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Mapping the Potential Distribution of Oak Wilt (Ceratocystis fagacearum) in East Central and Southeast Minnesota Using Maxent

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Mapping the Potential Distribution of Oak Wilt (*Ceratocystis fagacearum*) in East Central and Southeast Minnesota Using Maxent

by

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Abstract

Forest diseases and pathogens can cause significant damage to an ecosystem. Understanding where they are going to occur and what variables are important in their distribution can stave off the detrimental effects they have on established and at risk ecosystems. With the advancement of spatial analysis and remote sensing technology, these diseases can now be managed through modeling. Modeling allows researchers to determine the extent of the disease, which variables lead to the increase in infection centers, and predict the distribution of the disease. This study used Maxent, a presence-only species distribution model (SDM), to map the potential probability distribution of the invasive forest pathogen oak wilt (*Ceratocystis fagacearum*) in eastern and southeastern Minnesota. The model related oak wilt occurrence data with environmental variables including climate, topography, land cover, soil, and population density. Results showed areas with the highest probability of oak wilt occur within and surrounding the Minneapolis/St. Paul metropolitan area. The jackknife test of variable importance indicated land cover and soil type as the most important variables contributing to the prediction of the distribution. Multiple methods of analysis showed the model performed better than random at predicting the occurrence of oak wilt. This study shows Maxent has the potential to be an accurate tool in the early detection and management of forest diseases.

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Chapter 1: Introduction

The health of many of the world’s forests is at risk due to humans’ unique ability among animals to significantly alter their environment (Millar and Stephenson 2015; Lindenmayer, Laurance, and Franklin 2012; Cushman and Meentemeyer 2008). An increase in forests pests and pathogens is just one consequence of increased human interaction with the natural world (Weed, Ayres, and Hicke 2013). The importance of forests cannot be overstated; they are sources of raw materials and food, they prevent soil erosion, purify the air and water, and provide habitat for countless species. An increase in forest pests or pathogens would be devastating (Anagnostakis 1987; Needham et al. 2016). With the advancement of spatial analysis and remote sensing technology, management of these pests and pathogens is possible through modeling to determine the extent of the disease, which variables lead to an increase in infection centers, and prediction of the future distribution of the disease.

This research sets out to discover if the potential distribution of oak wilt in east central and southeastern Minnesota (Figure 1.1) could be mapped using Maxent version 3.4.1 species distribution model (SDM) and to determine which variables were important in the creation of that distribution. Oak wilt is a considerable threat to the health of forests in the state because of its ability to spread rapidly through oak stands. Oak wilt occurrence locations dated between 2007 and 2016 from the Minnesota Department of Natural Resources (MN DNR) and Three Rivers Park District (TRPD) were used. Environmental variables were carefully chosen to represent a wide spectrum of abiotic factors that are shown to have an effect on the distribution of oak wilt and other forest pathogens: climate, topographic, land cover, soil, and population data. With these variables, Maxent produced a better than random distribution for oak wilt in Minnesota. This research concludes by discussing whether the variables that were determined important by the model make ecological sense and are supported by current understanding and research.

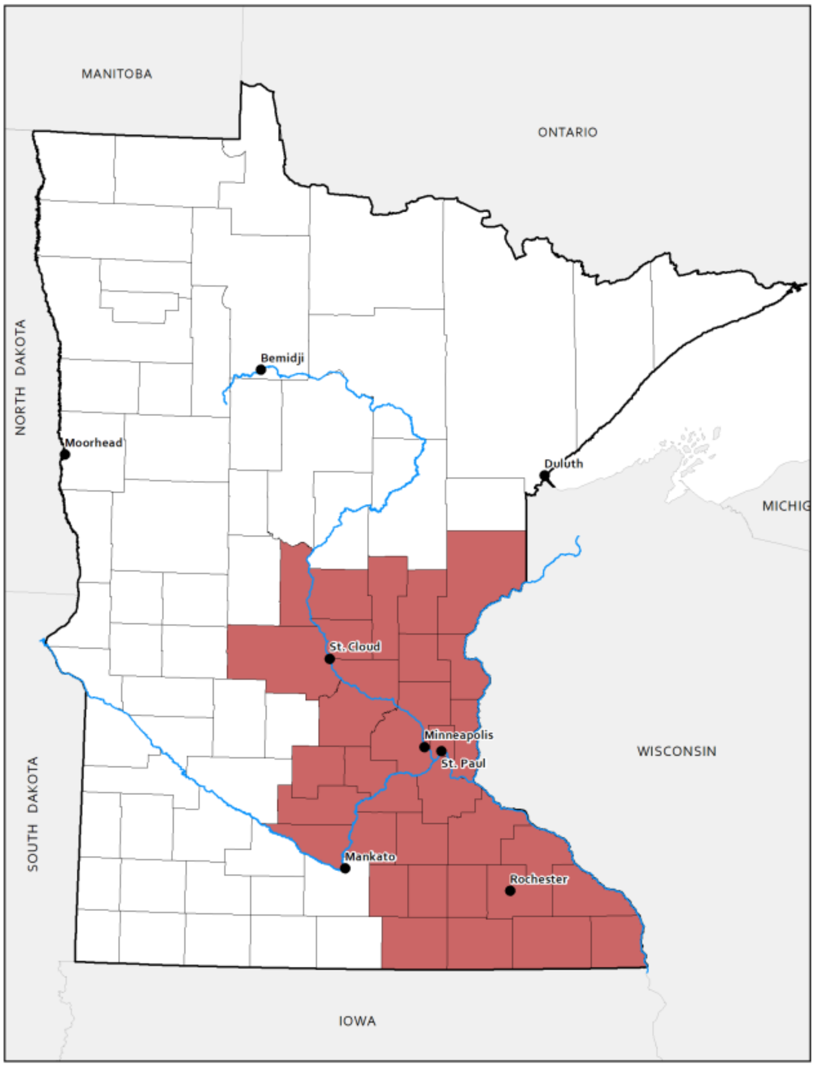

Figure 1.1: Study area consisting of 33 counties in east central and southeastern Minnesota.

Forest Pathogens

Forest pathogens thrive in most forests. Although most are innocuous and do not cause serious or long-term damage to the ecosystem, others such as Dutch elm disease and chestnut blight have the ability to devastate landscapes. Globalization in the form of increased travel and trade between and within countries creates new avenues for long distance dispersal of invasive forests pathogens into new habitats. Even locally, leisure and recreation activities, such as hiking, have been shown to carry pathogens short distances to new locations. The transport of firewood can carry pathogens hundreds of miles away to areas far distant from other infection centers (Cushman and Meentemeyer 2008). Change in land use through increases in agriculture land, deforestation, draining of wetlands, urban sprawl and landscape changes due to suppression of natural events such as fire can affect the prevalence of forest pathogens (Meentemeyer et al. 2008; King et al. 2006). Human-induced climate change affects the susceptibility of forests through shifting ranges of the pathogen or host species, adaptive reproductive responses, altering habitat and ecological community of a region, and through the social and economic responses of climate change (Venette 2013; Desprez-Loustau et al. 2011; Wilkinson et al. 2011). This results in forest fragmentation and loss of forest heterogeneity that allow forest pathogens to thrive.

When trees are lost because of a particularly devastating pathogen, the biology of a landscape, the human society tied to those trees, and the economies of the surrounding areas are impacted. The biological consequences are the most obvious. Tree loss can lead to decreased food supply and habitat for creatures that inhabit the area and change in the structure and composition of forest communities for decades to come. One striking example is the disease that affected American chestnut (*Castanea dentate*). In the early twentieth century, the American chestnut was an important species in the forests of the eastern United States comprising nearly 20 percent of forests in some regions (Faison and Foster 2014; Bratton and Meier 1998). With the introduction of chestnut blight (*Cryphonectrica parasitica*) from Japan in 1905, chestnuts numbers quickly declined and within 50 years, nearly 14,000 square miles of chestnuts were destroyed (Anagnostakis 1987). Today, chestnuts are struggling to regain its lost numbers and currently inhabit a mere fraction of their original range (Fei et al. 2012).

Less obvious but no less important, are the losses felt by society when a forest pathogen sweeps through a community. Trees can have an aesthetic and cultural value that is difficult to quantify (Haight et al. 2011). Elm trees once lined the streets of every American city with their tall, straight trunks and arching branches creating charming shaded boulevards. The introduction of Dutch elm disease from Europe in the 1930s left American streets bare (Marcotrigiano 2016). On a smaller and more personal scale, the loss of trees or just one significant tree from a yard can have an impact on both heart and mind that cannot be described in terms of biology or economy.

The economic effects of forest pathogens reach far. Costs associated with forest pathogens include tree removal, sanitation, detection, and management. Their effect can manifest as loss in property value, timber products, employment, and revenue from visitors (Haight et al 2011, Kokvacs et al. 2000, and Pimentel et al. 2000).

With the advancement in technology, remote sensing imagery, and the open availability of relevant data sources comes the ability to predict accurately the occurrence and potential distribution of forest pathogens using species distribution models. Utilizing these technologies can assist in the detection, management, and eradication of destructive forest disease and minimize the biological, societal, and economic impacts associated with them.

Species Distribution Models

Species distribution models (SDMs) are important tools in the fields of ecology, biogeography, conservation biology, and, more recently, climate change studies in understanding how the distribution of a species is dictated by local environmental factors (Guisan, Thuiller, and Gotelli 2005). SDMs create a distribution of a species by relating known species occurrence locations with environmental variables (Guisan and Zimmermann 2000). According to Austin

(2002), a proper SDM will include three parts: 1) an ecological model, 2) a data model, and 3) a statistical model.

Scientists use SDMs to understand the distribution of a species or predict where the species may occur. Most often, SDMs are used to understand or describe the distribution of one species (Ahmed et al. 2015). By using SDMs in such a way, scientists can better understand which variables are associated with the presence or absence of a species, information that can prove particularly beneficial in studies on rare or endangered species (Morinha et al. 2017; Maria Teresa et al. 2014; Wilson, Roberts, and Reid 2011; Elith and Leathwick 2009). In addition, with the continued acceleration of climate change, SDMs are becoming popular tools in studying the effects shifting temperature and precipitation will have on a species distribution (Abolmaali, Tarkesh, and Bashari 2018; Ikegami and Jenkins 2018; Aguilar, Farnworth, and Winder 2015; Venette 2013).

SDMs come in many different forms including regression models such as generalized linear and generalized additive models, machine learning software such as Maxent, artificial neural networks (ANN), support vector machines, BIOCLIM, DOMAIN, and ENFA to list just a few (Franklin and Miller 2010; Elith and Leathwick 2009). Choosing which SDM to use depends on the species being studied and the occurrence data available. SDMs can be used when absence data are available for a species and when they are not. Some scientists believe the addition of absence data is important because it gives valuable information on unsuitable habitat. However, others believe absence data can be misleading resulting in absence points where there may be suitable habitat simply because the species has not reached that location due to geographic barriers or slow spread. This is the case for species repopulating a location after a disturbance and invasive species (Franklin and Miller 2010; Elith and Leathwick 2009).

This research used the Maxent SDM to map the potential probability distribution of oak wilt in east central and southeastern Minnesota. Maxent utilizes computer software to create a probability distribution of a species based on the principle of maximum entropy. The algorithm used in Maxent modeling is complex but essentially attempts to create a statistical model that recreates the distribution of the training data by assuming a uniform distribution throughout the study area, then altering that distribution only as much as constraints allow (Phillips, Anderson, and Schapire 2006; Berger, Pietra, and Pietra 1996). Constraints are statistical values found using the values of environmental variables at the known occurrence locations. They can range from simple average values of environmental variables to complex statistics involving multiple variables.

The principle of maximum entropy states that within a probability distribution bound by specific constraint the distribution of maximum entropy (or closest to uniform) should be chosen because it agrees with what is known and does not assume anything that is not known. The uniformity of a distribution is summarized by:

$$H(p) \equiv -\sum_{x,y} \tilde{\mathrm{p}}(\mathrm{x})\mathrm{p}(\mathrm{y}|\mathrm{x}) \log \mathrm{p}(\mathrm{y}|\mathrm{x})$$

where H(p) is the conditional entropy $\tilde{p}(x)$ is the empirical probability of x, and p(y|x) is the probability (p) of species occurring (y) given context of x (Berger, Pietra, and Pietra 1996). A single set of constraints is capable of creating distributions of varying uniformities. Maxent will use the distribution that has the largest H(p), or most uniform distribution.

Maxent is machine learning software that requires only presence data to create a robust model of distribution and has quickly become a favorite tool amongst SDM users (Ahmed et al.

