Brown Hyena (*Hyaena brunnea*) Distribution: Nuances in Modeling a Generalist Species

by

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Executive Summary

This project served two primary purposes: increasing the knowledge of brown hyena (*Hyaena brunnea)* distribution and ecology across its global range, and exploring how best to model the habitat requirements of a generalist species.

Brown hyenas currently face a number of pressures on their distribution and population status including anthropogenic persecution, climate change, and declining populations of other predators that serve interspecific roles in brown hyena's ecological niche. There is currently insufficient understanding of how brown hyenas interact with their surroundings, and without this knowledge we are unable to predict or prepare for future changes in hyena range or status.

The Hyaena Distribution Mapping Project (HDMP) was formed in 2017 by my advisor Dr. Andrew Jacobson (then at Duke University) and has since been joined by Dr. Florian Weise (Ongava Research Center, Namibia). HDMP is currently working to update the global range map of the brown hyena, along with the rest of the Hyaenidae family, with the support of the IUCN Hyaena Specialist Group. They have received over 70,000 brown hyena occurrence records across southern Africa from formal research efforts, local expert submissions, and publicly available images from social media and news reports. I joined the project in 2018 and have since created this Masters Project to model brown hyena distribution.

Modeling brown hyena distribution on a global scale has yet to be done and is difficult because they are a generalist species. They are mobile, wide ranging, and adapt to a variety of habitat types including deserts, grasslands, and even sandy coastline. To account for the difference in habitats within their range, I created a set of distribution models. First, I built a general model across southern Africa. I then created two sub-models: one for the Desert and Xeric Shrubland biome and one for the Tropical and Subtropical Grasslands, Savannas, and Shrublands biome. I proposed that brown hyena habitat would vary across these biomes, and we could better describe how their ecology varies by comparing these sub-models to the general model prediction. I also performed a sensitivity analysis for the desert model to determine to what level habitat predictions of the inland region were influenced by the presence points along coastal habitat where hyena ecology is different.

I obtained presence data from the records collected by HDMP and tailored the points used in the model to account for observation and effort bias. After assembling a candidate set of environmental factors, I searched for publicly available geospatial data to describe these variables across southern Africa. I ran species distribution models using Maxent, a widely-used species distribution modeling software.

With Maxent, I generated predictions of habitat probability across southern Africa as well as for the desert and savanna biomes specifically. After comparing the biome models to the general model, I identified both regions in which the models had different predictions of habitat as well as the environmental variables causing these differences. This comparison revealed a number of important insights regarding the two goals of this project.

Insights into brown hyena distribution and ecology:

- In general, brown hyena presence is correlated with areas of lower livestock density.

- Brown hyenas in the desert are more often found in areas with greater tree cover while hyena presence in the savanna is correlated with relatively low tree cover.
- Hyena presence appears to be more strongly correlated with proximity to protected areas in the savanna than in other regions but further research is required.

Insights into modeling a generalist species:

- The global model benefitted from greater information than the desert model and avoided predicting habitat based on a misleading correlation between increasing urbanization and hyena presence.
- The global model also relied on livestock density to predict habitat in the savanna despite its irrelevance to that specific biome.
- The global model was unable to describe the difference in correlation with tree cover between hyenas in different biomes.

This analysis strongly indicates that brown hyena ecology and subsequent habitat preference differ based on the biome of an individual. Neither the general nor the regional models were without shortcomings, and they both introduced new insights into how brown hyena habitat varies. By combining the information from different modeling strategies and expert knowledge of hyena behavior, we can draw more informed conclusions about how this generalist species interacts with its surroundings. Future modeling efforts of wide-ranging, generalist species should account for how habitat selection can differ across a global range.

Acknowledgments

I would like to thank my advisor, Dr. Andrew Jacobson, for this opportunity and his support over the past two years. I have benefitted from joining him and the Hyaena Distribution Mapping Project in countless ways. His guidance and encouragement have been invaluable. I am grateful to Dr. Ingrid Wiesel and Dr. Richard Yarnell for sharing their work and expertise of the brown hyena as well as the entire Hyaena Specialist Group. Thank you to Dr. Dean Urban for taking the time to answer my questions about Maxent, Dr. Ram Oren for helping me communicate my results, and Dr. Stuart Pimm for the administrative support.

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Introduction

The brown hyena (*Hyaena brunnea*) relies on interspecific relationships with large predators across most of its range in southern Africa (Mills and Hofer, 1998). Many of these predators, including lions, leopards, and cheetahs, are facing serious population decline (Ripple et al., 2014). In part due to the severity of threats to their populations, these species benefit from intense research efforts, conservation initiatives, and representation and understanding in the global media. Influential species facing less severe population decline, such as the brown hyena, are not as well understood. Its generalist nature allows it to survive in a number of habitats including xeric deserts, subtropical grasslands, and sandy coastlines. Currently, there are a number of long-term studies on specific populations in different habitats, but we do not have a robust understanding of how the brown hyena interacts with its environmental surroundings on a global scale. In 2017, the Hyaena Distribution Mapping Project, in partnership with the International Union for the Conservation of Nature (IUCN) Hyaena Specialist Group, began work to establish the brown hyena's current range and population status. As an extension of their work, this analysis uses species distribution modeling to describe how brown hyena habitat varies across the ecosystems within its global range.

The IUCN Red List has ranked the brown hyena as Near Threatened with a declining population (Wiesel, 2015). While extinction of this species is not an immediate concern, there is still value in improving our knowledge of its habitat preferences and spatial ecology. Because its range overlaps with other top predators experiencing higher rates of population decline (Ripple et al., 2014), brown hyenas' role as large carnivores may become more important. In the United States, coyotes have expanded their range as wolf populations have disappeared (Benson et al., 2017). However, Benson et al. (2017) found that coyotes do not effectively fill the ecological niche left behind; their predation rate on large ungulates such as moose and deer is significantly smaller than wolves'. As larger competitors across brown hyenas' range decline, we are uncertain how brown hyenas will respond. For example, they may increase predation on wild ungulates as scavenging opportunities decrease, or perhaps they will increase their predation on livestock and scavenging in human refuse. The first step in understanding future brown hyena behavior is to examine what environmental factors are currently influencing their distribution and how.

Background on Hyaena Distribution Mapping Project (HDMP)

In 1998 the IUCN Hyaena Specialist Group released a Status Survey and Conservation Action Plan for all four members of the hyena family worldwide: brown hyena, spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*), and aardwolf (*Proteles cristatus*). This report detailed range distribution and population assessments for each species. Species ecology, threats, and management efforts were all considered in the final chapter which proposed an extensive if not detailed conservation action plan (Mills and Hofer, 1998). However, the Hyaena Specialist Group did not collectively pursue the strategies or follow-up on the recommendations from the 1998 publication until 2017 when a new director and members were instated. Dr. Andrew Jacobson (then at Duke University) began the Hyaena Distribution Mapping Project (HDMP) after realizing that there is a disproportionate research effort invested in Africa's other large carnivore species. He reached out to Dr. Florian Weise (Ongava Research Centre, Namibia), and Dr. Stephanie Dloniak (Michigan State University, Chair of the Specialist Group), and together they issued a call for any and all hyena occurrence records. Their efforts have tens of thousands of verified presence data points that are being used to update the range maps of each species. Next steps for the HDMP include the creation of distribution maps, identifying areas of contraction/expansion from the previous distributions, and estimating global population numbers for each species in order to update their conservation status. A critical follow-up to this larger work is to create a species distribution model for each of the four species to better describe the ecological drivers of their distributions. This analysis focuses on the brown hyena.

Brown Hyena Ecology

The brown hyena's range (Figure 1), when last defined in 2015, extended across southern Africa reaching both the eastern and western coasts. The northern edge of their range reached into Angola and Zimbabwe, falling further south toward the Indian Coast (Wiesel, 2015). Throughout this range, the brown hyena appears to fare well in harsh desert habitat as well as grasslands. Populations do not extend north into forested habitat, but they do require cover for denning and relief from the elements, either from rocks or vegetation (Mills and Hofer, 1998). They are not found in areas of high elevation (Wiesel, 2015). Brown hyena are predominantly scavengers, consuming the remains of other carnivores' prey, eggs, insects, and vegetation (Mills and Hofer, 1998). In arid regions, they have been observed to scavenge both wild and cultivated succulent plant species and so avoid a dependence on standing fresh water (Knight, 1995). In some cases, they will predate on small mammals; clans along the Namib desert coastline eat cape fur seal pups (*Arctocephalus pusillus*) (Wiesel, 2010). A study performed in pastoralist areas did not find any evidence that brown hyenas predate on livestock (Maude and Mills, 2005), but they do scavenge livestock kills from other predators. The primary threats facing brown hyena are anthropogenic. Though undeserved, they are subject to persecution from farmers who believe they steal livestock (Maude and Mills, 2005). Despite this, they are still found outside protected areas and in proximity to cattle, sheep, and urban areas (Maude and Mills 2005). Brown hyenas are predominantly nocturnal (Mills and Hofer, 1998). Depending on their sex and age, they either reside in small clans or as lone individuals. Their home ranges can be as small as a few hundred km^2 in areas with ample prey or larger than 1,000 km^2 (Welch et al., 2015, Maude et al., 2019). Overall, brown hyena ecology is understood from research efforts that focused on individuals or clans within their specific habitat rather than comparisons of such animals across habitat types. Using a set of species distribution models, we can examine what environmental factors drive differences in habitat utilization across their global range.

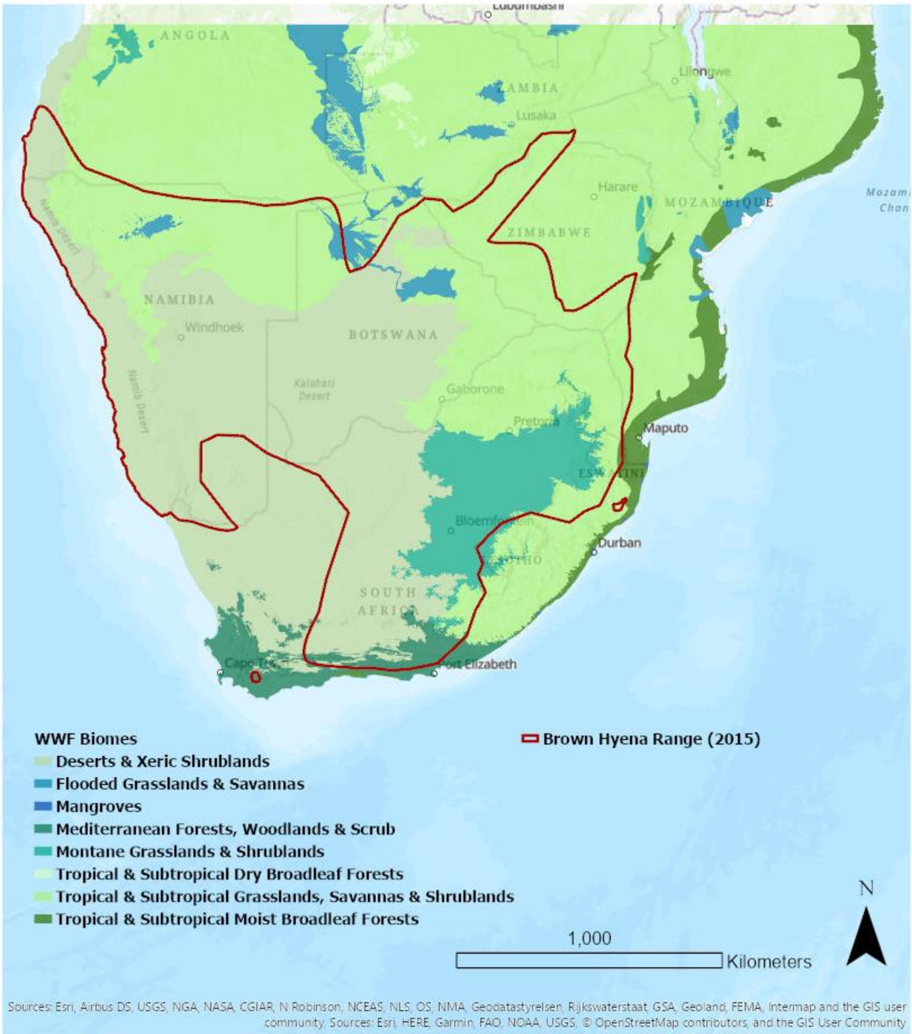

Figure 1: Brown hyena global range last updated in 2015 (IUCN). Overlaid on biome delineations (Wiesel, 2015, Dinerstein et al. 2017).

Species Distribution Models

Species distribution models (SDMs) are quantitative methods of analyzing the relationship between the presence of a species and selected environmental variables within its habitat. There are many different algorithms including random forest models, genetic algorithm for rule-set prediction, resource selection functions, artificial neural nets, and ecological niche factor analysis (Elith and Leathwick, 2009). Modeling methods should be chosen to fit the specific data, species, and goals of the analysis. Common goals of distribution models range from understanding evolutionary processes, estimating current habitat extent, predicting future habitat loss, and describing the environmental factors behind a species distribution (Elith and Leathwick, 2009).

Modeling a generalist species versus a specialist species introduces a particular challenge. Specialist species tend to occupy a very precise ecological niche regardless of its geographic location within its range. Generalist species, however, can have sub-populations with varying ecologies that take advantage of a range of habitat types. Modeling such sub-populations all at once runs the risk of overestimating a species' ecological breadth. This can affect the prediction of potential habitat and produce less precise, and therefore less informative, models (Regos et al., 2019). However, expanding the geographic range of a model can be useful. El-Gabbas and Dormann (2018) modeled a generalist bat species to test if using global presence points could improve a country specific model. Though they decided the large-scale model was indeed less accurate, it was still informative for their smaller model (El-Gabbas & Dormann, 2018).

For this analysis, I have chosen to use Maxent software for modeling species niche and distributions (Version 3.4.1; Philips, Dudik, and Schapire). Maxent is a popular software that predicts habitat with a high degree of accuracy, and it has been used in the past to handle similar datasets with mixed presence record types and no absence data (Angelieri CCS et al., 2016; Kanagaraj et al., 2013; El-Gabbas & Dormann, 2018). Maxent uses maximum entropy modeling to identify correlations between species presence points and a candidate set of environmental variables provided by the user. Based on these correlations, it then extrapolates across the entire range of the environmental variables to determine habitat similarity and subsequently predict the probability of habitat (Merow et al., 2013). One advantage of Maxent is that it does not require any absence data; it generates its own pseudoabsence background based on the size of the study area. However, Maxent results must then be interpreted appropriately. Any analysis of Maxent's predictive accuracy is based on its own generated background which is likely to inflate accuracy estimates. In addition, for this particular analysis, we must be wary of observation bias. Because HDMP's presence data is a combination of formal survey sites and incidental observations, Maxent is subject to overpredicting habitat in areas where greater research or other human observation is present such as along roads or in protected areas.

Similar analyses of other species have been performed with occurrence data acquired through both formal survey sites and opportunistic presence data. There are many examples in the literature for both types of data analysis (Angelieri CCS et al., 2016; Kanagaraj et al., 2013; El-Gabbas & Dormann, 2018), as well as an integrated approach that combined both data types and yielded a stronger model for the example species, Yellow-bellied glider (*Petaurus australis*) (Koshkina et al., 2017). By adequately accounting for effort and observation bias, Maxent can still be used to generate reasonable habitat probability predictions on mixed data sources.

Objectives

This project served two primary purposes: creating the first range-wide species distribution model of the brown hyena to increase our knowledge of its distribution and ecology, and exploring how best to model the habitat requirements of a generalist species.

Given the different biomes within the hyenas' range and the difference in individuals' home range size, a single distribution model may not be sufficient to capture their global distribution. I created a global model of the brown hyena as well as two sub-models, one for the deserts and xeric shrublands and one for tropical and subtropical grasslands, savannas, and shrublands as defined by Ecoregions 2017 (Dinerstein et al., 2017). I propose that brown hyena ecology varies based on the specific ecosystem of an individual and that by modeling their distribution at a biome level we can better predict habitat. However, a global model may still be useful and informative because individual hyenas do range widely, and one individual can take advantage of a variety of habitats. By comparing the predictions of habitat, we can create a more robust description of how brown hyena ecology varies throughout southern Africa. By comparing the models' performance, we explore the nuances of modeling a generalist species' habitat use.

Materials and Methods

I. Hyena Occurrence Data

Presence points were provided by the Hyaena Distribution Mapping Project. They issued a call for data submissions in 2017 from research efforts across the hyena's range. Any observation of hyena presence (or proven absence) between 2010 and 2019 was accepted including camera trap images, telemetry, scat, and spoor observations. In addition, a public records search was performed to find verifiable reports of hyenas on social media, news outlets, and other sources.

Each point was evaluated for its reliability, geospatial precision, and relevance to the model. I excluded any points that did not include a precise location of the observed hyena including data collected through a quadratic survey in Namibia. I also removed any duplicate records with identical latitude and longitudes. If occurrence data is acquired using standardized methods and effort, duplicate points can provide valuable information to an SDM. However, using duplicate points in addition to our incidental data would have unfairly biased the model towards parts of the study area in which formal research occurs.

To further account for the observation and effort bias in the data set, I thinned the remaining presence points using SDMToolbox 2.0 in ArcMap (Brown et al., 2017). Thinning intensity was based on brown hyena spatial ecology. Brown hyenas are mobile and far ranging. Their home ranges can be anywhere in size from 100 km^2 to over 1,000 km^2,and they often overlap with lone individuals' ranges or with clan members (Welch et al., 2015, Maude et al., 2019). Sex of individuals, physical constraints, and habitat were not factored into the spatial thinning as there was not readily available data. Because the pseudo-sampling intensity for our presence data was disparately stronger along the Namibian coast, thinning intensity was based on home range size in this region, 100-200 km^2. This accounted for the increased effort in the region without removing a significant number of presence points in the inland areas. Based on an average home range of 150 km^2, any point within 14 km of another presence point across the entire study region was removed, starting with a random seed point.

