MANAGEMENT IMPLICATIONS OF SEX-SPECIFIC HABITAT USE BY

NYCTICEIUS HUMERALIS IN NORTH-CENTRAL ARKANSAS

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A Thesis presented to the faculty of Arkansas State University in partial fulfillment of the requirements for the Degree of Master of Science in Biology

MASTER OF SCIENCE IN BIOLOGY

ARKANSAS STATE UNIVERSITY
AUGUST 2018

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ABSTRACT

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The goal of this study was to evaluate evening bat (*Nycticeius humeralis)* habitat use and provide a proxy strategy to evaluate habitat use by other species. I used the software Maximum Entropy to evaluate habitat suitability models for evening bats using three different modeling strategies; percent variable contribution, the jackknife test, and variable response curves. The predictors included in the models were 10 land use land cover classes, four forest management strategies, three stand types, slope, and the normalized difference vegetation index (NDVI). The results showed that distance to burned stands and proximity to edge habitat are the most important habitat features when determining probability of presence of evening bats in the study site. Habitat suitability maps were also generated to predict evening bat presence other areas of the habitat. These predictions were successful according to field technician observations, lending credibility to the predictive power of this analysis software.

ACKNOWLEDGEMENTS

I want to express heartfelt gratitude to my committee members, faculty, lab mates, coworkers, as well as friends and family who have participated in any way during this long and difficult journey. I could not have done it without each and every one of you. I'd like to give a very special thank you to Dr. Youngsang Kwon of the University of Memphis for his assistance with the MaxEnt modeling, Philip Jordan of the United States Forest Service for the ArcGIS layers and maps, Daniel Istvanko and his field technicians for gathering these data, and Kyle Edmonds who provided priceless insight to the field sites. I am not particularly eloquent in any form or fashion but unambiguous appreciation is best given in person and through actions. With that, thank you all again for your unwavering support and companionship.

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CHAPTER I

INTRODUCTION

Bats comprise the second largest mammal order and fill an important ecological niche due to their small size and their ability to achieve true flight. Bats are valuable biological indicators because they are widely distributed and are taxonomically and functionally diverse (Jones et al. 2009). Worldwide, bats provide many ecosystem services, such as pollination, seed dispersal, and pest management. In the New and Old-World tropics, bats are responsible for the pollination of 750 species of plants (Dobat 1985). The most well-known of these plants is the agave, which is the key ingredient in the production of tequila. In North America, bats primarily provide pest insect control; it is estimated that insectivorous bats save the agricultural industry at least $3.7 billion per year (Boyles et al. 2011). Despite their value, bats are faced with numerous threats affecting their survival. Bats are sensitive to human-influenced changes in habitat quality and changes in climate (Fenton 1997). Additionally, the onset of a devastating disease, White-Nose Syndrome (WNS), habitat loss, and increased implementation of wind energy, have caused drastic reductions in populations worldwide (Larsen and Madsen 2000; Warnecke et al. 2012; Thogmartin et al. 2014; White-Nose Syndrome 2017).

White-Nose Syndrome

Bats in the United States and to a lesser degree, Europe, are currently facing devastating population decline due to a disease caused by the fungus *Pseudogymnoascus destructans,* this disease, White-Nose Syndrome is caused by a fungal pathogen of European origin that is devastating bat populations in North America. The recently discovered psychrophilic (cold-loving) fungus has consistently been isolated from bats that meet the pathologic criteria for WNS. These criteria include colonization of skin by fungal hyphae, which causes characteristic epidermal erosions and ulcers that may progress to invasion of underlying connective tissue (Wibbelt et al. 2010). White-Nose Syndrome, named for the striking white fungal growth of *P. destructans* muzzles, ears, and/or wing membranes of infected bats, is characterized as a condition primarily affecting hibernating bats (Blehert et al. 2009). Blehert et al. (2009) found that over half of infected individuals did not have the necessary fat reserves to sustain themselves through winter hibernation. Warnecke (2012) found that either starvation and/or loss of electrolytic homeostasis could potentially explain these losses. White-Nose Syndrome is spread through contact with the fungal spores on roost surfaces or between individuals. Current WNS morbidity estimates approach 7 million, impacting more than 200 hibernacula within 30 states and five Canadian provinces (United States Geological Survey 2017). Research on habitat, roosting ecology, and the home range of various species will expand knowledge of pathogen susceptibility, and allow scientists a greater chance of reducing bat mortality caused by WNS (Menzel et al. 2001).