2015). It is easy to download, simple to use, efficient, allows the user to alter parameters, and calculates statistical tests. For these reasons, it was chosen for use in this study.

Oak Wilt

Oak wilt is an infectious forest caused by Ascomycetes fungus (*Ceratocystis fagacearum)* found in the eastern United States and has reached serious levels in Texas and the Upper Midwest. The pathogen targets primarily oak trees but all trees found in the family Fagacea that have been inoculated have shown susceptibility (Appel 2009; Harrington 2013). Within the oak family, susceptibility varies among species. White oaks (Sect. *Quercus*) are able to fight off the oak wilt pathogen, red oaks (Sect. *Lobatae*) are easily infected, most dying from the pathogen within months, while live oaks (Sect. *Protobalanus)*, the predominant group in Texas, have susceptibility between that of red and white oaks (Appel 2009; Juzwik, French and Jeresek 1985; Gibbs and French 1980; Jacobi and MacDonald 1980; Parmeter, Kuntz, and Riker 1956). Oak wilt enters a healthy tree through a fresh wound in the bark where it lodges in the xylem tissue. As the pathogen multiplies it chokes the xylem and prevents water from reaching the crown of the tree resulting in the eponymous wilt of the tree (Figure 1.2) (Gibbs and French 1980).

Transmission of oak wilt from an infected to a healthy oak occurs in one of two ways: overland and underground. Overland infection requires three events to happen concurrently. First, a spore mat must form on a red oak (Harrington 2013). Second, a fresh wound to the xylem tissue must be found on a healthy oak (Gibbs and French 1980). Finally, an insect vector must carry spores from the infected tree to the wound in the healthy oak (Juzwik, French, and Jeresek 1985). Underground spread takes place via root grafting and is the most common form of spread in Minnesota occurring most commonly among red oaks (Gibbs and French 1980; Parmeter, Kuntz, and Riker 1956). Regardless of the route of transmission, it is evident oak wilt is a rapidly spreading and serious forest disease.

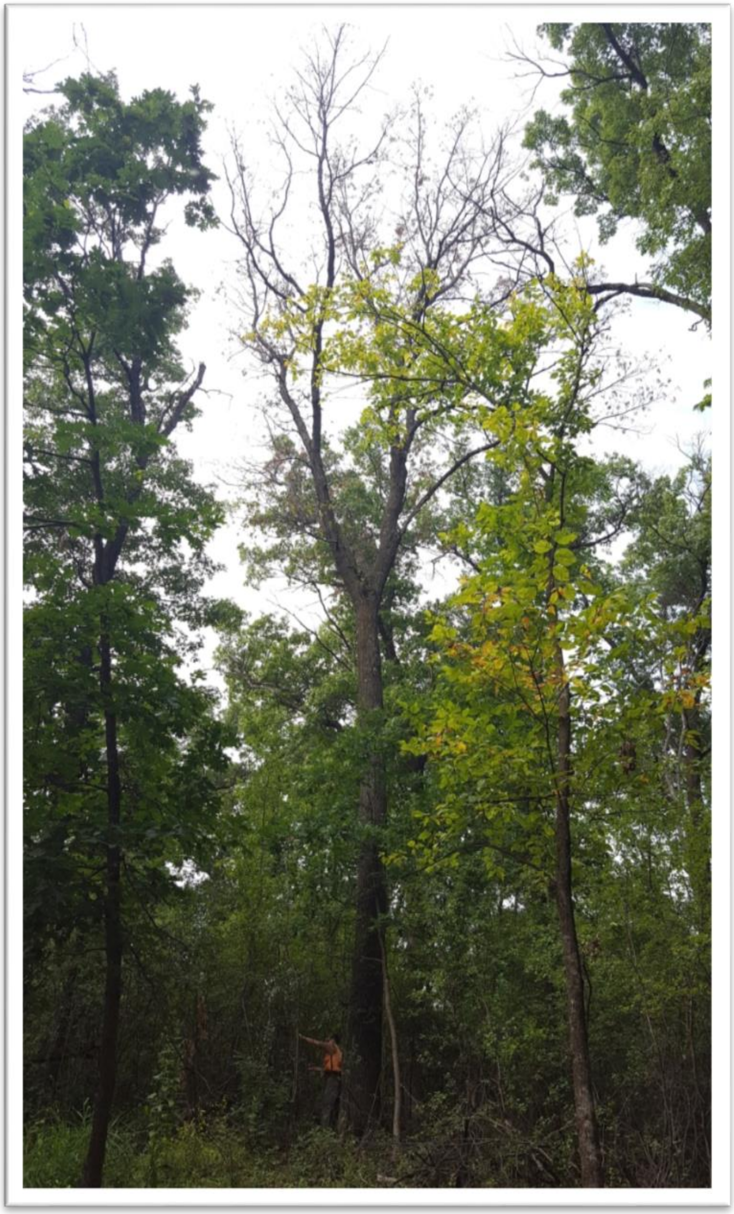

Figure 1.2: Oak wilt infected tree and a typical leaf from an infected tree. Photos by author.

As of 2016, 32 counties in Minnesota have had a confirmed case of oak wilt up from 29 in 2013 (USDA 2017). This forest pathogen has the potential to rapidly alter the makeup of forests making it an ideal candidate for modeling via species distribution models. Other invasive forest pathogens such as sudden oak death and Dutch elm disease have already benefited from the use of SDMs in their management. This research uses the Maxent SDM to model suitable oak wilt habitat within east central and southeastern Minnesota to assist in monitoring, prevention, and early detection and management of the disease.

Chapter 2: Methodology

Creation of a probability distribution of oak wilt in Minnesota using Maxent first required the creation of an oak wilt occurrence database and selection appropriate environmental variables. To minimize sampling bias found in the occurrence data, a bias file was then created. The model was then set up and run with the appropriate parameters followed by model evaluation using the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS).

Oak Wilt Occurrences

To create a database of oak wilt occurrences, current confirmed oak wilt locations were obtained from the Minnesota Department of Natural Resources (MN DNR) and Three Rivers Park District (TRPD). The MN DNR funded a program from the late 1980s to the early 2000s to which communities could apply for and receive funding for oak wilt management. The most recent year of data was 2016. TRPD has kept data on oak wilt occurrences within park boundaries since 2012. Annually, a forester surveys the forests from the air recording GPS points of possible oak wilt infection centers that are then ground checked for the presence of oak wilt in the trees.

Oak wilt occurrence data from 2007 to 2016 (n = 460) were used to produce the model (Figure 2.1). Using the Append tool in Arc Map version 10.5.1, the TRPD oak wilt occurrence data from 2012-2016 (n=135) were combined with the MN DNR data from 2007-2016 (n=325) to create a single database. Coordinates were added using the Add XY Coordinates tool using the NAD 1983 UTM Zone 15N projected coordinate system. The coordinate system in which the layers are in does not matter for running a Maxent model so long as the coordinate system of all inputs to the model are the same. Finally, the occurrence location data was exported into

Microsoft Excel where it was edited to include only necessary information (species name, latitude, and longitude) and saved as a comma-delimited file.

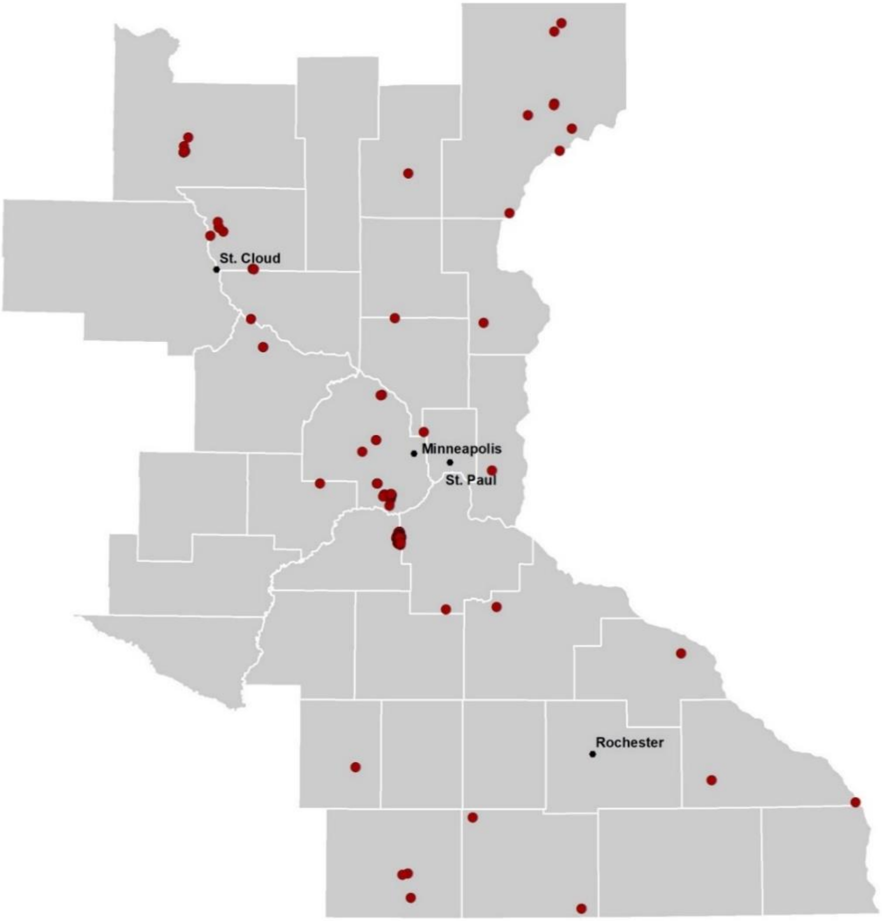

Figure 2.1: Oak wilt occurrence locations obtained from MN DNR and TRPD between 2007 and 2016.

Environmental Variable Selection and Modification

Machine learning and neural network SDMs have algorithms that are tolerant to faulty data meaning that any set of variables used in the setup of the model will produce an output distribution. To produce a meaningful model, selection of appropriate variables was vital. The second step of this research involved research and selection of variables considered important in the distribution oak wilt and other forest pathogens including climate, topography, land cover, soil type, and population density.

Climate Variables

Climate plays an important role in many SDM studies on forest pathogens (Ikegami and Jenkins 2018; Hubbart, Guyette, and Muzika 2016; Venette 2013; Desprez-Loustau et al. 2006). Different climate variables can make a host species more or less susceptible, change the suitability of the host habitat for the pathogen, or even alter the reproductive cycles of the pathogen (Desprez-Loustau et al. 2006).

This research used 30-year (1981-2010) normal climate variables from the PRISM Climate Group (http://prism.oregonstate.edu/) including average annual precipitation, average temperature for the two coldest months (December and February) and average temperatures of the three hottest months (June, July, and August). Each climate variable came in a nationwide raster dataset with a resolution of 800m and clipped to the study area using the Clip tool in ArcMap to make future processing more efficient. PRISM climate data had the best resolution and was chosen for this reason.

Topography

Alexander von Humboldt observed in his *Essay on the Geography of Plants* (1805) that different elevations have differing environmental characteristics and corresponding variation in biological diversity. Studying the effects of elevation on species distribution has continued ever since. Less studied is the importance aspect and slope play in species distributions, specifically on the distribution of forest pathogens. One study in Pennsylvania demonstrated aspect and slope affect oak wilt presence with hilly west-facing slopes and forest edges of forests and tall trees in flat areas showing greater incidences of the pathogen (Bowen and Merrill 1982). The study area in this research ranges from flat sand plains to steeply sloped bluffs (Figure 2.2). The range in elevation, slope, and aspect within the study area warranted inclusion into this study.

This research used a digital elevation model (DEM) of Minnesota: statewide, 1:24,000, Level 2, raster which was created from a United States Geological Survey (USGS) DEM to use as the elevation layer. With a standardized grid size of 30m, the resolution was a perfect fit for use in this research. Using the corresponding tools in ArcMap, slope and aspect layers were both created using the DEM raster.

