USING A SPECIES DISTRIBUTION APPROACH TO MODEL HISTORIC CAMAS (*CAMASSIA QUAMASH*) IN SOUTHERN IDAHO AND IMPLICATIONS FOR FORAGING IN THE LATE ARCHAIC

by

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ABSTRACT

Camas (*Camassia quamash*) is well documented as a traditional native food source throughout the Northwestern United States and Canada. A better understanding of the historic distribution of camas in Idaho would help to distinguish root foraging in this region from the Pacific Northwest. Modern grazing, development, climate change, and other factors have decimated native camas in this region. This study uses a species distribution model (MaxEnt) to provide a well-informed geospatial projection of the historic distribution and habitat characteristics of camas in Southern Idaho. Understanding the most significant landscape and climate characteristics for camas allows us to estimate suitable habitats, and therefore the potential influence of camas on human diet breadth and mobility in the Late Archaic.

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CHAPTER ONE: INTRODUCTION

Camas (*Camassia quamash*) has been documented as a traditional food source throughout the Northwest United States and Canada. Camas is a perennial plant with an edible bulb that grows in seasonal wetlands. Research on the Northwest Coast has provided a vast amount of literature about the importance of camas as a traditional food source and the potential for impressive return rates (N. J. Turner et al., 2011; Thoms, 1989; Leach and Osher, 2007; Lepofsky et al., 2005; N. Turner, Deur, and Lepofsky, 2013; Deur and Turner, 2005; Beckwith, 2004; Gritzner, 1994). However, this important food source is relatively unexplored on the Snake River Plain.

Most of the literature on the productivity, bulb size, and return rates of camas are based in the Pacific Northwest (Thoms, 1989; N. J. Turner et al., 2011; Beckwith, 2004). Thoms and Statham note the importance of drainage, soil pH, and patch density but do not quantify the relationship between those variables and camas productivity (Thoms, 1989; Statham, 1982). The data on productivity and return rates of camas from the Northwest would not be applicable to the camas on the Snake River Plain due to the variation of productivity due to environmental variables. If camas productivity is significantly affected by environmental factors such as soil drainage, precipitation, and soil pH, then camas will not be as productive on the Snake River Plain as it is on the Northwest Coast.

The patch choice and prey choice model of Human Behavioral Ecology provide a way of examining resource use through an evolutionary framework. The location, distance, and productivity of patchy resources can have an impact on that resource's ranking in the diet breadth. Due to modern grazing, agricultural development, and climate change the locations of camas habitat has been severely constrained. Species distribution models can provide a better picture as to the habitat range of a species and those environmental variables that could affect its productivity.

Theoretical Background

The Cultural Ecology of Julian Steward aims to provide a level of explanation of human adaptation to the environment (Steward, 1955). Cultural Ecology seeks to accomplish this through three steps: examining the relationship between the environment and technology, analyzing the behavior related to use of the environment, and exploring how those behaviors affect other aspects of culture (Steward, 1955). Steward views the features of the culture related to subsistence and economy as the culture core which is most related to interactions with the environment. Steward argues that this methodology can be used to provide a level of explanation of the relationship between culture and the environment and how they might change (Ibid).

Winterhalder and Smith (2001) state that the early goals of Human Behavioral Ecology "were to set the cultural ecology of Steward… on sounder theoretical footing by allying it to emerging neo-Darwinian approaches to behavior (p. 51)." They outline that HBE derives testable hypotheses based on models developed from the principles of evolution (Ibid), and argue that the goal of HBE models is to strive to be as simple as possible and capture the essence of an adaptive problem (Ibid). These authors state that a complete HBE model combines models of circumstances (how the environment affects costs and benefits) with models of mechanism (how does natural selection acts on those effects) (Ibid).

HBE models are set up to examine opportunity costs and tradeoffs of behaviors by measuring a goal, currency, constraints, and an alternative set of behaviors (Winterhalder and Smith, 2001). The goal of foraging theory is to optimize the acquisition of energy per set amount of time which is generally measured in calories per hour (Ibid). The optimal outcome results in a set of resources that have the highest rate of return for energetic expenditure (Ibid). This set of resources would be optimal for resources that are evenly distributed across the landscape. According to optimal foraging theory, the likelihood that a lower-ranked resource is added to the diet breadth is a result of the availability of higher-ranked resources, not the abundance of the lower-ranked resource (Ibid).

The patch choice model is useful in addressing those resources that are not evenly distributed across the landscape (MacArthur and Pianka, 1966). The patch choice model also looks to optimize the foragers' time spent within a resource patch before moving to a new patch (Ibid). In patchy environments, the distance between patches and the density within the patches is what determines the optimal time spent within each patch (Ibid). In environments where the resources are evenly distributed, if a prey item is already in the diet and becomes scarce it will still be in the diet (Ibid). The same is not true for patches, if the prey within a patch becomes scarce than the patches could drop out of the diet because of the travel time to the patch and not being able to collect enough resources within the patch to outweigh the travel time (Ibid). MacArthur and Pianka (1966) noted that more productive environments lead to specialization and a lower number of different prey species in fine-grained environments, yet patchy environments favor generalists as this reduces the travel time between patches. This is important in the Great Basin and the Snake River Plain.

Winterhalder and Smith (2001) state that HBE models should be used to develop hypotheses to test, rather than directly testing the models themselves. This is an important distinction as the models are not a snapshot of reality. There is often not enough archaeological data to fully test an HBE model.

The usefulness of HBE models in archaeology is through the development of hypotheses rather than testing of the models. Human behavioral ecology is most applicable to understanding why the differences of the environment condition the productivity of camas and how this applies to our understanding of the use of camas on the Snake River Plain in the Late Archaic. This can be seen by the successful application of the use of HBE models in archaeology by Elston and Zeanah (2002) and Plew (2009). In both instances, the authors were able to successfully use HBE models to develop hypotheses that were able to be tested using archaeological evidence. They both demonstrated how lower ranked resource gathering could be embedded into the pursuit of highly ranked prey without a significant negative impact to mobility.

The Study Area

The environment of the Snake River Plain can be characterized as a desert steppe environment with sagebrush and perennial grasses (Omernik, 1987; Davis, 1939). The summers are hot and dry with the winters receiving most of the precipitation (Plew, 2016; Thompson, 1996). This results in a diverse and patchy environment both temporally and spatially. There is a diverse set of animal resources on the Snake River Plain with many species of mammals, birds, and fish. Camas and balsamroot (*Balsamorhiza sagittata*) as two of the more important plant resources (Plew 2016).

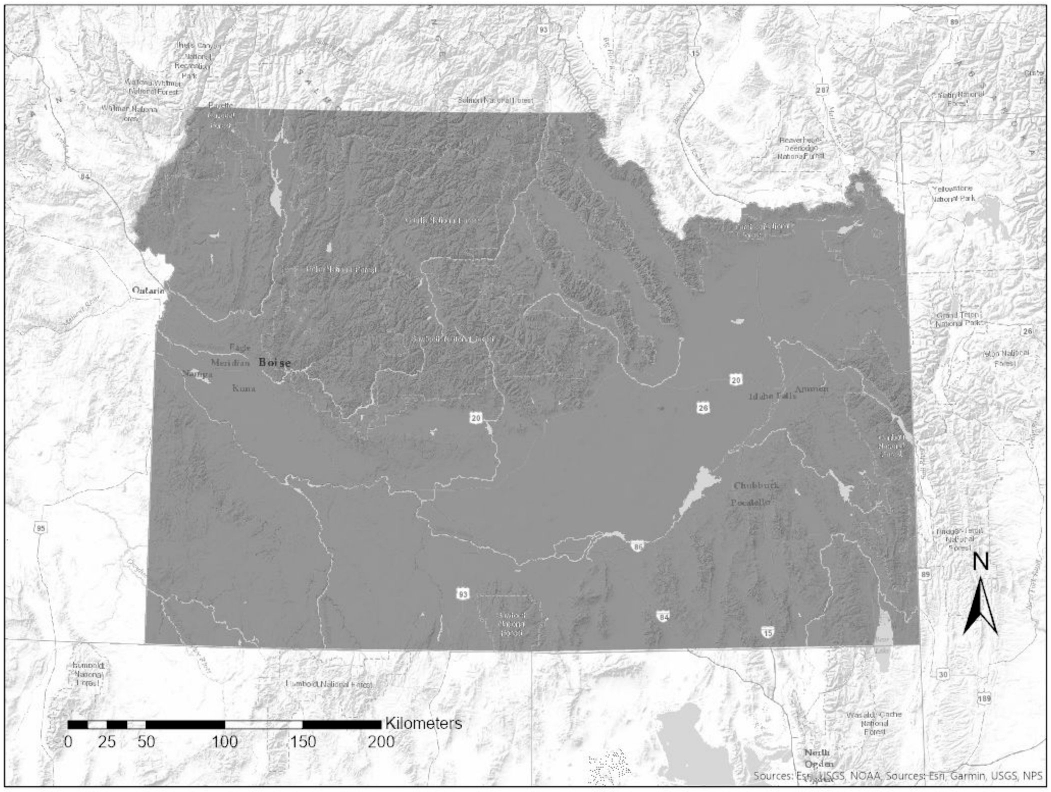

Figure 1. Extent of Study Area (Southern Idaho)

The indigenous peoples of the Snake River Plain were hunters and gatherers who exploited a large number of resources. The Late Archaic period (2000-250 B.P.) is characterized by logistical foraging task groups and seasonal rounds, with three major site types as identified by Plew on the Snake River Plain: field camps, harvesting locations, and processing locations (Plew, 2016). The Late Archaic Period saw an intensification of resources with an increase use of plant and aquatic resources (Plew, 2009; 2016).