While WNS is decimating bat populations in species across North America, bats that use caves for roosts and hibernacula, including tricolored bats (*Perimyotis* *subflavus*), Indiana bats (*Myotis sodalis*), little brown bats (*Myotis lucifugus*), and Northern long-eared bats (*Myotis septentrionalis*), appear to be the species most affected by WNS (Blehert et al. 2009). Tree-obligate bats, including evening bats, remain largely unaffected and therefore are important species to understand and protect as numbers of individuals of affected cave-dwelling species continue to decline. Pannkuk et al. (2013) found that evening bats have higher free fatty acid and lower sterol ratios in sebum than other species, which may have disease resistance implications. In addition to these differences in lipids from other bats, evening bats also show higher cholesterol. The high percentage of cholesterol in evening bats may be due to low percentages of lanosterol, considering that the lanosterol is a common intermediate in the biochemical conversion of squalene to cholesterol (Moran 2012). This difference in lipid content could also explain the peculiar odor that evening bats emit, especially the males. In addition to using tree roosts, evening bats can roost in underground cavities (Boyles et al. 2005) and may also roost in leaf litter on the forest floor (Moorman and Robbins 2007). The evening bat (*Nycticeius humeralis)* does not seem to be susceptible to WNS. This is primarily due to their roosting ecology because evening bats prefer to roost in trees whereas other species affected by WNS are cave-obligate during hibernation. Further study of evening bat habitat, home range, and roost characteristics will help researchers and land managers to better preserve species that are not experiencing dramatic declines due to WNS. Importantly as evening bats are unaffected by this disease, management of this species may be vital as they could be one of the only few not severely impacted by WNS and thus provide most of the ecological services provided by insectivorous bats in forests.

Forest Management Techniques

Forests that are well managed provide numerous benefits to the native flora and fauna in addition to aesthetically pleasing scenery and products of economic value such as paper products. Poorly managed forests are often unhealthy and unproductive due to overcrowding, disease, insects, and competition for light, water and nutrients among trees (North Carolina Forestry Association 2018). The Ozark-St. Francis National Forest, the study site for this research, implements four broad categories of management practices to maintain a healthy forest and provide suitable habitat for wildlife.

The first management category is tree harvest in which some trees are removed to harvest timber for commercial use, attract certain species of wildlife, and improve access to areas for recreational users. The first method of tree harvest includes a thinning harvest where a land manager removes trees in the early stages of growth (~10-15 years of age). This reduces competition amongst trees for water, sunlight, and nutrients as well as promotes understory growth. The understory includes weeds and wildflowers that are important food items and cover for wildlife. The second harvest method is clear cutting, wherein all trees in a stand are removed. When applying this method, all canopy cover is removed. This creates edge habitat and foraging opportunities for insectivores and wildlife that eats perennial plants and low grasses as well as the carnivores that hunt them. The third harvest method used by the Ozark-St. Francis National Forest is a shelterwood harvest. Shelterwood harvests remove mature trees in two or three harvests over 10 to 15 years. This management strategy allows shade-tolerant species to thrive as a "shelter" of larger trees' canopies are left to protect the shade-tolerant species from direct sunlight. This encourages young trees to grow and develop with the decreased competition for sunlight, water, and nutrients.

The second management category includes prescribed burning, which is performed often in the Ozark-St. Francis National Forest. Prescribed burning provides benefits to the forest such as removal of detritus to reduce fuel for wildfires, allows for the growth of new foliage, and decreases the spread of disease and pest insect infestation (North Carolina Forestry Association 2018). Silviculture is the third management category that includes activities such as weeding, pesticide use, and herbicide treatment. The fourth category, reforestation, can be accomplished by natural and/or artificial regeneration. Natural regeneration allows the forest to regenerate without human interference after a harvest. New trees are grown from seeds that are transported by animals or the wind or by seeds that drop from mature trees to grow nearby. Artificial regeneration is a method by which land managers plant seedlings or seeds. This method allows for greater control over tree placement and the tree species that are present in the forest. It also results in a more productive stand in less time.

Effects of Forest Management on Habitats

Forest management impacts bats and their habitats both directly and indirectly through forest composition. Aging stands have different structural characteristics when compared to new growth stands. New growth stands do not provide an adequate selection of roost sites. For example, there is greater distribution and availability of roosts in older stands due to an increased presence of large-diameter snags and trees. Older stands may have more complex vertical strata, presenting more foraging opportunities than young forests (Burford et al. 1999). Alternatively, open habitat, such as meadows and young stands (< 10 years), lack clutter and are directly used as activity and foraging areas but also indirectly provide more prey (Muller et al. 2012).

