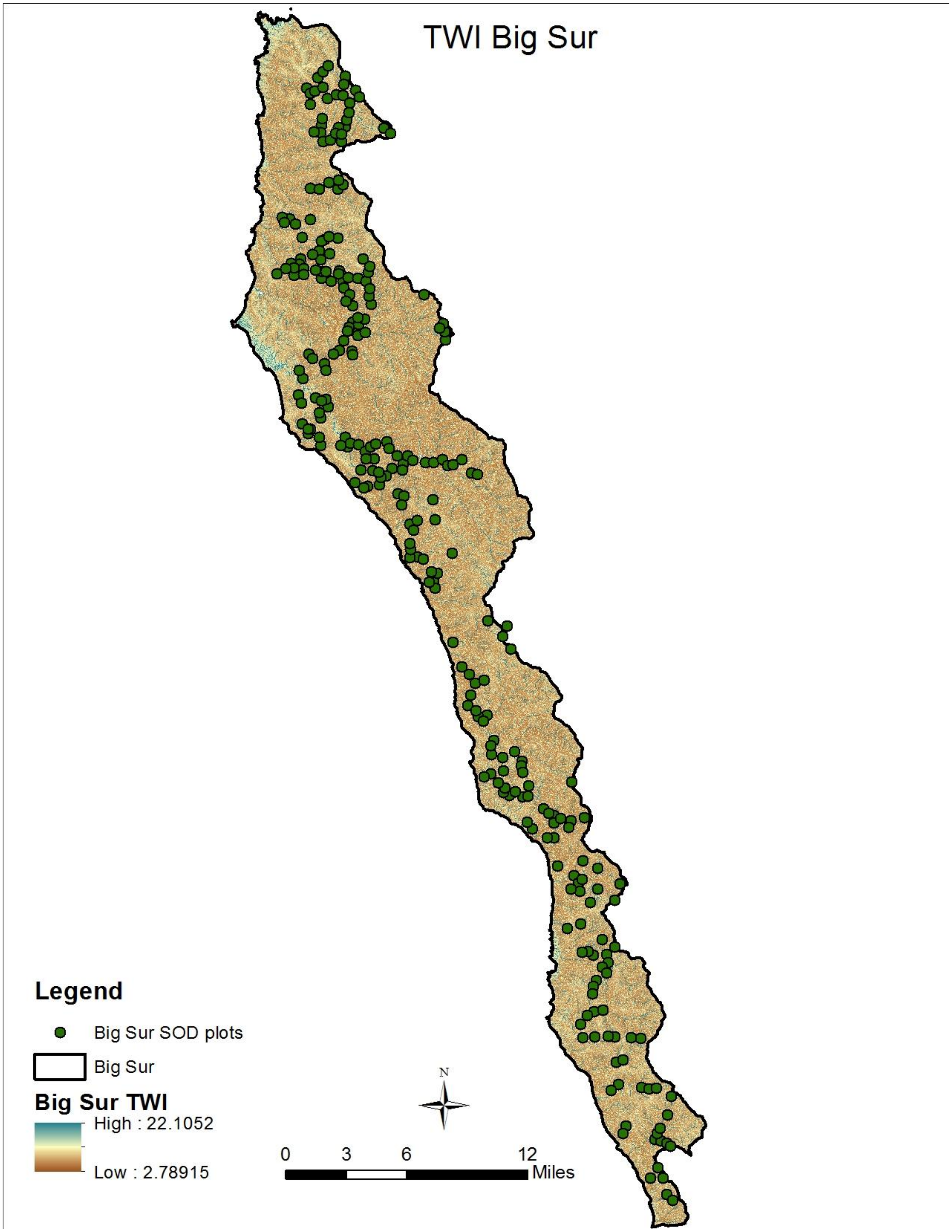

Figure 2: Plot locations in the Big Sur and Topographic Wetness index.