Murphy and Murphy (1960) and Steward (1938) provide the main ethnographic account of Native American peoples on the Snake River Plain. They describe a focus on salmon runs in the spring and fall along the Snake River, gathering of camas and other roots in the summer in the uplands, and reliance on stored food in the winter. The description of the reliance on salmon has been called into question (Plew, 1990; Gould and Plew, 1996; Plew, 1983). However, the ethnographic descriptions provide some information on the method of preparation of camas and the importance of hunting. Camas was prepared through boiling in clay pots, which differs from the large pit oven cooking method described on the Northwest Coast. Both ethnographies mention the importance of hunting ungulates in conjunction with the gathering of camas.

CHAPTER TWO: PREVIOUS RESEARCH

Geophyte Use in Cool Arid Environments

Research throughout the wider Great Basin and Pacific Northwest on geophyte use by hunters and gatherers can provide reference information for the use of camas in Southern Idaho. There is generally little evidence of the direct use of geophytes in the archaeological record even though it makes up an important part of the expected diet breadth (Herzog and Lawlor, 2016; Scholze, 2010; Smith and McNees, 2005). Geophyte use in prehistory is generally inferred through reference information from ethnobiology, ethnography, and optimal foraging models (Scholze, 2010).

Great Basin and Pacific Northwest

Simms (1985) uses optimal foraging theory to examine the diet of hunter gatherers within the Great Basin. To do this he outlines the processing costs and nutritional data of plant and animal resources to establish a return rate of calories per hour. Sims used these results to rank resources and make some simple predictions of resource exploitation. Based on his ranking, he notes that large game should be taken when encountered as they are the highest-ranking resources. On examination of the plant resources, he states that seed resources should be included in the diet breadth as they are ranked very low - but he does not address the use of roots.

Elston and Zeanah (2002) examine the structure of the environment, the diet breadth, and substance patterns of hunter gatherers in the Great Basin during the Early Holocene. Their work follows the work of Simms (1985) in an effort to explain low ranked resource acquisition that appears to not fit into the optimal diet breadth. They use the diet breadth model of Simms (1985), patch choice model, and an understanding of the different environment and resource structure of the Early Holocene to argue that an abundance of wetlands in the Early Holocene allowed for high mobility that maximized big game hunting while gathering lower-ranked plant resources, including geophytes, that could be embedded into their mobility without having to make the tradeoff between highly mobile prey and patches of plant resources (Elston and Zeanah, 2002).

Smith and McNees (2005) examined biscuitroot (*Cymopterus bulbosus)* in the Green River Basin in Wyoming. They analyze patch size, density, and nutritional information to develop return rates for the geophyte and how it relates to other resources in the diet breadth as modeled by Simms (1984). They argue that biscuitroot is ranked high enough that it could have affected the camp locations of prehistoric hunter gatherers (Smith and McNees, 2005).

Anderson (1997) examines the relationship between humans and geophytes through selective harvest, burning, and tillage. She examines the exploitation of geophytes in California by foragers and how harvesting geophytes can have a positive impact on their growth and reproduction. She argues that the relationship between geophytes and foragers can be better understood through three areas, ethnobotanical studies, observational studies of the resource, and greenhouse and field experiments (Anderson, 1997).

Research on camas has been conducted through ethnobotanical studies (Leach and Osher, 2007; N. J. Turner et al., 2011; Kuhnlein and Turner, 1991; Beckwith, 2004). Observational studies have shown an interesting relationship between ungulates and camas in which grazing negatively impacts camas bulb size (Gonzales and Arcese 2008), and field experiments that examine the relationship with fire and tillage to camas productivity (Stucki, 2018; Beckwith, 2004; Storm and Shebitz, 2006; Proctor, 2013).

Research into camas productivity, density, and habitat characteristics has been primarily conducted in the Pacific Northwest. Thoms (1989) represents one of the most comprehensive studies conducted with camas in the Northwest (Thoms, 1989). He observed that although the camas fields appear flat there is some relief to the ground. The higher portions tend to dry out faster and produce shorter bulbs while the lower reliefs retain more moisture and produce taller plants (Ibid). Thoms found that the highest density of camas occurred in the lower relief areas (Ibid). This suggests that there is a relationship between the drainage (soil moisture) and density of camas.

Thoms also found a correlation between the age and depth of the camas bulbs. He notes that harvesting camas bulbs is laborious, made more difficult by harder soil and deeper bulbs (Thoms, 1989). Harvesting bulbs could serve to break up the soil making subsequent harvests easier and reducing the number of older, deeper bulbs. These factors could influence the productivity of harvesting camas rather than having a positive effect on growth and reproduction. Thoms argues that the most efficient way to harvest camas would be to target bulbs of moderate size and depth before the soil has completely dried out allowing for an extended harvest period. This could facilitate different harvest times at different patches of varying elevation as some would dry out sooner than others (N. J. Turner, Deur, and Mellott, 2011). Further examination is needed of the effects of drainage both on the bulb size and density. and also harvesting rates.

Thoms found that the plant density of camas in the Clearwater Mountains of Northern Idaho was high relative to those of the surrounding states (Thoms, 1989). The density varied in locations in different states, from the lowest in Washington at 84 plants per square meter up to 410 plants per square meter in Northern Idaho and up to 928 plants per square meter in an artificially managed garden setting. The density measures collected in Northern Idaho represent a small area of 0.25 square meters. Thoms notes that this might not be representative of the density of the entire patch, and these are estimated from a relatively small sample size. He defines a typically productive camas meadow to be 300 bulbs per square meter (Thoms, 1989).

Idaho and the Snake River Plain

Statham (1982) examined some of the ecological factors of camas on the Snake River Plain, noting that the majority of camas in Southern Idaho grows between 5,000 and 7,000 feet in flat valleys that are wet for at least part of the year. Camas grows predominantly in rich mollisols with low clay content (Ibid). Statham notes that the soil's clay content would affect water drainage at camas locations but that the relationship between drainage and camas needs further examination. Statham also found that a relationship between soil pH, bulb size, and the color of the camas flower: that more acidic soils produce smaller bulb size, while the largest bulb size occurred in the more neutral soils. There was a loose relationship between the color of the camas flower and the pH of the soil, with the color of the flower changing from purple to blue before neutral pH values. Statham does note that the pH values were not collected in the field and that field study could provide more information on this relationship. This relationship could provide a visual indication of the size of the camas bulbs.

Plew (1992) examined the nutritional composition of camas in Southern Idaho. He harvested camas from three separate locations to provide nutritional information for camas in relation to Statham's (1982) work in identifying the importance of drainage and soil pH on the distribution, density, and bulb size of camas. Plew's work further suggests a significant relationship between camas density and bulb size to soil pH and drainage. His findings suggest that camas density is higher in better drained soils and more neutral pH. As noted by Plew, this could produce selective use of camas patches, focusing on those that are more productive. These factors are important in our understanding of the diet breadth and the use of camas.

Camas reproduces both through seeds and offsets of bulbs, which Thoms notes makes it well adapted to exploitation (Thoms, 1989). An additional study done in Idaho by Stucki (2018) examined the effects of harvesting and burning on the productivity of camas. Stucki notes that drainage and landscape hydrology are a likely control for camas density but does not explore this relationship further. An experiment was performed to test the effects of both harvesting and burning, both together and separately. Other variables were controlled with plots of camas being the same density and soil characteristics (Stucki, 2018).

Stucki found that after the first year, the plots where harvesting occurred were shown to have a reduction in density of camas. The same occurred in the plots that were both harvested and burned. Stucki notes that a further examination would be needed after three years. This is due to camas's maturation of 3 to 5 years and the ability of camas to lay dormant underground for long periods of time (Thoms, 1989). The positive effects of both traditional harvesting and burning are based on accounts from the Northwest Coast and might not be applicable to habitats of the Snake River Plain.

Plew (2009) examines the faunal record on the Snake River Plain using foraging theory to look at shifts in subsistence throughout the Early, Middle, and Late Archaic period. Plew looks at the frequency of highly ranked prey in relation to the changing environmental conditions and their relationship to low ranked, small-bodied prey species. Plew concludes that the increase in encounter rates of large-bodied prey in the Late Archaic could be due to an increase of aridity and the congregation of prey around water. Also, he notes that there is an increase in the abundance and ubiquity of salmon and fish remains in the Late Archaic, argued to be a result of the increased use of riverine settings (Plew, 2009).

It is possible that hunter gatherers were drawn to the animals that like to eat camas rather than camas itself. There are references in the plant and gardening literature that ungulates like to eat camas ("Native Plant: Common Camas | Beaverton, OR - Official Website" n.d.; Anne G. Andreu n.d.; Stevens et al. n.d.). A study in British Columbia found that a moderate ungulate population had a significant negative effect on the bulb size camas. They found that those camas patches protected from grazing had bulb sizes three times larger (Gonzales and Arcese, 2008). This effect could reduce the return rates of camas harvesting causing a reduction in importance in the diet breadth, while a reduction in the population of ungulates could cause the return rates of camas to increase.

Plew (2009) argues that artiodactyl populations aggregating near water would be a draw by hunters and gatherers to these high ranked resources based on the prey choice mode. This would also create a situation in which broadening of the diet breadth to include aquatic resources would be beneficial. This approach could also be used to examine the increased presence of camas in the Late Archaic. Highly ranked prey (artiodactyls) are drawn to camas patches that would provide an attraction for hunter gatherers and a broadening of the diet breadth to include geophytes. This is similar to the addition of aquatic resources with highly ranked prey drawn to riverine settings.