Most bat species in North America tend to avoid using highly cluttered habitat (Lacki 2007), thus forest management can directly influence habitat suitability. Evening bats have a low aspect ratio which is associated with low maneuverability during flight, and high wing loading that is related to fast flight speed (Findley et al. 1972; Lacki 2007). Therefore, evening bats frequently use edge habitat for commuting and foraging, presumably because of low tolerance to clutter due to morphological characteristics in combination with prey availability (Furlonger et al. 1987; Clark et al. 1993; Walsh and Harris 1996; Wethington et al. 1996; Grindal et al. 1999; Zimmerman and Glanz 2000). Therefore, management of edge habitat is of paramount importance to forest managers who wish to positively impact some forest bat populations.

Prey abundance, and therefore availability, is influenced by management practices such as prescribed fire, timber harvests, silviculture practices, and reforestation efforts (Lacki 2007). These changes occur directly through tree mortality or indirectly by changes in soil properties and/or vegetation characteristics (McCullough et al. 1998). Some studies have examined influences of forest structure and forest management on insect populations, showing that regional variation in insects and forest structure after prescribed burns precluded determination of general patterns that are useful for predicting bat response to fire (Burford et al. 1999; Humphrey et al. 1999; Lewis et al. 1999). Some of the structural implications of prescribed fire mimic those of thinning (Peterson and

Reich 2001). For example, a reduction in forest understory results in less clutter through which bats must navigate to travel and forage (Webala et al. 2011).

Forest management practices also influence the availability and quality of aquatic habitat, which is crucial to some bat populations. Bats have relatively high rates of evaporative water loss and consequently require a comparatively greater intake of water to maintain their water balance (Kurta et al. 1989; McLean and Speakman 1999; Webb et al. 2009). Various studies have shown that riparian zones have high levels of foraging and commuting activity, which is most likely due to high insect density and the availability of water (e.g., Racey and Swift 1985; Brigham and Fenton 1991). For an aquatic habitat to be suitable, it must include two important features; 1) a smooth water surface, which reduces acoustic clutter associated with riffles, that does not produce a high frequency sound like fast-moving water, and 2) forest cover in riparian areas, which is directly influenced by forest management practices. Evening bats in particular are very responsive to a variety of forest management techniques and thus allow researchers to examine the effects of these management practices on these and similar species.

Study Species

The evening bat is a medium-sized vespertilionid with a geographic range that extends from the Gulf of Mexico to the southern Great Lakes (Watkins 1981; Kurta et al. 2005). This species is easily identifiable by its dark coloration of both skin and fur. It resembles a smaller version of the big brown bat (*Eptesicus fuscus*), but is distinguishable by its two upper incisors as opposed to the four of the big brown bat. Evening bats begin to forage for insects such as beetles, moths, and leafhoppers shortly before or after sunset (Sealander and Heidt 1990; Whitaker and Clem 1992). These bats are bimodal in their hunting patterns with a spike of activity immediately after leaving the roost, with little activity throughout the night, then another peak of activity 9-10 hours after sunset (Whitaker and Clem 1992). These bats prefer to hunt over water, but will hunt above the tree line (>30 meters) until it becomes completely dark (Menzel et al. 2005; Vindigni et al. 2009). Given their proclivity for water, lake habitats and other riparian areas, these resources and surrounding landscape need to be managed accordingly (Grindal et al. 1999). While roosting in the summer, male evening bats remain solitary, whereas females form maternity colonies where communal nursing has been observed (Watkins and Shump 1981). Young are born in late May or early June and are volant within 30 days (Sealander and Heidt 1990).

Evening bats are strict forest dwellers, commonly roosting beneath exfoliating bark on snags within mature hardwood stands (Istvanko et al. 2016). Although they occasionally roost in abandoned human structures, evening bats always roost near water (Kalcounis-Ruppell et al. 2005). The most important factor concerning roost selection for evening bats is reproductive status. Boyles and Robbins (2006) showed that evening bats did not select the same winter roost trees as they did during the summer. During the spring and summer seasons, reproductive females form maternity colonies for the birthing and raising of young. The maternity roost must provide several options for thermoregulation such as temperature gradients across the roost, hold humidity, and provide adequate protection from predators. As certain species thermoregulate during periods of their reproductive cycle (Stones and Wiebers, 1965; Studier and O'Farrell, 1972), the selection of a predator-free thermal environment would be energetically advantageous by eliminating the physiological processes needed to regulate body temperature (Watkins and Shump 1981). As evening bats and other tree-roosting species appear to be unaffected by WNS, their conservation and protection should receive focus and study as bat populations continue to decline. If the cave-obligate bats in its range become superseded, evening bats and other forest bats are going to have a large ecological niche to fill.

