Predicting Abiotic Preferences of Three Roadside Plant Invaders

A Technical Report Prepared for the Integrated Roadside Vegetation Management Program,

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Executive Summary

Invasive species have degraded many habitats, including the Tallgrass Prairie in the Midwestern United States, such that prevention and site prioritization for management are challenging priorities. Unfortunately, specific environmental conditions in which these species thrive are not well understood (preference of elevation, direction, and proximity to human disturbance, etc.), particularly regarding predicting sites of prioritization for management and protection. Using data from 440 plots gathered along roadsides in Scott County, Iowa, we determined binomial predictive models of species presence and absence for three dominant invasive plant species, as well as principal components analyses and decision trees combining environmental predictors. Smooth Brome (*Bromus inermis*), is cosmopolitan but concentrated in north-facing, flatter areas; Reed Canary Grass (*Phalaris arundinacea*) primarily dominates in low elevations with proximity to water; and Wild Parsnip (*Pastinaca sativa*) in most restricted, primarily in areas of steep landscape slope and proximity to water. This model increases scientific understanding of understudied invasive species establishment, demonstrates where all three species may spread in the future, and identifies which areas of American Midwest may be best suited for restoration to prairie with lowest risk of invasion.

Introduction

In North America, humans first began impacting the landscape, flora, and fauna during and after the last Ice Age. Later, during the Age of Discovery, the European colonization of North America is when the threat to unique native ecosystems began to grow (Donlan and Martin 2004). In what is now the Midwestern United States, the region has long been classified by its temperate continental climate and native species that occupied the land; this vast, biologically diverse mixture of grasses and forbs was called the prairie (Anderson 2009, Smith 1992). The rich organic soils driving its great species diversity led to this biome's demise; since the sharp ascent of agricultural technology in the 19th century, over 90% of the prairie has been destroyed for farm use (Dornbush 2004). In Iowa in particular, the Tallgrass Prairie has been reduced to only 0.1% of its historical range (Samson and Knopf 1994). Besides the takeover of industrial-scale agriculture, the extirpation of the American bison crippled a key component of the prairie's health: selective grazing (Anderson 2009). These factors, in combination with wildfire suppression, chemical herbicide use, and irrigation over the last two centuries allowed trees to grow in the rich soils, further weakening the prairie's ancient foothold in the Midwest (Anderson 2009). These detrimental elements allowed invasive species to easily and quickly colonize the American Midwest; in particular, invasive plants by abundance may be the largest threat to the surviving native Tallgrass Prairie species (Gaskin et al. 2021).

While many invasive species have established in this biome, three common species in particular pose great threat to the survival of the prairie: *Bromus inermis* Leyss (Smooth Brome), *Phalaris arundinacea* L. (Reed Canary Grass), and *Pastinaca sativa* L. (Wild Parsnip). Smooth Brome was originally introduced to North America in the late 19th century from eastern Asia to enhance pastureland and land reclamation after mining, likely due to its hardiness and ability to spread rapidly (Fink and Wilson 2011). Smooth Brome can greatly reduce native plant abundance and diversity and often outcompetes native forbs due to the density of stands that form (Fink and Wilson 2011, Wasser and Dittberner 1986). Similarly, Reed Canary Grass was introduced by Iowa farmers in 1930 from Europe, over time becoming one of the major invasive concerns due to its high tolerance for mesic environments that Iowa farmlands can provide (Molofsky et al. 1999). Like Smooth Brome, Reed Canary Grass is perennial, though it can spread by both seed and vegetative propagation, further enhancing its invasive ability (Molofsky et al. 1999). Wild Parsnip has a much longer history in North America than its two counterparts; earliest estimates suggest the cultivated variety was introduced from Europe into the Virginia colonies in the early 17th century (Averill and DiTommaso 2007). It is thought that this particular variety of *Pastinaca* then escaped cultivation, reverting to the wild-type present across much of the United States today (Averill and DiTommaso 2007). Wild Parsnip is a forb of particular interest to human, pet, and livestock health due to its ability to produce a myriad of toxic chemicals in its tissues. One family of compounds in particular, furanocoumarins, can cause severe irritation and skin blistering after exposure to UV radiation from the sun (Averill and DiTommaso 2007).

These three invasive species pose a great ecological threat to the last few existing patches of prairie, especially since management is inconsistent or largely nonexistent throughout the Midwest (Gaskin et al. 2021). Despite their concerning history, very little is understood about where and under what conditions these species propagate in native Midwestern ecosystems. Beyond an ethical obligation for preservation, prairie has several benefits to both science and industry: it is well understood that prairie benefits plant and animal diversity (up to 20 times the original concentration for some species), thereby increasing ecosystem health as a whole (Schulte et al.

2017, Travis et al. 2018). Furthermore, prairie acts as a refuge for keystone and endangered species of mammals, avians, and insects; this increased pollinator count and productivity associated with prairie, as well as water uptake and release by the diverse root system, supports higher theoretical yields for farmers (Asbjornsen et al. 2007, Kwaiser and Hendrix 2008, Nippert and Knapp 2007).

Given the well-established benefits of biodiverse and healthy prairies, priority expectations for management of invasive species have the opportunity for great benefit to biologists and property managers. Previous literature has established the importance of early detection in management of invasive species (Reaser et al. 2020). The Tallgrass Prairie is no exception to this; however, the limited research on species known to invade this biome requires further exploration of where these species are most likely to invade. With the last of the prairie struggling to survive fragmentation, invasive species, and mismanagement, all of these concerns prompted us to ask the question: in Scott County, IA, is there a predictable relationship between environmental conditions and invasion presence of these three major plant species? Our statistical model hypotheses, reflecting available literature (or null hypotheses in cases of lack of research support), are presented in Table 1. Relationships that are bolded represent the most important hypothesized relationships in determining each species' distributions.

Table 1. Hypothesized relationships and most predictive environmental characteristics (bold) for distribution of each of the three focal invasive species. Where previous literature suggested a potential relationship, that literature was used (footnotes below). A lack of literature led to presentation of the null hypothesis.

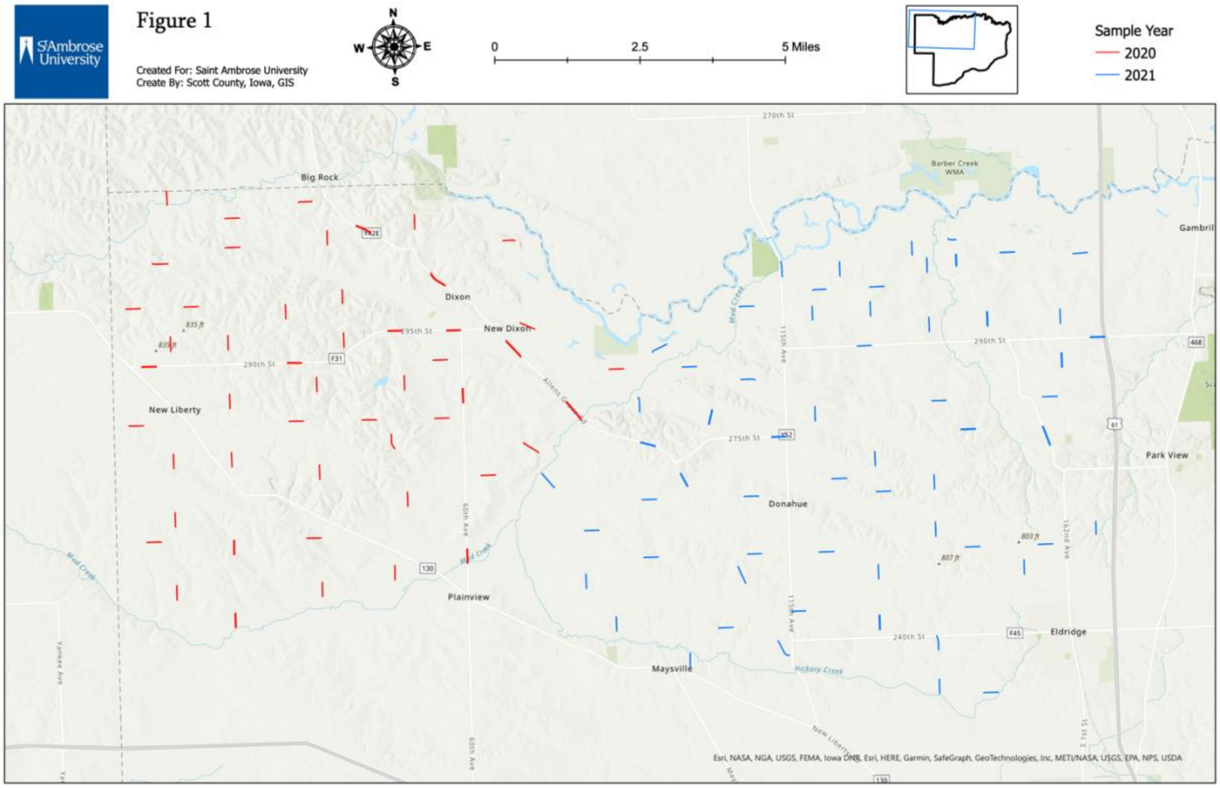
Environmental Characteristic	Description of Characteristic and Units	Smooth Brome	Reed Canary Grass	Wild Parsnip
Slope	The angle of the roadside relative to the horizon in degrees; higher values indicate a steeper slope	Null	Null	Null
North Facing	The degree to which the center of the plot faces due north; -1 is due south, 1 is due north; cos-transformed from aspect	**Positive[1]**	Positive[2]	**Negative[3]**
East Facing	The degree to which the center of the plot faces due east; -1 is due west, 1 is due east; sin-transformed from aspect	**Positive[1]**	Positive[2]	**Negative[3]**
Elevation	Feet above sea level	Negative[4]	**Negative[5]**	Null
Distance to Nearest Water Body	Feet from the nearest county-identified pond, lake, stream or river	Negative[1,4]	Negative[2]	Positive[6]
Distance to Nearest Culvert	Feet from the nearest culvert (on the same road or an adjacent)	Negative[4]	**Negative[2]**	**Positive[6]**
Distance to Nearest Cropland	Feet from nearest land cover defined as cropland via ArcGIS (on the same road or an adjacent)	**Negative[4]**	**Negative[7]**	Null