II. Literature Review and Expert Consultation

In order to identify relevant environmental variables, I conducted a literature review of brown hyena habitat and ecology. Using Google Scholar and Duke University Library, I searched terms including "brown hyena habitat," "hyaena brunnea habitat," "brown hyena ecology," "brown hyena environmental constraints," and "southern African climate." I compiled a list of proposed variables that affect brown hyena ecology and distribution and shared them with Dr. Ingrid Wiesel and Dr. Richard Yarnell of the Hyaena Specialist Group. They provided feedback including further sources and personal expert knowledge. I finalized the environmental variable candidate list and began to search for available geospatial datasets to include in the Maxent model.

III. Study Area and Environmental Data Collection

After determining what environmental factors affect brown hyena habitat, I sought publicly available data to translate these variables into separate geospatial layers for input into Maxent. I gathered geospatial data from a range of publicly available sources (Table 1). Using ArcGIS Pro, I converted each variable layer to WGS 84, resampled them to a spatial resolution of 1 km^2, and clipped the layers' extents to the study area. The study area (Figure 3) was defined as all of continental Africa south of the 12^{th} parallel south. The 12^{th} parallel is approximately 330 km north of the most northern brown hyena presence point. This study area size provides the model with the flexibility to predict habitat further north than is implied by the presence data while still limiting potential range to avoid statistically significant but uninformative predictor variables.

Table 1: Environmental Variable Layers

Variable	**Source**	**Date**	**Ecological Relevance**
Elevation	SRTM (Jarvis et al., 2008)	NA	Brown hyena are thought to prefer lower elevations (Mills & Hofer, 1998).
Slope	SRTM (Jarvis et al., 2008)	NA	Brown hyena are not known to frequent steep slopes (Mills & Hofer, 1998).
Tree Cover	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Grassland	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Shrubland	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Cropland	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Bare Land**	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Urban Land Cover	Copernicus Fractional Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena inhabit arid to semi-arid deserts and grasslands. They den and rest in areas with vegetative or rocky cover. They frequent pastoral areas to raid crops and livestock (Mills & Hofer, 1998).
Distance to Fresh Water	Calculated from Copernicus Land Cover V2.1.1 (Buchhorn et al., 2019)	2015	Brown hyena are not directly dependent on water; they supplement their diet with succulent vegetation (Knight, 1995). However, prey species distribution may be affected by water sources.
Productivity	NASA Visible Infrared Imaging Radiometer Suite (VIIRS) (Didan & Barreto, 2018)	2010-2017 Average	EVI can be used to assess vegetation cover (Evrendilek & Gulbeyaz, 2008). Expect BH to be in areas of sparse cover but not barren. (Mills & Hofer, 1998).
Mean Annual Temperature	WorldClim 2.1 (Fick, S.E. and R.J. Hijmans, 2017)	1970-2000 Average	Brown hyena prefer warmer climate zones. This may be due to elevation preference. (Mills & Hofer, 1998)
Minimum Temperature of Coldest Month	WorldClim 2.1 (Fick, S.E. and R.J. Hijmans, 2017)	1970-2000 Average	Brown hyena prefer warmer climate zones. This may be due to elevation preference. (Mills & Hofer, 1998)
Precipitation of the Wettest Quarter	WorldClim 2.1 (Fick, S.E. and R.J. Hijmans, 2017)	1970-2000 Average	Brown hyena are not known to be dependent on standing water; they supplement their diet with wild melons during the dry season (Knight, 1995). Hyenas do not extend into areas of dense vegetation growth (possible because of higher precipitation).
Global Human Modification	TNC (Kennedy, M et al., 2018)	2018 v.1	Includes all quantifiable human activity including cities, roads, agriculture, mining, dams, etc.
Human Population	Africa Continental Population Datasets (WorldPop, 2016)	2000-2020	BH avoid dense urban areas but frequent pastoral zones (Mills & Hofer, 1998)
Distance to Protected Areas	WDPA (IUCN and UNEP-WCMC, 2014)	2016	BH are protected in these areas, positive observation bias, etc. Distance to protected area was calculated for each pixel in a 1 km^2 raster layer.

Cattle Density	Gridded Livestock Data of the World (GLW v3) (Gilbert et al., 2018)	2010	Brown hyena predate on livestock but experience threats from associated farmers (Mills & Hofer, 1998).
Sheep Density	Gridded Livestock Data of the World (GLW v3) (Gilbert et al., 2018)	2010	Brown hyena predate on livestock but experience threats from associated farmers (Mills & Hofer, 1998).
Distance to Seal Habitat	Calculated from IUCN Cape Fur Seal Range Map (Hofmeyr, 2015)	2014	Brown hyena along the coast predate on seal pups. Individuals within 60 miles of the coast may display distinct habitat preferences due to their awareness of different prey sources (Wiesel, 2010).

**Not included in final models due to strong correlation with the productivity, distance to seal habitat, and grassland layers.

All variable layers were included in the form in which they were downloaded unless otherwise noted. To determine distance to seal habitat, I used ArcGIS Pro to calculate the Euclidean distance from every pixel in the study area to the closest point within the Afro-Australian fur seal (*Arctocephalus pusillus)* range (Hofmeyr, 2015). I then scaled the results so that pixels along the coast had the highest score (1) and inland pixels had the lowest (0). The linear rate of decay from 1 to 0 was based on telemetry data provided by Dr. Ingrid Wiesel. Any distance from the coast within the range of the coastal hyenas (20 miles inland) was considered to be consistently affected by proximity to seal habitat and was given a score of 1. Any pixel outside this range but within the range of a male who occasionally visited the coast was scored between 1 and 0 according to its Euclidean distance (20 to 60 miles inland). All pixels outside of this range (further than 60 miles inland) were determined to be too distant from the coast for a resident hyena to be aware of the presence of seals and given a score of 0.

Distance to fresh water was also determined by the Euclidean distance from each pixel and the nearest, permanent body of water in the Copernicus land cover dataset. Water sources were taken from the vector dataset for land cover rather than the fractional land cover (Buchhorn et al., 2019).

Vegetative productivity was approximated using NASA Visible Infrared Imaging Radiometer Suite (VIIRS) Enhanced Vegetation Index (EVI) data averaged from 2010 to 2017 (Didan & Barreto, 2018). EVI is a popular method of translating remotely sensed imagery to reveal vegetation productivity in a landscape. I chose EVI because it is particularly well suited to identify vegetation in sparsely vegetated landscapes with high soil reflectance (Evrendilek & Gulbeyaz, 2008).

Distance to protected areas was expressed as the Euclidean distance of each pixel from the closest protected area included in Protected Planet's 2014 version of the World Database of Protected Areas (IUCN and UNEP-WCMC, 2014). This year was selected as the midpoint in the data collection period.

Cattle and sheep density were obtained from Gridded Livestock of the World (GLW 3) (Gilbert et al., 2018). Values are expressed in animals per pixel; the original data layers used 5 arcminute resolution. The only manipulation of these datasets was a resampling to match the 1 km^2, but it is important to note that the livestock layers were the coarsest datasets included in the models.

Human population data was taken from the Africa Continental Population Datasets (2000-2020) version 2.0 (WorldPop, 2016). The data was resampled from 30 arcseconds to 1 km^2. Pixel values represent the average number of people per pixel across the 20 year time span.

The global human modification came directly from The Nature Conservancy's 2018 v.1 dataset; no manipulation was applied (Kennedy et al., 2018).

After organizing each variable layer, I extracted the value of every variable at each presence point. I then assessed the correlation among all the variables and removed variables that were highly correlated. Based on the standard threshold of 0.7 (Dormann et al., 2013), I removed bare land cover from the dataset as it was highly correlated with grassland, productivity, and distance to seal habitat. Removing the single variable was the most parsimonious solution.

IV. Maxent Models

After determining the final occurrence and environmental datasets, I ran three Maxent models. A general model was created for the entire study region to encompass any and all potential habitat both suitable and accessible to the brown hyena. The first comparative model was limited to the extent of Deserts and Xeric Shrubland biome (Dinerstein et al. 2017), using the same Maxent parameters as the full model (Figure 1). The second comparative model was based on Tropical & Subtropical Grasslands, Savannas & Shrublands biome extent (Dinerstein et al. 2017).

These two biomes encompass 96% of the observation points. Remaining points fall into three other biomes: Mediterranean woodland (five points), Montane grassland (eleven points), and flooded grasslands (nine points). These biomes were not modeled individually due to lack of sufficient data points.

In addition to the suspected ecological difference between hyenas in the savanna and hyenas in the desert, there is a possibility that hyena ecology within the desert biome varies as well. The presence of cape fur seals along the coast may alter the predictions of the desert model. I performed a sensitivity analysis of the desert model to presence points of individuals along the coast to account for this potential confounding factor (Appendix I).

After creating a model, Maxent assesses its accuracy with the reserved test points. Accuracy can be evaluated with a receiver operating characteristics curve which graphs the model's true positive rate against its false positive rate. The area under the resulting curve (AUC) should equal 0.5 for a random model; AUCs higher than 0.5 indicate the model is more informative than a random prediction (Phillips, 2009). Because Maxent uses pseudoabsence points rather than true absence data, the resulting AUCs should be interpreted carefully. Pseudoabsence points are inevitably misclassified. While the AUC is still helpful in interpreting the model's strength, it can only describe how well the model fits the generated background data.

Maxent allows the user to determine how closely habitat predictions must be fit to the presence points by adjusting the regularization multiplier (beta value). I ran all three models with varying beta values to determine how the AUC was affected (Figure 2). Choosing an appropriate beta value based on the resulting AUC values depends on the goal of the analysis. In general, smaller beta values generate more localized predictions, fitted to the presence points. Increasing the beta value loosens the model and will typically lower the AUC (Phillips, 2009). Because the goal of this project is to compare the two biome specific models to the full, global model, the same beta value should be implemented. Beta value 1.5 was selected as it performed well across all three models and allowed for a looser fitting of the model around the presence points. Hyenas are mobile and generalist in nature (Mills & Hofer, 1998), so a higher beta value is more ecological appropriate.

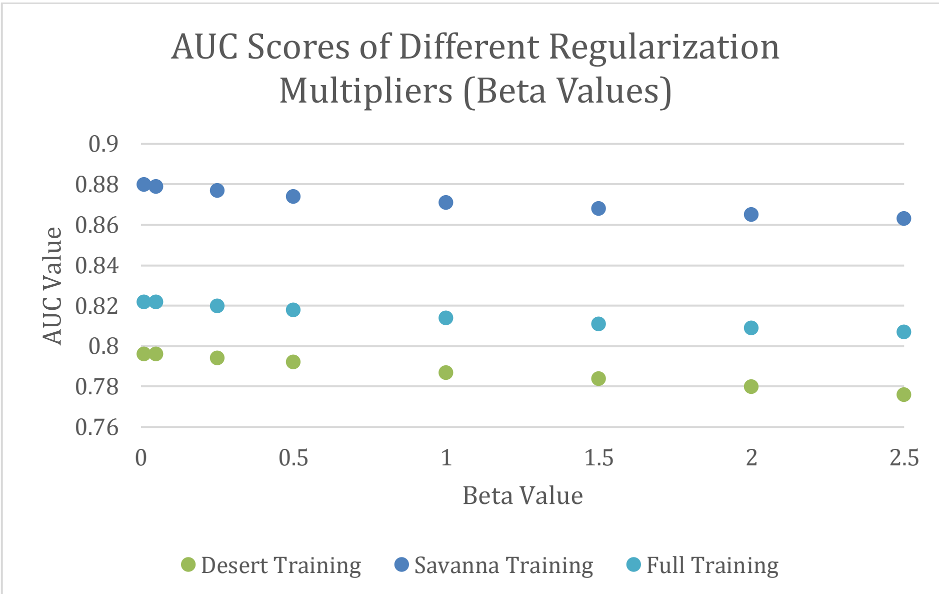

Figure 2: AUC values from Maxent runs with differing β values for each model extent.

Maxent also allows the user to select how responses to each predictor variable can be calculated. Environmental variables can be fit to linear, quadratic, product, threshold, and hinge feature classes. Linear features are drawn so that the average value of a predictor variable within the predicted habitat is the same as the average value at the training points. Quadratic features force the variance of a variable between where the species is predicted and where the species is observed to match (Merow et al., 2013). Only linear and quadratic features were allowed; product, threshold, and hinge features are more complex. Because of the sparse number of presence points relative to the size of the study area, these features would likely have generated complicated response curves that would be ecologically insensible.

All three models were run with a beta value of 1.5, up to 10,000 background points, and allowing for linear and quadratic features. Ten percent of the presence data was reserved as test points for all three models. After finalizing each model, Maxent assessed the model's performance based on both the input presence points as well as the reserve points. Similar model performance between training points and test points indicates a well fit model.

Final models were brought back into ArcGIS for comparison. I subtracted the raster layers of both biome specific models from the full model raster. This created a new map where pixels equal or close to zero had similar values from both models, positive pixels were predicted greater in the global model, and negative pixels had higher predicted habitat scores in the biome model. Using these new maps and the importance of variables to each model, I identified regions of the study area in which the two models disagreed most strongly. Based on the location of these regions and the relative importance of different variables, I examined how and why habitat predictions differed and the implications these differences had regarding hyena ecology and model suitability.

Results

I. Occurrence Data Submissions

HDMP obtained approximately 70,000 records for the brown hyena. 22,000 data points remained after removal of imprecise and duplicate records. Thinning the dataset to 14 km between each point left a total of 738 points across the entire study area. The full dataset was used in the global model (Figure 3). The deserts and xeric shrubland model was run using the 444 points that fell within the biome; 269 points were within the savanna and grasslands biome. Of the 444 desert presence points, 85 were within 60 miles of the coastline within the range of cape fur seals. The other 359 presence points were used to perform the sensitivity analysis of the desert model to coastal individuals' ecology.

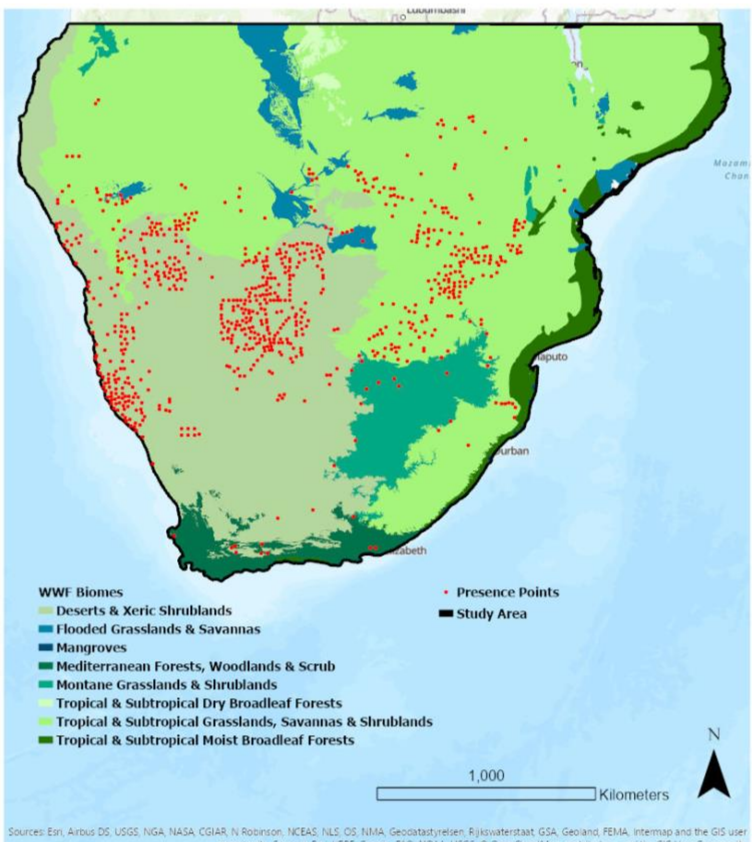

Figure 3: Presence points included in the models displayed across the study area.

II. Global Model

The global model produced a range wide prediction of habitat probability based on the correlation between presence training points and the environmental variables' values at each point. The regions with highest probability of habitat were concentrated in Namibia and Botswana. Parts of South Africa and Lesotho had very little probability of habitat (Figure 4). The greatest probability Maxent calculated was 0.899, indicating no pixel can be labelled as habitat with 100% confidence.