Habitat, Habitat Use, and Habitat Selection

A habitat is defined as any space that offers resources and surroundings promoting residence by a species. The study of habitats allows researchers and wildlife managers to gather information about resource utilization in a particular area. Habitats can be studied narrowly at the microhabitat level or more broadly on the macrohabitat level. Although the entire macrohabitat, such as a forest, appears to be suitable, only a small part, such as a stand of trees may be used by a species (Kotliar and Wiens 1991; Danell et al., 1991; Bergin 1992; Schmidt 1993; Ward and Saltz 1994). The knowledge gained from studies that focus on habitat also influence conservation and management approaches.

Habitat selection is the behavior by which an animal chooses which habitat and resources to use. Factors that influence habitat selection include the availability of food, shelter, mates, and nest sites for raising young. Animals may also select their habitats based on experience or natal circumstances. For example, if an individual is reared in a pine tree as a neonate, it is more likely to choose a pine tree to raise its own young

(Stamps and Swaisgood 2007). Once an animal has selected a habitat, it must use its resources effectively. For example, a bat that selects a habitat for its abundance of a certain species of moth, will not prey on the moths if their daily caloric requirement is already met.

Habitat use is defined as how an organism uses the resources and conditions of the habitat they have selected. Habitat use is behavior specific because feeding, hiding, roosting, and breeding cannot all take place concurrently in the same area of the habitat. Habitat use is generally measured as the comparative amount of time an organism spends in separate zones within a habitat (Owen-Smith et al. 2015). Observed habitat use patterns can be completely motivated by competition and predation and are also subject to seasonal variability. There are two common approaches to studying habitat use: 1) the manipulative or experimental approach, which consists of altering variables to influence use, either in the lab or in the field, and 2) the mensurative or observational method, where variables are not altered, and the data collected reflect natural variation, rather than observer influence (McGarigal and Cushman 2002).

Defining available habitat is typically an arbitrary decision that has a major effect on data analysis. Studies either assume that all habitats are available to all individuals (designs I and II; Thomas and Taylor 1990), or that a different area of available habitat, such as a home range, may be defined for each individual (design III). Either way, available habitat is defined once and applied to all observations of habitats used by the study species. For my purposes, I have defined habitat use by detection of an actively moving evening bat outside of its roost.

Objectives

The goal of this study was to evaluate evening bat (*Nycticeius humeralis)* habitat use in a heavily managed forest. On a finer scale, the goal was to evaluate habitat use based on sex and reproductive status. I have addressed these aims by considering 1) forest management techniques such as burning, timber harvest, reforestation, and other silviculture activities; and 2) habitat types with emphasis on stand composition and characteristics.

My research answered the following questions concerning habitat use in terms of foraging habitat:

1) What habitat features are evening bats selecting?

   Foraging activity is often greatest in edge habitat where flight and orientation are likely easier due to reduced spatial clutter (Kalko 1993; Brigham et al. 1997). I predicted that foraging sites would be located closer to the forest edge and roads than a random location.

2) Do sex and reproductive status influence habitat selection and use?

   Istvanko et al. (2016) demonstrated that solitary males had smaller home ranges with more core foraging areas than reproductive females. Moreover, males and females generally foraged in different locations. I predicted that females would forage in larger, homogeneous stands more than predicted by their availability, whereas males would forage in smaller, heterogeneous stands more than predicted by their availability.

This prediction was made before I had a complete understanding of how the maximum entropy software analyzed data and what kind of outputs I would receive after running the models. The techniques the software uses did not allow me to quantify homogeneous and heterogeneous stands in a meaningful way. Therefore, my adjusted prediction is that species distribution maps will show larger core foraging areas with higher probability of presence for females than males.

3) What forest management practices could influence habitat selection and use?

Research has demonstrated the general conservation value of managed pine stands in the Southeast for a variety of bats (Wigley et al. 2007). Intensive management of these forests should increase open areas under the canopy to create foraging habitat. Burning and timber harvest can increase edge habitat by creating habitat discontinuity with the mature forest; bats frequently use edge habitat for commuting and foraging, presumably because of low tolerance to clutter in combination with prey availability (Furlonger et al. 1987; Clark et al 1993; Walsh and Harris 1996; Wethington et al. 1996; Grindal et al. 1999; Zimmerman and Glanz 2000; Hogberg et al. 2002). I predicted that areas managed by prescribed burn and harvested areas would be more selected for foraging locations than unmanaged areas.