Plew (1990) modeled three alternative winter subsistence strategies for the Snake River Plain. The first strategy is a riverine resource-focused subsistence strategy. Riverine focused subsistence groups did not travel far from the river and were able to focus on the exploitation of aquatic resources. The second strategy is seasonally mobile hunter gatherers that focus on resources that have an extended harvest window; those resources with a high processing cost and short harvesting windows would not be optimal. They would focus on stored roots rather than salmon. The third strategy is mobile groups that focused on large game during winter months and not the storage of salmon or roots. This third strategy has a low acquisition cost but high risk. Plew (1990) was able to make a prediction based on the costs and return rates of the various resources, large body prey, root crops, and salmon. He demonstrated that, based on the availability and return rates that salmon focused diet is not optimal but rather the low acquisition costs make root crops a more desirable resource with continued focus on continued hunting (Plew, 1990).

Summary

The overview of the literature of camas and geophyte used by hunter gatherers has demonstrated the usefulness of some of the models from Human Behavioral Ecology to our understanding of their use by hunter gatherers in prehistory. This is especially useful reference information with a general lack of direct evidence for their use in the archaeological record.

Different environmental conditions have been shown to affect the currencies in the HBE models. Soil type, pH, drainage, elevation, temperature, and moisture have all been demonstrated to affect distribution, density, and bulb size of camas. Changes in the distribution, density, and bulb size can affect the ranking within the diet breadth and how long a forager will stay within a particular patch. Hunter gatherers were able to forage longer in patches with higher density and larger bulb sizes.

The understanding of these Human Behavioral Ecology models can be used to develop hypotheses about the use of camas in prehistory. According to optimal foraging theory, highly ranked prey items will always be taken upon encounter with the addition of lower-ranked resources into the diet breadth until the optimal average return rate is reached. Large bodied prey animals would be a focus of mobile hunter gatherers. As Plew (1990, 2009) has demonstrated this through his work in Southern Idaho, boiling camas rather than roasting in a pit oven significantly reduces the processing costs of camas but the effects of boiling on nutritional value are not yet known. With a lowering of the processing costs by boiling rather than roasting, camas would have a higher ranking for a more mobile hunter-gather population.

The literature review has identified two possible strategies for the exploitation of camas. The first is intensive harvesting meant to maximize the returns of camas. This is accomplished through harvesting at the optimal time right after flowering, bulk harvesting and roasting, and management of camas fields through tillage and burning to increase the yield that limits mobility, as seen in the Northwest coast. The second is an embedded strategy of camas exploitation. This is accomplished through including camas as part of a suite of targeted resources, boiling camas to reduce processing time, and exploitation through the extended harvest window of several months. This negates the need to collect and process camas in bulk so that the benefits will outweigh the processing costs. The second strategy does not heavily limit mobility but rather could be embedded into the exploitation of large game based on our knowledge that large-bodied prey species are also drawn to camas fields. The Human Behavioral Ecology models are useful in generating a hypothesis to explore these two alternative strategies of camas subsistence. If hunter gatherers are highly mobile and focused on highly ranked large-bodied prey then we can expect an embedded strategy of camas gathering, except under conditions where the benefits for intensive camas exploitation outweighs the cost of reduced mobility. Understanding how changing environmental variables affect the productivity of camas is important to our understanding of its inclusion into the diet breadth. A geospatial approach can show how these environmental changes could affect the spatial and temporal changes in the exploitation of different camas patches. The destruction of camas habitat makes species distribution modeling important in our understanding of the distribution of camas patches on the landscape and how this can affect the mobility of hunter gatherers.

CHAPTER THREE: METHODS

Species distribution modeling is especially useful for species like camas, where the habitat has been constrained or reduced. MaxEnt (Maximum Entropy) is a niche-based model of species distribution that uses known locations of a species and environmental variables to produce an estimation of the habitat suitability (Phillips and Schapire, 2004). MaxEnt compares probability densities using a suite of covariates attempting to reduce the relative entropy between two sets of probability densities. MaxEnt aims to make a prediction of the probability of species distribution from incomplete information. This method of species distribution modeling is valuable because it uses presence-only data and does not require absence data that is used in more standard statistical methods and is resistant to the issues of overfitting and correlation between variables (Phillips, Anderson, and Schapire, 2006; Elith et al., 2011).

There have been two instances of MaxEnt being used to model the species distribution of camas in other areas. Elliot (2013) used MaxEnt to model the species distribution of camas across the state of Oregon, using only precipitation and maximum temperature and attempting to improve the model by adding in the cultural environment. Ingegno (2017) used MaxEnt to model the distribution of camas and other rare plant species in the Blackfoot-Swan Landscape Restoration Project. She used a wider suite of variables but noted that there was no access to soil survey data in the area for analysis.

The occurrence data of camas used in this study was obtained from the Consortium of Pacific Northwest Herbaria (CPNWH, 2020). The CPNWH compiles and digitizes specimen records from the Pacific Northwest over a long period of time. Many of these older records have unreliable estimated location or no location information attached, and must be filtered. The specimen records for *Camassia quamash* were downloaded and clipped to the geographic area of interest. The data was then filtered to remove those records with unreliable or missing data and redundant entries. Records with missing location information or location uncertainty greater than 800m were removed. Phillips et al. (2006) note that the temporal and geographic scale of the variables should match. Due to the temporal properties of the environmental variables, only those records collected in the last 50 years were used. After filtering the occurrence data, 89 records were used in this model (Figure 2).

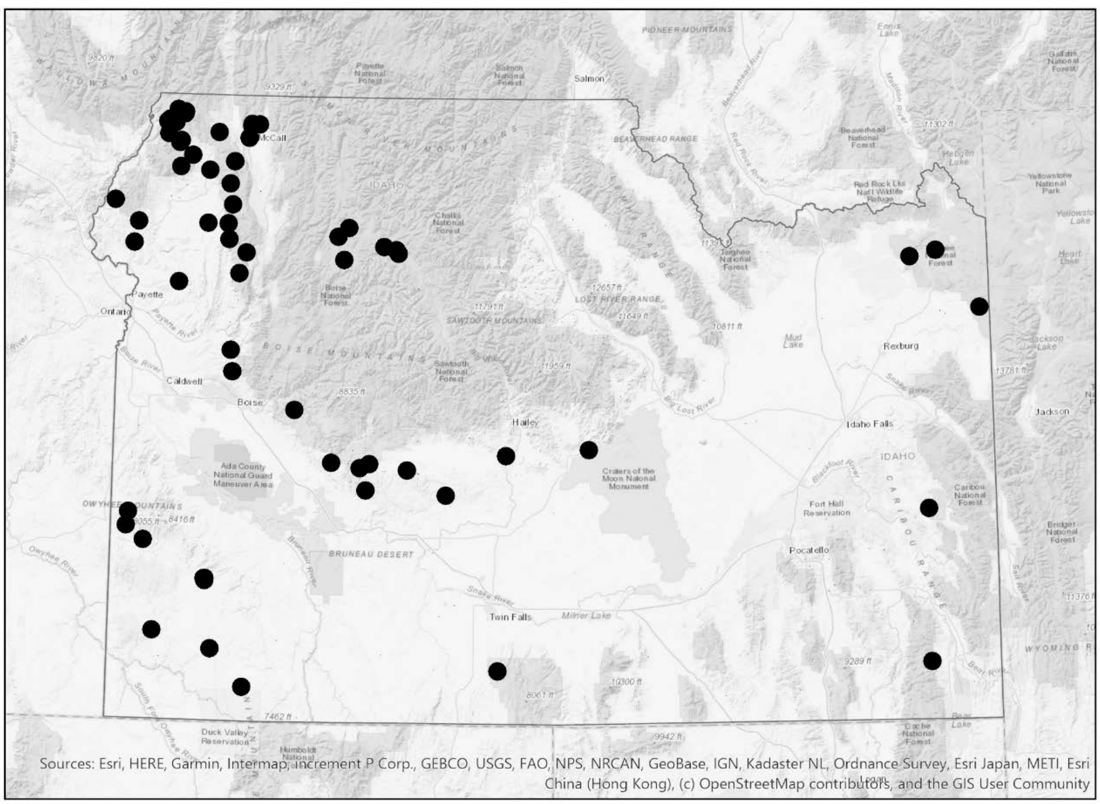

Figure 2. Location of Known Camas Locations Used in the Study

Selection of the environmental variables used in MaxEnt must be chosen based on information about the ecology of the species (Feng et al., 2019). Based on this information the environmental variables chosen for this model are based on relevant ecological factors identified in the literature review. These include topographic variables (elevation, slope, and aspect), climatic variables (precipitation), and soil characteristics (soil composition, pH, and drainage). The environmental variables were prepared for MaxEnt using ArcGIS. Each of the variables was converted to equalize the extent and raster cell size in the same geographical projection.

Table 1. Environmental Variables Used in Camas Distribution Modelling

Variable	Data Type	Resolution or Scale	Measurement	Source
Elevation (DEM)	Raster	30m	Meters	National Elevation Dataset
Slope	Raster	30m	Degrees	Calculated from DEM
Aspect	Raster	30m	Degrees	Calculated from DEM
Precipitation	Raster	800m	Millimeters per Year	PRISM Climate Group
Clay	Vector	1:250,000	Percetage by Weight	STATSGO2
Sand	Vector	1:250,000	Percetage by Weight	STATSGO2
Silt	Vector	1:250,000	Percetage by Weight	STATSGO2
Organic Matter	Vector	1:250,000	Percetage by Weight	STATSGO2
pH	Vector	1:250,000	pH scale	STATSGO2
Kstat	Vector	1:250,000	micrometers per second	STATSGO2

The general practice for statistical models is to use variables that are not highly correlated. However, MaxEnt has been demonstrated to be robust against the effects of collinearity among the environmental variables (Feng et al., 2019). Highly correlated variables can show an over-importance in statistical analysis because the researcher is unable to separate the effects of one variable from the other. Environmental variables should be chosen based on their relevance and not necessarily removed due to collinearity due to environmental variables' tendency to be correlated (Feng et al., 2019; Dormann et al., 2013). However, the issue of collinearity among variables is still addressed. General practice in statistics is to remove those variables that are correlated greater than 0.7 (Feng et al., 2019). Band statistical analysis was used in ArcGIS to create a correlation matrix (Table 2). There were only three variables with a correlation greater than 0.7. Silt and clay were highly negatively correlated (-0.91155). Among those correlated variables the only one removed from the model was silt, as the other two soil composition variables, clay and sand, can still provide a measurement for silt.