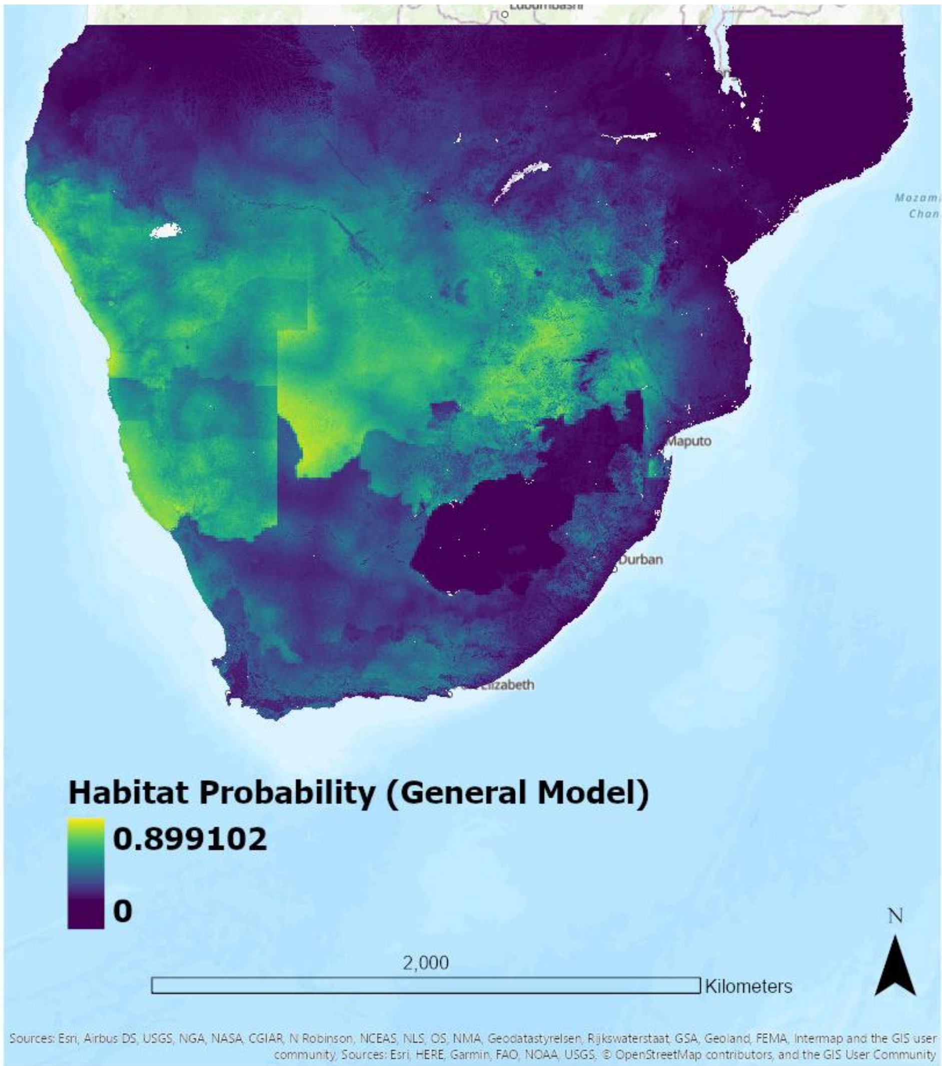

Figure 4: Habitat probability across brown hyena's entire range. Scores of 0 (blue) are areas predicted to be unsuitable for hyenas; greatest scores (yellow) indicate areas most likely to serve as habitat.

The global model had an AUC of 0.811 for the training data and 0.803 for the test data (Figure 5).

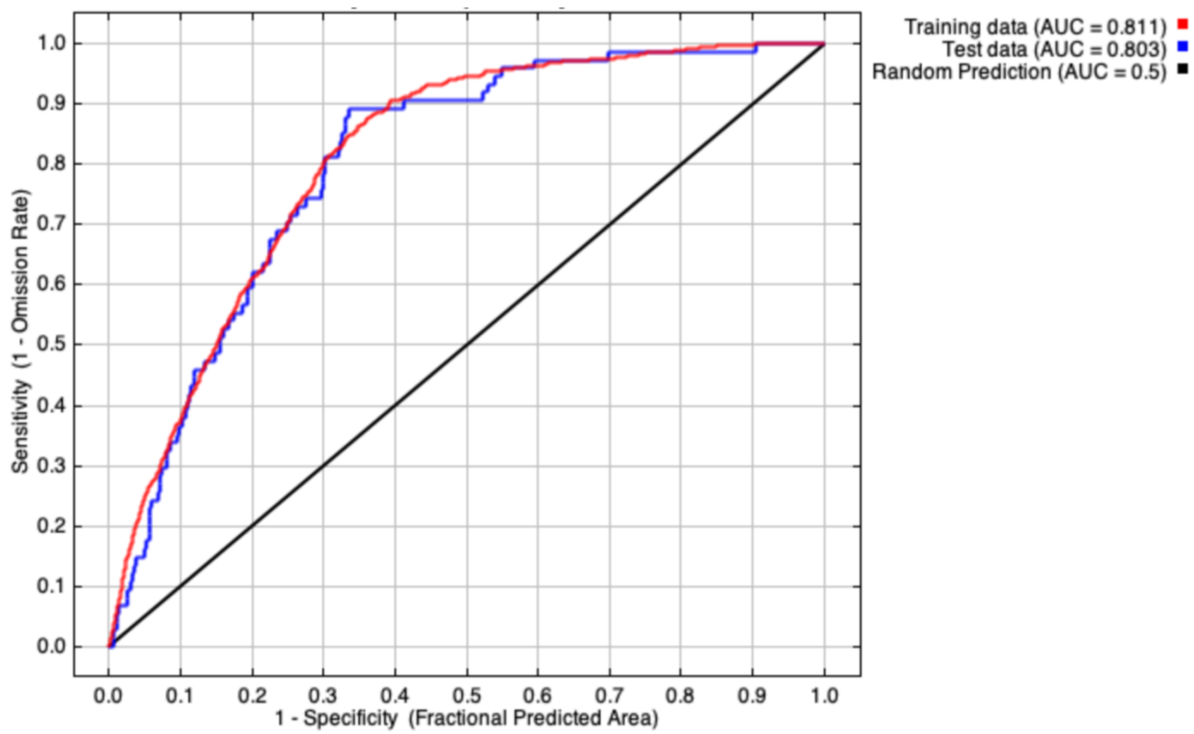

Figure 5: Receiver operating characteristics curve for the global Maxent model.

Maxent calculates both the percent of contribution each variable as well as the permutation importance of each variable. Percent contribution is determined by the cumulative increase (or decrease) in regularized gain after inclusion of the variable for each iteration of the algorithm (Merow et al., 2013). Essentially, percent contribution indicates how much of the model's habitat prediction relies on each variable. It reflects the strength of the distinction each variable can make between the presence and background points. To find permutation importance, Maxent randomly permutes values for each environmental layer at both the presence and pseudoabsence points (Phillips, 2009). The accuracy of model is re-calculated on the new values, and the subsequent change is noted for each environmental variable. Change is AUC is reported as a normalized percentage and reported as the permutation importance (Merow et al., 2013). Permutation importance assess the relationship between the species presence (and background) points and the range of the values of each variable. Both tests of variable importance are relevant to determining how presence points correlate with environmental factors. Percent contribution describes which variables the model relies on for its predictions, but these values should be interpreted carefully. They are a direct result of the specific order in which Maxent assessed variables to arrive at the final model. It is possible to generate a similar model with different variables and result in different percent contribution scores (Kalle et al., 2013). Permutation importance shows an underlying correlation within the range of values of a variable and presence points, but again these results should be interpreted correctly. The values are dependent on the chosen model; a variable could be correlated with hyena presence but not result in a loss of AUC depending on the final model (Kalle et al., 2013). Figure 6 shows the variables scoring over 5% in both categories for the global model.

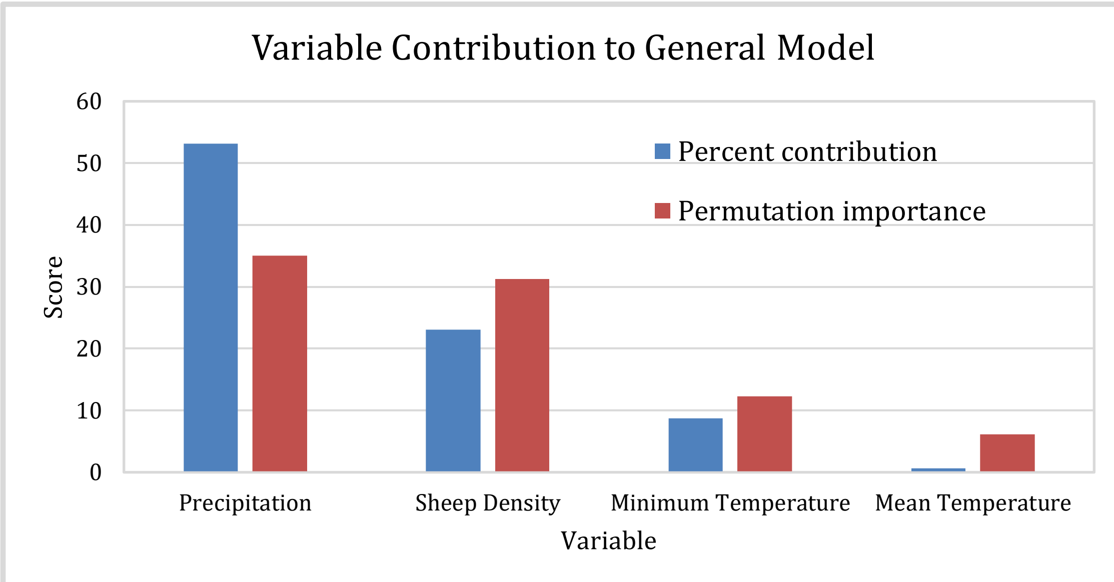

Figure 6: All variables with a score greater than 5 for either percent contribution to the global model or permutation importance.

We can further describe how predicted habitat was determined by investigating the shape of response curves of the identified environmental variables (Appendix III). Response curves show the relationship between the entire range of values of a variable and the predicted probability of habitat. The algorithm generated predicts hyena are most likely to be found habitats with little precipitation, low density of sheep, and minimum temperatures ranging between zero and ten degrees. In addition, the model experiences a decrease in its overall AUC when the values of these variables or mean temperature are randomly permuted. Hyena presence is correlated with cooler mean temperatures.

III. Savanna Model

The savanna model produced a prediction of habitat probability based on the correlation between presence training points and the environmental variables' values at each point constrained to the savanna biome. Habitat is most probable in the southern half of the savanna (Figure 7).

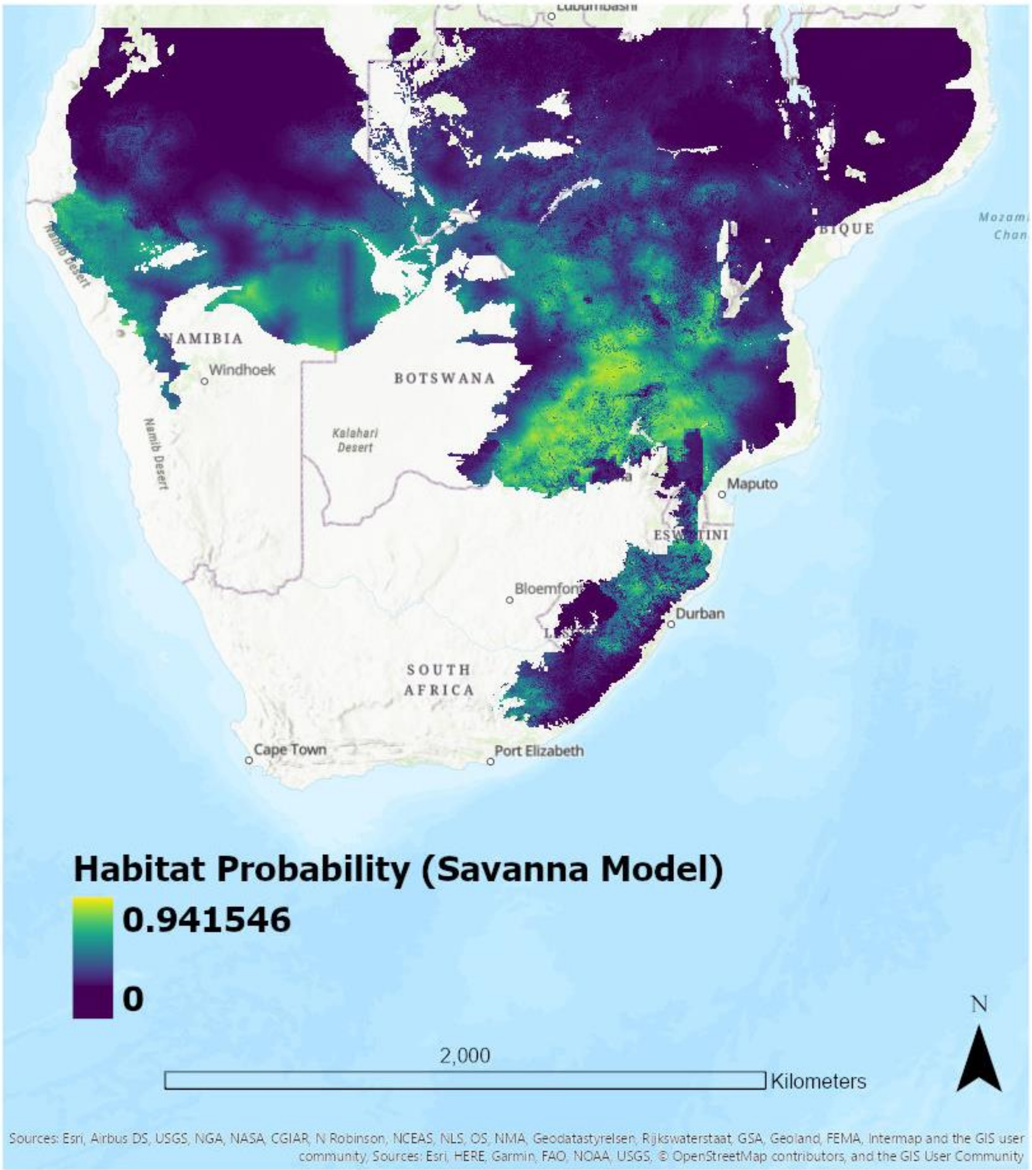

Figure 7: Habitat probability across the Tropical and Subtropical Grasslands, Savannas, and Shrublands biome. Scores of 0 (blue) are areas predicted to be unsuitable for hyenas; greatest scores (yellow) indicate areas most likely to serve as habitat.

The greatest probability Maxent calculated was 0.942, indicating no pixel can be labelled as habitat with 100% confidence (Figure 7). AUC scores of 0.868 and 0.835 indicate the model performed better than a random model (Figure 8).

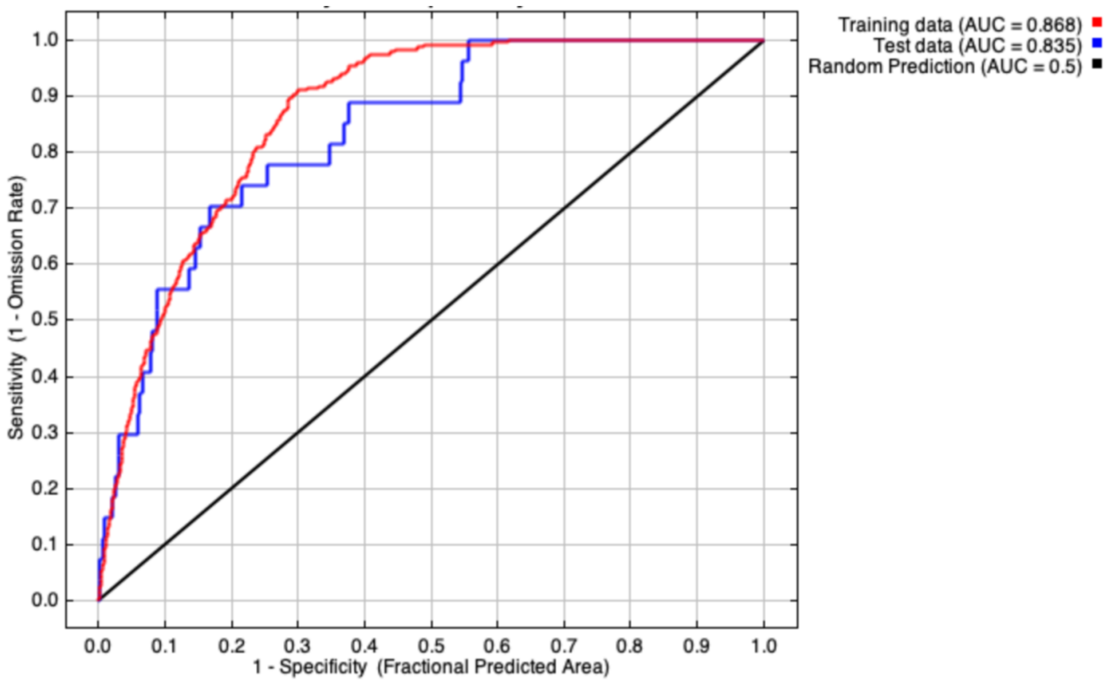

Figure 8: Receiver operating characteristics curve for the savanna Maxent model.

Figure 9 shows the six variables that had scores greater than 5 for either percent contribution or permutation importance. The algorithm generated predicts hyena are most likely to be found in habitats with little precipitation, closer to protected areas, either in close proximity or far from water sources, cooler minimum temperatures ranging around freezing, cooler mean temperatures, and lower elevations.

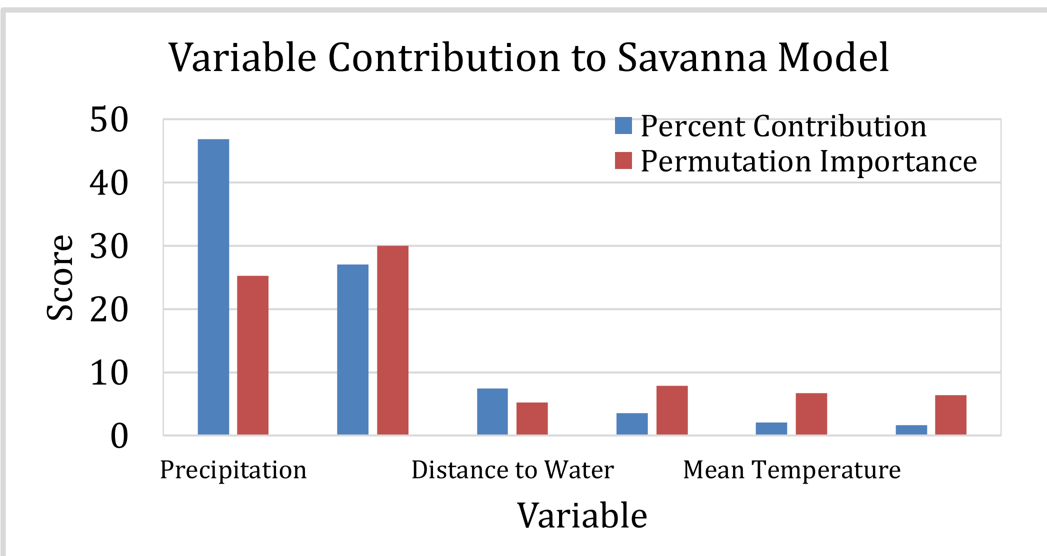

Figure 9: All variables with a score greater than 5 for either percent contribution to the savanna model or permutation importance.