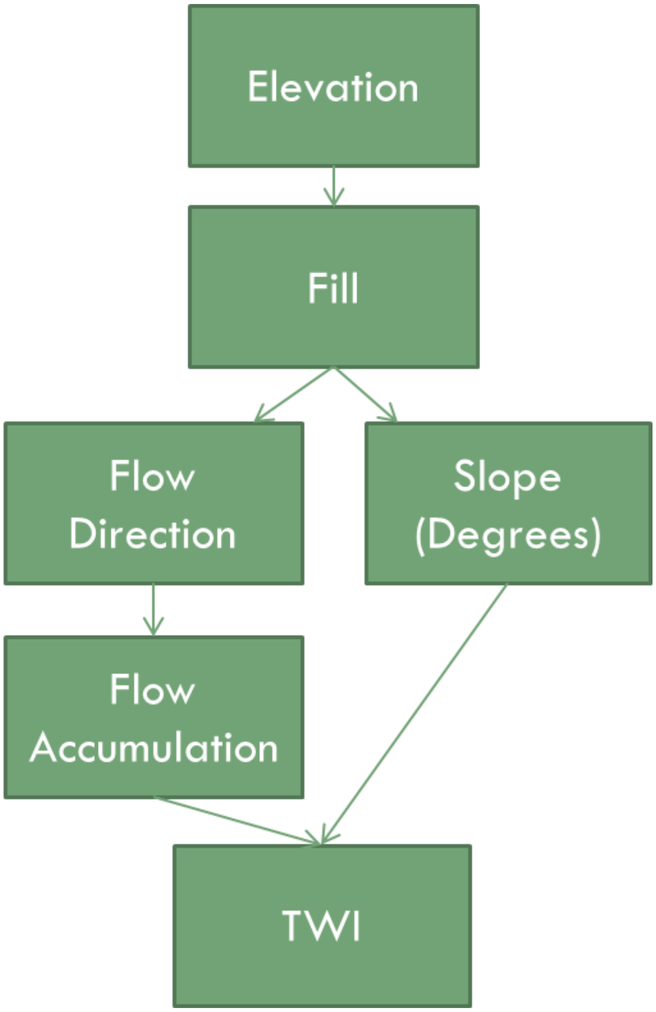

Figure 3: Topographic Wetness Index steps.