Table 2. Correlation Matrix of Environmental Variables

	Silt	Sand	Clay	Precipitation	Elevation	Slope	Aspect	Kstat	pH	Organic Matter
Silt	1									
Sand	-0.91155	1								
Clay	0.20931	-0.58461	1							
Precipitation	-0.25058	0.2582	-0.11638	1						
Elevation	-0.14194	0.1423	-0.0535	0.673	1					
Slope	-0.28883	0.27733	-0.09577	0.6111	0.55393	1				
Aspect	0.00827	0.00059	-0.01907	0.01949	-0.01817	0.01421	1			
Kstat	-0.64781	0.81536	-0.69478	0.24131	0.10772	0.19361	0.01572	1		
pH	0.36137	-0.30929	0.04749	-0.72759	-0.42813	-0.5046	-0.02492	-0.31048	1	
Organic Matter	0.13254	-0.19239	0.20765	0.41081	0.30397	0.22916	0.01115	-0.21279	-0.40313	1

The topographic data used in the model are elevation, slope, and aspect. The National Elevation Dataset was used to obtain the 30-meter DEM (digital elevation model) raster for Idaho measured in meters above sea level (USGS, 1999). This raster was clipped to the study area of Southern Idaho and re-projected in the Idaho NAD 1983 TM projection. Slope and aspect were both calculated in ArcGIS using this elevation raster. Slope is a measure of the steepness of the terrain measured in degrees. Aspect is a measure of the direction the slope is facing, measured in degrees.

The only climatic data used in the model was precipitation. This is due to the resolution of the precipitation data fitting our study area. Temperature is at a broader scale and would be a useful variable with a slightly larger study area. The precipitation raster was obtained from the PRISM Climate Group as a long-term average dataset for a 30-year period (1981-2010) at an 800m resolution (PRISM, 2020). The precipitation raster is a 30-year average of precipitation values measured in inches per year. The raster was resampled to a 30m resolution, projected in the Idaho NAD 1983 TM projection, and clipped to the study area.

The soil data used in the model were clay content, sand content, organic matter content, soil pH, and saturated hydraulic conductivity (Kstat). The soil variables were obtained from the Digital General Soil Map of the United States (Soil Survey Staff, 2020) at 1:250,000 scale. These soil data were extracted from the STATSGO2 database as a vector format that was then converted to a raster format at 30m cell size. The data layers were extracted from the database using the representative value as weighted averages for all layers and each map unit. Clay content is measured as a percentage by weight of soil particles less than 0.002 mm in diameter. Sand content is measured as a percentage by weight of soil particles from 0.05 mm to 2 mm in diameter. Organic matter measures the available organic matter in the soil as a percentage by weight of soil less than 2 mm in diameter. Soil pH is a measure of acidity or alkalinity using the 1:1 water method. Saturated hydraulic conductivity (Kstat) is a measure of how water moves through the soil, in micrometers per second.

MaxEnt requires that each of the environmental layers has the same extent, raster cell size, and projection in the ASC file format. Each of the environmental layers was clipped to the same extent, resampled at 30 m resolution, and projected in the Idaho NAD 1983 TM projection. The MaxEnt software is a stand-alone package that uses the occurrence points and environmental layer data to perform the analysis (MaxEnt, Version 3.4.1). The following settings were chosen when running the analysis based on the literature review, regularization multiplier of 1 (a measure of how the model fits the data), random seed (a different random seed used for each run), random test percentage of 25% (percentage of presence points to be set aside as test percentage), and 10 replicate runs using the bootstrap method. Unless otherwise stated, the default settings were used.

CHAPTER FOUR: RESULTS

The main indicator of the accuracy of the model is measured by the receiver operating characteristic area under the curve (ROC AUC). This number measures how accurately the model predicted presence and absence. The mean AUC for the replicate runs is 0.950 with a standard deviation of 0.008 (Figure 3). A model with an AUC of 0.5, represented as the black line in figure 1, is a random prediction. A model with a perfect prediction would have an AUC of 1. Because the model only uses presence data and does not have absence data to test against the model, it is viewed in its usefulness and not its correctness (Pearson, 2007). An AUC above 0.9 is considered to be very good (Swets, 1988). Those species that have more narrowly defined habitat characteristics will generally have a higher AUC than those with a wide range of habitat characteristics.

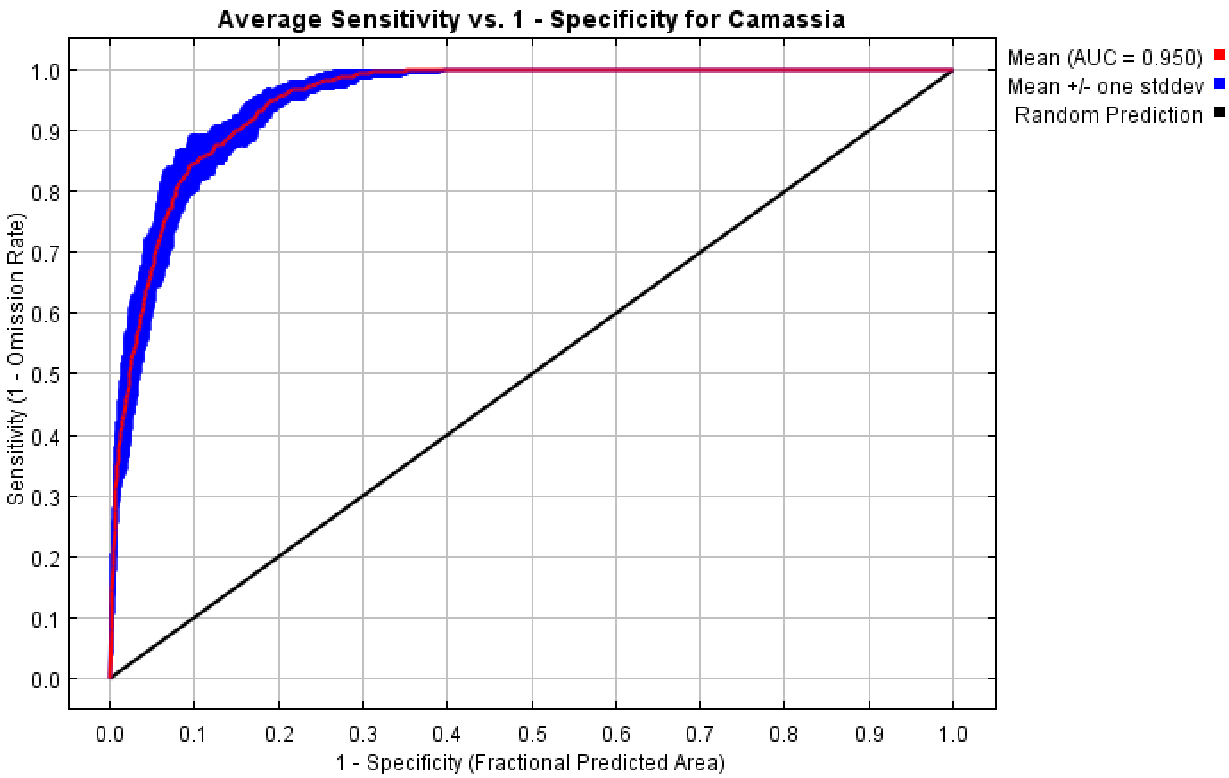

Figure 3. AUC Curve for Camas

The variable that was the highest percentage contribution to the model of camas habitat was soil pH, which has a 30.7% contribution but had a very little drop in the model's AUC when removed from the model (4.9% permutation). This suggests that the soil pH is the most useful variable by itself, but the information may be contained in other variables due to its low permutation importance. Elevation and precipitation both had the next highest percent contribution with 17.2% and 17.3% respectively. These two variables had the highest permutation importance which suggests that they have the most useful information that is not present in other variables. The reason that these two variables have a similar percent contribution and higher permutation importance could be due to the slight correlation between these two variables. Saturated hydraulic conductivity (Kstat) has a very low percent contribution (1.5%) and permutation importance (3%). It is possible that soil texture (sand and clay) provides a better representation of drainage than saturated hydraulic conductivity.

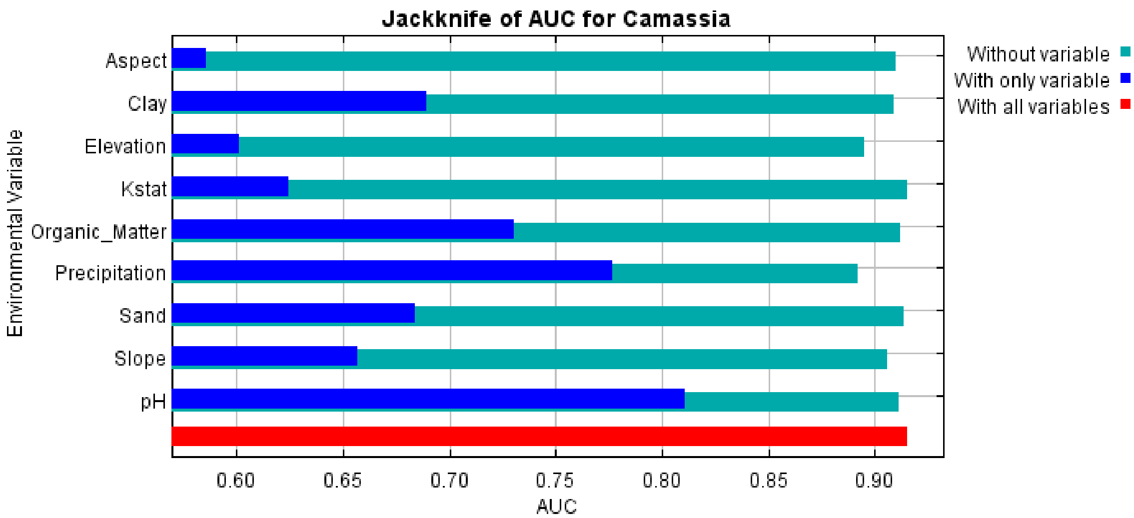

Figure 4. Jackknife Test of Individual Environmental Variable Importance

MaxEnt provides a jacknife for each variable showing the importance of the individual variable to the model and how much the model's AUC decreases when the model is removed. This controls for highly corelated variables in the model. The variable that had the highest contribution to the model was soil pH. The variable that reduced the AUC the most when removed from the model was precipitation, suggesting that this variable has the most information for the model that is not explained by the other variables. Aspect had the least importance and the least effect on the AUC when removed from the model.