IV. Desert Model

The desert model produced a prediction of habitat probability based on the correlation between presence training points and the environmental variables' values at each point that fell within the desert biome. Regions of Namibia and Botswana were predicted as probable habitat while much South Africa and Angola are predicted to be less suitable (Figure 10).

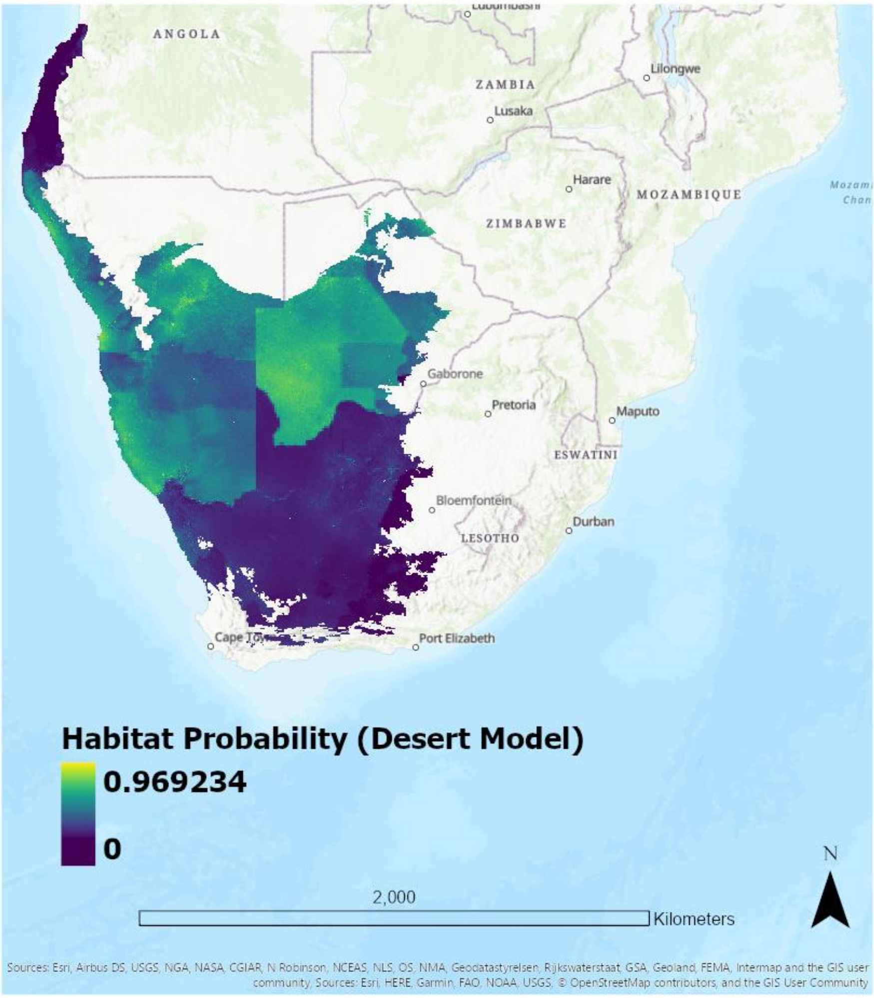

Figure 10: Habitat probability across the Deserts and Xeric Grasslands biome. Scores of 0 (blue) are areas predicted to be unsuitable for hyenas; greatest scores (yellow) indicate areas most likely to serve as habitat.

The greatest probability Maxent calculated was 0.969, indicating no pixel can be labelled as habitat with 100% confidence. AUC scores 0.784 and 0.735 are the lowest of the three models, but still higher than a random prediction (Figure 11).

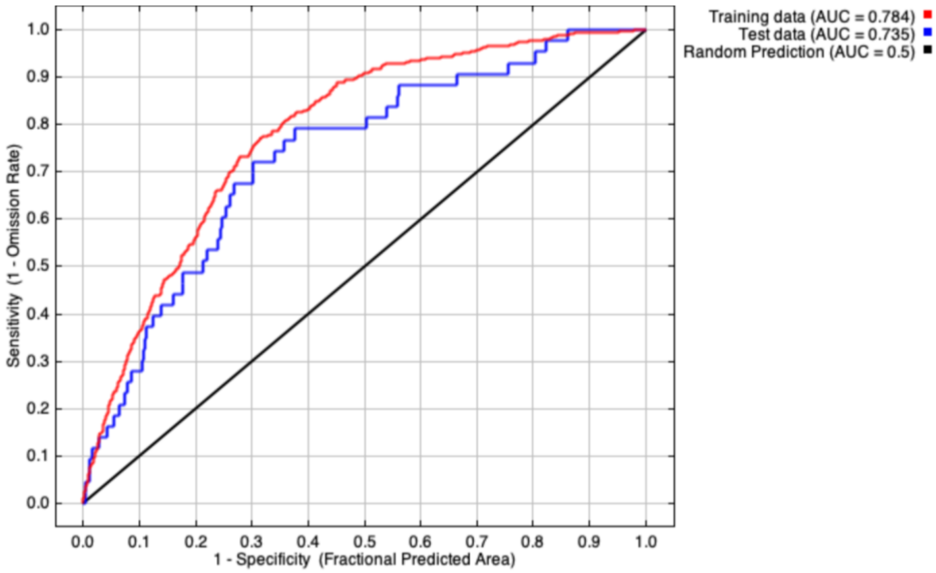

Figure 11: Receiver operating characteristics curve for the desert Maxent model.

The desert biome model predicts hyena are most likely to be found habitats with minimum temperatures around five degrees, higher relative tree cover, closer to protected areas, and higher urbanization. The desert model had a stark difference in the variables that contributed information to the algorithm and the variables with a high permutation importance (Figure 12). Sheep and cattle density did not contribute to the model, but their permutation scores indicate there is a strong correlation between hyena presence and lower density of both livestock species.

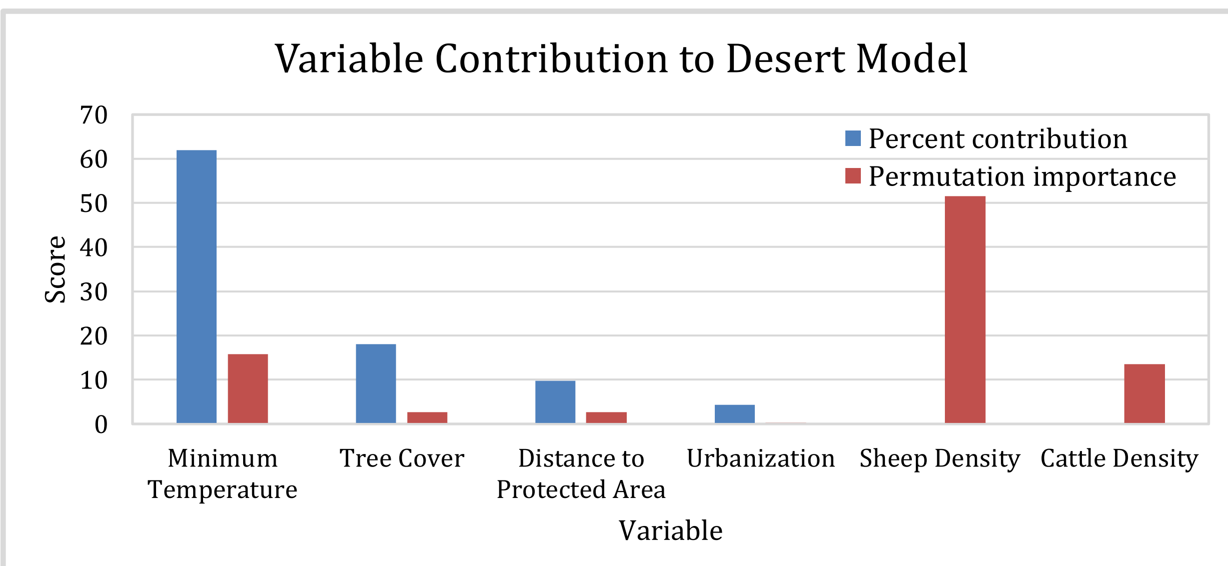

Figure 12: All variables with a score greater than 5 for either percent contribution to the desert model or permutation importance. Urbanization scored at 4.4 for percent contribution but is included in this graph because it has further implications.

The sensitivity analysis did not indicate that the desert model's prediction of inland habitat was influenced by the presence points along the coast (Appendix I). Model comparison proceeded between the general model and the desert model including the presence points from animals along the coast.

V. Model Comparisons

Subtracting the biome predicted habitat from the general model predicted habitat identified areas in which the models disagreed most strongly. Based on the contributing variables of the general (Figure 6) and sub models (Figures 9 and 12), we can explain why different levels of modeling produces such different results.

Overall, the model of the entire study area generated higher probabilities of habitat across much of the desert biome. The few areas that the desert model predicts greater habitat are driven by urban land cover and tree cover. The majority of the difference between the two models is information provided by sheep density. Variation in sheep density is due in part to human activity and is therefore subject to human constructs in addition to ecological factors. In Figure 13, the Namibian border appears clearly as this line relates to shepherding practices.

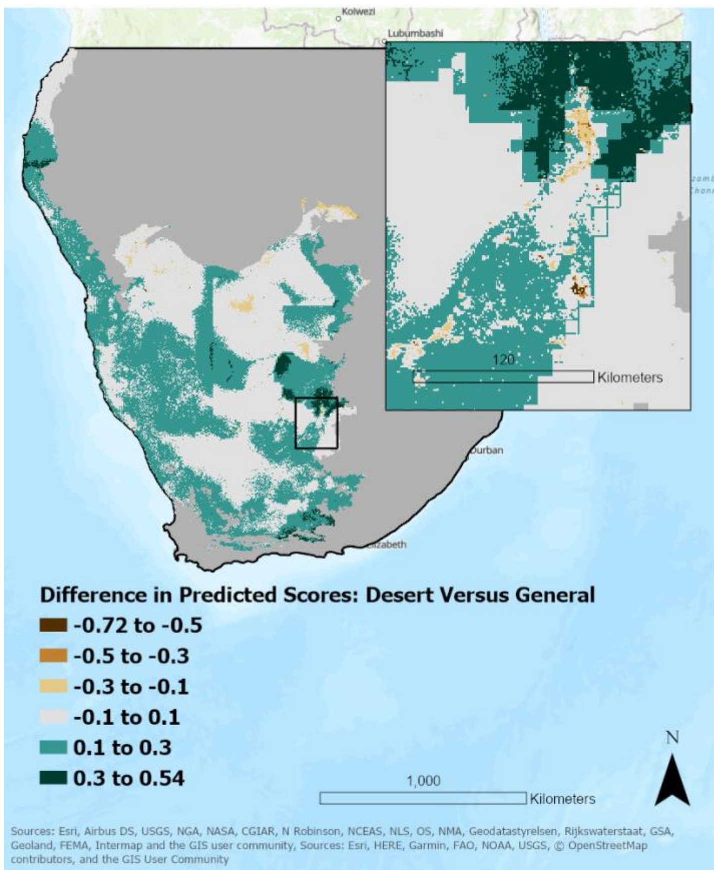

Figure 13: Difference in habitat probability predictions between the desert model and the general model. Areas in brown had higher predictions of habitat in the desert model. Areas in teal had higher predictions in the general model. White indicates pixels that had similar predictions of habitat probability.

The primary cause for higher probability in the savanna biome model compared to the full model (Figure 14) is the importance of the distance to protected areas variable. The model of savanna habitat predicts that brown hyena are more likely to be found closer to protected areas, visible in the southeast region of the study area. The majority of teal regions in the northwest are further from protected areas that the global model predicted to be more probable habitat but the biome model did not. Conversely, sheep contributed a much greater amount to the global model than the savanna model. Overall, the two models resulted in very different predictions across the savanna biome. The two models consistently provide similar results only for the northern region in the study area which is largely north of distributional limits of the species.

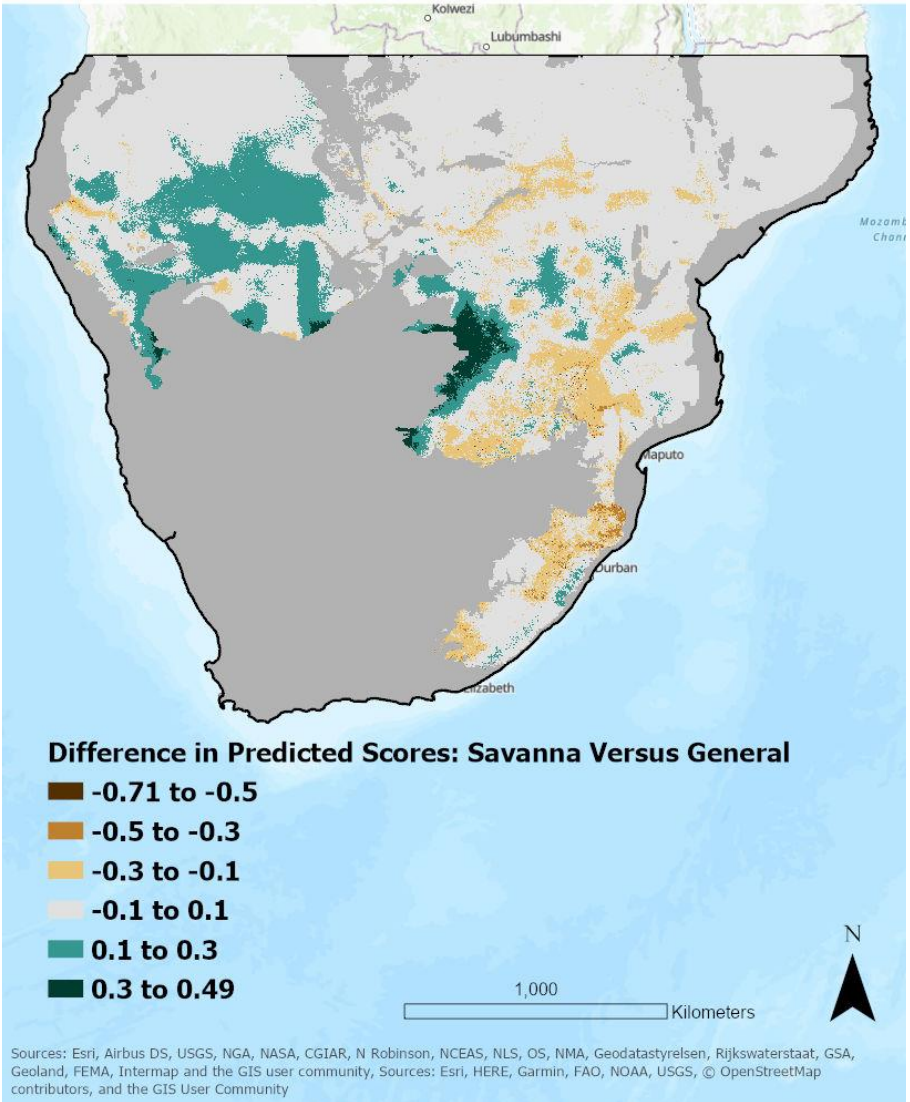

Figure 14: Difference in habitat probability predictions between the savanna model and the general model. Areas in brown had higher predictions of habitat in the savanna model. Areas in teal had higher predictions in the general model. White indicates pixels that had similar predictions of habitat probability.

Discussion

This analysis serves as the first range-wide species distribution model of the brown hyena (*Hyaena brunnea).* The set of models revealed new information regarding its distribution and ecology including a stronger affinity displayed by hyenas in the desert for tree cover and a similar affinity of savanna dwellers for protected areas. In addition, modeling brown hyena distribution at different geographic levels identified some pitfalls in modeling a generalist species. The biome level models generally revealed more specific relationships between hyenas the environmental variables including tree cover and protected areas. However, in one instance, the general model benefitted from more information and avoided a misleading correlation between urbanization and hyena presence.

The general, savanna, and desert models were all evaluated to have high performance based on the presence data and pseudoabsence background. If the goal of this analysis were to simply identify regions of potential habitat, any one of the models could be accepted as a solution. However, modeling habitat at different levels allows us to assess their ecological fit in addition to their statistical performance. Here I discuss how the models assigned weight to different variables of note and the subsequent implications these variables have on model fit. I also address a number of limitations to this analysis and make a few suggestions for future research.

Tree cover

Tree cover may be the most interesting variable across the three models. The desert model ranked it as the most important with a percent contribution of 18% and permutation importance of 2.6 (Figure 12), while the global model found it 1.5% and 2.2 respectively (Figure 6). The savanna model ranked tree cover as 0.7 percent contribution and 4.7 permutation importance (Figure 9). By far, the desert model weighted it the heaviest. Furthermore, each model found a different correlation between percent tree cover per pixel and hyena presence. The desert model showed a positive, linear correlation as tree cover increased from 0 to 60% across the biome (Appendix III). The general model found a quadratic relationship that peaked at 40% tree cover and had lower predictions of habitat for 100% cover versus 0% (Appendix III). The savanna model found an opposite relationship to the desert model; hyena presence had a linear negative relationship with increasing tree cover from 0% to 100% (Appendix III).