Notes on Table Citations: Null indicates there was no predictive relationship determined from published literature.
1. Fink and Wilson 2011
2. Inferred from Figiel et al. 1995, Molofsky et al. 1999
3. Inferred from Baskin and Baskin 1979, Sternberg et al. 1999
4. Wasser and Dittberner 1986
5. Barnes 1999
6. Averill and DiTomasso 2007, Sternberg et al. 2007
7. Kercher and Zedler 2004, Lavergne and Molofsky 2004

Materials and Methods

Study sites and locations

We conducted our research in patches of the Tallgrass Prairie, including replanted, historically mowed, and invaded areas in Northern Scott County, Eastern Iowa, USA, centered on ~41.681209, -90.679402. The vast majority of Northern Scott County is rural, with most of our plots being very close in proximity to corn and soybean fields; data collection sites were chosen away from human made structures that could cause interference in consistency, most notably being houses, bridges, and mowed areas. Furthermore, there were some areas with cedar (*Juniperus virginiana*) windbreaks, but otherwise plots were mostly devoid of mature trees along the roads. Sampled areas could, and often did, include steep ditches, standing water, and difficult to access areas. However, very few areas were actually deemed unsuitable for sampling; those that were determined as such were due to the presence of creeks, culverts, or bridges that made it impossible to sample continuously. Most areas could be sampled on all sides. To select specific sites to collect data, we used a stratified sampling technique throughout the region to be representative of the geographic span of the sample area. We worked in partnership with Scott County GIS to choose predominantly gravel roadsides or low speed limit paved roads (Fig. 1), and we only sampled from roadsides that were managed by the county.



Sampling methods

All data were collected July 6-August 10, 2020, and June 14-July 23, 2021. In one standard day, the researchers responsible for data collection would generally sample between 2-4 roadsides, depending on weather conditions. Per day, the timeframe spanned ~4-5 hours total in the field; a single plot averaged ~1.5 hours to complete. Each plot was started and completed on the same day. A total of 440 plots were sampled between 2020 and 2021; Smooth Brome was present in 416, Reed Canary Grass in 240, and Wild Parsnip was present in 205 plots.

In order to be sampled, a plot had to consist of a continuous quarter mile on both sides of the road, and it could not be mowed. The researchers assessed sites in the stratified sample for representativeness and suitability; if sites were unsuitable, the team would move down the road to sample a more representative area in the same general vicinity. Once at an appropriate location, both quarter mile segments along either side of the road were marked with orange flags, splitting them up into four segments, each ~0.2 km in length. GPS coordinates were taken at this central location. All vascular plant species were then identified in each 0.2 km section; species observation began at the edge of the road and continued ~3 m into the ditch. Occasionally, some ditches were unsafe to walk in, submerged in water, or too steep of an embankment to traverse, and therefore visual estimation of all species was done as best as possible. If one or more species were found that the researchers could not identify, they were collected for later identification and analysis. Taxonomic keys were used to identify the unknowns, which were then pressed for preservation.

Data preparation

Topographic and landscape data were collated from Scott County GIS layers of abiotic conditions. Landscape data for each individual plot was determined by Scott Country Geographic Information Systems (GIS) using ArcGIS and ESRI ENVI software. These data included slope, elevation and aspect at the plot midpoint; as well as straight-line distance to the nearest creek or stream, the nearest culvert, and the nearest cropland. Aspect values were transformed from degrees to "northness" and "eastness" measures, ranging from -1 (fully south facing or west facing, respectively) to 1 (fully north facing or east facing, respectively).

Data analysis

The data collected was analyzed using binomial regression models in the MASS package of R software (OS "Kick Things", v. 4.1.1). Specifically, generalized linear models were developed to prevent concerns of overdispersion of absence data. This system determined which factors best correlated with species presence and absence. These models utilized Akaike Information Criterion (AIC) values, with lower AIC values representing models that best balance accuracy and simplicity to avoid overfitting data (Legendre and Legendre 2012). The AIC assessed each variable in relation to the others for a given focal species, resulting in a range of predictiveness; the three most influential variables with lowest AIC values were not only compared in every combination additively, but also multiplicatively via mixed-effects models. For Smooth Brome and Reed Canary Grass, the three most predictive variables could combine into five distinct additive and interactive models for evaluation. In contrast with the other two invasive species, Wild Parsnip was determined to have four most predictive individual variables, leading to the development of fourteen distinct mixed-effects models. These models, coupled with a stepdown model of all additive variables, were compared to the original individual models for best fit by AIC value.

Decision trees to summarize the conditions throughout the data were also utilized using the tree package. These trees mapped the most important specific conditions that affect each species individually, emphasizing probability of presence or absence of the focal species. To prevent concerns with overfitting probability values, we pruned the tree for Reed Canary Grass to its first eight branches; the other two focal species produced trees with six or fewer branches and were not pruned.

Three principal component analyses (PCA) were developed using the factoextra package to demonstrate how the variables combined to impact species presence in a general sense. PCA was chosen for this dataset because there are a great number of variables and relationships that impact the presence of the invasive species, resulting in many predictive axes in need of condensing for one general predictive envelope.

Results

Table 2 demonstrates the slope and AIC values for individual binomial regressions for each invasive species compared to the seven unique environmental variables. This information can be used to determine which variables are most predictive of presence, with lowest values indicating highest probability.

Table 2. Binomial fit as described by AIC of generalized linear model between presence of three invasive species in a plot and the single predictive variables shown. Bolded AIC values indicate the most predictive individual variables for that species, based on AIC fit.

Variable	Smooth Brome Slope	Smooth Brome AIC	Reed Canary Grass Slope	Reed Canary Grass AIC	Wild Parsnip Slope	Wild Parsnip AIC
Slope	0.0151	189.7	-0.021	**604.5**	0.0264	**602.7**
Northness	0.705	**184.6**	0.0275	610.3	0.046218	611.8
Eastness	-0.14	190.1	0.0927	609.9	0.10963	611.3
Elevation	0.0113	**184**	-0.00575	**602.2**	0.00345	**609**
Distance to Water	0.0000697	190	-0.0000705	608.7	-0.00014	**605.8**
Distance to Culvert	-0.00032	189.4	0.00062	**599.1**	-0.0001	611.5
Distance to Cropland	-0.00136	**184.8**	0.0005	609.4	-0.0012	**608.5**

Smooth Brome

For Smooth Brome, the three most predictive individual variables were a positive relationship with northness and elevation, and a negative relationship with proximity to croplands (Table 2), each with an AIC between 184 and 185. In combining these three predictors in mixed effects models (Supp. Table 1), the presence of Smooth Brome was best predicted by an x-axis defined by Northness*Elevation+Cropland with an AIC of 176.7074, suggesting an interaction of effects between northness and elevation improves predictive ability compared to each individual variable.