The variable response curves show how each environment variable affects the model. The graphs show the probability of presence as the variable changes while keeping the other variable at their average value. These figures can help show the ideal values for each of the variables in the model. Soil pH shows a high peak at 6.5 pH dropping off significantly on either side. Precipitation shows a definite peak at 700 mm per year. Elevation shows the majority of the values falling between 1000 to 2000 feet above sea level. Slope shows the peak at 5-degree slope with the values falling off sharply with an increase in slope. Aspect shows a relatively flat curve only dropping on after 250-degree and before 50-degree aspect, the north-facing slopes. The clay percentage peaks at 28% and the sand percentage peaks at 38%. From those two values, we could estimate the silt percentage to be 34%. The makeup of the soil according to the soil texture triangle is a clay loam with a 2% organic matter (Groenendyk et al., 2015). Finally, the saturated hydraulic conductivity is not well represented as a curve but with a sharp peak at a very low value of approximately 5. It is possible that due to the relatively low contribution of saturated hydraulic conductivity that it is not a good measure for this model, but drainage might be better viewed by the soil texture characteristics.

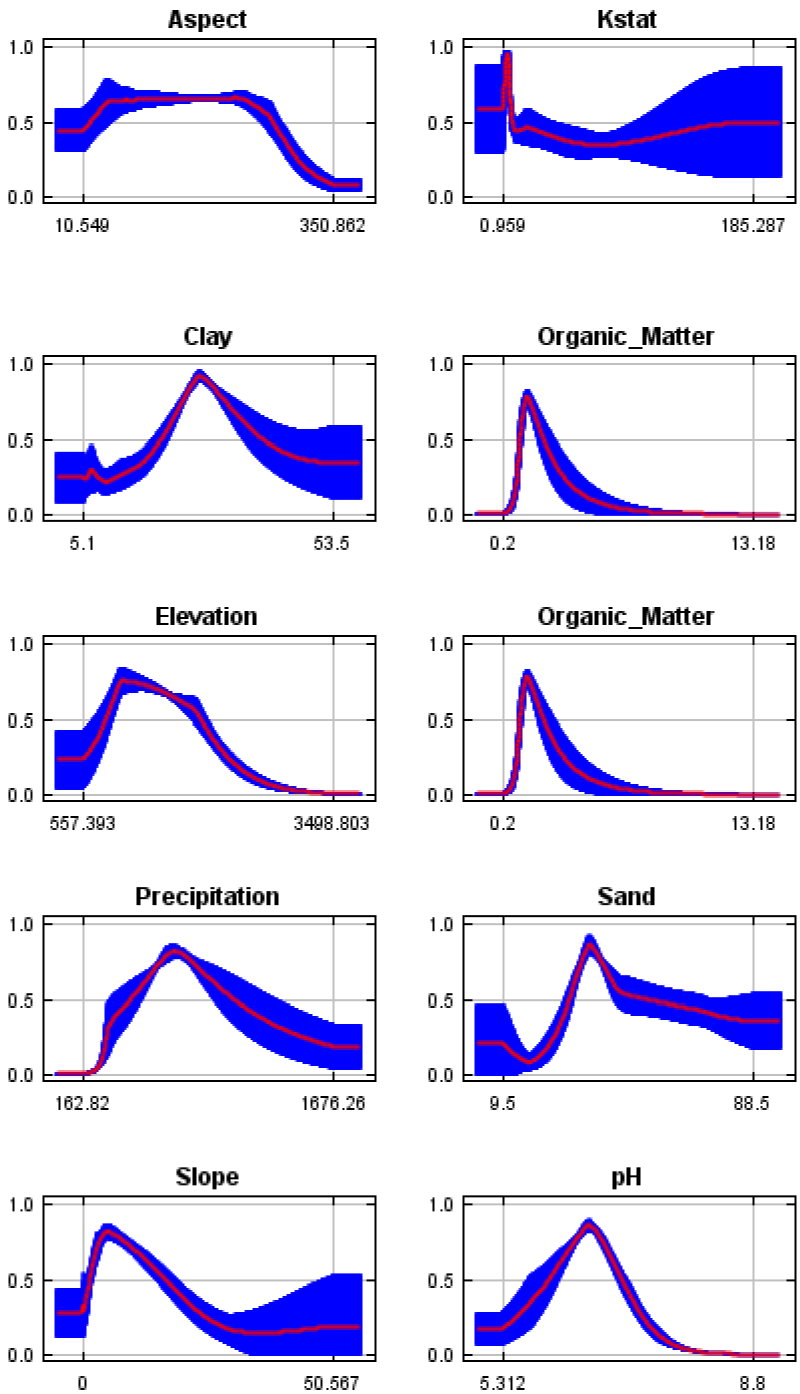

Figure 5. - 11. Variable Response Curves for the Model

MaxEnt's last product is a raster image of the model, applied to the study area. In this raster, those values close to 1 are a higher probability of camas. This can be seen by the red areas on the map (Figure 12) as good camas habitat (> 0.9). There is a large amount of good camas habitat in the uplands to the North and South of the Snake River in the Western half of Southern Idaho. There is much less camas habitat in the Eastern half of Southern Idaho with almost a total absence on the Snake River Plain itself.

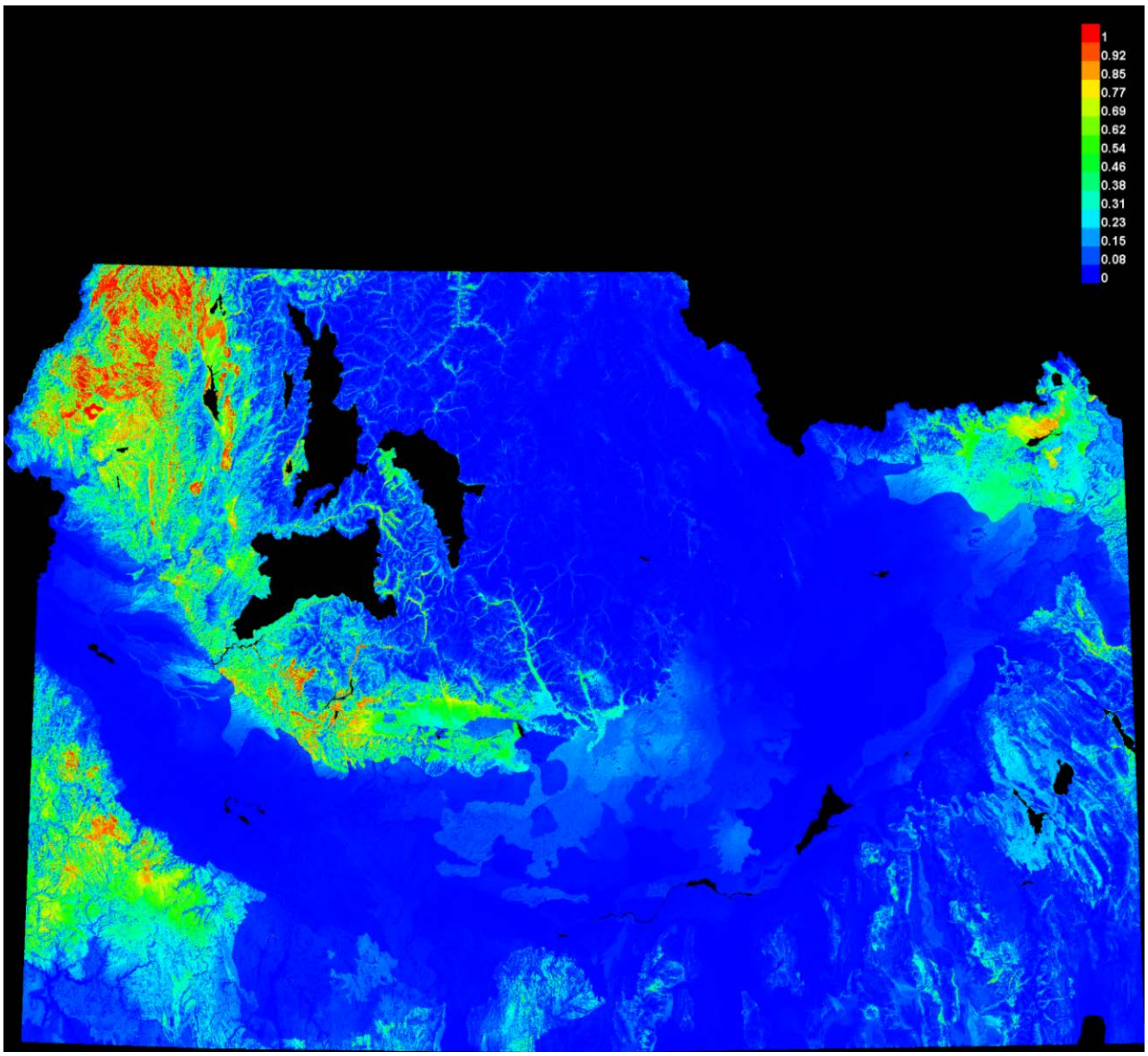

Figure 12. Camas Habitat

CHAPTER FIVE: DISCUSSION AND CONCLUSION

The overview of the literature of camas and geophytes has demonstrated the usefulness of some of the models from Human Behavioral Ecology toward understanding their use by hunter gatherers in prehistory. This is especially useful reference information given a general lack of direct evidence for their use in the archaeological record. The increase in aridity during the Late Archaic in Idaho constrained camas distributions and concentrated large-bodied prey.