The cause for such drastically different correlations is likely biologic. In the desert, tree cover and vegetation as a whole are much scarcer (Buchhorn, 2019). Brown hyena may seek out tree cover as relief from the sun or as cover for denning (Mills & Hofer, 1998). Trees may also serve as territory markers or other communication between individuals (Mills & Hofer, 1998). In the savanna, tree cover is more common, denser, and likely a less limiting factor (Buchhorn, 2019). If hyenas have more opportunities for denning, respite, and communication, they may not seek out tree cover as intensely. This is an example of how the biome level models provide more specific insights into a generalist species’ habitat than the general model. While the general model demonstrates the same relationship between hyenas and tree cover – preference for scarce but not absent– it fails to show how an individual in the desert is predicted to behave versus an individual in the savanna.

Protected Areas

The savanna model had attributed much more importance to proximity to protected areas than the desert and particularly the general model. There are a number of factors to consider when interpreting this phenomenon. Within the savanna biome, there is a wide range of distances to protected areas. In the southeast region, there are many small, disparate protected areas which decreases the overall distance between them. However, in the northwest, there is a large area in which no protected areas have been established and so the range of possible values for each pixel is large (IUCN and UNEP-WCMC, 2014).

The general model only gained 4.9% (Figure 6) of its information from the protected area layer while the savanna model gained 27% (Figure 9). At first glance, this may be due to the disparity between pseudoabsence points falling in the northwest region with higher distances to protected areas. Indeed, more pseudoabsence points would fall in pixels with higher distance scores in the savanna model than in the general model. The general model's permutation importance was 3.9 while the savanna model's was 30 (Figure 9); this indicates that the general model did not find nearly as strong of a correlation between proximity and presence. The pseudoabsence points could cause a stronger correlation between proximity to protected areas and hyena presence within the savanna biome, but it is unlikely that this alone is causing such difference between the scores.

There may also be a lingering observation bias in the savanna biome specifically. Because there so many smaller protected areas in the southeast, and these areas happen to coincide with higher population density, it is possible that hyenas are simply seen and reported more often. However, the majority of data points in this region were provided by formal research groups and similar research efforts provided occurrence data outside of the savanna biome. It does not seem that we can attribute the difference in variable importance to incidental observations.

It is worth considering ecological explanations for why hyenas in the savanna are more often found near protected areas than the average brown hyena. The savanna is a forgiving environment for human activity including farming and residency. The savanna model did show that while human modification was not an important variable on its own, brown hyena presence was negatively correlated with areas of greater anthropogenic influence. Brown hyenas may be utilizing proximity to protected areas to avoid persecution from humans actively impacting the environment including farmers and sheepherders (Mills & Hofer, 1998). Or perhaps the explanation is less direct. Other large carnivores may gravitate to these protected areas creating hotspots for foraging opportunities.

This analysis alone is not comprehensive enough to explain why hyenas in the savanna are more strongly correlated with proximity to protected areas. It may be due to the methodological constraints, but given the strength of the relationship, further research into the phenomenon should be pursued.

Livestock

Sheep and cattle play a different role between the global model and the regional models. Globally, values for both livestock species vary greatly with higher densities in the southeastern regions of the study area. At the biome level, the variation decreases significantly, causing these variables to contribute less to the models. In the desert model, though cattle and sheep did not contribute much information to the algorithm itself, there is still enough variation that the permutation importance for sheep and cattle were quite high, 44% and 14 % respectively (Figure 12). This indicates that though the model does not rely on these variables, brown hyena presence is still very much correlated with livestock density. However, in the savanna biome, there is much less variation for either species. Neither cattle nor sheep has a high percent contribution or permutation importance (<5%) (Figure 9). The general model gained 22% of its information from the sheep variable layer and was susceptible to a 31% decrease in AUC after random permutation (Figure 6). Because sheep are not as prevalent in the savanna (Gilbert et al., 2018), the global model may be predicting brown hyena habitat based on an irrelevant variable for this specific biome. This indicates that it is a less ecologically descriptive model, even if its predictions of habitat are ultimately sensible. Of course, without further presence or absence data, it is difficult to say definitively that its predictions are a better fit to hyena presence than the savanna model. It should also be noted that the livestock variables were the coarsest layers included. This is not ideal for a variable that has a disputed impact on brown hyena presence; proximity to livestock provides foraging opportunities but introduces anthropogenic persecution (Mills & Hofer, 1998). The general and desert model indicate that hyena presence is correlated with decreasing livestock density (Appendix III), but more research with better livestock density data could reveal more about this relationship.

Urbanization

The desert model shows hyena presence to have a positive correlation with increasing urban land cover (Appendix III). However, the global model shows a no relationship between hyena presence and urban land cover (Appendix III). Past research has shown that hyenas can survive near urban areas, but they do not commonly reside within them (Mills and Hofer, 1998). The relationship found in the desert model may be misleading. There is less urbanized area in the desert region (Buchhorn, 2019), but a few presence points do overlap with these pixels. The pseudoabsence points generated in the desert model are less likely to fall in the smaller urban areas than the points generated in the full model. Therefore, even the small number of presence points in desert, urban pixels could lead to a positive correlation within the desert biome. The global model benefits from more available information and may better describe the relationship between hyena presence and urbanization. At the very least, the global model has highlighted a flaw that should be accounted for in the desert biome model.

Study Limitations

The primary limitation of this study is a lack of presence data as well as unequal sampling effort throughout the study area. As with most research, better data would yield better results. Ideally, presence points would be obtained through a formal survey extending across the entire range. As this is near impossible, the current dataset could be reasonably improved by seeking occurrence records in areas known to be habitat that were not identified in this model such as the Kalahari Gemsbok National Park. Occurrence data should also be sought for regions that were predicted to be habitat but had few points to validate these predictions.

Species distribution models created in Maxent often carry a number of standard limitations. The test of model performance using AUC is based on the background generated by Maxent. Reserving records to use as test points can help provide a stronger test of true positive predictions of habitat, but the measure of false positives relies on pseudoabsences. While the AUC is still helpful in interpreting the model's strength, it can only describe how well the model fits the generated background data (Philips, 2009). In addition, both measures of variable importance are subject to changes depending on how Maxent builds the model. For example, a variable may have a low percent contribution because it was the last to be included in the model, and the model could not gain any new information from it. However, if it had been included first, it may have had a higher contribution (Kalle et al., 2013). Permutation importance is similarly dependent on the final algorithm. Changing the values of a variable that is correlated with hyena presence may not necessarily create a loss of AUC which would result in a low permutation importance (Kalle et al., 2013). Maxent models can also be limited by our understanding of the species ecology. If the most relevant environmental variables are not included, Maxent will nonetheless create a model that is potentially a strong fit. For example, if a species is dependent on an elevation gradient that is not included as a variable in the model, Maxent may instead indicate that the temperature variable is important instead (Philips, 2009).

Finally, home range size is a question of ongoing research within the Hyaena Specialist Group and should be considered a critical component of future modeling. This analysis assumed that home range size was informed by the habitat of an individual and that habitat was dependent on the specific biome. If home range could be determined for each point in the dataset, thinning could have been based on more tailored estimates rather than a blanket average.

Conclusion

Brown hyena play a critical ecological role as a member of the large carnivore guild, but they are understudied as a species. In order to predict how ecosystems will respond to anthropogenic pressures, climate change, and biodiversity loss, it is important to begin with a general understanding of all of an ecosystem's major factors. This analysis is a first step in describing how brown hyena are interacting with their environment as it varies across multiple biomes. It showed that brown hyenas in the desert are more likely to be found in areas with greater tree cover while hyenas residing in the savanna are more likely in areas with sparser tree cover. In addition, livestock density proved a useful predictor of hyena habitat across their range; they are more likely found in areas of lower density for both cattle and sheep. Hyenas in the savanna were also predicted to be found closer to protected areas than in other regions. Based on these findings, we not only have a stronger understanding of brown hyena ecology as a whole, but we can also demonstrate that brown hyena ecology does vary across its range.

Species distribution models are can aid a wide range of research and management goals, but they must be tailored to the species in question. This analysis demonstrates that a generalist species can display different ecology based on the specific biome it inhabits, and modeling a species distribution at different scales can reveal these differences. The global model was unable to describe the difference in correlation with tree cover between hyenas in the savanna and desert biomes. It also relied heavily on livestock as a predictor variable though this variable was not comparably relevant within the savanna biome specifically. However, the global model benefitted from greater information than the desert model and avoided predicting habitat based on a misleading correlation between increasing urbanization and hyena presence. This analysis demonstrates that a generalist's species ecology cannot be fully described by a single model. Modeling efforts that intend to describe a wide-ranging species should consider how individuals utilize habitat and select modeling scales that best fit any differences.

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Appendix

I. Sensitivity Analysis

Following the assertion that hyena ecology may vary between biomes, I performed a sensitivity analysis of the desert specific model to the proximity of individuals to the coast. Within the Desert and Xeric Shrublands biome model, the presence of cape fur seals may alter the types of habitat in brown hyena are predicted to reside. I removed any presence points within 60 miles of the coastline in the desert biome and ran the desert model again, using identical environmental variables and Maxent parameters. I then compared the two models (with and without coast individuals) to assess to what extent the coastal individuals influenced habitat prediction within the desert. Comparison was performed using the same raster subtraction method as the comparison between the desert and general model predictions.

The sensitivity analysis generated predictions of habitat probability (Figure 15) across the same range as the Desert and Xeric Shrubland biome model based on identical variables and parameters but a different presence dataset.

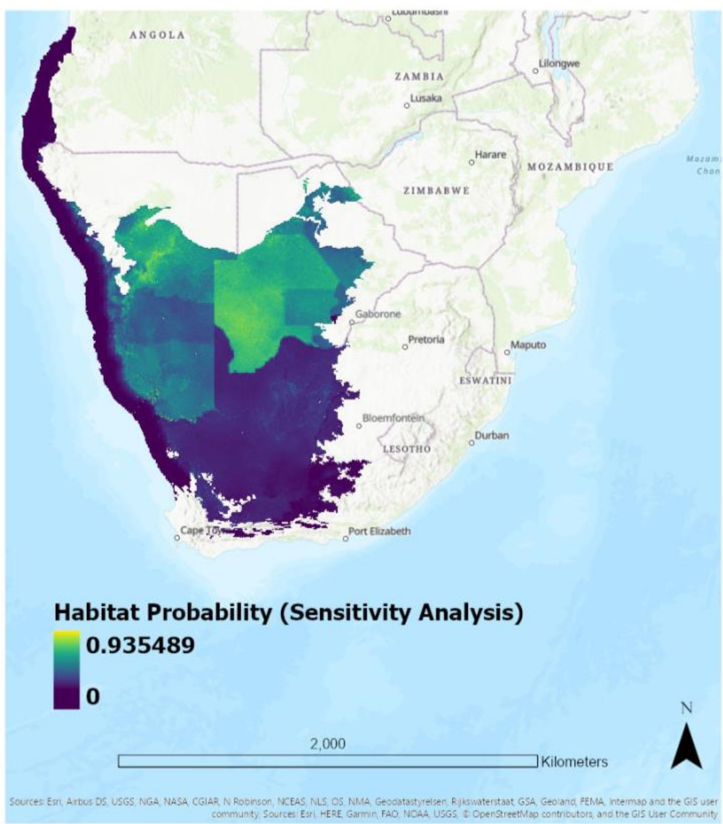

Figure 15: Habitat probability across the Deserts and Xeric Grasslands biome after exclusion of coastal individuals. Scores of 0 (blue) are areas predicted to be unsuitable for hyenas; greatest scores (yellow) indicate areas most likely to serve as habitat.

The model found that habitat along the coast was highly improbable after exclusion of presence points in this area. This is also due to the inclusion of the distance to coast variable layer, as no presence points fell within the defined 60 miles from the coast. This exclusion of the coast as predicted habitat was expected. Inland, habitat is still predicted as having a probability of up to 93.5%.

Differences in habitat prediction between the models falls almost entirely along the coast in which presence points were removed (Figure 16). Overall, the two models generated similar habitat predictions of inland desert.

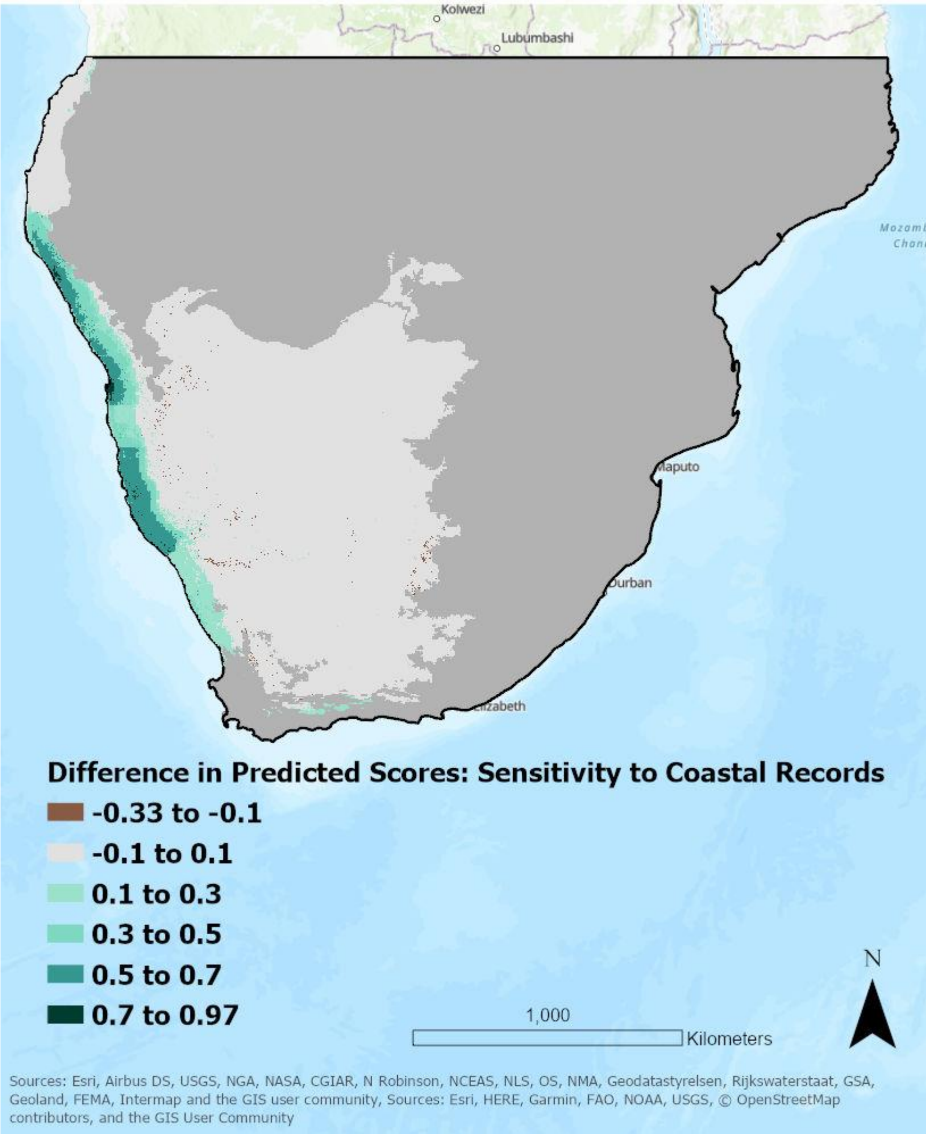

Figure 16: Difference in habitat probability predictions between the desert model and the sensitivity analysis model. Areas in brown had higher predictions of habitat in the sensitivity model. Areas in teal had higher predictions in the desert model. White indicates pixels that had similar predictions of habitat probability.

Implications

The sensitivity analysis did not indicate that the desert model is overly biased toward coastal individuals. Habitat prediction values across the inland region of the desert model were not significantly affected by the removal of coastal presence points in the model. The models with and without these points relied on the same variables to predict habitat except that the sensitivity model relied on distance to seal habitat to determine the coast as unsuitable habitat (Figure 16). Overall, there is no concern that the desert model was unreasonably altered by difference in ecology between inland and coastal individuals. Future efforts could examine if coastal habitat is better modeled separately.