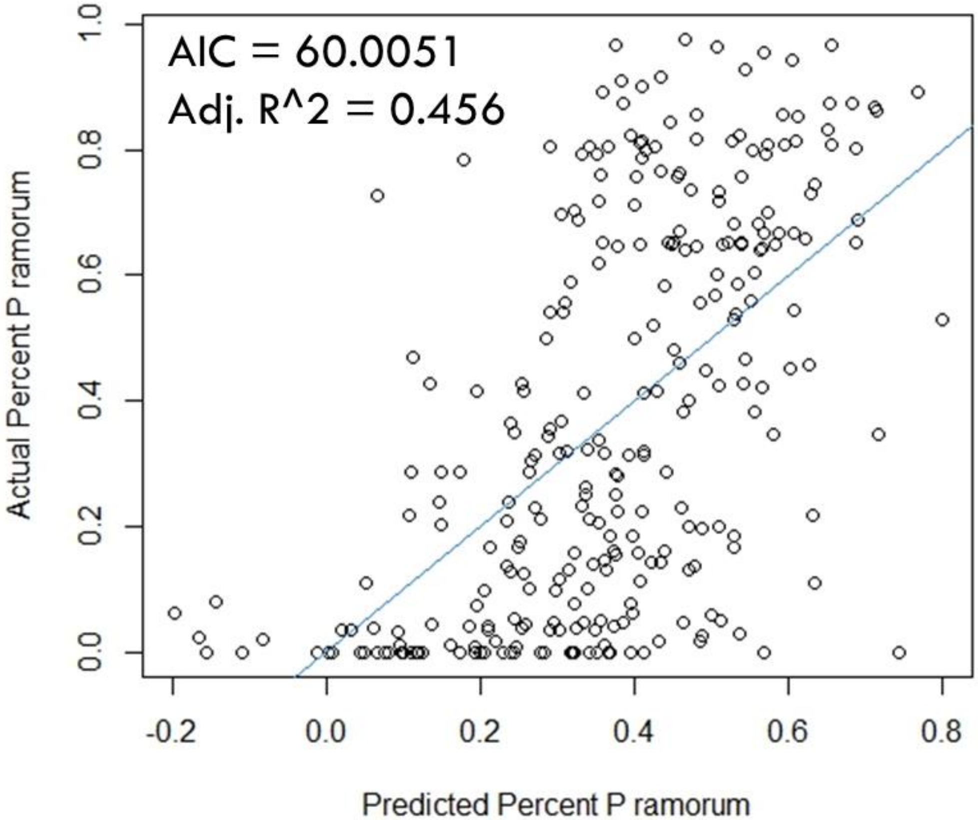

Figure 4: Actual vs. Predicted percentage of trees infected with *P. ramorum*

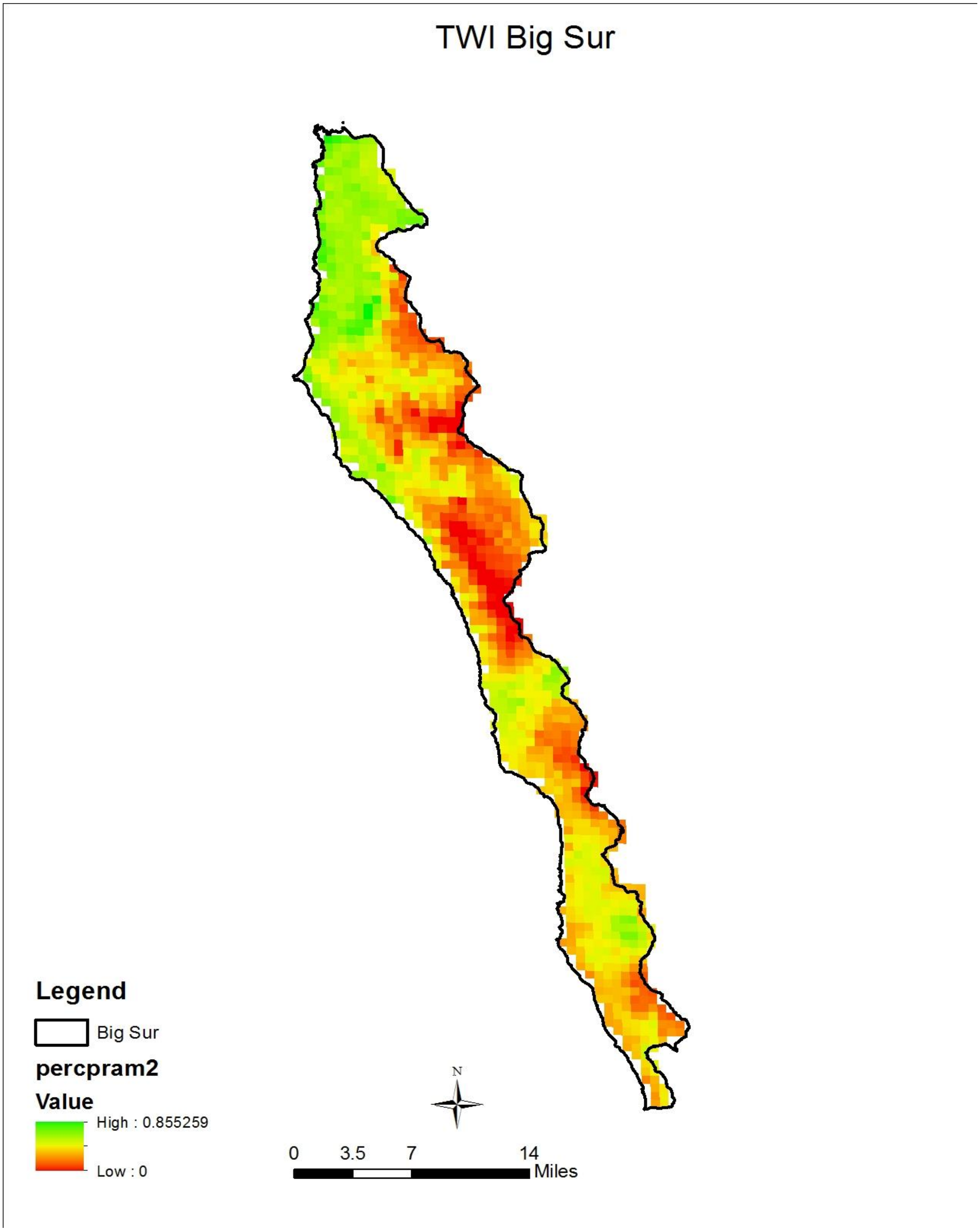

Figure 5: Predicted *P. ramorum* infected percent over the entire Big Sur using coefficients from the model developed in R

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