Different environmental conditions have been shown to affect the currencies in the HBE models. Soil type, pH, drainage, elevation, temperature, moisture have all been demonstrated to affect distribution, density, and bulb size of camas. Changes in the distribution, density, and bulb size can affect the ranking within the diet breadth and how long a forager will stay within a particular patch. Using our understanding of the workings of these Human Behavioral Ecology models we can develop hypotheses about the use of camas in prehistory and the conditions for which it can be included into the diet breadth without negatively impacting large-bodied prey exploitation.

Optimal foraging theory has demonstrated that highly ranked prey items will always be taken upon encounter with the addition of lower-ranked resources into the diet breadth until the optimal average return rate is reached. Large bodied prey animals would be a focus of mobile hunter gatherers. As Plew (1990, 2009) has demonstrated this through his work in Southern Idaho, boiling camas rather than roasting in a pit oven significantly changes the processing costs of camas. With a lowering of the processing costs by boiling rather than roasting, camas would have a higher ranking for a more mobile hunter-gather population.

The results of the MaxEnt species distribution model has demonstrated the relationship that camas has with environmental variables. Soil pH, precipitation, and elevation are all important variables identified in the model. There is a correlation between these three environmental variables. Elevation has an effect on precipitation, with higher elevations receiving more precipitation. Precipitation has an effect on soil pH with more precipitation lowering the soil pH. Precipitation is the variable with the most temporal variability. As annual precipitation decreases it reduces and constrains the available camas habitat moving it to higher elevations. As precipitation increases it would increase the available camas habitat, causing to be more dispersed on the landscape.

Based on the literature review and the results of the species distribution model, two possible strategies for the exploitation of camas have been identified. The first is intensive bulk harvesting and processing meant to maximize the returns of camas. This is accomplished through harvesting at the optimal time right after flowering, bulk harvesting and roasting, and management of camas fields through tillage and burning to increase the yield that limits mobility. The second is an embedded strategy of camas exploitation, accomplished through boiling camas to reduce processing time and the exploitation through the extended harvest window of several months. This negates the need to collect and process camas in bulk so that the benefits will outweigh the processing costs. The second strategy does not heavily limit mobility but rather could be embedded into the exploitation of large game based on our knowledge that large-bodied prey species are also drawn to camas fields. The Human Behavioral Ecology models are useful in generating a hypothesis to explore these two alternative strategies of camas subsistence. If hunter gatherers are highly mobile and focused on highly ranked large-bodied prey then we can expect an embedded strategy of camas gathering, except when the benefits for intensive camas exploitation outweigh the cost of reduced mobility.

These results would have implications for the distribution and composition of archaeological sites in Southern Idaho. With focus on large body size prey embedded with camas exploitation one could expect to find an increased concentration of archaeological sites around these productive camas patches with evidence of an increase in both camas and large-bodied prey exploitation during the Late Archaic. Higher aridity in the Late Archaic would constrain the available camas habitat and concentrate large-bodied prey. This would result in seasonal rounds with more established archaeological sites and multiple occupations as resources are not as widely distributed across the landscape.

The results of this research have opened up other avenues of inquiry about the use of camas in Southern Idaho. First would be to explore how the important variables identified in the MaxEnt model influence measures of productivity like patch density and bulb size. A smaller scale examination of the relationship between camas distribution, ungulate ranges, and archaeological sites could further our understanding on the mobility of hunter gatherers in Southern Idaho. It would be useful to explore the results of a species distribution model of camas in surrounding regions using the same variables. Differences in the results could speak to how camas is exploited using different strategies. The destruction of camas habitat and the loss of wetlands makes camas restoration projects important. Finally, projecting camas distributions in to changing climate conditions could help facilitate camas restoration projects and prepare for future climate change.

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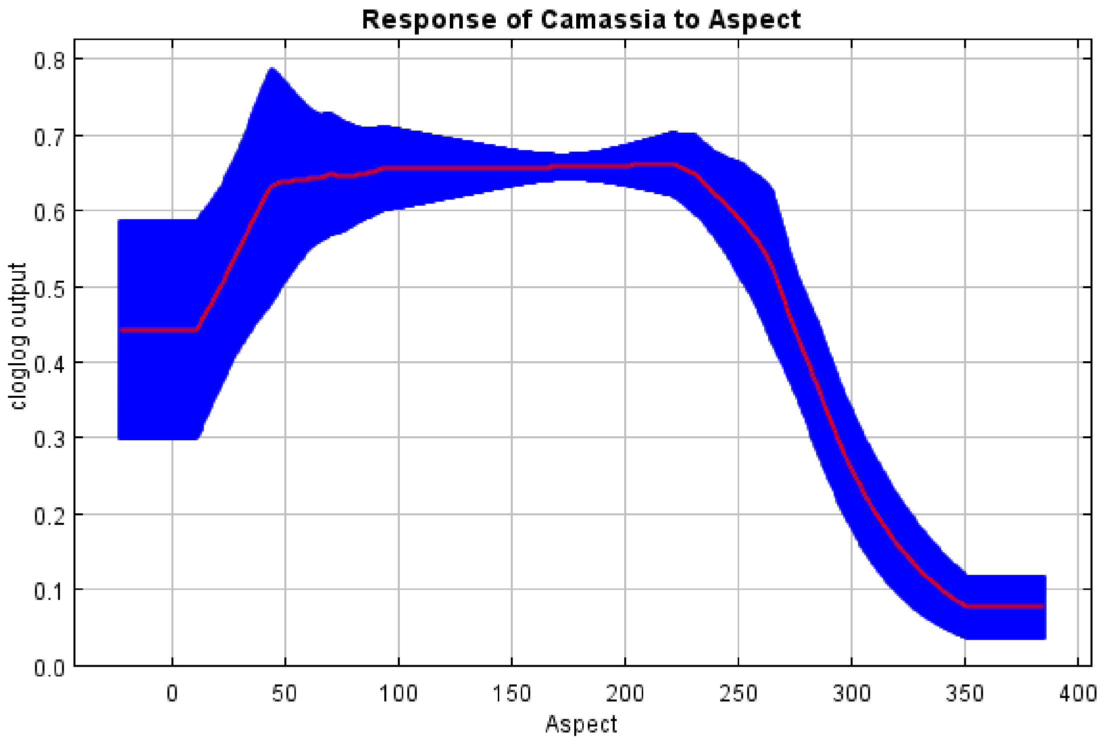
APPENDIX A