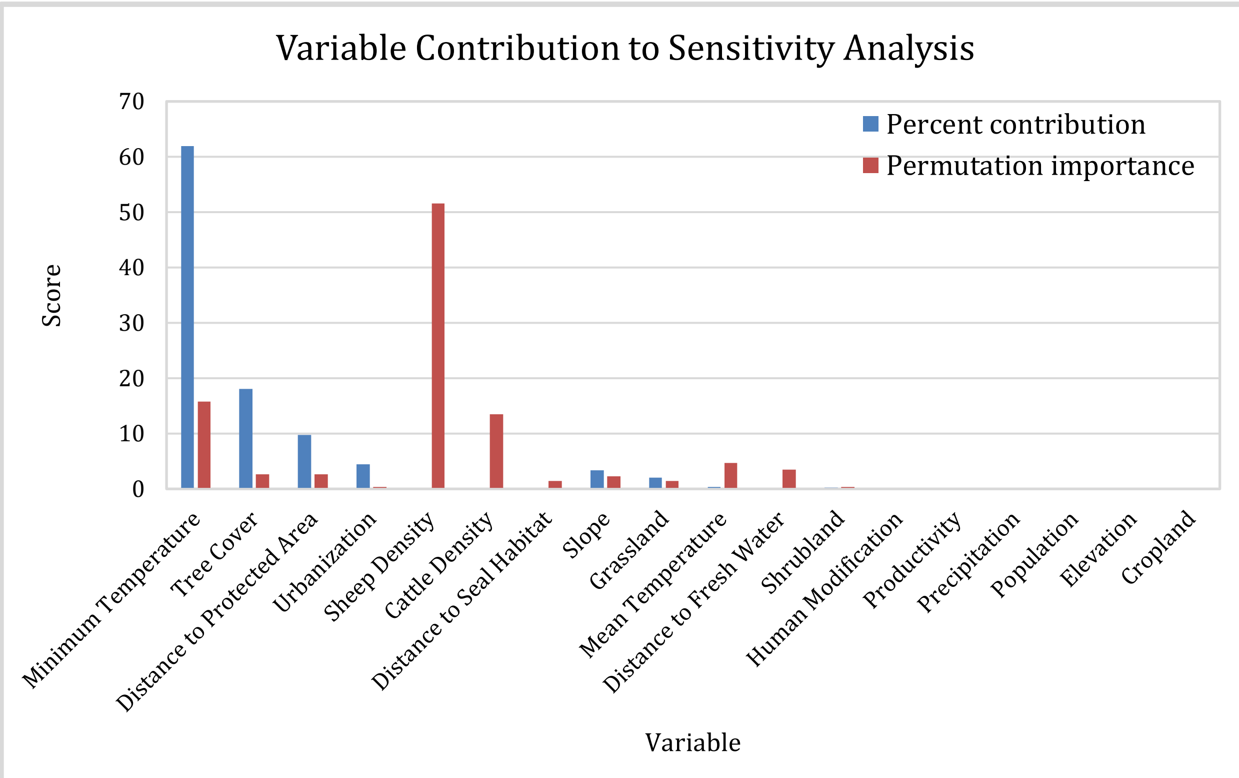

Figure 17: Percent contribution and permutation importance scores for all variables included in the sensitivity analysis model.

II. Variable Importance to Models

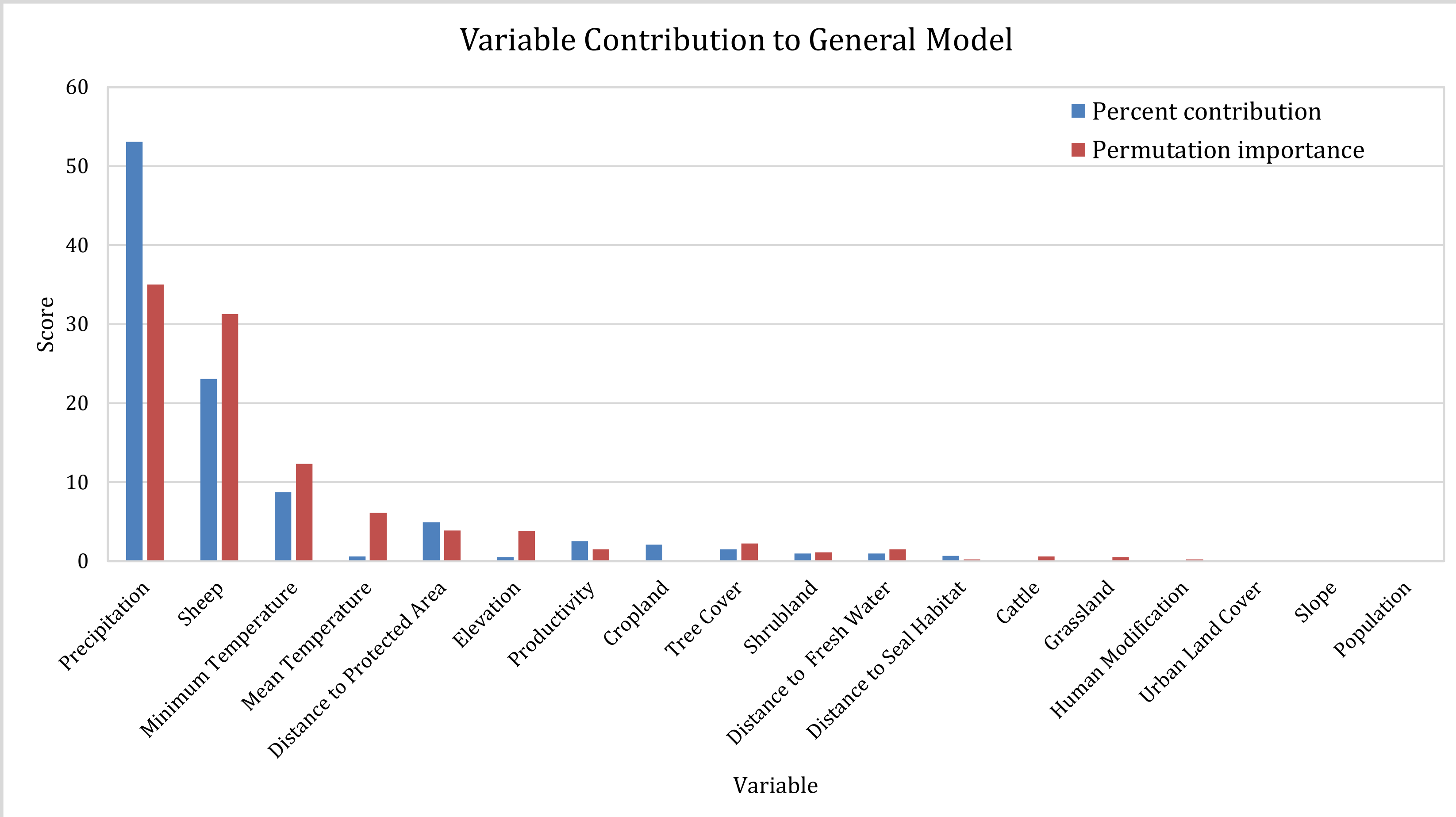

Figure 18: Percent contribution and permutation importance scores for all variables included in the general model.

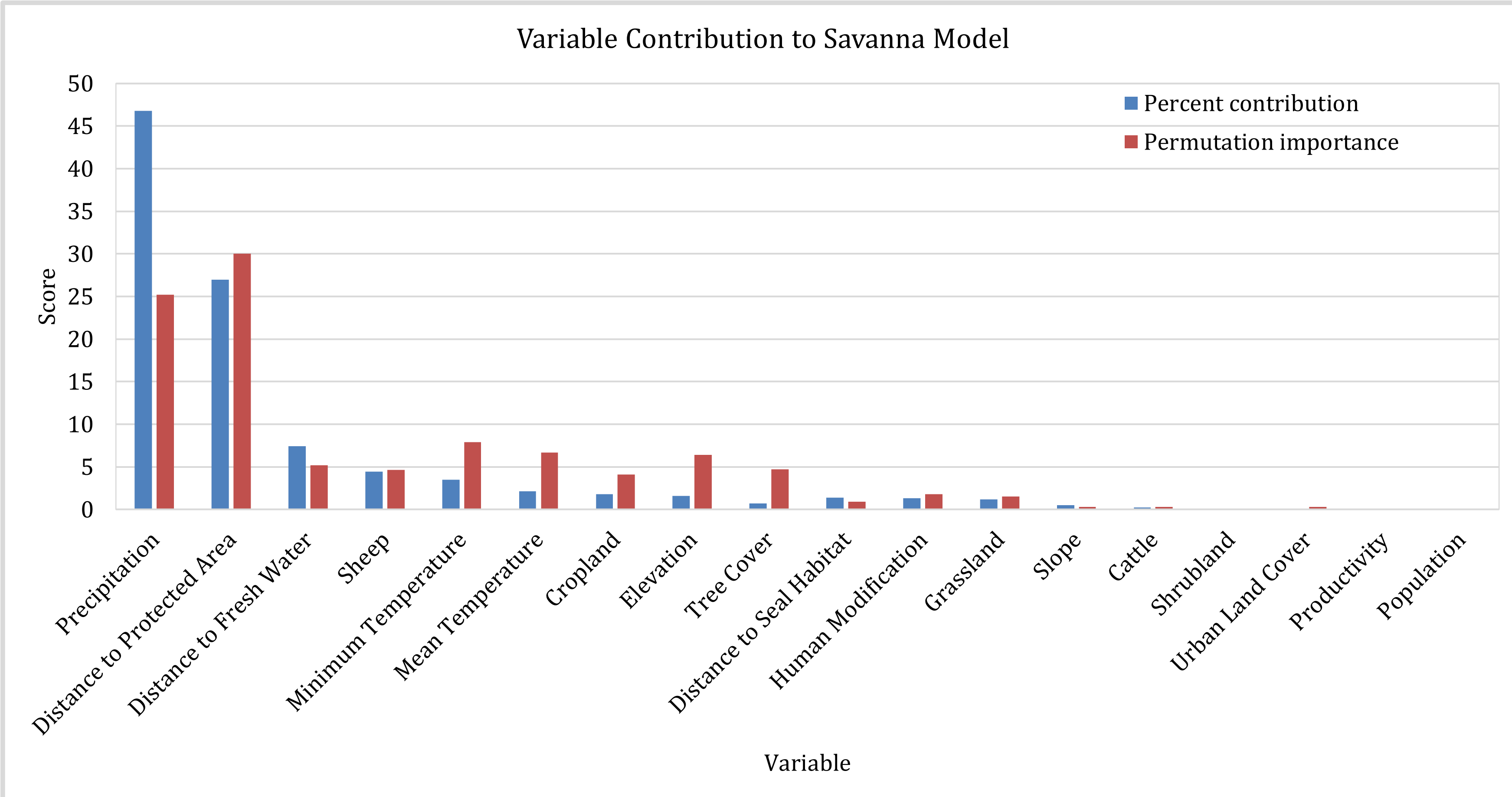

Figure 19: Percent contribution and permutation importance scores for all variables included in the savanna model.

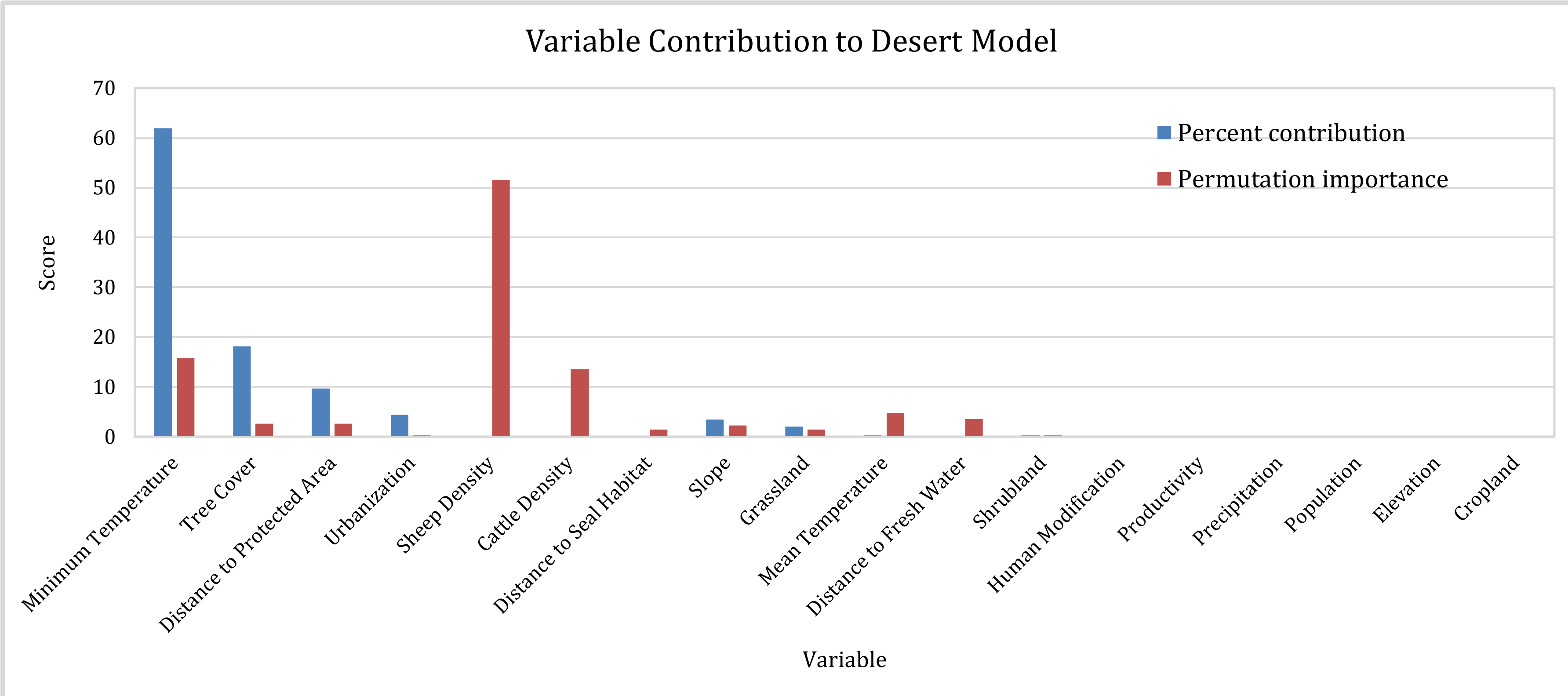

Figure 20: Percent contribution and permutation importance scores for all variables included in the desert model.

III. Response Curves of Each Variable Within the Three Models

Response Curve: Cattle

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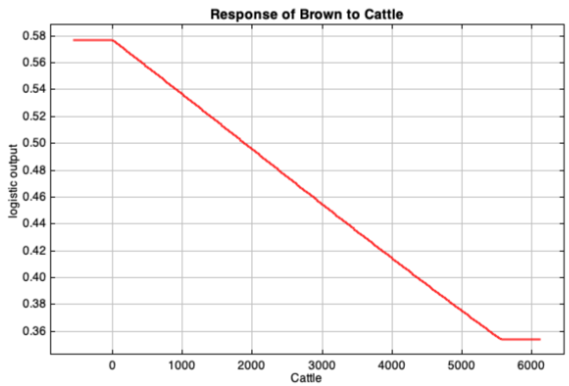
<td>
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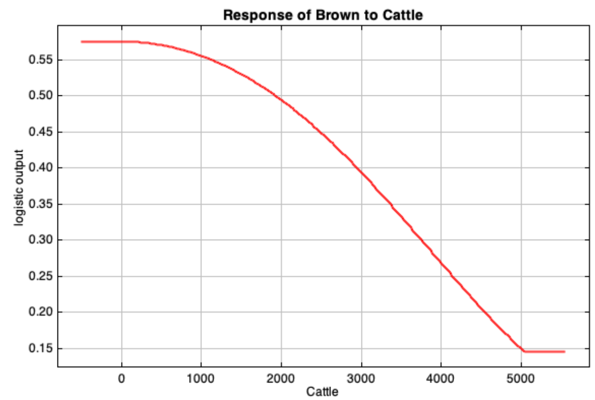
<td>
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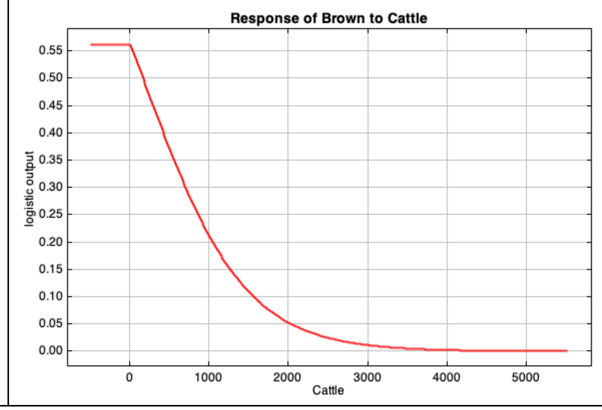
<td>
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Response Curve: Cropland