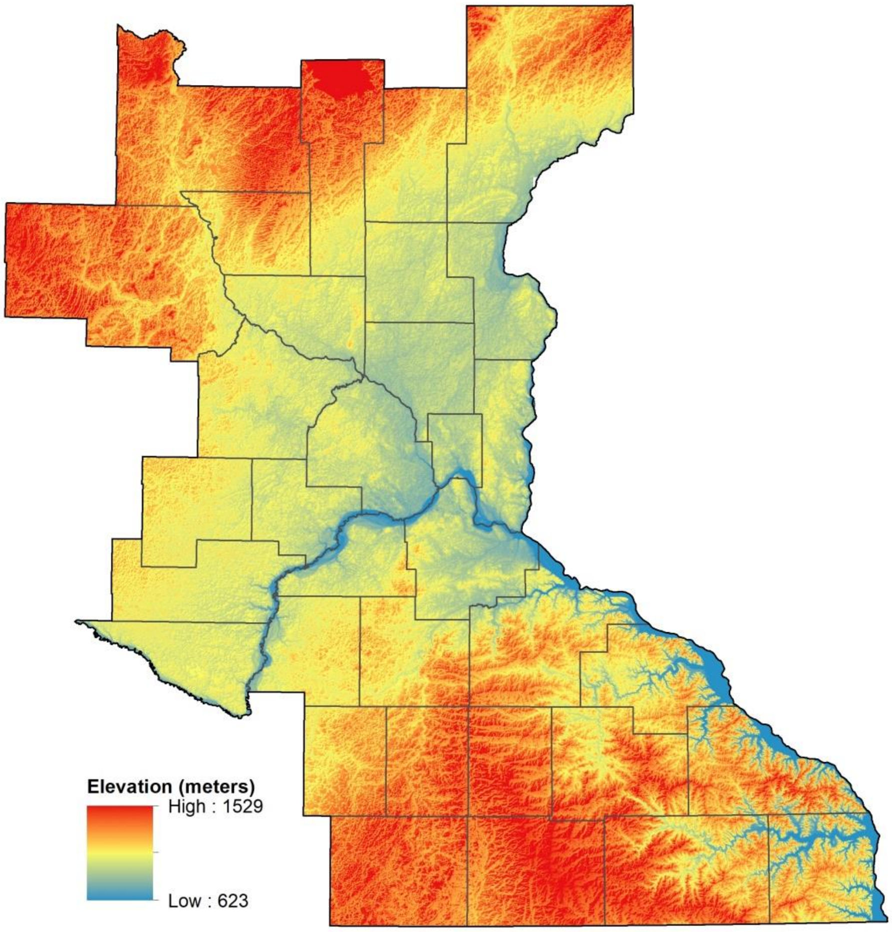

Figure 2.2: Elevation raster of the study area.

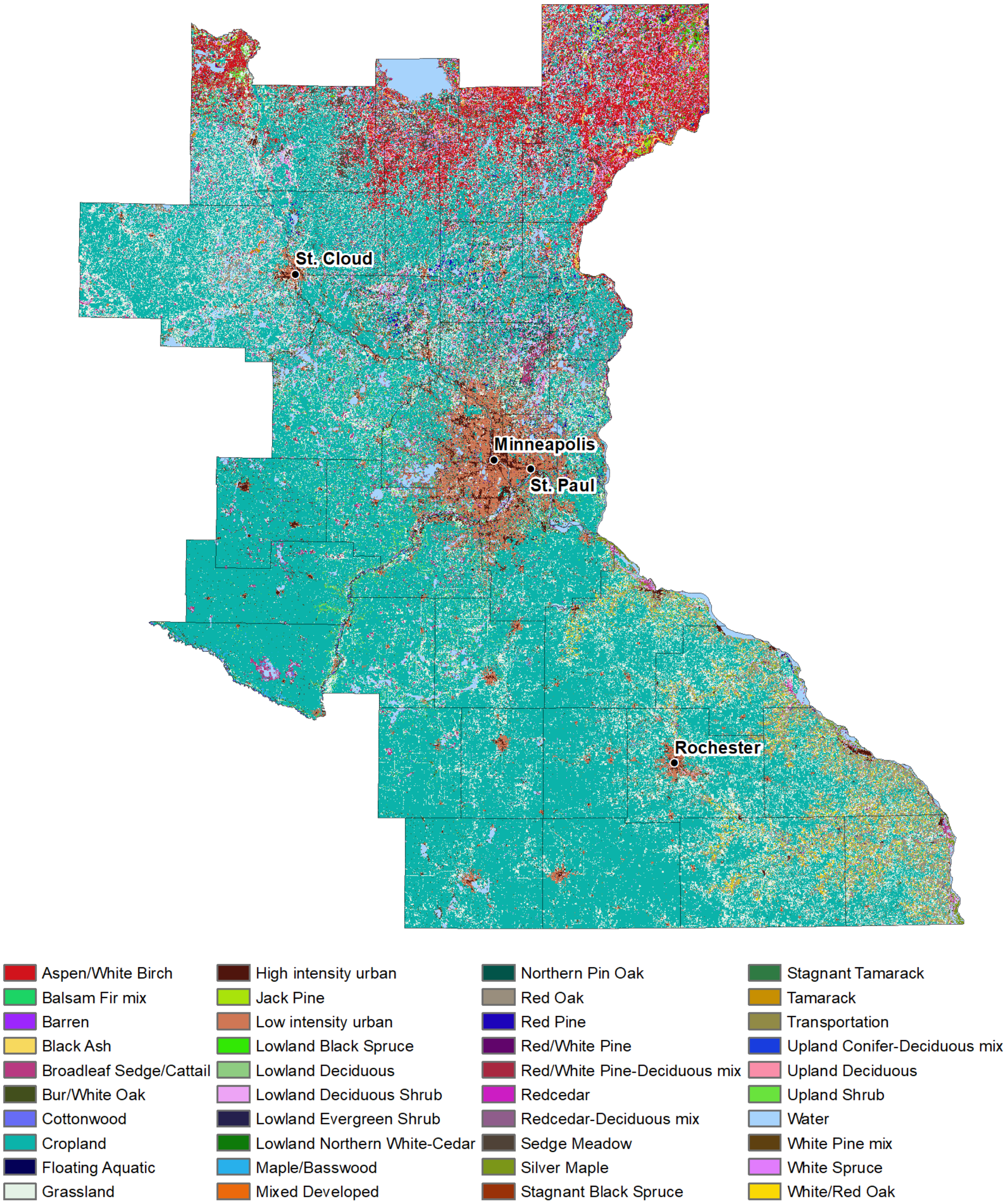

Figure 2.3: GAP-derived land cover.

Land Cover

Forest composition is thought to determine whether oak wilt is capable of maintaining a presence in an area. Forests with high diversity of plant species may have lower incidences of oak wilt simply because the distance separating oak trees inhibits the transmission of the pathogen (MacDonald, Double, and Haynes 2009; Gibbs and French 1980). Conversely, a more homogenous forest with many oaks growing close together is more likely to sustain an oak wilt infection (Haugen et al. 2009; Juzwik 2009).

The Minnesota Land Cover 1991-1992 map, a product of the USGS Gap Analysis program, which used satellite imagery to produce detailed vegetation maps with a resolution of 30m, was used for this research. The data used divides the land cover in Minnesota into 49 classes, 40 of which are found in the study area (Figure 2.3). The last accuracy assessment of this data took place between 1995 and 2000. Although 20 years have passed since the last accuracy assessment and much development in the metropolitan areas has occurred, the level of detail found in this layer made it the ideal choice for this research. This layer was downloaded as a file geodatabase raster from the Minnesota Geospatial Commons (https://gisdata.mn.gov/).

Soil Types

The underground spread accounts for the majority of oak wilt infections. Spread takes place through grafted root systems between oak trees of the same species or group. The texture of the soil plays a large role in how far the roots can spread and whether or not significant amount of grafting occurs. .

Soil suborder data was acquired through the Natural Resources Conservation Service's (NRCS) Soil Survey Geographic (SSURGO) database (https://websoilsurvey.nrcs.usda.gov/), a massive database covering detailed soil characteristics of the entire United States. The download included a spatial element and dozens of tables of soil data that link to the spatial element via a map unit key. Using this key, the component table was joined to the shapefile to create a map with an attribute table that included soil order information. To make analysis and alterations run faster, unnecessary fields were deleted leaving only the ObjectID and Soil_Order. This layer was in vector format and in order to run within Maxent it was converted using Polygon to Raster conversion tool in ArcMap (Figure 2.4).

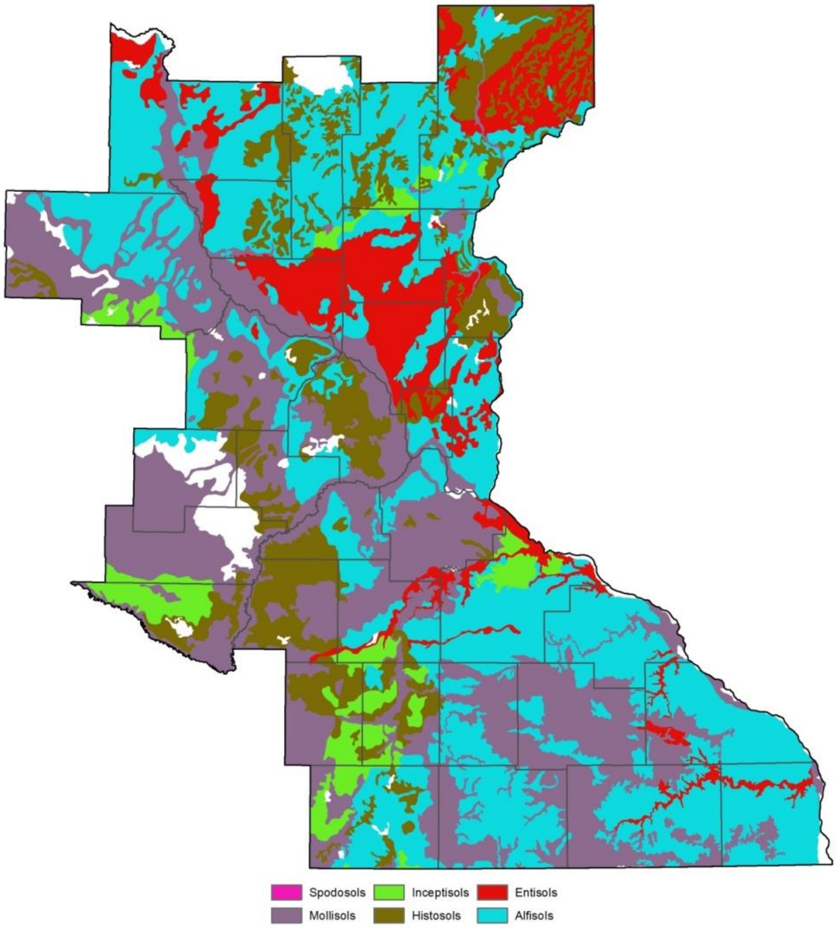

Figure 2.4: Soil suborder classification found within the study area.

Population Density

The creation of new infection centers by overland spread of oak wilt requires a wound in a healthy oak tree. This wound could be the result of storm damage, animal activity, or human disturbances. Humans have a demonstrative impact on the spread of forest pathogens and it makes sense that higher population densities would lead to an increase in pathogen incidence with at least one study showing it was an important factor in oak wilt distribution (Downing et al. 2009).

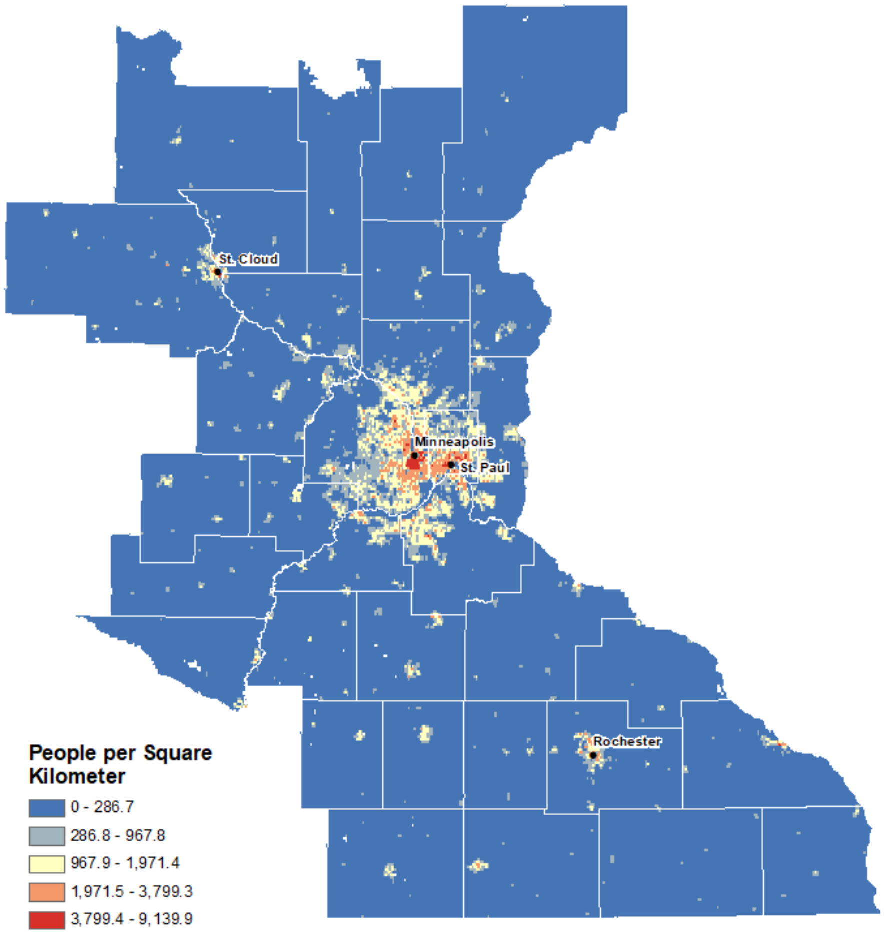

Figure 2.5: Population density of the study area.