The Decision Tree (Fig. 2) demonstrates that, at elevations less than 646.5 feet, Smooth Brome occurred the vast majority of times in north-facing environments. Even more specifically, Smooth Brome was present 100% of the time when distance from a cropland was over 0.5 and the distance to a culvert was under 925. On the other hand, when the elevation was above 646.5 and when the northness was a strong negative value (i.e., it occurred in a south-facing environment), Smooth Brome had a very high correlation with those conditions. However, when the environment was less south-facing and the distance from the nearest body of water was less than 3407 meters, there was also a very strong correlation with Smooth Brome presence.

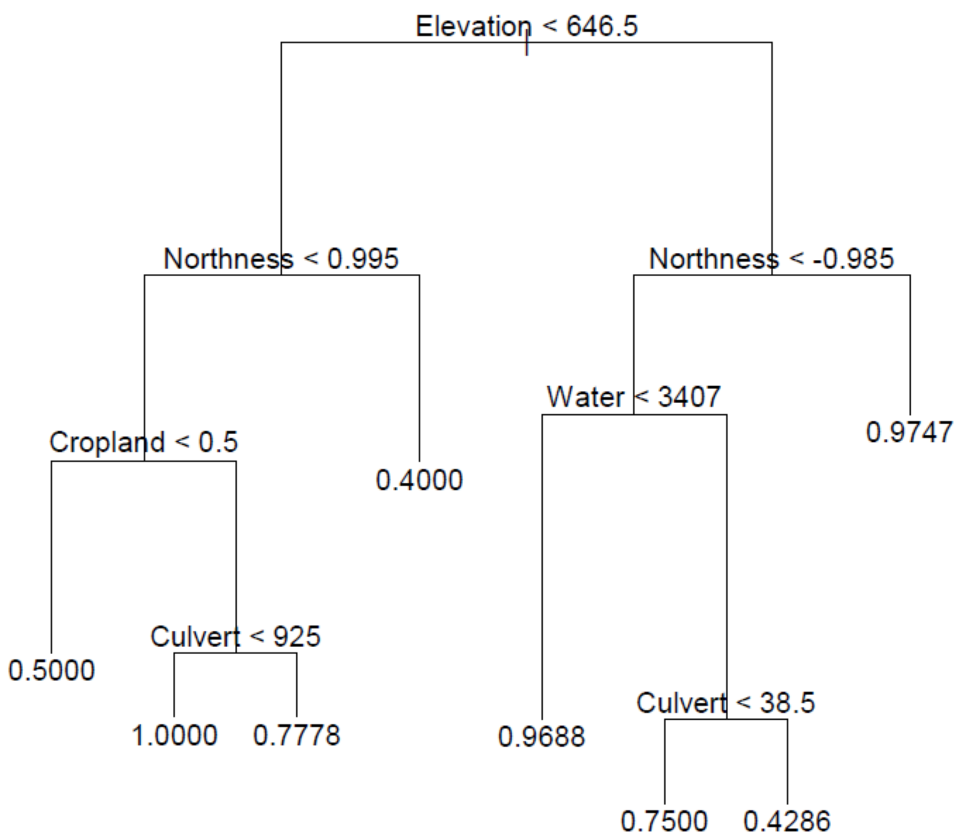


Figure 2. Decision tree showing the summary of conditions that most affect the presence of Smooth Brome. At each fork, the left side is “true”, whereas the right side is “false” with the condition presented. Numerical values from 0-1 indicate the percentage of plots meeting that unique set of conditions with the focal species present.

The PCA (Fig. 3) demonstrates that there is significant overlap between environmental conditions where Smooth Brome is present and those where it is absent. Although only ~40% of environmental variation was captured in the two axes, there was not a clear delineation between its presence and absence. It is worth noting that the ellipsis of Smooth Brome presence did fit almost entirely within the ellipsis of its absence, suggesting that moderate conditions, devoid of any extreme environmental characteristics, are most likely to host this species.

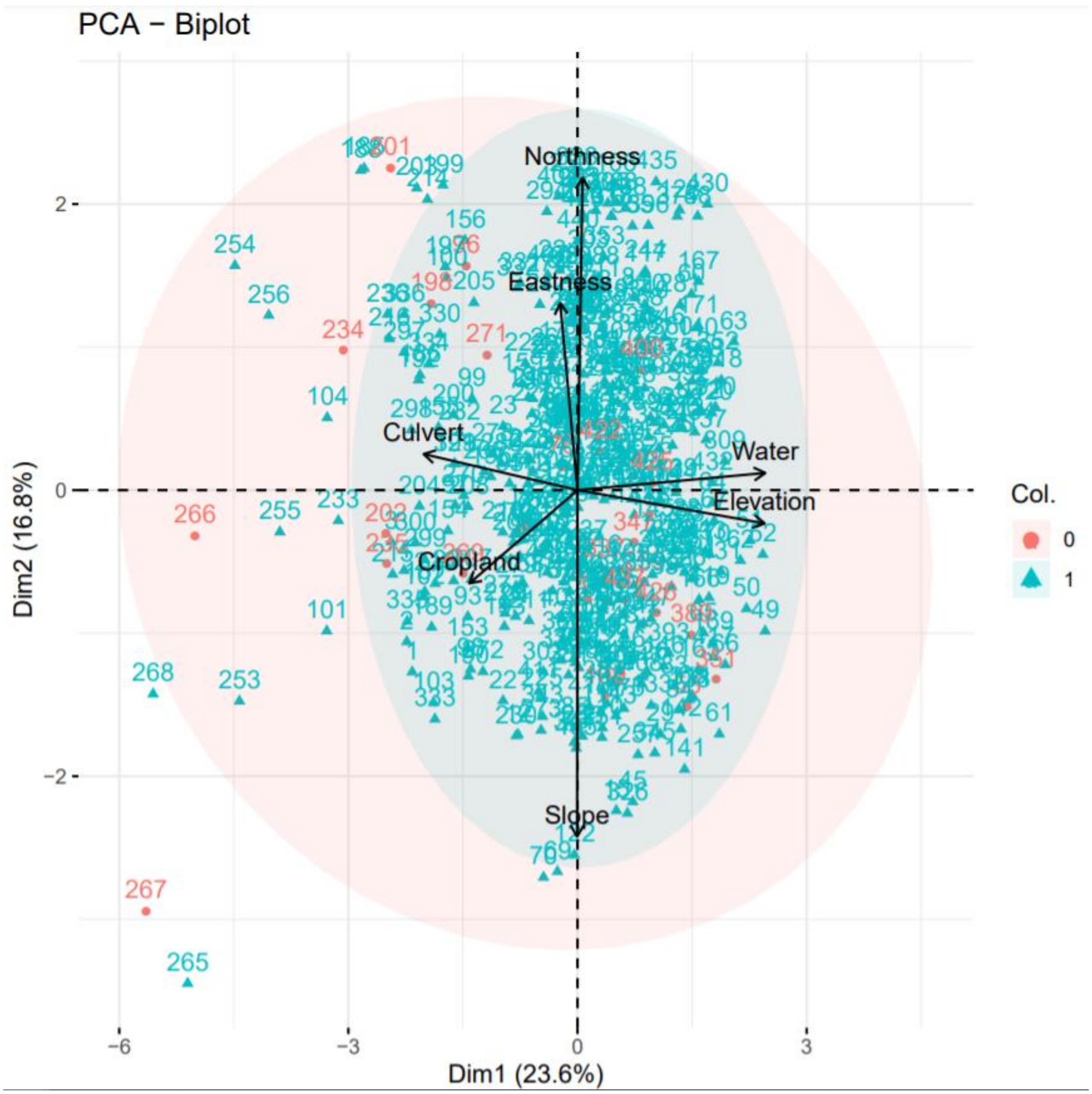


Figure 3. The principal components analysis showing the coordinates of which conditions are most predictive to finding Smooth Brome. As a cosmopolitan species, plots containing Smooth Brome overlapped extensively with plots not containing it, suggesting a preference for intermediate conditions and the chance for future invasion.

Reed Canary Grass

For Reed Canary Grass, the three most important predictive variables were negative slope, negative elevation, and positive proximity to a culvert (Table 2). With an AIC of 593.6, the presence of Reed Canary Grass was best predicted by an x-axis defined by Slope + Elevation + Culvert with no interactive terms among the three variables (Supp. Table 2).