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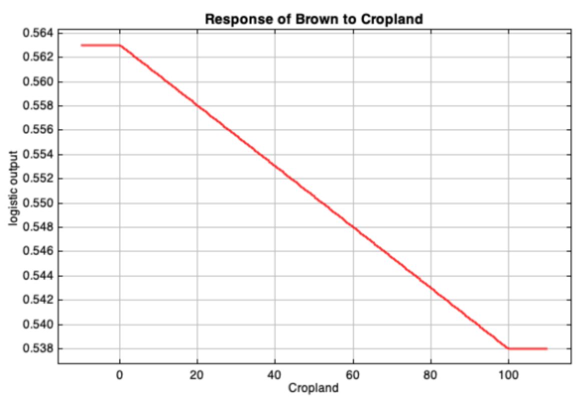
<td>
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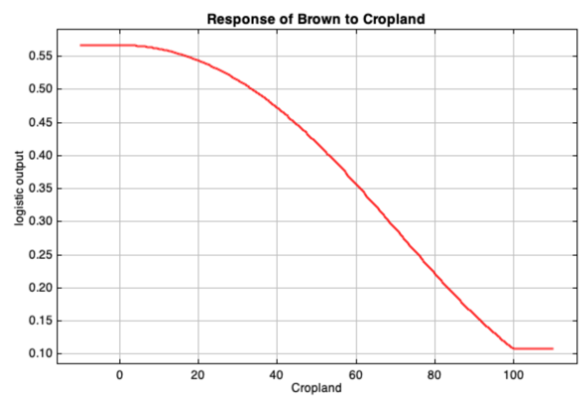
<td>
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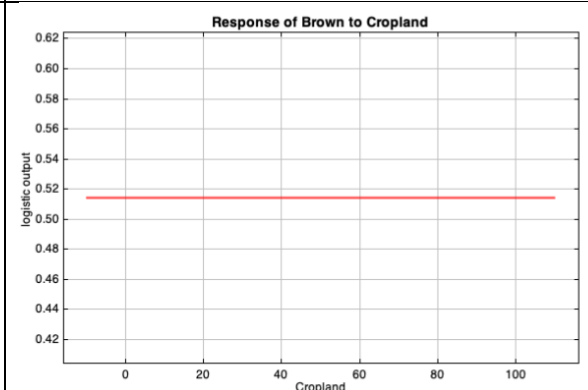
<td>
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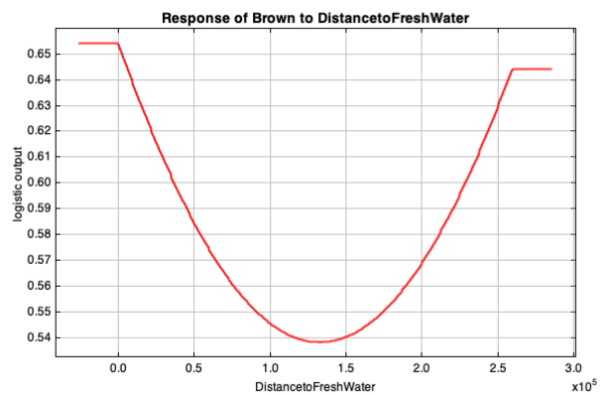
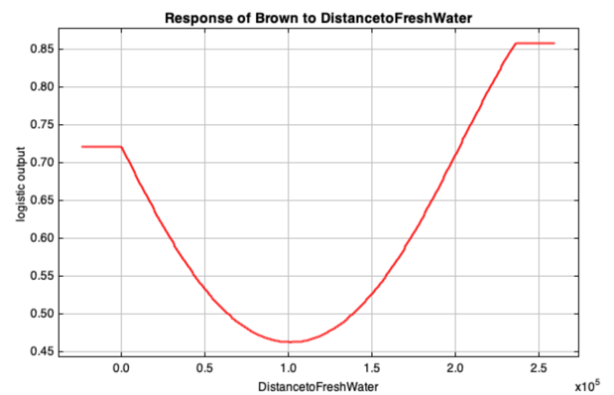
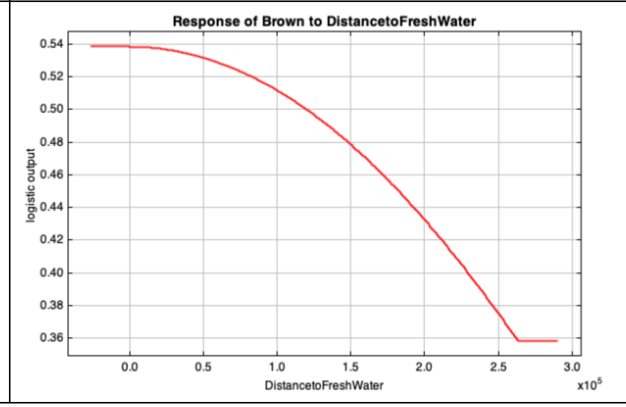
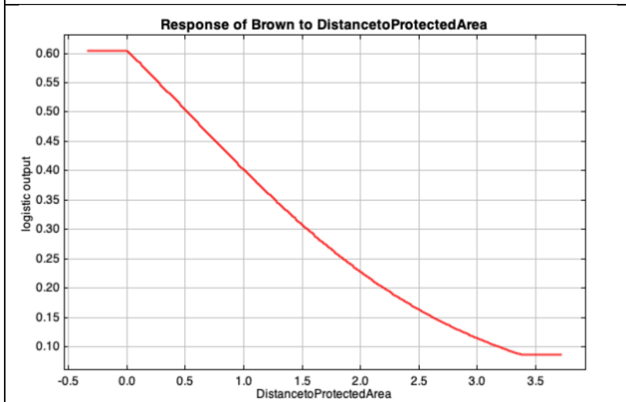
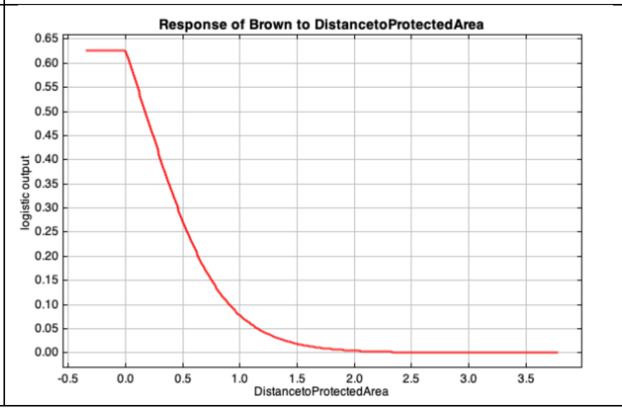
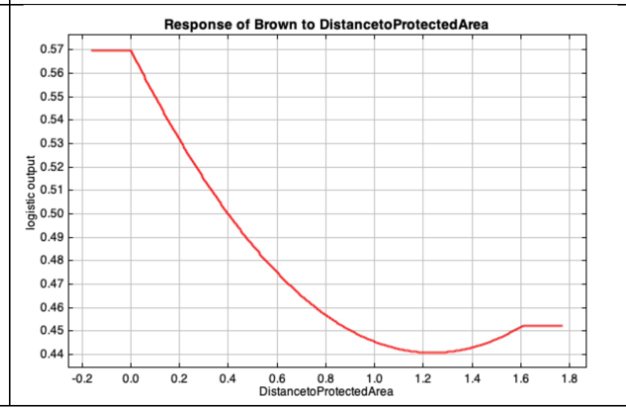
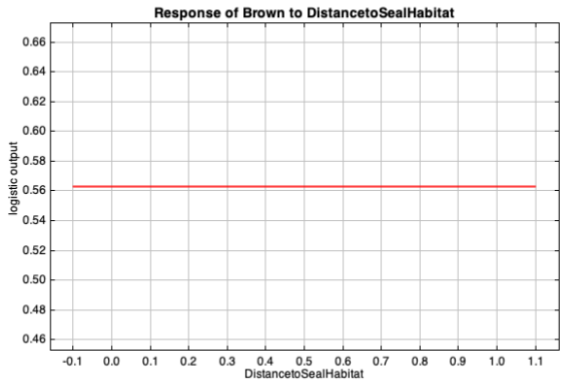
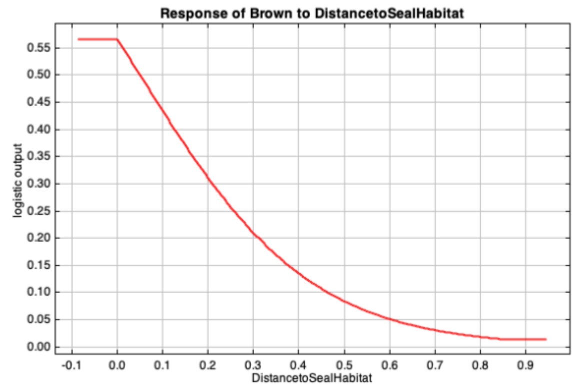
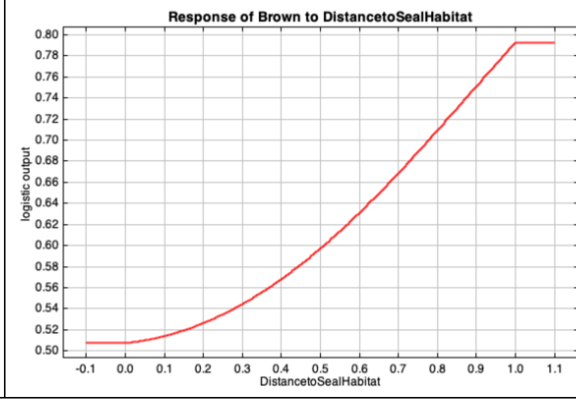
Response Curve: Distance to Fresh Water

General Model	Savanna Model	Desert Model
		

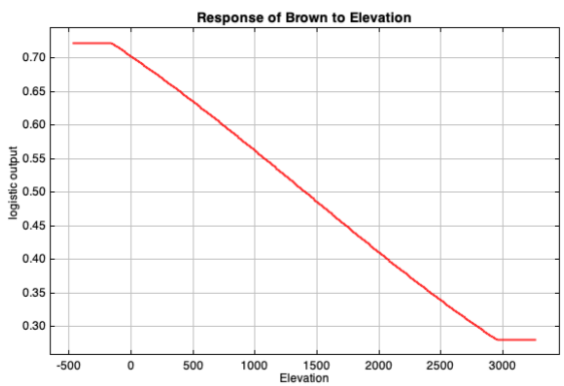
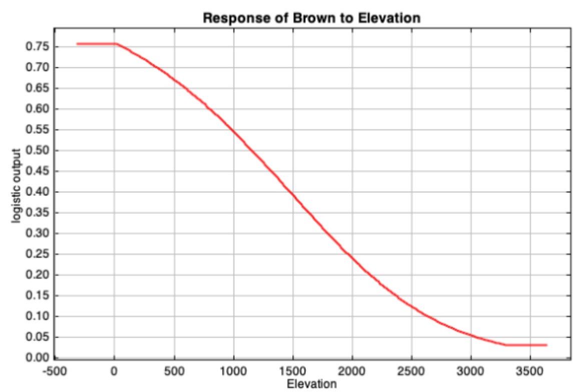
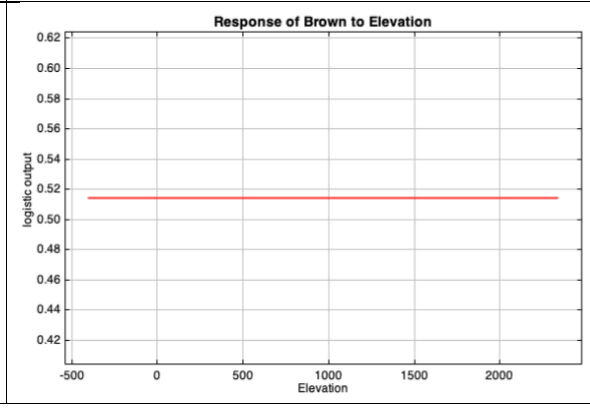
Response Curve: Distance to Protected Area

General Model	Savanna Model	Desert Model
		

Response Curve: Distance to Seal Habitat

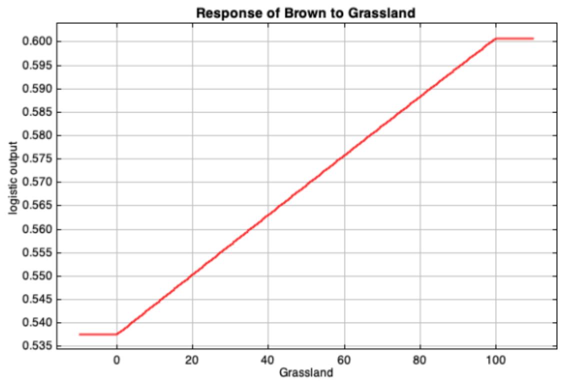
General Model	Savanna Model	Desert Model
		

Response Curve: Elevation

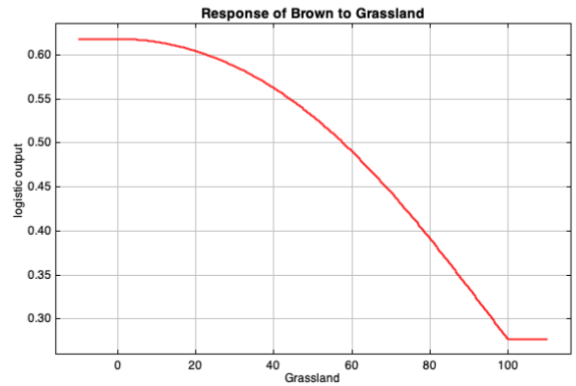
General Model	Savanna Model	Desert Model
		

Response Curve: Grassland

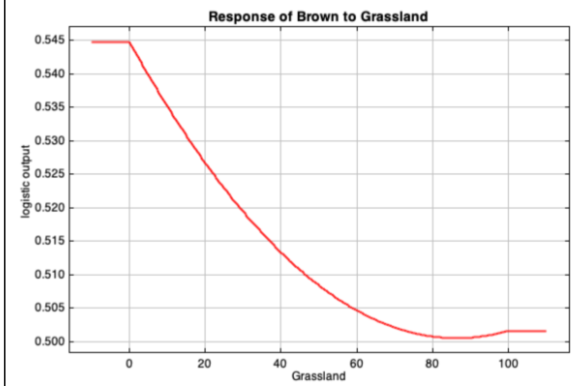
General Model



Savanna Model

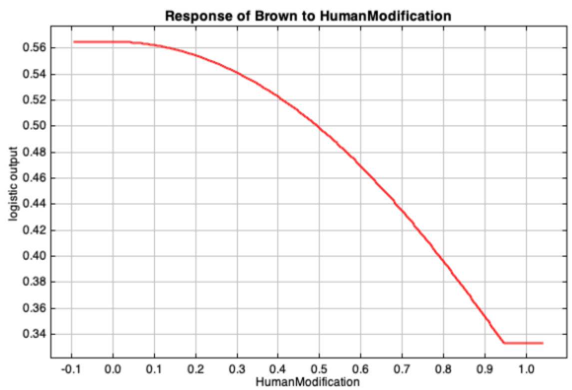


Desert Model

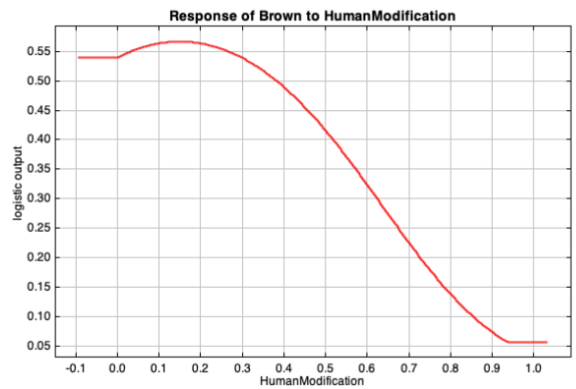


Response Curve: Human Modification

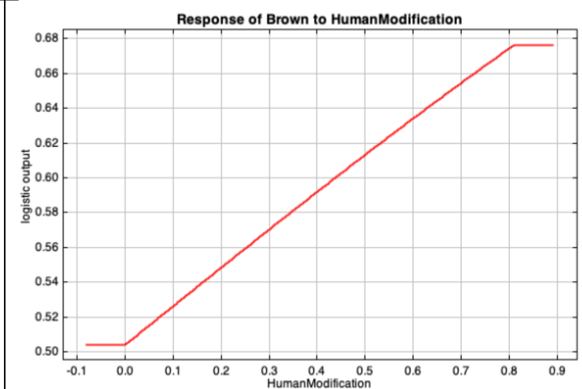
General Model



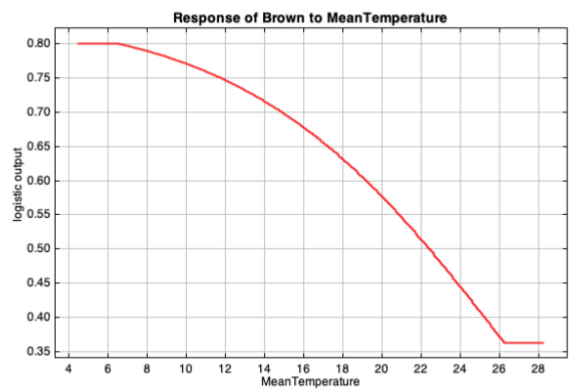
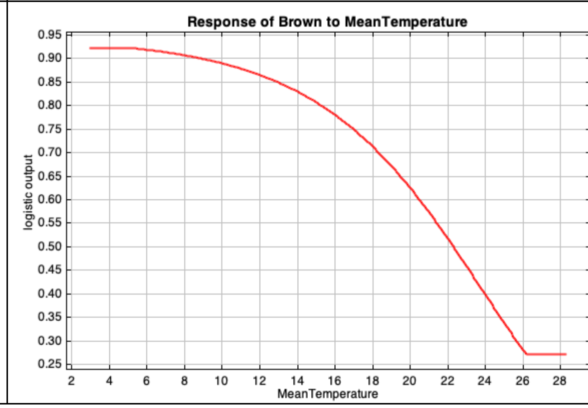
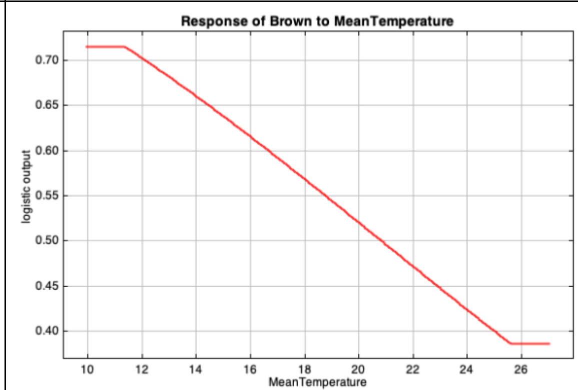
Savanna Model