For this research, the Gridded Population of the World (GWP), Population Density version 4.10 for the year 2015 from the Socioeconomic Data and Applications Center (SEDAC) (http://sedac.ciesin.columbia.edu/) was used. This layer showed the estimated number of people per square kilometer using national census numbers (Figure 2.5). Although the resolution for this data is coarse, SEDAC provides the only gridded (raster) datasets on population counts and density that is not constrained to political boundaries.

Variable Modification

After selecting and downloading the environmental variables, the layers were converted into a format that was useable by the Maxent software. First, all cells in each layer had to line up with each other. Second, all layers needed to be in ASCII (.asc) format. To do so, the Extract by Mask tool in ArcMap was used to clip the GAP layer raster to the study area boundary. For the first layer, the "Environments…" settings were changed so the coordinate system corresponded with that of the oak wilt occurrence data (NAD 1983 UTM Zone 15N). Following that, the Raster to ASCII tool was run to convert the layer into an ASCII text file (.asc).

Once the first layer was complete, I used Model Builder in ArcMap to create a simple model that iterated through the environmental variable layers running the Extract by Mask and Raster to ASCII tool in succession (Figure 2.6). Under the environment settings of the Extract by Mask tool, I selected the GAP layer raster as a template for the coordinate system, processing extent, snap to raster, and cell size. This step ensured all corresponding cells in the variable layers lined up with each other. Proper running of the Maxent model requires that the area covered by a particular cell to be the same in every variable layer. This simple model ran using all the remaining variables resulting in ASCII files for each environmental variable.

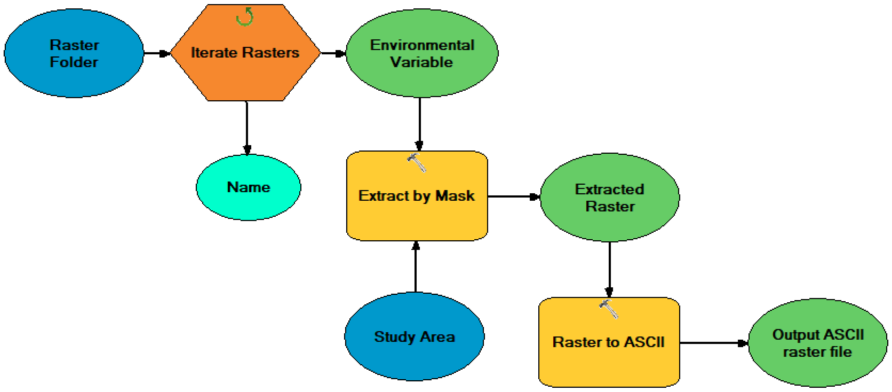

Figure 2.6: Variable modification mode built in ModelBuilder in ArcMap used to speed the process of converting environmental variables.

Bias File Creation

Sampling bias was an issue with the oak wilt occurrence data. It showed bias toward communities with high oak wilt incidences, areas with high red oak densities, and areas with forestry programs (Schwingle, Personal communication). To minimize the effect this bias would have on the testing, a bias file was created. This file told the Maxent software to collect background points only from counties with oak wilt occurrence data. These background points are necessary in the testing and evaluation of the model.

The bias file was created by selecting the 23 counties within the 33-county study area with confirmed oak wilt occurrences and exporting that data into a new shapefile. Then, the shapefile was converted into a raster using the same method as the soil type layer. Using the Raster Calculator tool, the values of the cells within the bias file were set so the Maxent model would read all counties with oak wilt as a value of one and all other counties as zero. Finally, this layer was converted into an ASCII file, changing the coordinate system, processing extent, snap to raster, and cell size to match that of the GAP layer.

Maxent Setup

This research utilized Maxent software version 3.4.0 (https://biodiversityinformatics.amnh.org/open_source/Maxent/). The oak wilt occurrence data comma delimited (.csv) file was uploaded into the pane labeled Samples and the ASCII variable files into the Environmental variables pane. Data type was selected from the drop-down menue for each environmental variable: aspect, GAP, and soil types as categorical and the remaining variables as continuous. Below these panes were options to include in the final output folder. Create response curves, make picture of predictions, and do jackknife to measure variable importance were all selected.

Overfitting is a common issue with Maxent but one that can be controlled through altering specific parameters within the model. As stated before, Maxent uses a set of constraints to create a distribution and overfitting occurs when the model adheres too closely to these values. Preventing this issue requires one of two parameters to change. First, increasing the regularization parameter will relax the constraints allowing for a greater range of values around the constraint. Second, and the method chosen for this research, the feature class can be selected manually from a choice of linear, product, quadratic, threshold, and hinge feature classes. The feature class chosen determines how constraints are calculated (Phillips, Anderson, and Schapire 2006). Maxent defaults to “Auto features” and selects the feature class based on the number of occurrence points used in the model. Hinge features only were selected because research done on the accuracy of models using specific feature classes showed hinge feature created the most accurate models without becoming overly complex and overfitting the occurrence locations (Phillips and Dudik 2008).

Within the settings of Maxent, various parameters can be changed to customize the model to fit the species and data being modeled. This research used random seed to set aside a random 25% of the occurrence data for testing. The bias file was uploaded in the advanced settings page, and ‘Write background predictions’ was chosen under the experimental settings tab. All other settings were left at their default selections.

Model Evaluation

The best method for evaluating a Maxent distribution from presence-only data is still debated (Elith and Leathwick 2009; Gusian, Thullier, and Gotelli 2005). This research used multiple methods to evaluate the performance of the model. Maxent produced a receiver operating characteristics (ROC) area under curve (AUC) and an analysis of omission/commission to evaluate the model. In addition, I calculated the true skill statistic (TSS) as an independent measure of validity. The TSS is calculated from the model’s sensitivity and specificity, or the proportion of accurately predicted presences and the proportion of accurately predicted absences (Allouche, Tsoar, and Kadmon 2006):

$$\text{TSS} = \frac{ad - bc}{(a+c)(b+d)} = \text{Sensitivity} + \text{Specificity} - 1$$

In this equation, *a* are true presence cells, *b* false presence cells, *c* false absence cells, and *d* true absence cells. The result of this equation is a value between +1, a perfect model, to -1 with any number above zero better than random. For this research to find *a*, *b*, *c*, and *d* I used the 10 percentile training presence (0.24) as the presence/absence cutoff. This value denotes the value at which the model includes 90 percent of the training data. For this model, *a* represented the number of test points above the threshold value (n=97), *b* the number of background points above the threshold value (n=1657), *c* the number of test points below the threshold value (n=11), and *d* the number of background points below the threshold value (n=8343).

Chapter 3: Results

Potential Distribution

The image generated by the model (Figure 3.1) shows the potential of distribution ranging from zero, or no probability, to one, definite probability. The image is also color coordinated with blues indicating low probability and reds high probability. According to the model, the areas with highest probability of oak wilt are found in the center of the study area near the Minneapolis-Saint Paul metropolitan area and to the north and west near the Mississippi River. The model placed the highest probability areas mainly surrounding known occurrence locations.

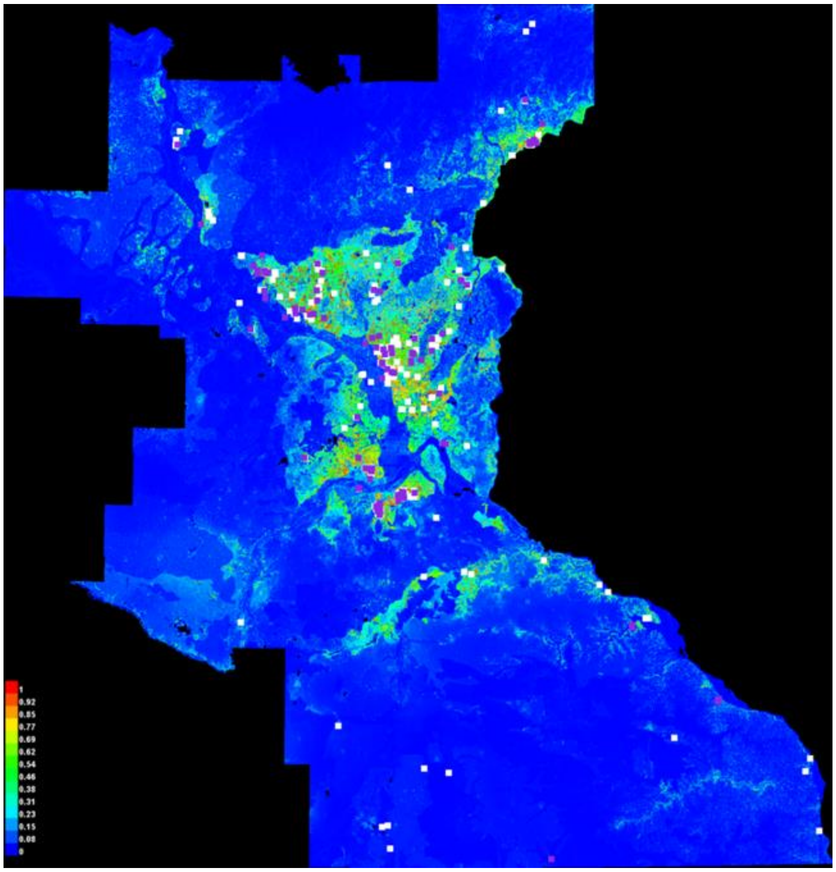

Figure 3.1: Maxent picture output in cloglog format. Red and orange indicate areas of higher probability of oak wilt occurrences. Blue indicates low probability areas. White squares represent oak wilt occurrence locations and purple squares represent test occurrence data locations.

The raw Maxent image is useful but better understanding can be garnered with some alterations. Figure 3.2 takes the original raster output and classifies it into five probability categories: very high, high, medium, low, and very low. Very high probabilities can be found in nearly half of the counties within the study area. Hennepin, Ramsey, and Anoka counties have significant areas classified as very high or high followed closely by Sherburne, Isanti, and Washington counties. Counties in the far north or far south of the study area show very low probabilities of oak wilt distribution with the exception of Pine County along its border with Wisconsin. The Maxent model also predicted high probability for regions in southern Dakota county, northern Rice county, and western Goodhue county although they have few occurrence locations.

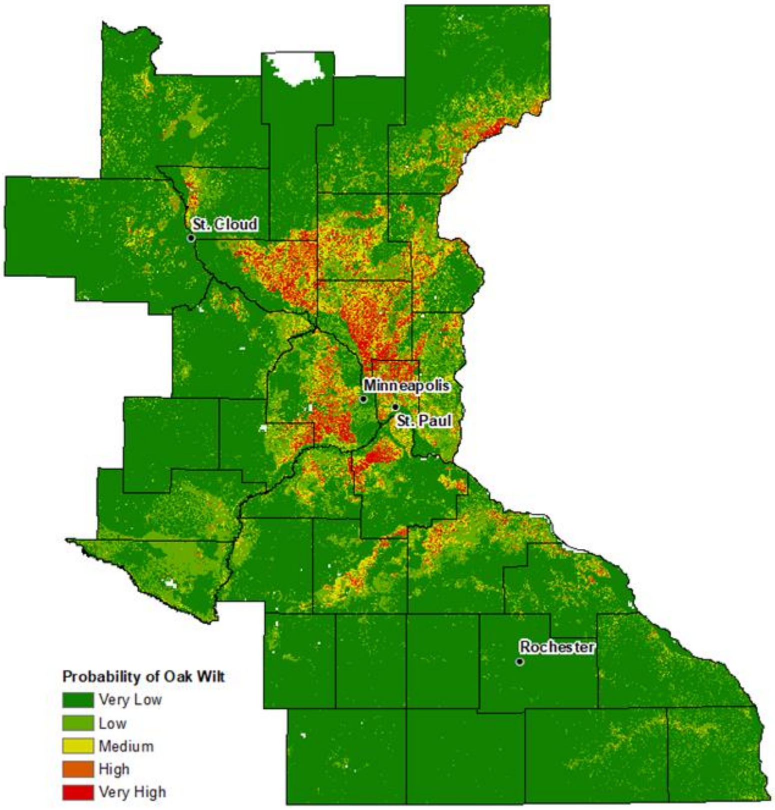

Figure 3.2: Reclassified Maxent output into 5 categories representing the probability of oak wilt occurrence using Jenks classification in ArcMap 10.5.1.