Variable Response Curves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0.2
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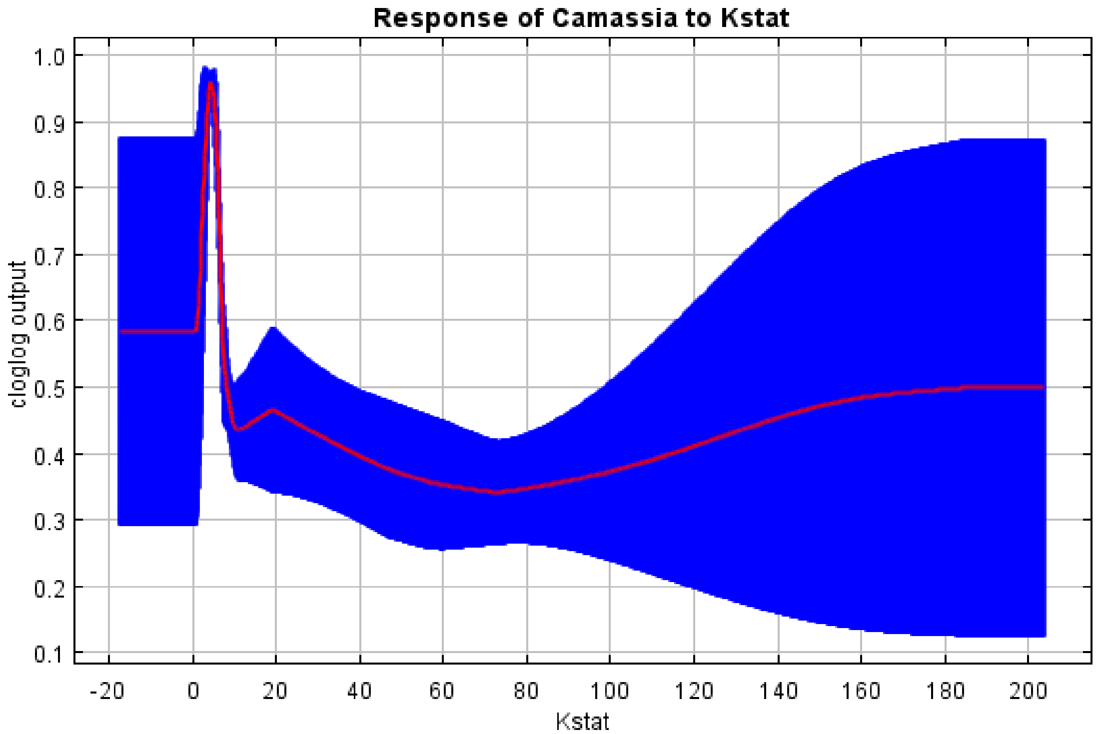
0.4
0.5
0.6
0.7
0.8
0
50
100
150
200
250
300
350
400
Aspect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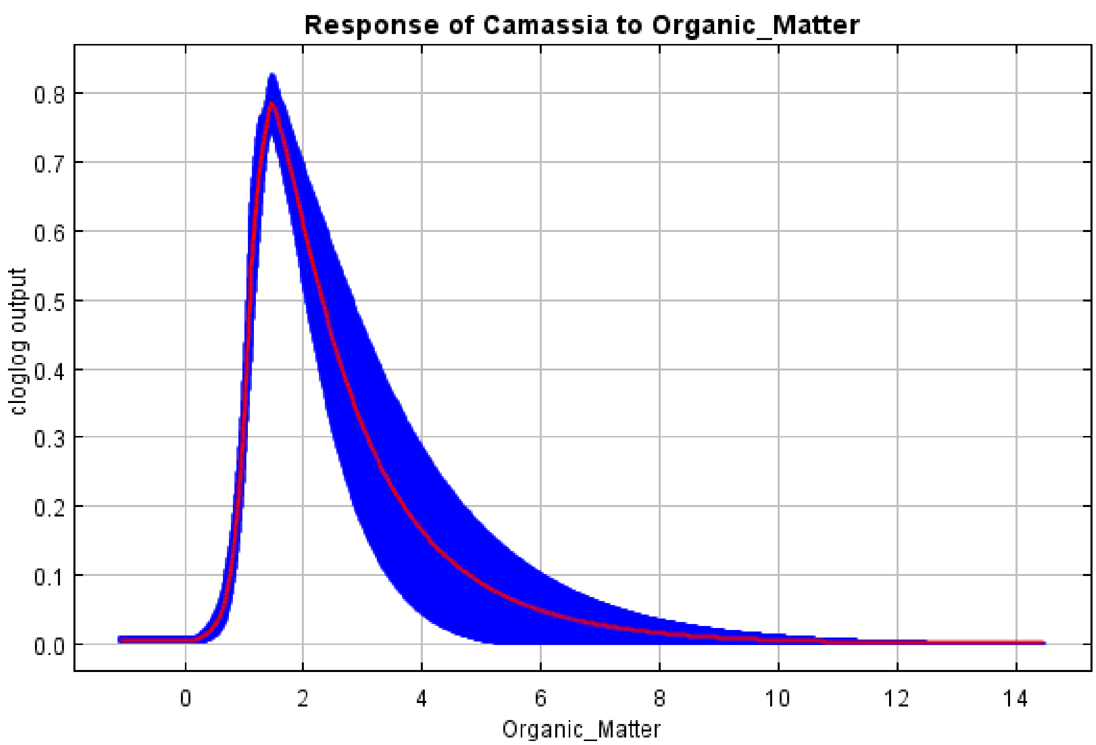
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
-20
0
20
40
60
80
100
120
140
160
180
200
Kstat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0.6
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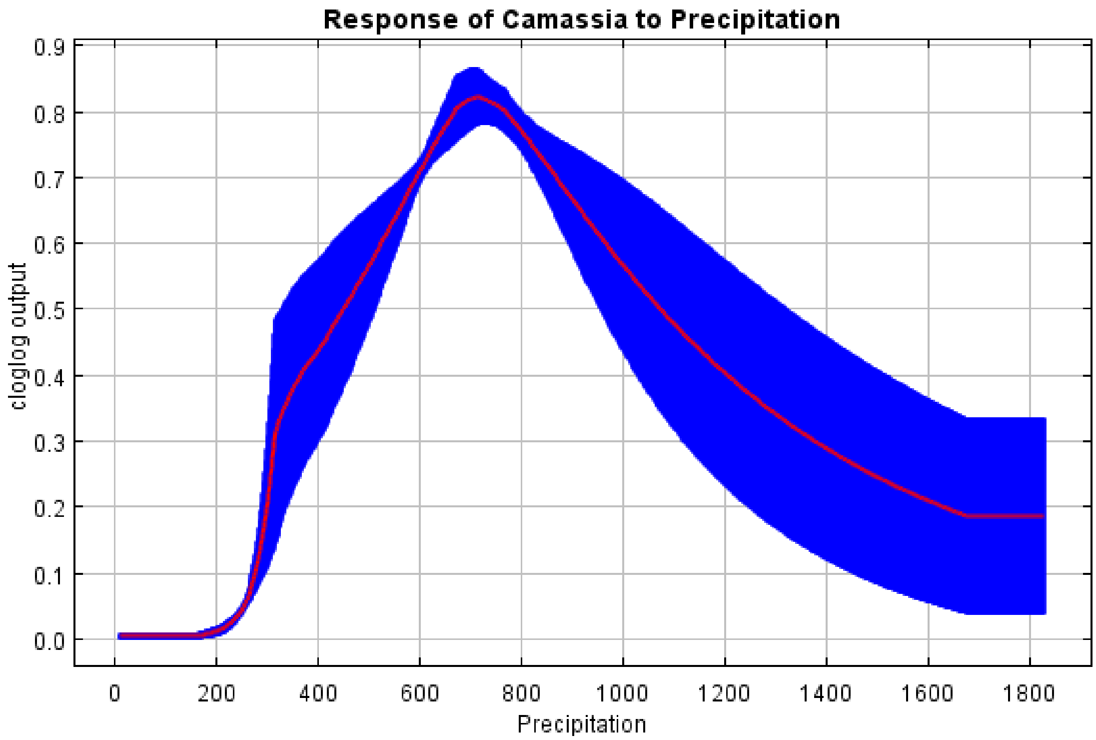
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
Organic_Matter



Response of Camassia to Precipitation
cloglog output
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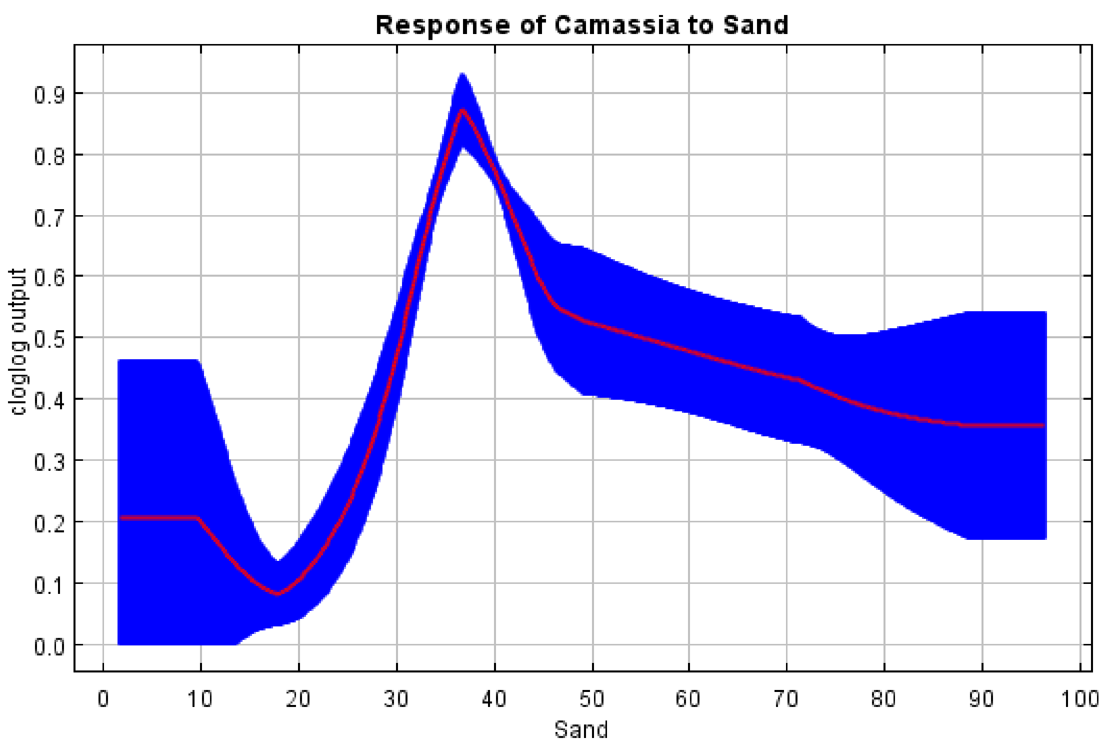
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
200
400
600
800
1000
1200
1400
1600
1800
Precipitation