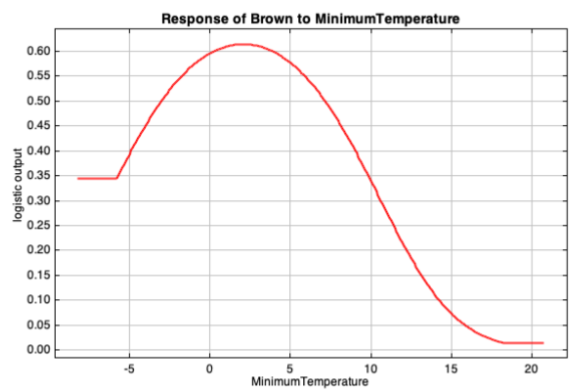
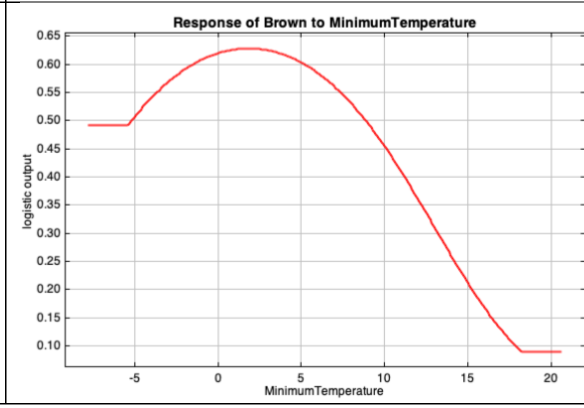
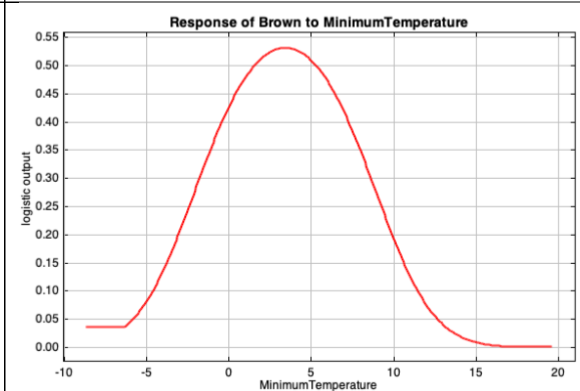
Desert Model



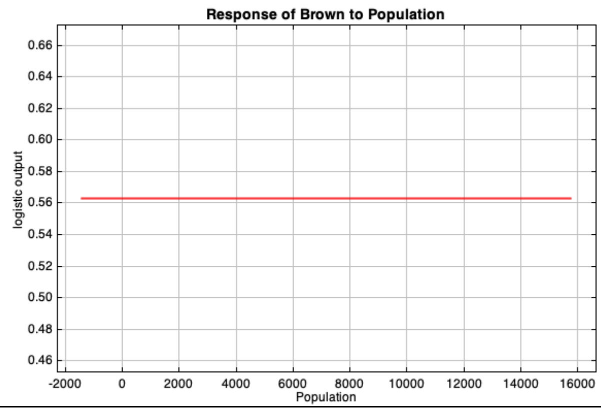
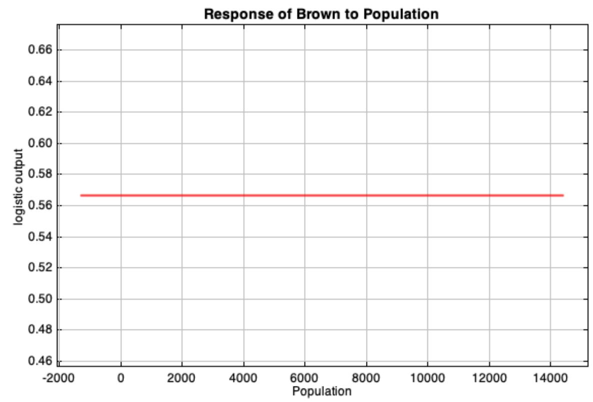
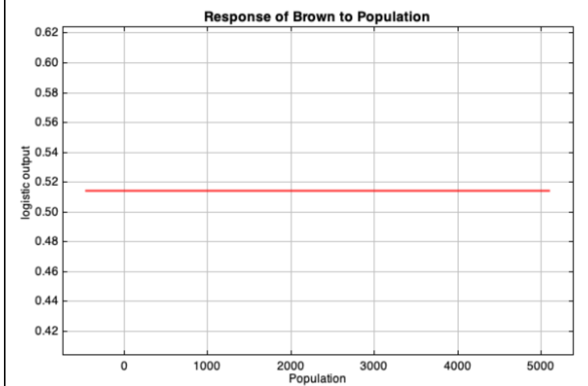
Response Curve: Mean Temperature

General Model	Savanna Model	Desert Model
		

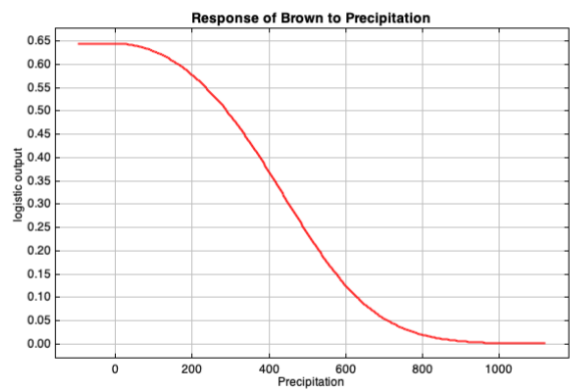
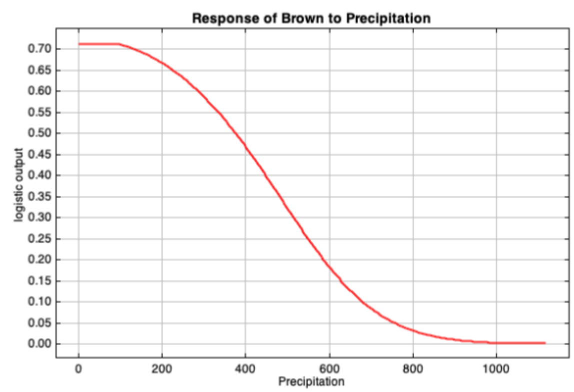
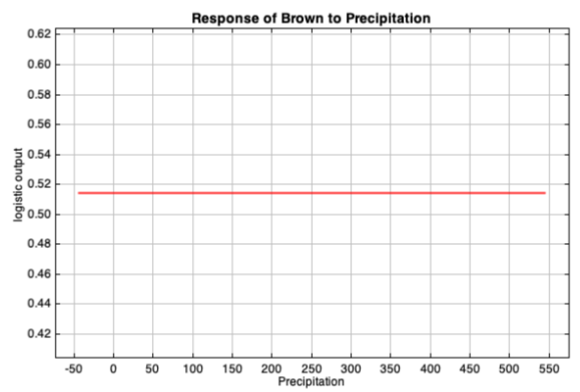
Response Curve: Minimum Temperature

General Model	Savanna Model	Desert Model
		

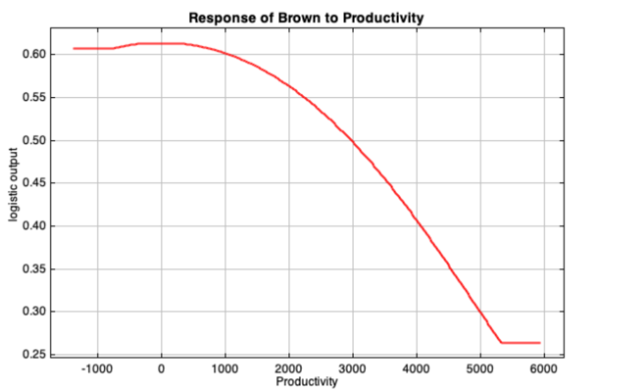
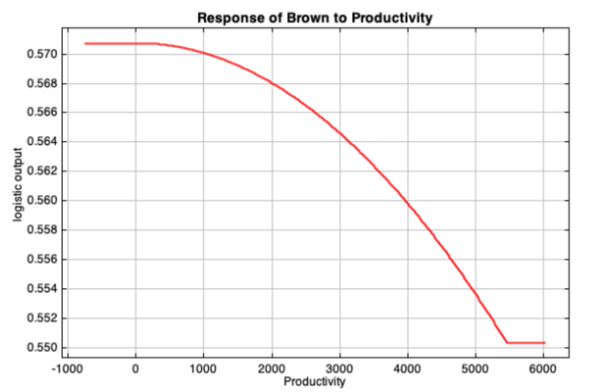
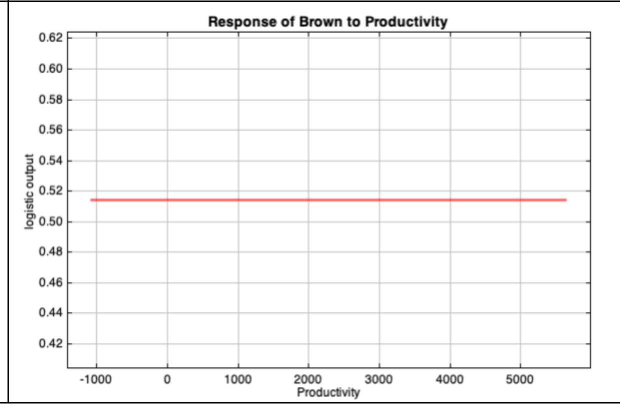
Response Curve: Population

General Model	Savanna Model	Desert Model
		

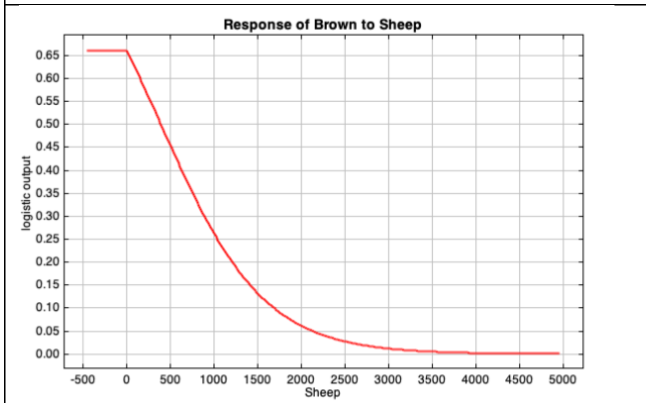
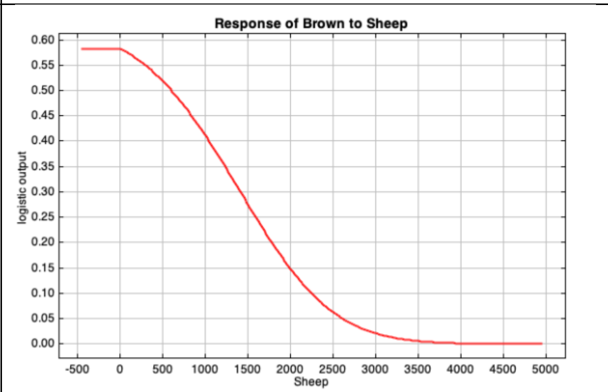
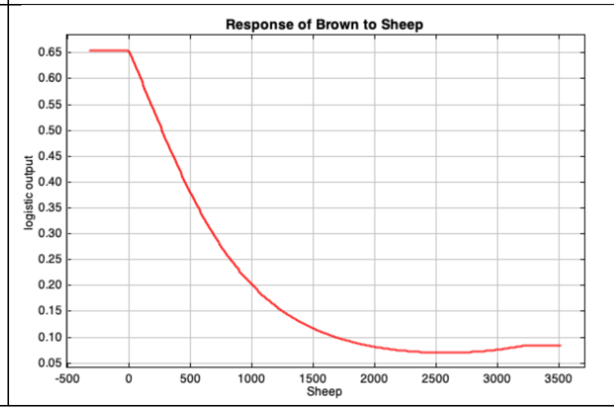
Response Curve: Precipitation

General Model	Savanna Model	Desert Model
		

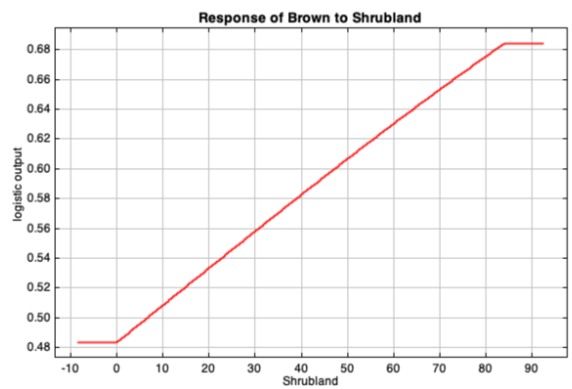
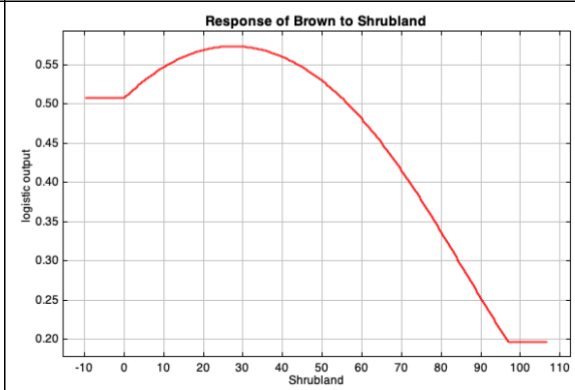
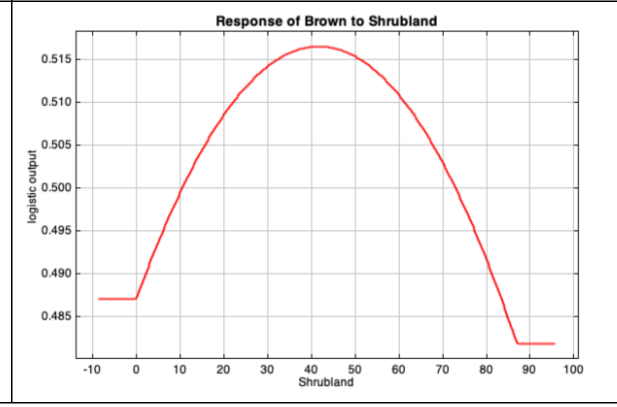
Response Curve: Productivity

General Model	Savanna Model	Desert Model
		

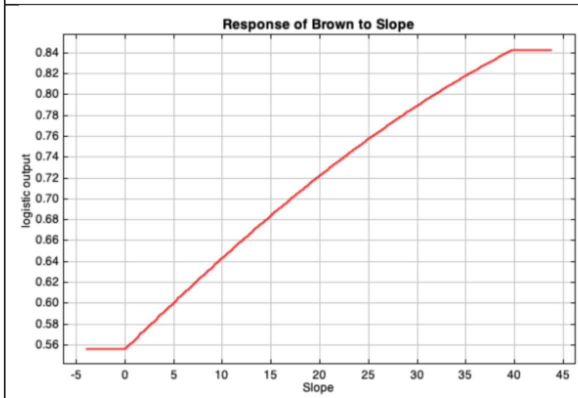
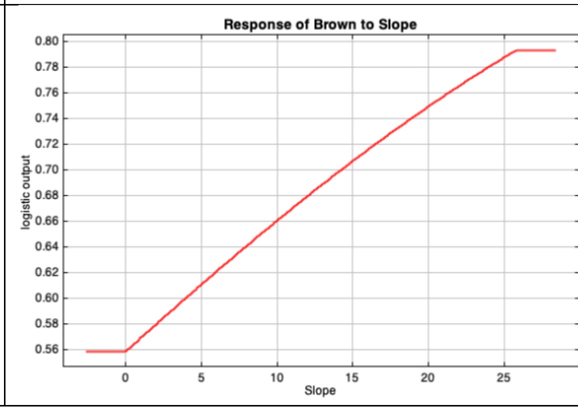
Response Curve: Sheep

General Model	Savanna Model	Desert Model
		

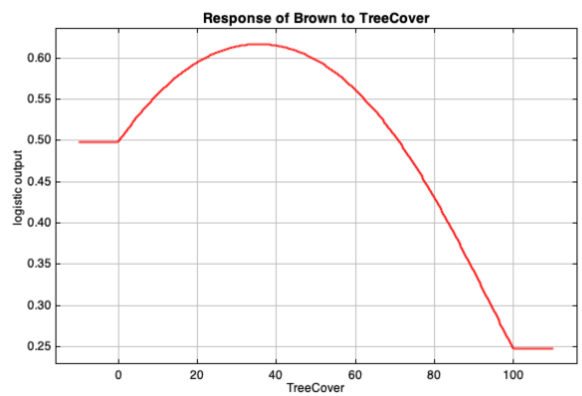
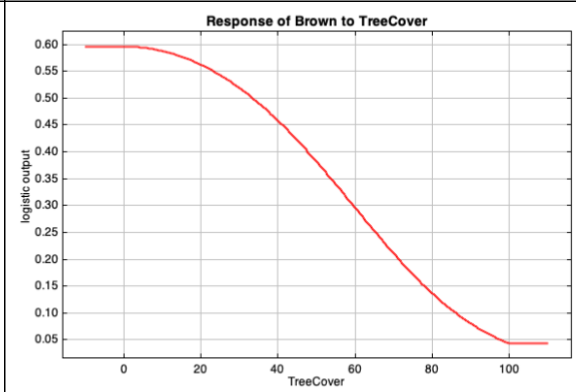
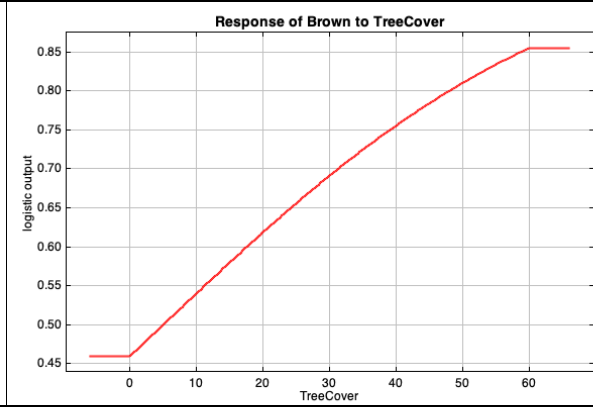
Response Curve: Shrubland

General Model	Savanna Model	Desert Model
		

Response Curve: Slope

General Model	Savanna Model	Desert Model
		

Response Curve: Tree Cover

General Model	Savanna Model	Desert Model
		

Response Curve: Urban Land Cover

General Model	Savanna Model	Desert Model