The presence/absence map (Figure 3.3) shows the locations where oak wilt is likely to be found currently. Using the 10-percentile training presence threshold (0.175), the map was classified into two categories with values above the threshold indicating oak wilt presence areas. The 10-percentile training presence threshold means 90 percent of the testing data of occurrence locations is included in the present category. Thresholds at other values can be used depending on the confidence the researcher has in the environmental variables chosen.

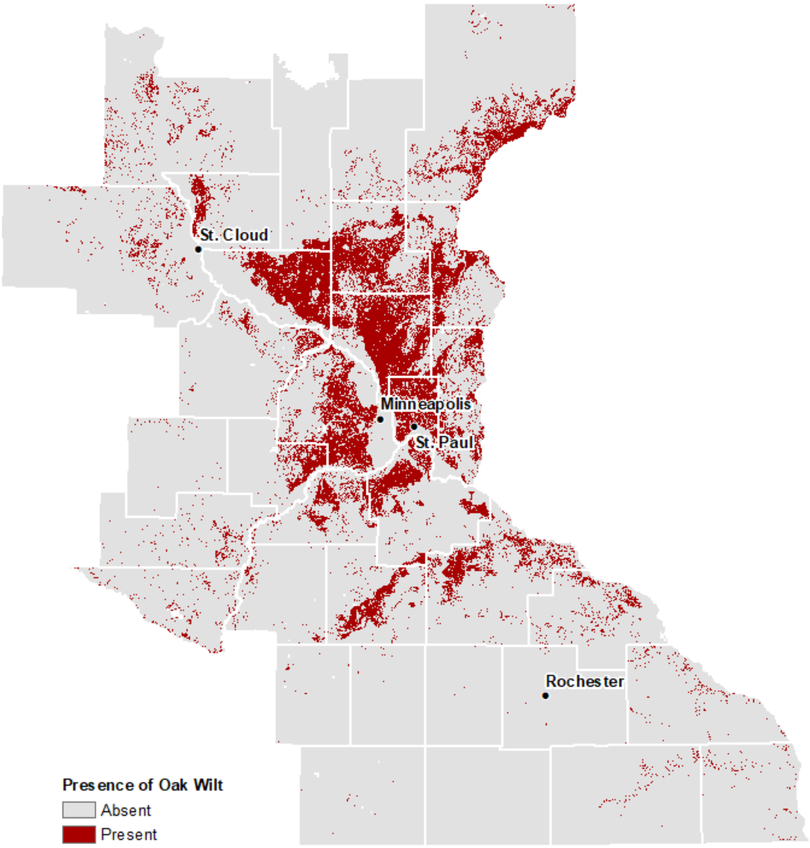

Figure 3.3: Oak wilt presence and absence locations based on a 10 percent training threshold.

Variable Importance

Variable contribution shows how much the model relied on each variable to create the final output (Table 3.1). The GAP-derived vegetation cover variable contributed the most (37.1%) to the model with soil type (23.0%) and population density (22.2%) rounding out the top three environmental variables. Of the 12 variables used in the study, nine contributed only 17.6%. It is important to note the table of variable importance represents only the model created, alternate models using the same data will generate a table with different percentages.

Table 3.1: Percent contribution of each variable to the creation of the final Maxent model. The higher percentages mean the model placed greater weight on those variables when creating the distribution model,

Variable	Percent Contribution
GAP	37.1
Soil type	23.0
Population density	22.2
Elevation	5.3
Annual precipitation	4.3
Dec min temp	2.3
Jun max temp	2.2
Aspect	1.4
Feb min temp	0.9
Slope	0.5
Jul max temp	0.4
Aug max temp	0.3

The jackknife test of variable importance shows the amount of useful and unique information within each variable. To create the plot, Maxent runs three models: one with all variables, one with only a single variable, and one with all but one variable. The red bars indicate the usefulness of the information within each variable toward the creation of the model while the blue bar indicates the uniqueness of the information within the variable. In the plot created by this model (Figure 3.4), the vegetation cover variable has both the longest red bar and the shortest blue bar, indicating this variable has the most useful and unique information of all the variables. Soil type had the second greatest uniqueness of information. Other highly useful variables include soil types, elevation and July maximum temperature.

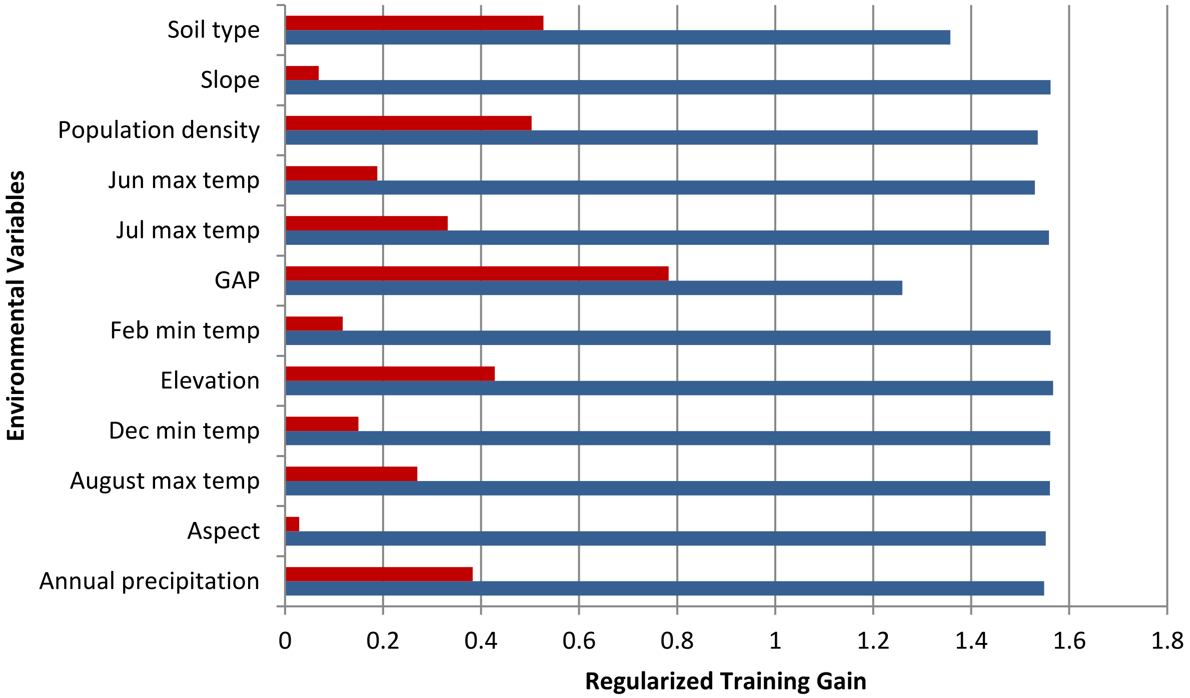

Figure 3.4: Jackknife test of variable importance. The red bars indicate the model run with only that variable and the blue bars indicate the model run excluding that variable. High red bars and low blue bars indicate unique or important variables to the model**.**

Response curves are yet another option to study the effects of each environmental variable on the model (See Appendix A). The curves, for continuous data, and bar graphs, for categorical data, created for this thesis are based on the model using only that variable and represent how the probability of oak wilt differs when that variable changes. The plot for GAP, the largest contributing variable to the model, shows areas with land cover primarily made up of northern pin oak and bur/white oak almost guarantees the presence of oak wilt. Low intensity urban and red oak land cover resulted in about an 80 percent chance of oak wilt occurrence. Interestingly, areas in the study area covered in jack pine and red/white pine-deciduous mix also had an almost 100 percent probability of oak wilt presence. Two soil suborders stand out above the rest in terms of probability of oak wilt occurrence. The presence of Psamments and Hemists soils will result in an about 88 percent and 81 percent chance of oak wilt occurrence respectively.

Model Evaluation

The area under the receiver operating characteristic curve (AUC) value for this mode (0.926) indicates that the model fit the training data much better than average. The AUC is calculated from the receiver operating characteristic curve which plots the true positive rate on the Y-axis and the false positive rate on the X-axis (Figure 3.5). However, because Maxent is a presence-only modeling technique, no true absence points were available to calculate the false positive rate. Instead, the model took background points for this purpose. A perfect model would have an AUC value of one represented by a right angle on the graph, indicating all known occurrence locations were labeled as such in the model and no areas absent of oak wilt were labeled as present by the model. The high AUC of this model shows Maxent did far better than random in creating a model to represent oak wilt occurrence locations.

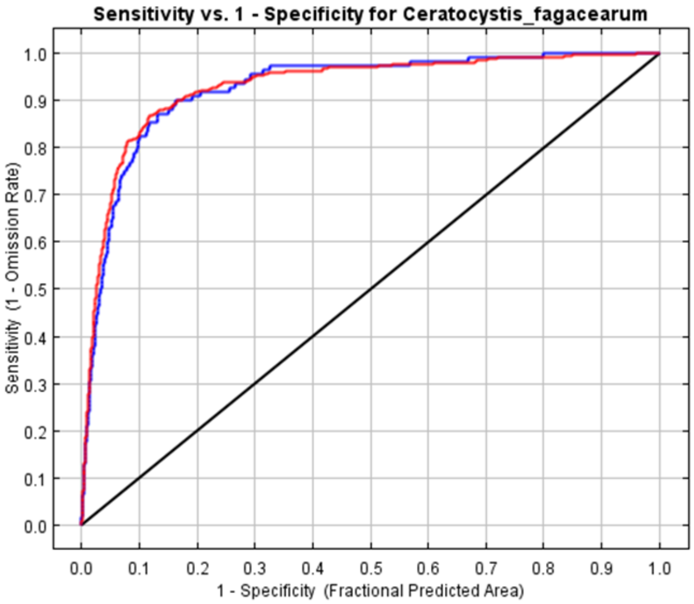

Figure 3.5: Receiver operating characteristic (ROC) curve created for the Maxent model. The red and blue lines represent the training and test data respectively.

When calculating the true skill statistic (TSS) I used the same threshold, the 10 percentile minimum training percentile, as was used in the creating of the presence/absence map. The TSS value for this model was 0.748 indicating a model statistically better than random.

Chapter 4: Discussion

The results indicate the Maxent approach is capable of creating a potential distribution model of oak wilt in Minnesota. However, the results are simply based on the data the model was given, which does not ensure that the results are ecologically meaningful. To understand how well the model predicted distribution based on ecological terms, I compared the top three variables the model deemed important for the presence of oak wilt (GAP-derived land cover, soil type, and population density) with research that has been completed on the subject.

Environmental variables must be carefully chosen due to the fact that Maxent models create the best output possible regardless of the quality of the variables. Careful consideration of which variables to use is necessary as irrelevant or unnecessary variables may change the accuracy of the variables or display variables as important when, in reality, they are not (Elith and Leathwick 2009). Even when caution is taken, understanding the important variables in the Maxent output leads to greater understanding of the model and its performance.

Spread of Oak Wilt

Oak wilt can spread in one of two ways: above ground via insect vector or underground through root grafting. Overland spread requires a spore mat to form on an infected oak, a sap beetle to visit the spore mat and pick up spores, and the insect to visit a fresh wound on a healthy oak tree (Juzwik et al. 2011). Root grafting is the creation of a shared root system. The oak wilt pathogen can spread rapidly through the shared xylem tissue found within these shared roots with the possibility of infecting a large number of trees in a single year (Juzwik et al. 2011; Appel, 2009). Land cover, soil type, and population density may all contribute to the establishment and spread of oak wilt, as explained below.

Land Cover and Oak Wilt

The land cover (GAP derived) layer had the largest contribution to the creation of the model. Presence of northern pin oak had the biggest increase in probability of oak wilt occurrence while bur or white oak and red oak categories also ranked high (see Appendix A). Land cover plays an important role in both the above ground and underground spread of oak wilt. Aboveground spread of oak wilt requires the presence of both healthy oak trees to infect and inoculum in the form of spore mats. The availability of inoculum is related to the composition of the forest in areas with a higher concentration of oaks having more inoculum, which leads to an increase in probability of spreading oak wilt and developing new infection centers (Juzwik 2009).