Figure 4 provides the summary of abiotic factors which are most determinant of Reed Canary Grass presence or absence. As noted in previous literature, Reed Canary Grass is greatly affected by and dependent on highly water-saturated soil. Our findings support this with the third bifurcation on the left side being a greater than 90% chance of finding Reed Canary Grass when less than 156 feet from water. Furthermore, there are several points at which there is a greater than 70% chance of finding Reed Canary Grass due to each variable being one that affects the presence or absence of water. For example, a low elevation, low distance to a culvert, and high eastness value all point towards conditions that would allow for high groundwater saturation. Contrary to the Smooth Brome decision tree, this tree provided much less specific data about Reed Canary Grass and the factors that most influence its presence.

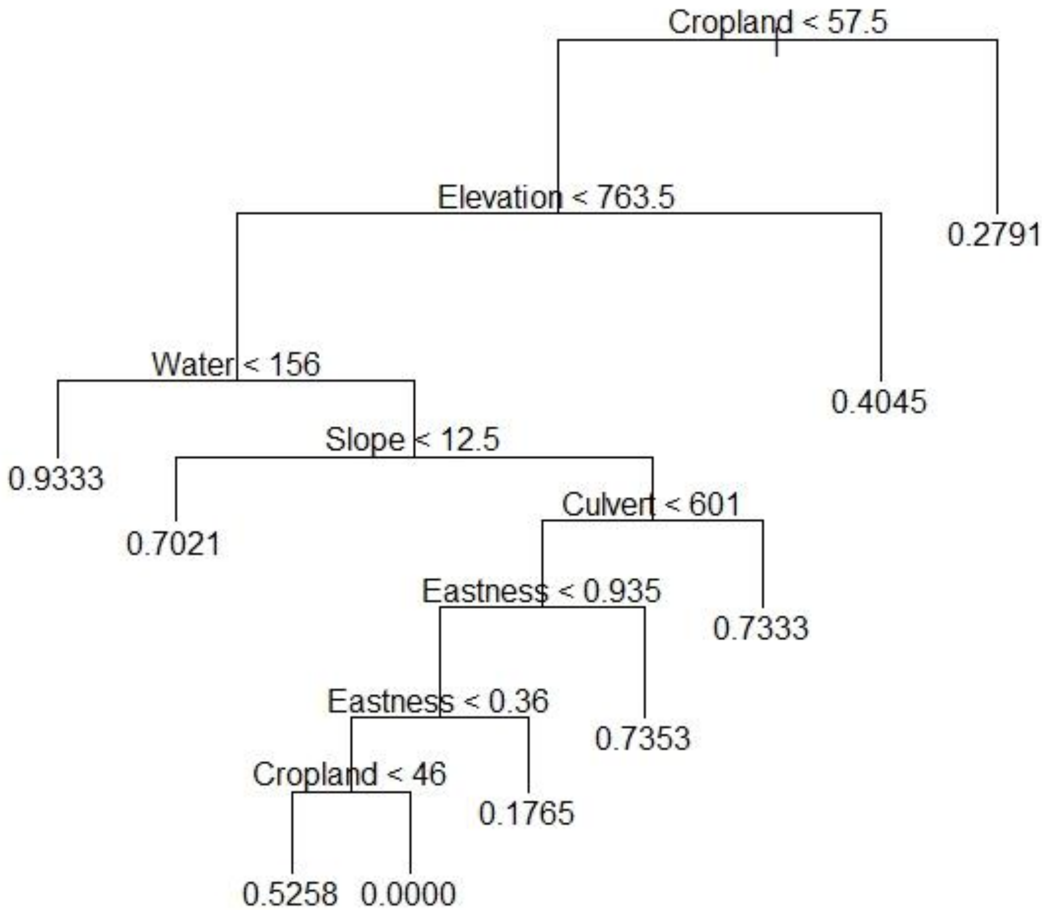


Figure 4. Decision tree showing the summary of conditions that most affect the presence of Reed Canary Grass. At each fork, the left side is "true", whereas the right side is "false" with the condition presented. Numerical values from 0-1 indicate the percentage of plots meeting that unique set of conditions with the focal species present.

The PCA (Fig. 5) demonstrated significant overlap between plots with and without Reed Canary Grass, though there was a distinct pattern of presence in low-elevation, low-slope conditions, with greater likelihood of absence in high-elevation, high-slope conditions.

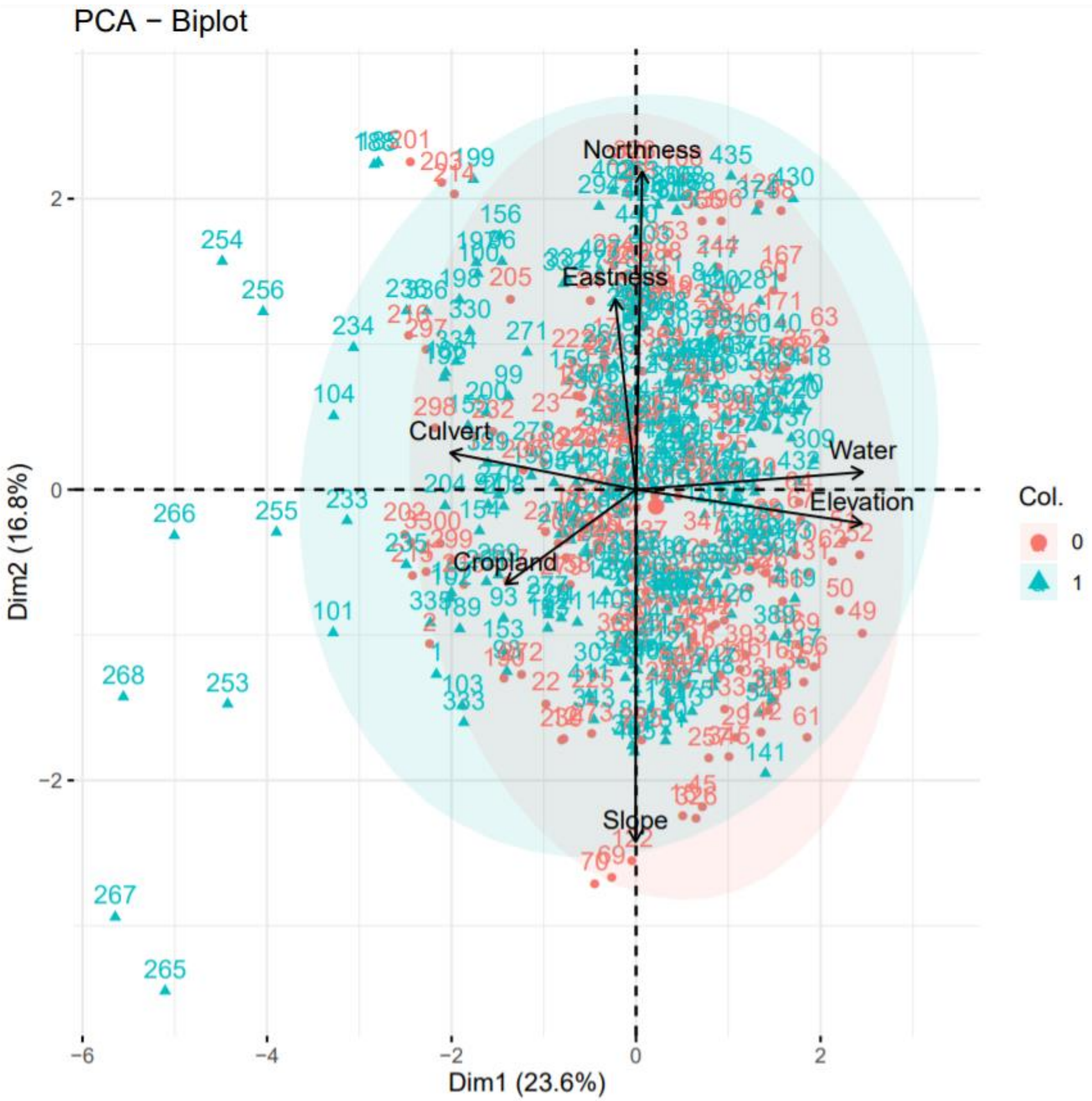


Figure 5. The principal components analysis showing the coordinates of which conditions are most predictive to finding Reed Canary Grass.