Response of Camassia to Sand
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0.7
0.6
0.5
0.4
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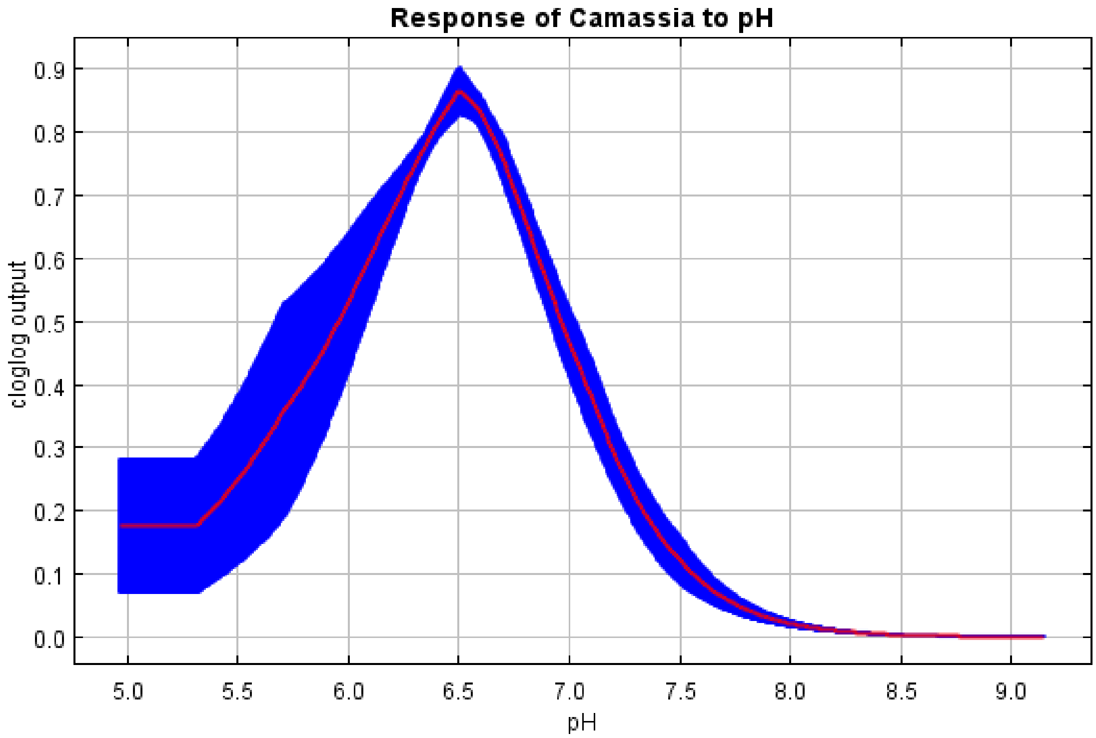
0
10
20
30
40
50
60
70
80
90
100
Sand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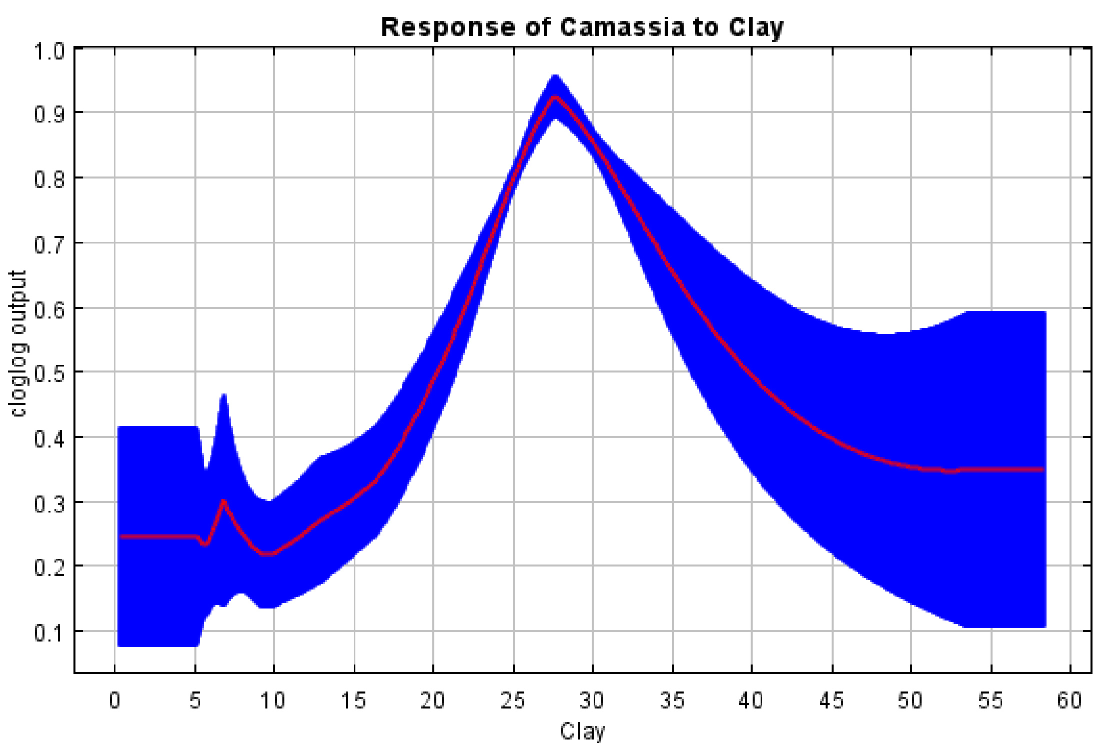
pH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55
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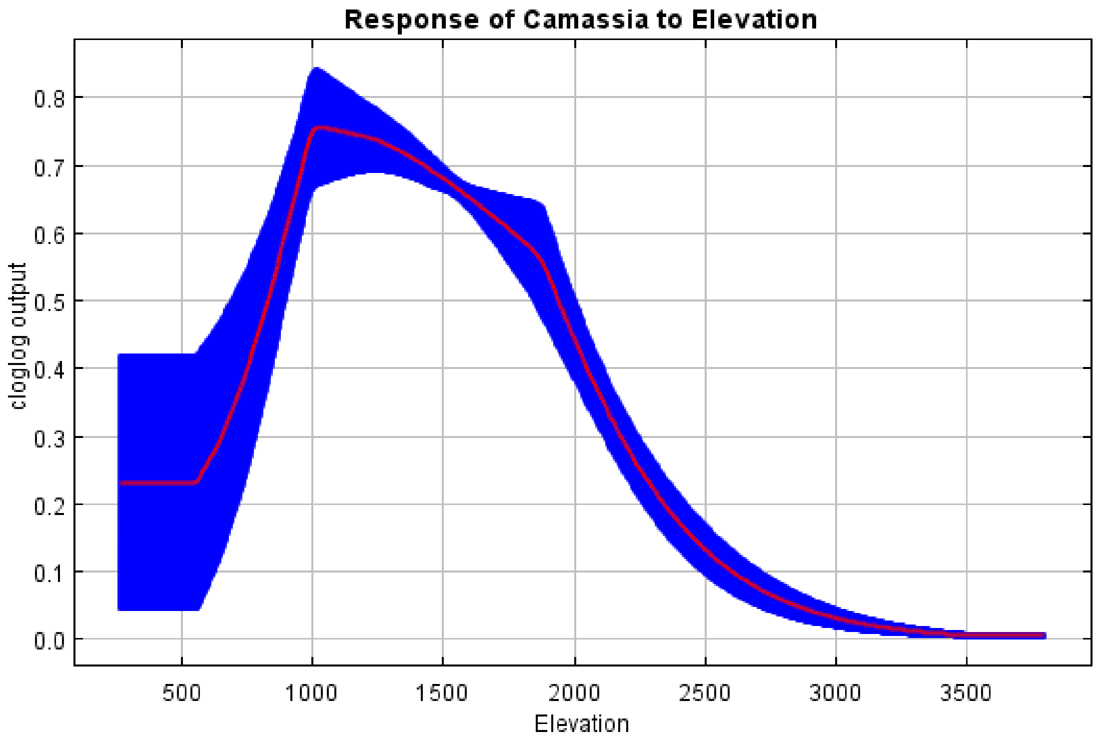
Clay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0.5
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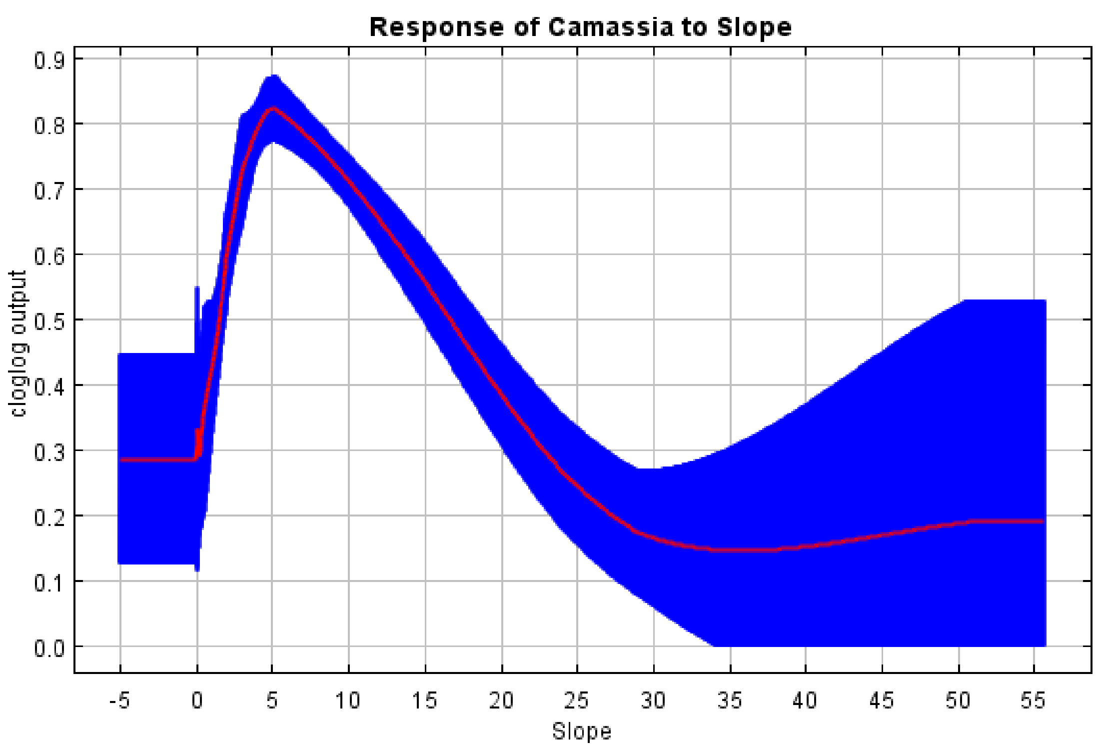
1000
1500
2000
2500
3000
3500
Elevation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0.6
0.7
0.8
0.9
-5
0
5
10
15
20
25
30
35
40
45
50
55
Slope