Aboveground spread of oak wilt depends on the variety of trees found in a forest but it also can depend on the different groups of oaks found in a forest. Oaks found in the white oak and red oak sections have varying susceptibility to oak wilt. White oaks, including bur oaks, are less vulnerable to oak wilt than other species with highly resistant white oaks such as *Quercus alba* showing dieback of a few branches a year, taking a decade to die. if at all (Juzwik et al. 2011). On the other hand, northern pin and red oaks are highly susceptible and will die the same year in which they are infected (Harrington 2013; Koch, Quiram, and Venette 2010). Differences in susceptibility are thought to be due to anatomical and physiological differences between the species. Within infected white oaks, the pathogen, once it enters the xylem, is unable to move laterally and is often soon surrounded by a new layer of xylem tissue (Jacobi and MacDonald, 1980; Beckman et al. 1953). These two events essentially isolate the pathogen and prevent it from spreading. Northern pin and red oaks do not have such advantages and the pathogen is free to spread rapidly both laterally and vertically throughout the tree’s vascular system.

Underground, root grafting most commonly occurs among trees of similar species. Among oaks, roots can graft among and between species. Oaks of similar species or in the same section of the genus tend to graft more commonly than oaks of different species or sections (Juzwik 2009). In areas where oak wilt is present but at low levels, root grafting plays a role in its spread; however, the diversity of the forest and the relative isolation of oak trees to small groupings prevent the pathogen from spreading widely (MacDonald, Double, and Haynes 2009). The frequency of root grafting also differs among oak species in Minnesota. Grafting is not common in bur oaks (Parmeter, Kuntz, and Riker 1956) but is far more common in red oaks, with one study showing all northern pin oaks within 15 meters having grafted together (Beckman and Kuntz 1951).

The GAP-derived land cover variable also showed low intensity urban and jack pine land covers as also having high levels of oak wilt probability. In Minnesota, large numbers of oak trees can be found in the regions labeled as low intensity urban and the reason for the large oak wilt probability will be discussed in the population density section of this discussion. Jack pine, on the other hand, is an interesting anomaly. The GAP land cover layer used in this study shows jack pine is only located in a few counties in the northern range of the study area. Thirty-seven of the 460 oak wilt occurrence points used in this study were found in approximately a two-square mile area of jack pine in northern Pine County on the Wisconsin border. The high density of oak wilt occurrence so far from other major oak wilt infection centers may be because of a local introduction into a small oak stand, spread from infected trees across the border in Wisconsin, or simply because of a sampling bias.

Soil Type and Oak Wilt

The response curves for soils show two suborders whose presence significantly increase the chances of oak wilt occurring. The existence of Psamments results in an approximately 88% probability of oak wilt while the occurrence of Hemists results in an approximately 82% likelihood of oak wilt. To understand why these two soils lead to a greater probability of oak wilt occurring, one needs to understand the makeup of these soils and what the literature says about their role in oak wilt distribution.

Psamments are a member of the order Entisols. Entisols are unique in that they do not have soil horizons, or layers, like others due to the fact that these soils typically do not stay long enough on the land to form horizons. Psamments have a sandy texture, consist of less than 35% rock fragments, and have a low water holding potential (USDA 1999). In Minnesota, this soil type is found along a few rivers and in a large area north of the Minneapolis-St. Paul metropolitan area known as the Anoka Sand Plain subsection of the Minnesota and Northeast Iowa Morainal section of the Ecological Classification System used by the Minnesota DNR.

Hemists are a member of the Histosols order. The defining characteristic of Histosols is that they are made up primarily of organic material. Hemists are wet soils with an intermediate level of decomposing material with a bulk density below $0.3 g/cm^3$, making it a very light and porous substrate (USDA 1999). These soils can be found throughout Hennepin County and in pockets of northern Pine County.

The sandy characteristics of Psamments and the lightness of Hemists make them ideal substrates for roots to reach out and graft with the roots of other trees. The distance and frequency at which roots graft rely heavily on soil composition and texture. Studies have shown the distance roots are able to reach out and the amount of grafting occurring increases from heavy and dense to light and sandy soils (Prey and Kuntz 1995; Bruhn et al. 1991; Anderson and Anderson 1963). The expansion of oak wilt due to grafted roots varies between regions. In Michigan’s Upper Peninsula oak wilt expansion through root grafting has been shown to be as much as 12 meters per year, in Minnesota it can range from 1.9 to 7.6 meters per year, while in Texas oak wilt can spread up to 50 meters per year (Appel 2009; Juzwik 2009; Bruhn et al. 1991). Overall presence of very sandy or organically rich porous soils may facilitate the spread of oak wilt.

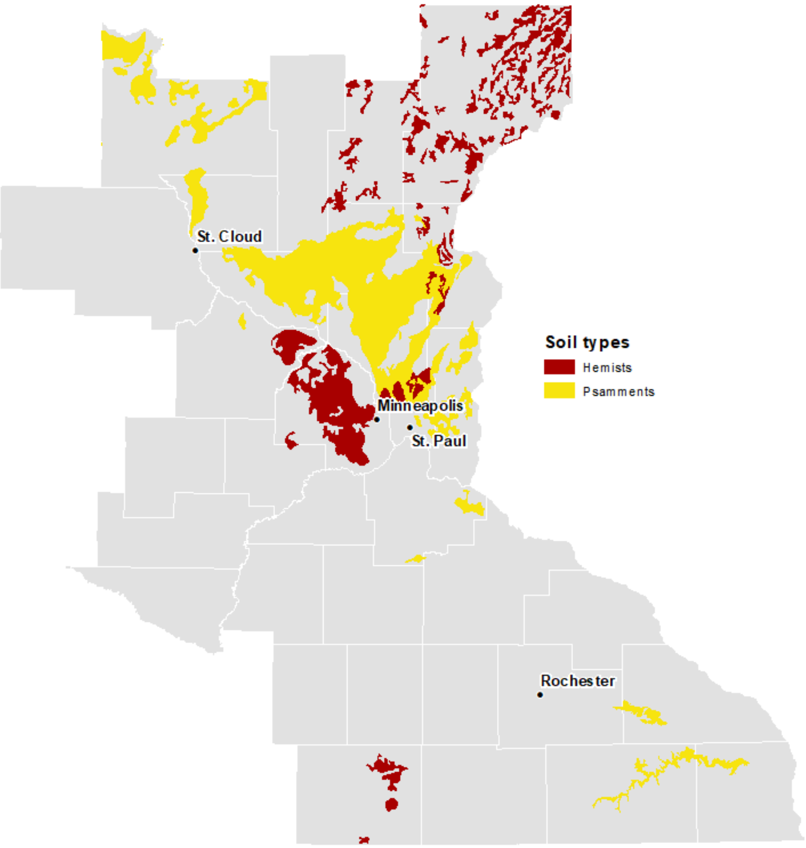

Figure 4.1: Location of soil suborders Psamments and Hemists within the study area.

Population Density and Oak Wilt

Human population density may not, at first glance, seem as important a variable when determining the distribution of most forest pathogens. However, as stated before, humans have the capability of promoting the spread of forest pathogens through trade, travel, recreation, and land use change.

This research showed, through the population density response curve, that the probability of oak wilt was high and steady at moderate population densities with a rapid and continuous decline of probability when population density reached around 1,700 people per square kilometer. This corresponds to the response curve for land cover that shows low intensity urban land cover had a high probability of oak wilt presence (about 79%) while high intensity urban areas had a very low probability of oak wilt presence (about 14%).

Population density plays a role in the overland spread of oak wilt. In order for a healthy tree to become infected, a fresh wound has to be present. In populated areas, that damage is often caused by human activity. Juzwik, French, and Jeresek (1985) gathered observations of tree pruning and wounding between 1953 and 1979. They demonstrated how the pruning or wounding of trees between May and June would result in greater occurrences of oak wilt while the swift application of wound dressings prevented infection. Downing et al. (2009) used classification tree analysis to predict the distribution of oak wilt and discovered population and population change as important factors although the authors did not discuss reasoning for its importance.

Conclusion

Forest pathogens have the ability to alter a landscape quickly. Species distribution models have the potential to limit the effects of forest pathogens if they are used in the detection and monitoring of said pathogens. The purpose of this research was to test a popular species distribution model, Maxent, in its ability to predict the potential distribution of an invasive forest pathogen. Using oak wilt presence locations and a set of 11 environmental variables, the potential distribution of oak wilt was successfully modeled in east central and southeastern Minnesota with Maxent.

In addition to creating a potential distribution, the model was also able to highlight areas of concern, including locations that currently have very little oak wilt but have highly suitable habitat. One such area is south of the Minneapolis-St. Paul in southern Dakota and northern Rice counties where a line of high probability habitat can be seen in the raw Maxent output but only one oak wilt occurrence location was in the area. Highlighting areas of concern is where Maxent can do the most good in bringing attention to these locations to assist in monitoring and managing forest pathogens.

Limitations and Future Research

In the course of this research, a number of limitations presented themselves. First, the presence data is very biased. The points were taken in communities that requested and received funding from the Minnesota DNR to manage oak wilt from the 1980s to the early 2000s. Second, the GAP-derived land cover data was created 20 years ago and important areas within my study area have undergone significant urban development in that time period. Third, this research was only capable of predicting potential distribution because it did not utilize dispersal constraints to limit distribution from currently infected locations.

Future research in oak wilt distribution modeling can be improved by addressing these three issues. Minimizing the bias in presence data would require the use of systematic sampling of random plots. This would also include the added benefit of the creation of true absence data which can be utilized in evaluating the distribution model more accurately than randomly generated background points. Updating the land cover data would require detailed classification of high quality up-to-date aerial photography or satellite imagery. Finally, the use of dispersal constraints would create an accurate model of current distribution of oak wilt. In addition, understanding the distance at which the oak wilt pathogen can disperse in a given time period (e.g. per year), would allow for the analysis of year-by-year distribution of the pathogen. With these additions, the accuracy and precision of distribution modeling would increase, improving detection and monitoring capabilities.