Wild Parsnip

For Wild Parsnip, four variables proved most predictive instead of three; this was due to the AIC value of two variables being almost identical (Table 2). These four variables were a positive slope, positive elevation, negative distance to nearest water source, and negative distance to nearest cropland. With an AIC of 585.6, the presence of Wild Parsnip was best predicted by an x-axis defined by Elevation * Cropland + Slope + Water, suggesting an interaction between the terms cropland and elevation (Supp. Table 3).

The decision tree (Fig. 6) gives evidence to how Wild Parsnip exists, in contrast with its other invasive counterparts, in very specific environmental conditions. For example, Wild Parsnip was never found when the distance to water was under 163.5 feet, or when it was a great distance from water (above 5648.5 feet). It was always found when the slope was less than 21.5, the elevation was less than 771.5, the distance to water was less than 1524 but greater than 163.5, the eastness was greater than 0.17, and the distance to the nearest culvert was less than 207.5. These findings suggest that Wild Parsnip occurs in much more specific environmental conditions than what was previously thought or known in the Midwestern United States, but can be highly invasive in the areas that do suit it well.

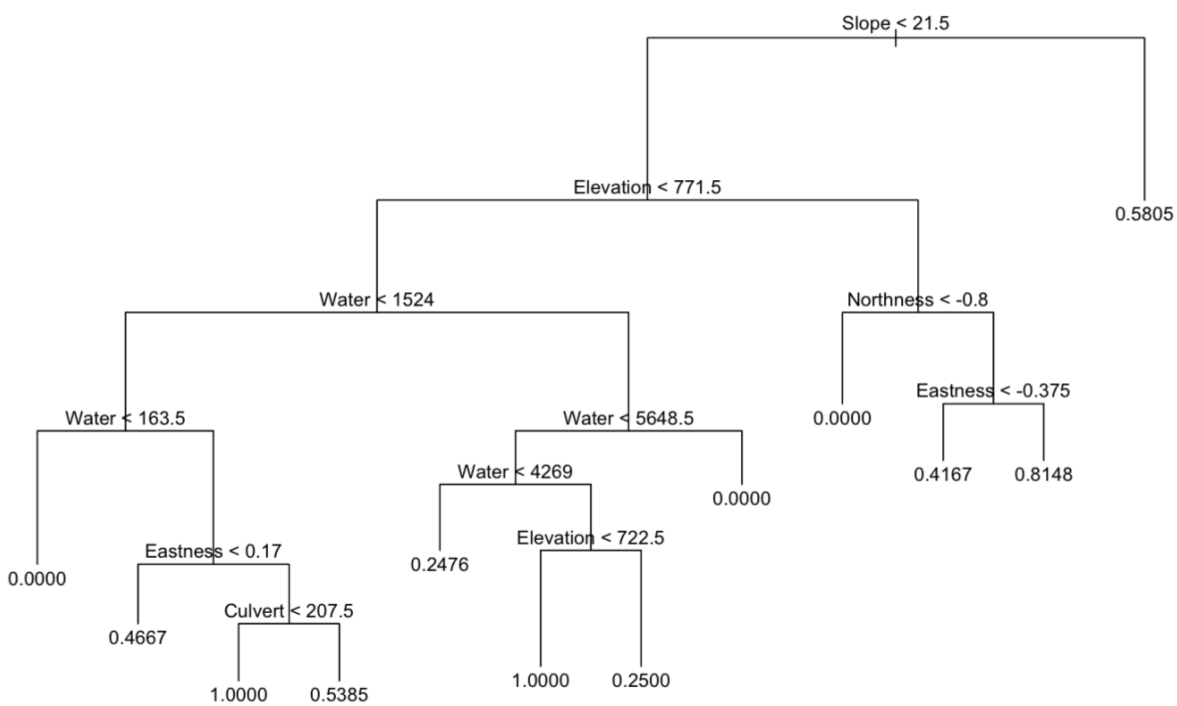


Figure 6. Decision tree showing the summary of conditions that most affect the presence of Wild Parsnip. At each fork, the left side is “true”, whereas the right side is “false” with the condition presented. Numerical values from 0-1 indicate the percentage of plots meeting that unique set of conditions with the focal species present.

The PCA (Fig. 7) demonstrated significant overlap between plots with and without Wild Parsnip, though there was a distinct pattern of absence in low-elevation, low-slope conditions, with greater likelihood of presence in high-elevation, high-slope conditions.

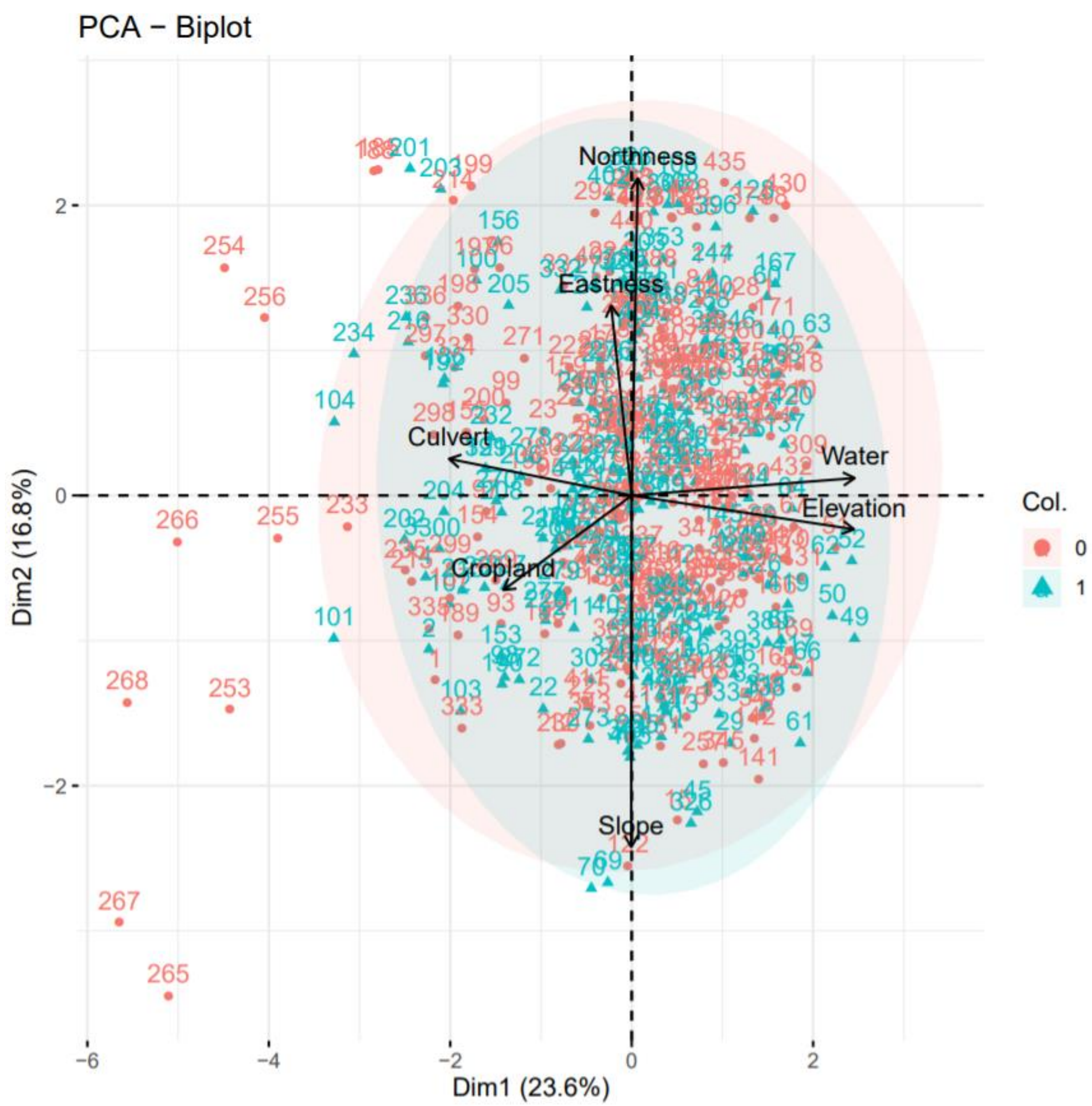


Figure 7. The principal components analysis showing the coordinates of which conditions are most predictive to finding Wild Parsnip.