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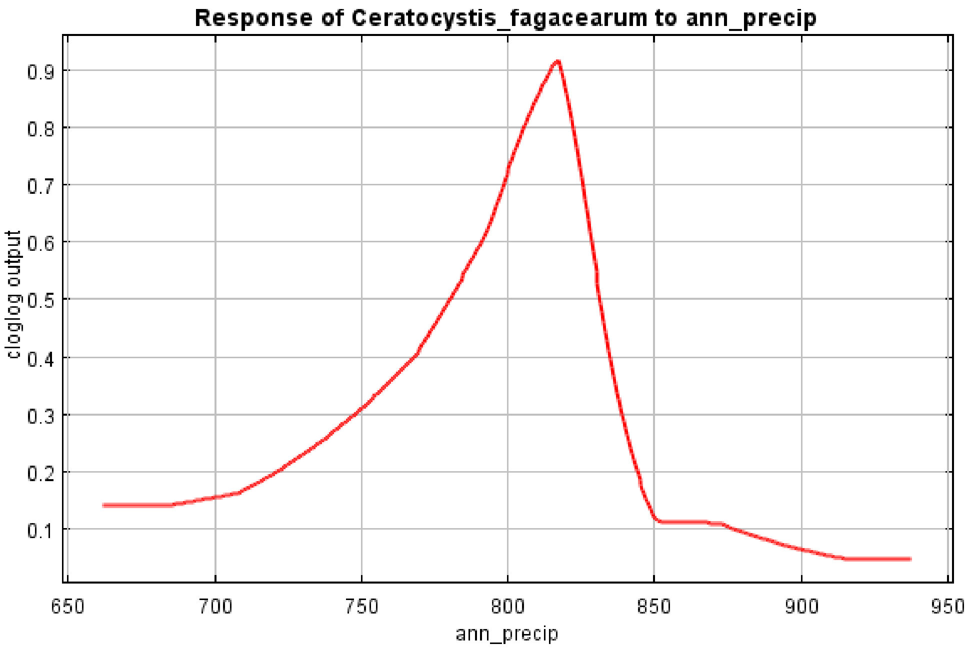
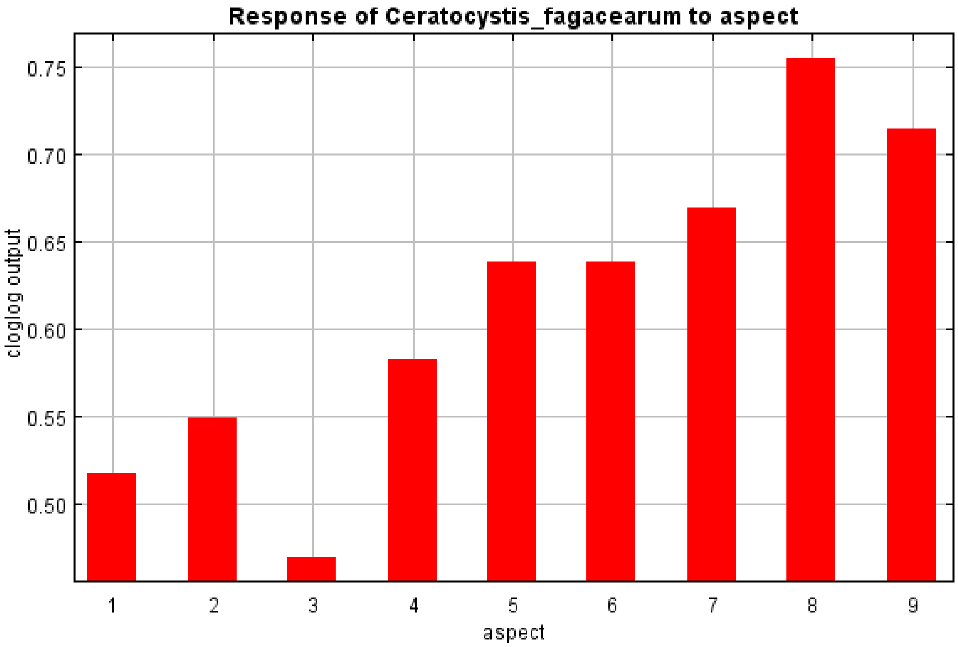
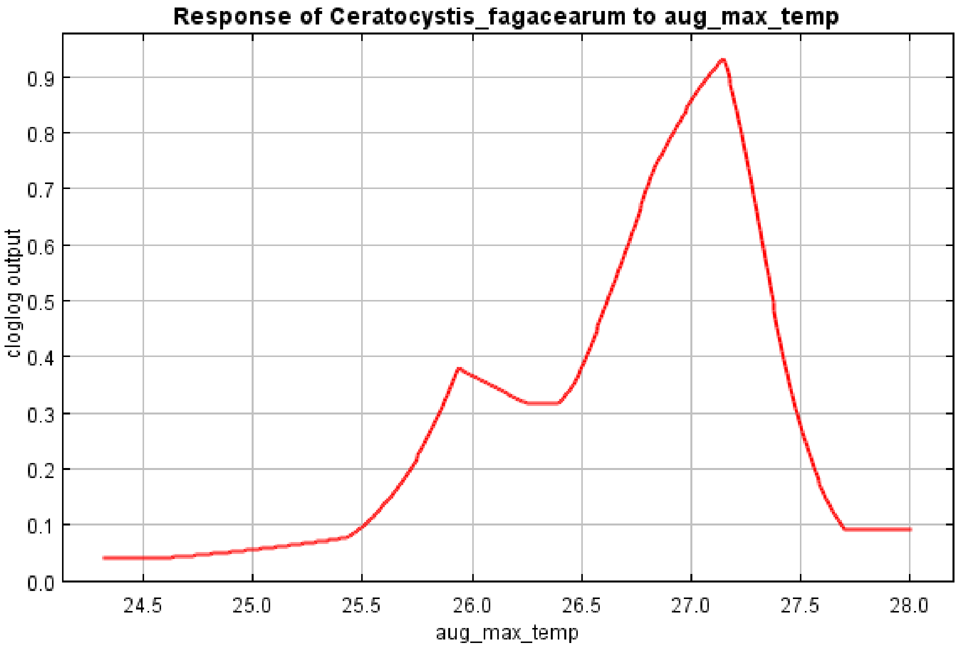
Appendix: Response Curves





1. No slope
2. North
3. Northeast
4. East
5. Southeast
6. South
7. Southwest
8. West
9. Northwest


Response of Ceratocystis_fagacearum to aug_max_temp
cloglog output
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0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
24.5
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25.5
26.0
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27.0
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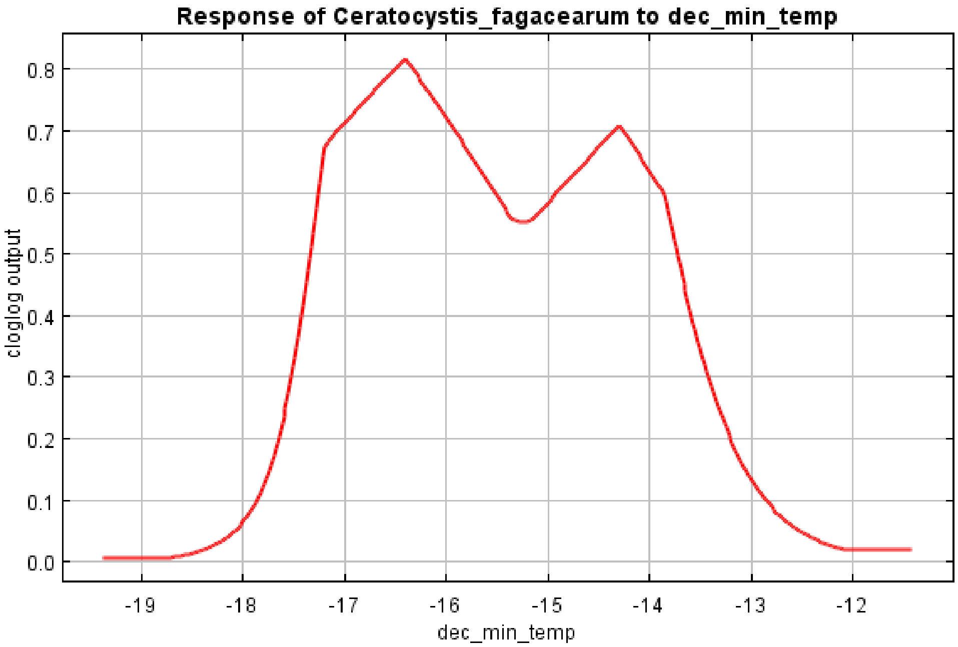
28.0
aug_max_temp


Response of Ceratocystis_fagacearum to dec_min_temp
cloglog output
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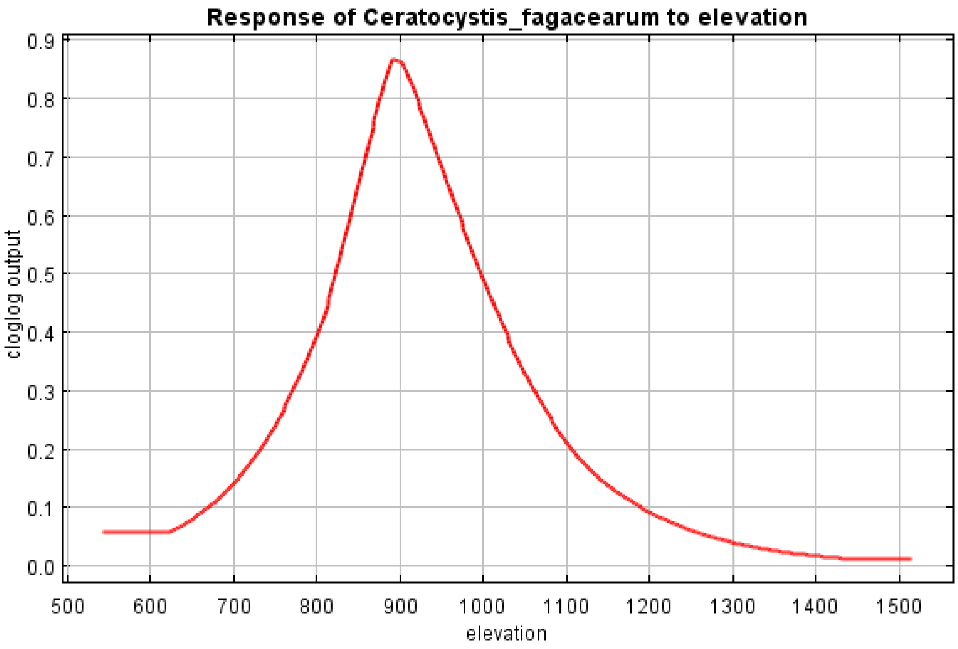
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-19
-18
-17
-16
-15
-14
-13
-12
dec_min_temp