Discussion

Smooth Brome

Before any data was analyzed, we hypothesized that positive northness, positive eastness, and negative distance to cropland were the most important abiotic factors to influence the presence of Smooth Brome based on previous literature (Fink and Wilson 2011, Wasser and Dittberner 1986). As exemplified in Table 1, northness and distance to cropland were found to have two of the three lowest AIC values (184.6 and 184.8 respectively). Contrary to our prediction, elevation was considerably lower in AIC value than was eastness. This led us to rejecting our hypothesis on Smooth Brome.

The decision tree exhibits the abiotic factors that led us to rejecting the hypothesis. The first separator is elevation, indicating its importance in determining the presence of Smooth Brome. Overall, the decision tree reveals that Smooth Brome can and does colonize a wide variety of environmental conditions as a competitively dominant species (Grime 1974). Smooth Brome has the ability to thrive in environments that have high and low northness, as shown by the first two bifurcations on the decision tree, as well as close to water (in the case of a culvert) or far from a water source (such as a pond or creek) as the tree branches. It is important to note that Smooth Brome was found in 100% of the plots that were north facing environments near farm fields that were relatively close to a culvert. Additionally, there were very few plots where Smooth Brome was not found, but the lowest probability of finding it was in lower elevations with a very strong northness value, as well as at higher elevations close to water sources and a culvert (likely where water could be trapped). This may be due to Smooth Brome having a low tolerance for flooding, relative to other invasive species like Reed Canary Grass, with its native habitat mimicking the mesic prairie's natural dryness rather than some areas in Iowa that could be considered wetland prairie (Wasser and Dittberner 1986).

The PCA biplot yielded information on where Smooth Brome was found, giving a visualization of all the plots that contained it and those which did not. As seen in the PCA, there were far more plots that had favorable abiotic conditions for Smooth Brome than did not. It is also important to notice that the environments that Smooth Brome was found in were very similar to the environments that it was not found, with most "absent" markers being found within the "present" envelope.

Interpreting all of these analyses together, it is very evident that our data supports Smooth Brome being a generalist invasive, meaning that it can thrive in environments with variation in abiotic conditions. This property, in combination with how densely and quickly it infects the landscape, makes it a very dangerous threat to Tallgrass Prairie native ecology.

Reed Canary Grass

We determined negative landscape elevation, negative distance to the nearest culvert, and negative distance to the nearest cropland as being the most likely determinant abiotic factors in Reed Canary Grass presence based on previous studies done on this species (Barnes 1999, Figiel et al. 1995, Kercher and Zedler 2004, Lavergne and Molofsky 2004, Molofsky et al. 1999). Elevation and distance to the nearest culvert matched our predictions; as with Smooth Brome, one of our hypothesized abiotic factors was not consistent with the data, which actually supported the pattern of slope being more impactful to finding Reed Canary Grass.

A variety of abiotic factors influenced the presence of this species, but one of the most important was proximity to water. As shown by the third bifurcation on the left side of the decision tree, Reed Canary Grass was found almost always when the distance to water was low in low elevations, near croplands. Additionally, in areas even closer to farm grounds that are more westward-facing with steeper ditch slopes, Reed Canary grass was not found at all in our dataset. Environmental conditions like these are much more specific than what was found for Smooth Brome, indicating that Reed Canary Grass is much more specialized in the locations it is evolved to inhabit.

The PCA biplot suggests that there are specific conditions that must be met in order for invasion by Reed Canary Grass. In comparison to Smooth Brome, Reed Canary was found far less often in our plots, which is indicated by the much greater amount of red markers on the biplot itself.

These three interpretations together support Reed Canary Grass being less of a cosmopolitan species, and more of a specialist. This species in particular seems to show strong preference for areas near farm fields at low elevation; this may be explained by the large amounts of field runoff which can occur in the Midwest due to field tiling and seasonal rains in the spring and summer (National 2020). Additionally, due to poor drainage in ditches and roadsides in comparison to cropland, water can often accumulate and become stagnant to the point of creating an artificial wetland, which may promote the growth and spread of Reed Canary Grass. These preferences could be important in determining where to put tiling and where to reseed prairie-native species due to these factors reliably predicting where Reed Canary Grass could invade and propagate.

Wild Parsnip

Before data analysis, we hypothesized for negative northness, negative eastness, and positive distance to the nearest culvert to be the most impactful abiotic factors on Wild Parsnip (Averill and DiTomasso 2007, Baskin and Baskin 1979, Sternberg et al. 1999). Inferences had to be made for two of the three abiotic factors due to Wild Parsnip being an understudied species in terms of its invasiveness. None of our findings supported our hypotheses, but instead found slope, elevation, distance to the nearest water source, and distance to the nearest cropland as being the most predictive environmental factors (Table 2); the values calculated for elevation and distance to the nearest cropland were so numerically close that we determined four most predictive abiotic factors would be more helpful in evaluating our hypotheses than would three.

The decision tree visualizes the trends presented multiple conditions that contradicted our expectations; for example, as shown by the third bifurcation on the left side of the decision tree, Wild Parsnip was not found within any plots when extremely close to water, leading one to believe that it might prefer dry environments. Conversely, the right side of the water bifurcation shows that Wild Parsnip rarely or never existed when very far away from a source of water; Wild Parsnip was found in all plots which existed between near and far conditions to a water source, and relatively close to a culvert on East banks, as well as at low elevations when far away from water. All of these observations may indicate that this species persists best in a "Goldilocks Zone" of intermediate wet and dry conditions as mediated by distance from water, exposure to wind, and exposure to sunlight, an intermediate in Grime's CSR framework (1974).

Furthermore, the PCA biplot corroborates the specificity presented in the decision tree. Much like the biplot for Reed Canary Grass, the PCA for Wild Parsnip shows much less generalist characteristics for this invasive species. The red envelope being much larger than the blue envelope indicates that there was a wider variety of plots and conditions where we did not find Parsnip, which is further exemplified by the outliers on the plot.

Synthesis

In synthesizing these conclusions, it is clear that our data supports Wild Parsnip being a specialist species. Based on our data, it seems that Wild Parsnip is governed most by soil moisture levels, making it predictable to certain environments. This may be one of the most important species to understand because out of the three invasive species we studied, Parsnip by far has the greatest immediate health concern to people, pets, and livestock. When the juices of Wild Parsnip get on exposed areas of skin, they often cause painful blisters similar to the irritation caused by poison ivy, which many people who are not aware of this species would not know. It is also reasonable to assume that the chemicals affect plants and insects around them due to the well-established connection between plant coumarins and allelopathy (Razavi 2011).

Between all three species, elevation was the abiotic factor that was commonly shared as a best predictor; this was predicted in previous studies for Reed Canary Grass, but an inference had to be made for Smooth Brome, and there was no previous literature to suggest any preference by Wild Parsnip. In general, all three species are understudied relative to the rate at which they are invading American landscapes (Gaskin et al. 2021), and therefore many inferences on environmental conditions had to be made when we were initially formulating our hypotheses. This was especially the case for Wild Parsnip, given that the many studies on this species are relating to its agricultural values in some cultures. Due to this limited body of literature, our study in several ways is the first to comprehensively evaluate the environments these species prefer, especially in what was historically the largest continuous biome in the continental United States.

Perhaps the largest difference between the species is not only where they occur, but how often they occur, as exemplified in the PCA biplots and AIC values of each species. Given the lower AIC value for Smooth Brome, it was found far more often than not (the majority of plots). This is also one of the limitations of our study: even though we evaluated 440 plots, there was no guarantee that we would find each species every day. Smooth Brome was found far more often than its counterparts, yielding potentially more informative data, yet this may be balanced out by Smooth Brome being a generalist species to the point that it can likely establish in almost any Midwestern environment.

In general, the three focal species are highly invasive with demonstrable impacts on invaded systems, such as the climax community that is the Tallgrass Prairie (Brown et al. 1983). Because the prairie landscape has been so drastically changed over the last several centuries, we can use the data we have gathered to potentially identify environmental conditions which species like these, and perhaps others, best invade; conditions which are "weak points" of threatened ecological landscapes can be better identified. This has great potential for utility in conservation biology, as well as governmental and private organizations which are dedicated to managing and preventing invasion by nonnative species. Furthermore, our experimental design can be modeled by researchers in other parts of the Midwest, the United States as a whole, or the world to analyze where species are likely to invade based on where we know they already exist.

Available published literature was limited in terms of what these species prefer. Out of the three species, Wild Parsnip is by far the least studied as an invasive one. This could be due to cultural reasons: due to its records since the 1600s, it has essentially established itself as a "normal" species to see in the Midwestern United States. Furthermore, it may not be considered a direct priority for treatment as an invader because it likely has a low impact on the crops farmers grow when it exists solely in roadside ditches, and it is less likely than the other two species to form dense monocultures. This makes our work valuable in determining and mapping the locations where Wild Parsnip prefers to invade.

Another distinction between the three focal species is not only where they occur, but how often they occur. Given the AIC values, it is clear to see that brome occurs far more frequently than reed or parsnip. This predominance throughout the sampled region comes despite plot selection often avoiding clear monocultures of Smooth Brome in favor of nearby patches of more biodiversity. The random stratification of the county plot sampling suggests that Smooth Brome truly is everywhere along these roadsides. Although we believe that all three species are particularly problematic and have potential for further eradication of the Tallgrass Prairie, these analyses demonstrate the significant threat posed by Smooth Brome (Fink and Wilson 2011). With a variety of locations and plots being chosen for examination and sampling, it is clear that Smooth Brome may singlehandedly be the most numerous invasive plant species in rural Scott County, Iowa, and perhaps, by extension, all of Iowa.

In general, many invasive species are excellent at upsetting the established order of an ecosystem (Gaskin et al. 2021). This finding is supported by our study. Our work could provide helpful insight into these species which lack recent or relevant study in the Midwestern United States and are quickly invading/changing the native landscape. Understanding how and where these species prefer to invade is just as important as understanding the biological features of the plants themselves; particularly, in areas of the Midwest that have prairie conservation sites, such as state parks, conservation managers could use the model we created to best predict the areas most at risk for invasion or most in need of management. Often, very few biologists and volunteers are left to manage properties with dozens or hundreds of acres. Using our model, they could drastically reduce the time spent on searching for predictable, hardy invasives like Smooth Brome that pose great risk to prairie survival and health.

Additionally, in areas like Eastern Iowa where the majority of areas that Tallgrass Prairie exists in is roadsides, this method could also help reduce the risks of habitat fragmentation in prairie biomes that are susceptible to division. Roadside management is a crucial step in this process -- knowing where invasives might try to gain a foothold means managers can better focus attention on prevention, reseeding, burning, and grazing efforts. In this way, long term care and management for the remaining relics of the Tallgrass Prairie may better be preserved for future generations. Additional research is required on the effects of different types of management strategies and invasion of the focal species in this study to better arm local governments (who are often the ones to make change happen) with relevant information and strategies to preserve what remains.

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Supplementary Tables and Figures

Supp Table 1. *Bromus inermis* mixed-effects models

Step down additive model of best fit: *Bromus* ~ Northness + Elevation + Cropland (AIC 179.4)

Interactive Models: *Bromus* ~ Northness * Elevation * Cropland: AIC= 181.3

Bromus ~ Northness * Elevation + Cropland: AIC= **176.7**

Bromus ~ Northness + Elevation * Cropland: AIC= 180.3

Bromus ~ Northness * Cropland + Elevation: AIC= 180.9

Supp Table 2. *Phalaris arundinacea* mixed-effects models

Step down additive model of best fit: *Phalaris* ~ Slope + Elevation + Culvert (**AIC 593.6**)

Interactive Models: *Phalaris* ~ Slope * Elevation * Culvert: AIC= 598.0

Phalaris ~ Slope * Elevation + Culvert: AIC= 593.7

Phalaris ~ Slope + Elevation * Culvert: AIC= 595.6

Phalaris ~ Slope * Culvert + Elevation: AIC= 594.9

Supp Table 3. *Pastinaca sativa* mixed-effects models

Step down additive model of best fit: *Pastinaca* ~ Elevation + Cropland + Slope + Water (AIC 591.3)

Interactive Models: *Pastinaca* ~ Elevation * Cropland * Slope * Water: AIC= 597.2

Pastinaca ~ Elevation + Cropland * Slope * Water: AIC= 594.4

Pastinaca ~ Elevation * Cropland + Slope * Water: AIC= 585.8

Pastinaca ~ Elevation * Cropland * Slope + Water: AIC= 590.2

Pastinaca ~ Elevation + Cropland + Slope * Water: AIC= 591.6

Pastinaca ~ Elevation + Cropland * Slope + Water: AIC= 593.1

Pastinaca ~ Elevation * Cropland + Slope + Water: AIC= **585.6**

Pastinaca ~ Elevation * Slope * Cropland + Water: AIC= 594.1

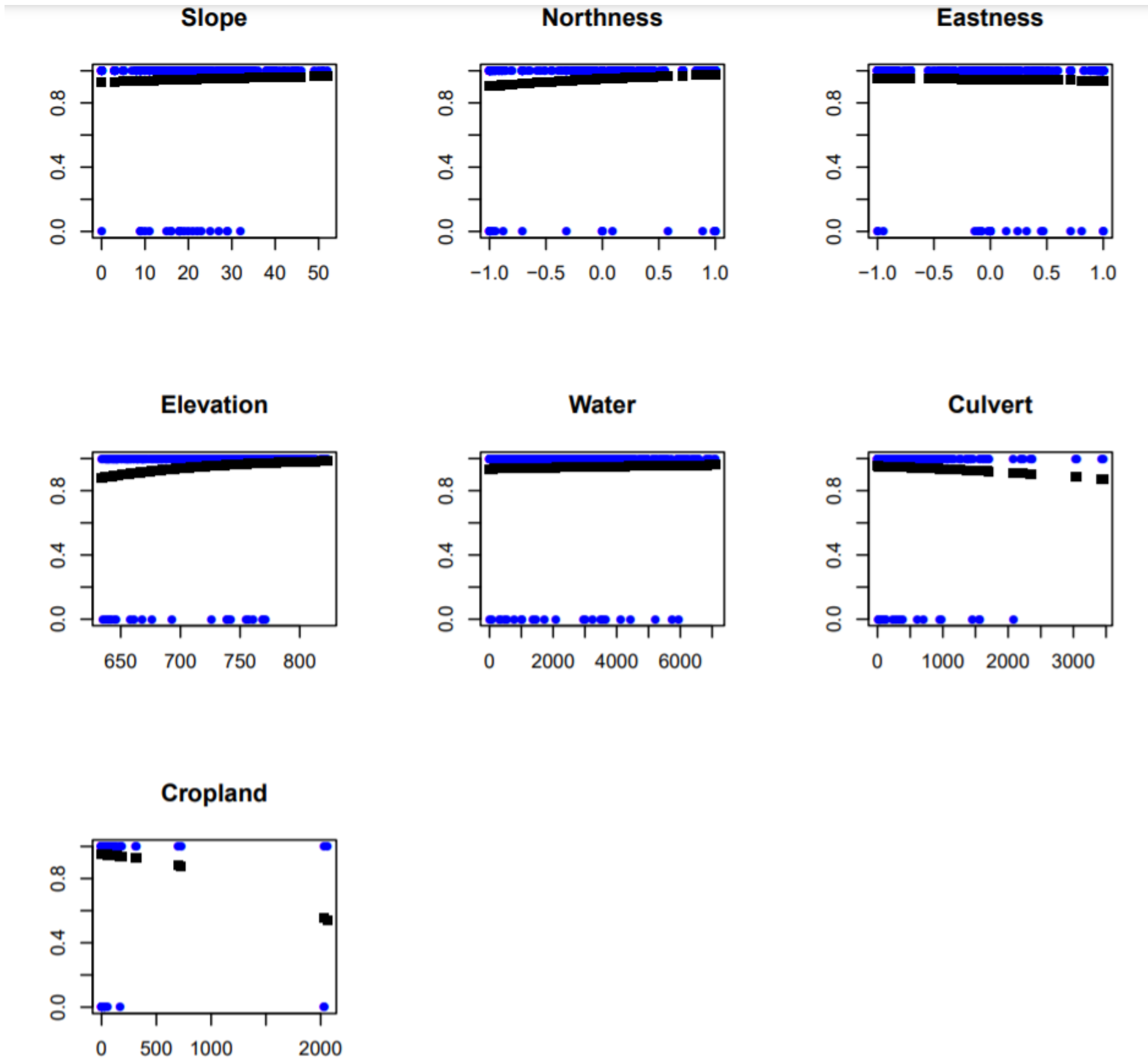
Pastinaca ~ Elevation * Slope + Cropland + Water: AIC= 593.3