Response of Ceratocystis_fagacearum to elevation
cloglog output
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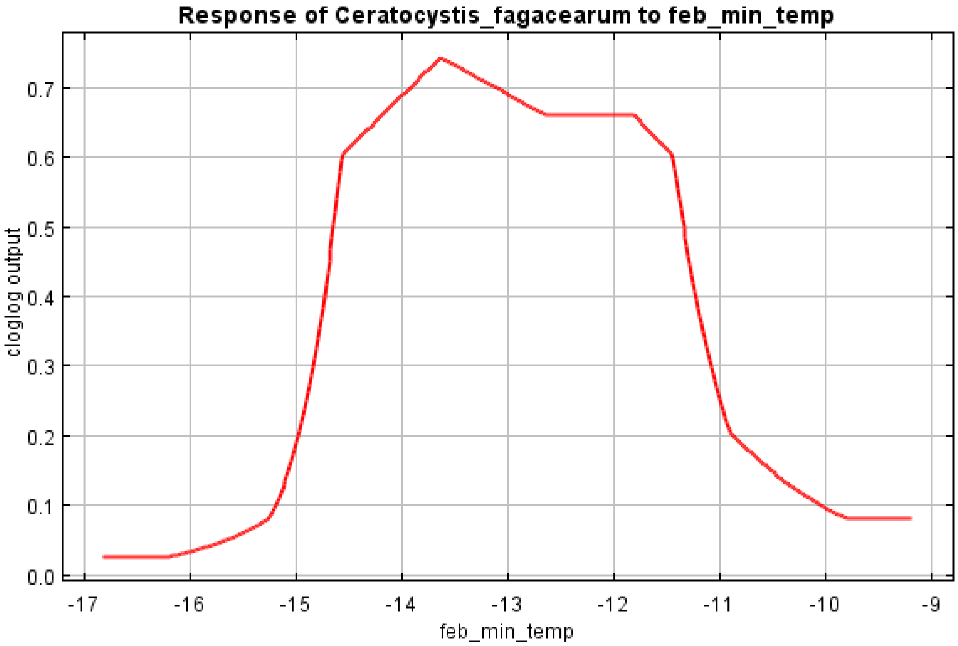
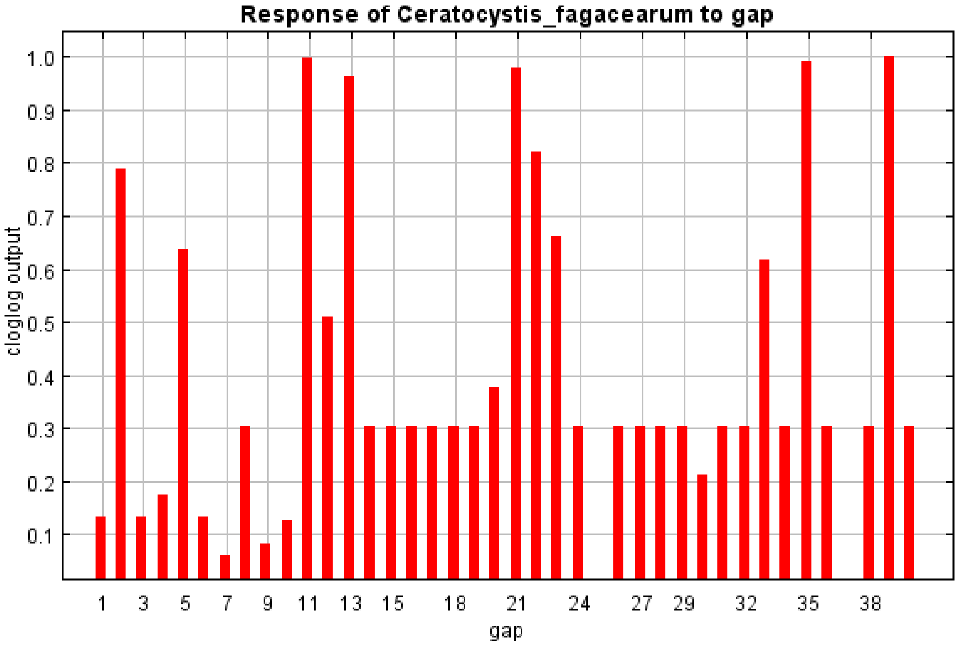
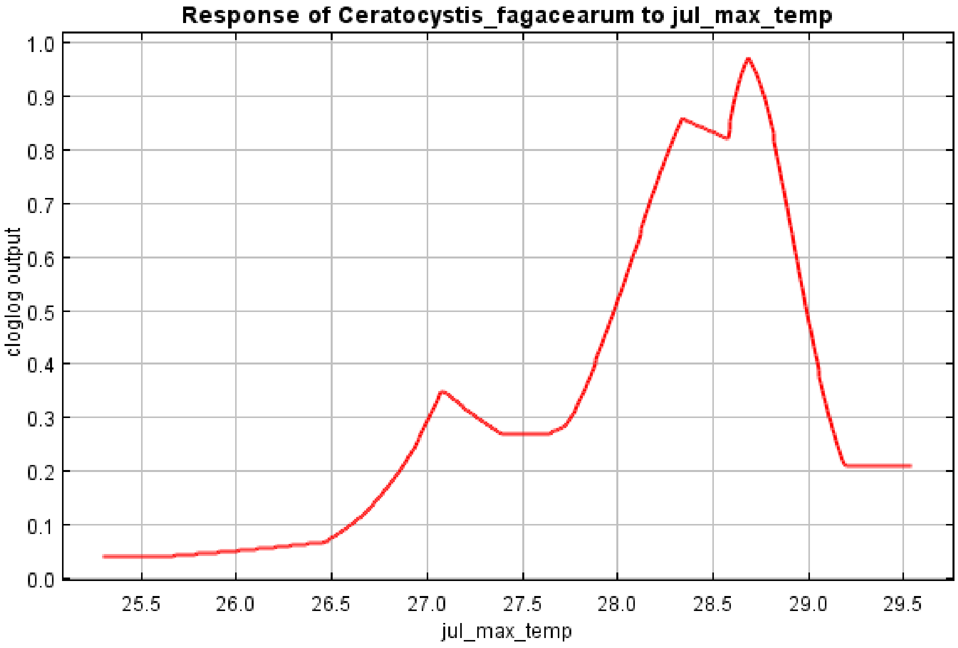
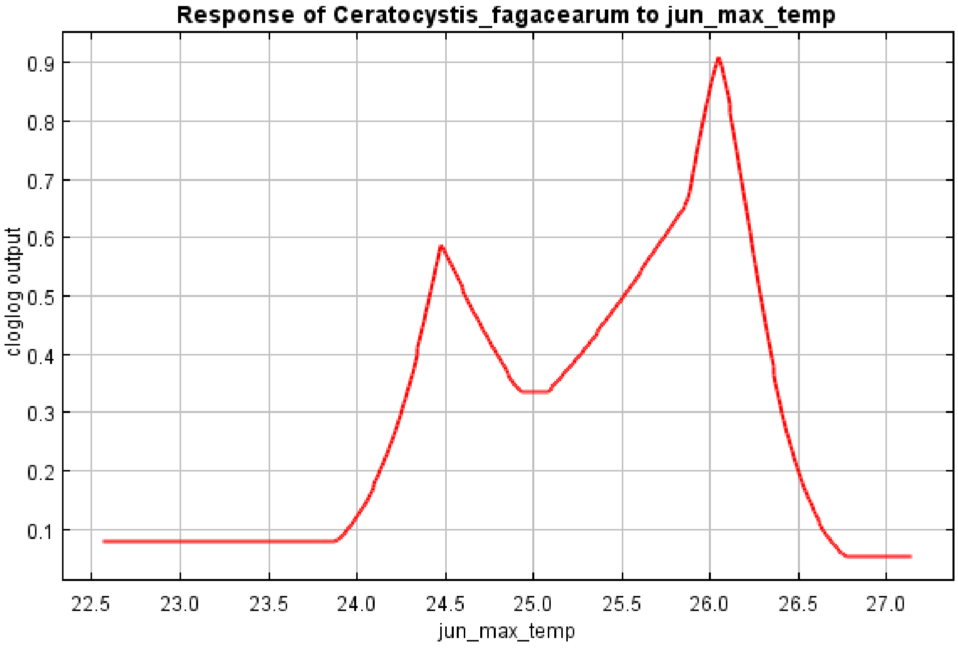
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
500
600
700
800
900
1000
1100
1200
1300
1400
1500
elevation

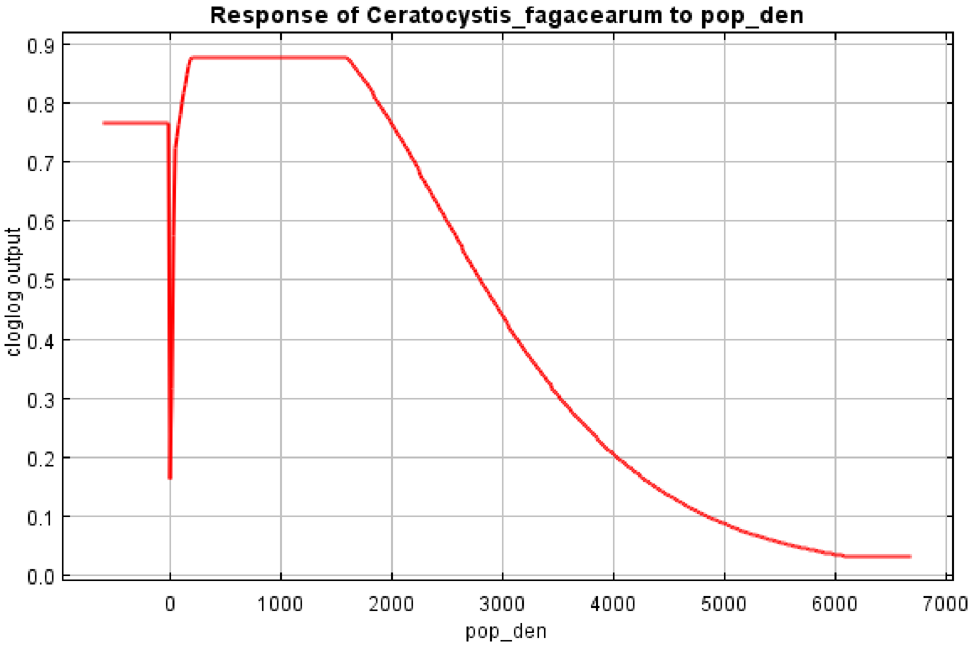

Response of Ceratocystis_fagacearum to feb_min_temp
cloglog output
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-17
-16
-15
-14
-13
-12
-11
-10
-9
feb_min_temp

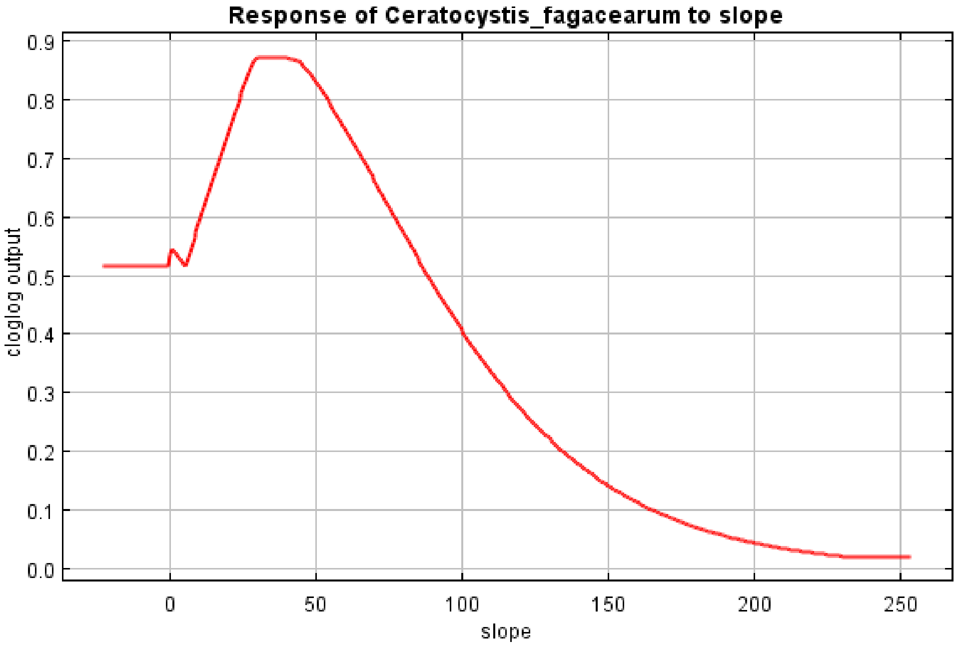


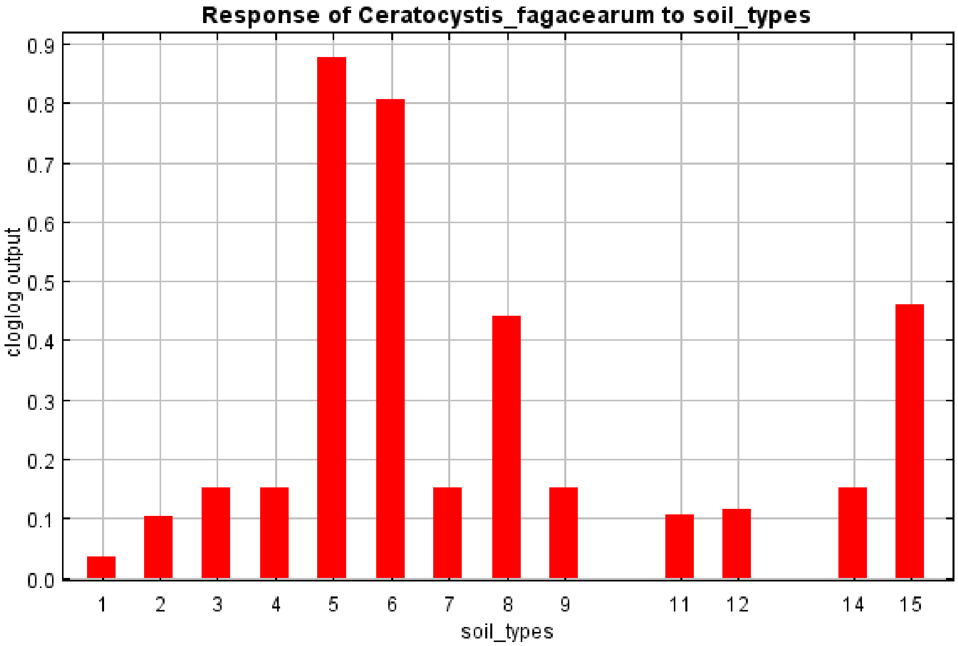
1. High intensity urban
2. Low intensity urban
3. Cropland
4. Grassland
5. Upland Shrub
6. Lowland deciduous shrub
7. Water
8. Floating aquatic
9. Sedge meadow
10. Broadleaf sedge/cattail
11. Jack pine
12. Red pine
13. White pine mix
14. Balsam fir mix
15. White spruce
16. Lowland black spruce
17. Tamarack
18. Stagnant tamarack
19. Lowland northern white cedar
20. Aspen/white birch
21. Bur/white oak
22. Red oak
23. Maple/basswood
24. Black ash
25. Mixed developed
26. Transportation
27. Barren
28. Lowland evergreen shrub
29. Stagnant black spruce
30. Upland deciduous
31. Silver maple
32. Cottonwood
33. Lowland deciduous
34. Upland conifer-deciduous mix
35. Northern pin oak
36. Red cedar
37. Red/white pine
38. White/red oak
39. Red/white pine-deciduous mix
40. Red cedar-deciduous mix


Response of Ceratocystis_fagacearum to jul_max_temp
cloglog output
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
25.5
26.0
26.5
27.0
27.5
28.0
28.5
29.0
29.5
jul_max_temp


Response of Ceratocystis_fagacearum to jun_max_temp
cloglog output
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
22.5
23.0
23.5
24.0
24.5
25.0
25.5
26.0
26.5
27.0
jun_max_temp


Response of Ceratocystis_fagacearum to pop_den
cloglog output
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
1000
2000
3000
4000
5000
6000
7000
pop_den


Response of Ceratocystis_fagacearum to slope
cloglog output
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
50
100
150
200
250
slope



1.	Aquolls	6.	Hemists	11.	Aqalfs
2.	Udolls	7.	Sparists	12.	Aquents
3.	Aquetpts	8.	Udalfs	13.	N/A
4.	Water	9.	Udepts	14.	Orthods
5.	Psamments	10.	N/A	15.	Fluvents