Pastinaca ~ Elevation * Slope + Cropland * Water: AIC= 592.3

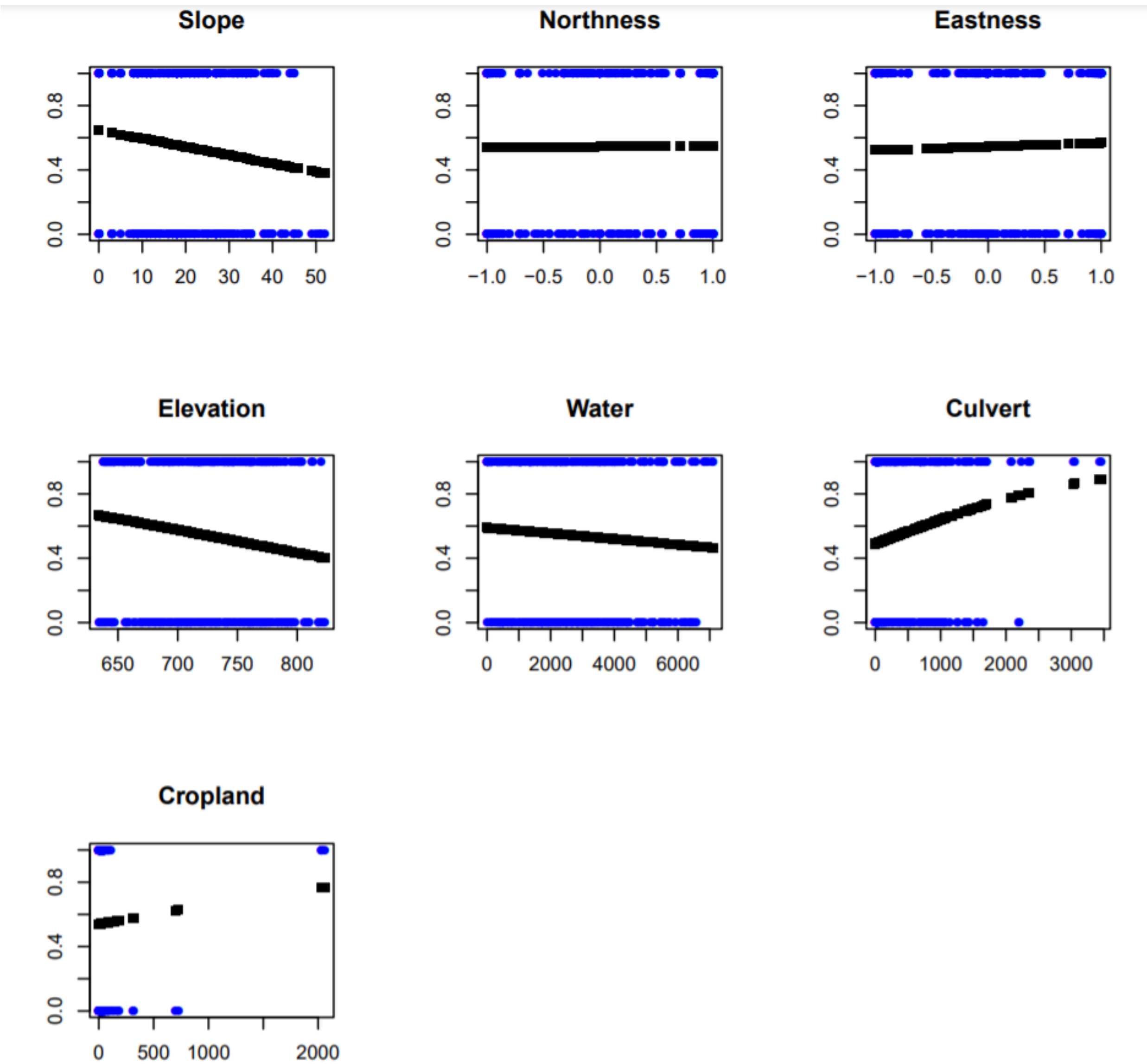
Pastinaca ~ Elevation + Slope + Cropland * Water: AIC= 588.0

Pastinaca ~ Elevation * Water + Cropland + Slope: AIC= 590.7

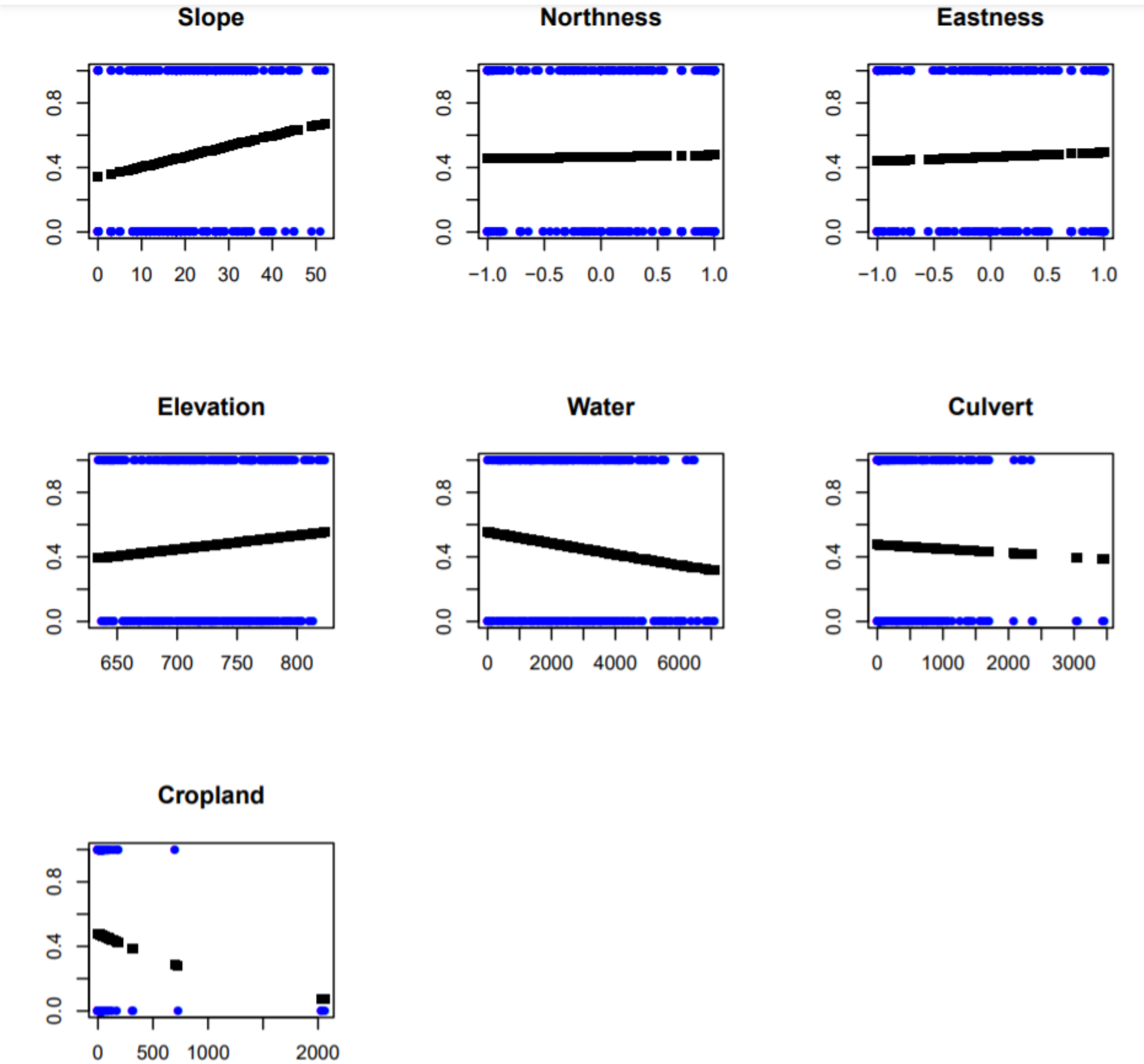
Pastinaca ~ Elevation * Water + Cropland * Slope: AIC= 594.3



Supp Figure 1. Binomial regression of the presence or absence of *Smooth Brome* with the line of best fit for each variable of the study. Northness, elevation, and distance from cropland were determined to be the most important factors in determining presence.



Supp Figure 2. Binomial distributions of the presence or absence of Reed Canary Grass with the line of best fit for each variable of the study.



Supp Figure 3. Binomial distributions of the presence or absence of *Wild Parsnip* with the line of best fit for each variable of the study. Slope, elevation, distance from nearest water source, and distance from nearest cropland were hypothesized to be the most important factors in determining presence.