4) What is the overall habitat availability of the Ozark- St. Francis National Forest for evening bats?

Foraging activity is often greatest in edge habitat where flight and orientation are likely easier due to reduced spatial clutter (Kalko 1993; Brigham et al. 1997). I predicted that foraging sites could be considered available if they contained sufficient edge habitat.

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CHAPTER II

MATERIALS AND METHODS

Study Area

The study area is located at the USDA Forest Service's Sylamore Ranger District (Fig. 1), Ozark-St. Francis National Forest, approximately 10 km northwest of Mountain View, Arkansas (35.8683° N, 92.1175° W).

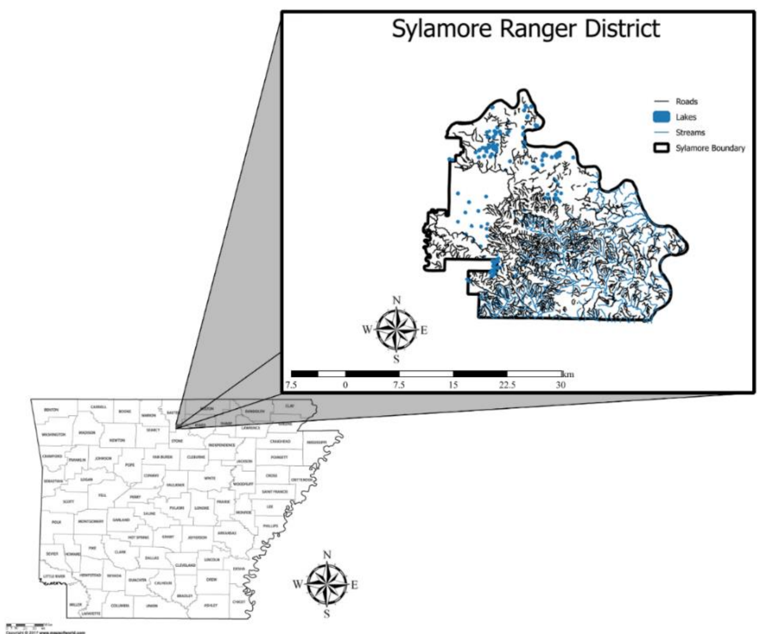

Figure 1. Map of Arkansas indicating the location of the Sylamore ranger district in relation to other state locations.

The Sylamore Ranger District encompasses about 53,000 ha within the counties of Stone, Searcy, Marion, Baxter, and Izard in the Ozark Highlands Ecoregion of north-central Arkansas. The lower elevations of the district (average of ~ 98 m) are composed of hardwood and pine forests, and characterized by steep mountainous slopes consisting of limestone and sandstone ridges. The higher elevations of the district can extend upwards to 381 m (Arkansas Game and Fish Commission 2017). The main drainages are the North Sylamore Creek, the South Sylamore Creek, and the White River. The average temperature of this area is 27°C in July, and the average summer rainfall is 10 cm. Wildlife management practices in the Sylamore are a cooperative effort between the Arkansas Game and Fish Commission and the U.S. Forest Service (Arkansas Game and Fish Commission 2017). These practices are intended to enhance wildlife habitat by manipulating forest openings and also through timber management. Timber management practices range from small regeneration cuts to seed tree and shelterwood cuts. Some prescribed burning is conducted in timber patches to reduce fuel and stimulate new growth. The wildlife management practices are primarily focused on the deer and turkey populations, with some large field systems being managed for quail and rabbit. More recently, intensive management has also targeted habitat enhancement for Indiana bats (*Myotis sodalis*) (Perry et al. 2016).

Data Origin and Program Information

I used Istvanko et al.'s (2016) data, collected from June to early August of in 2013 and 2014. These data included home range estimates on 32 individuals and a total of 71 roost locations. The methods for data collection are detailed in Istvanko et al.

(2016). In brief, bats were captured using mist nets typically placed in proximity to ponds and streams. Model LB-2X transmitters (Holohil, Ontario Canada) weighing 0.33 g were attached with surgical cement to selected bats. TRX-1000s receivers and 5-element folding Yagi antennas were used to track bats daily to their respective roosts and during their first foraging bouts of the night, which began when the bats emerged from their roosts and ended when all bats returned. Each bat was monitored for an average of 6 days after capture and approximately 2 hours per night during the first foraging bout. Although Istvanko et al. (2016) report individual home ranges for 12 females and 20 males that had 20 or more telemetry location points, I pooled the individual data to address sex-specific foraging habitat differences based on known presence locations. These presence data were integrated into ArcGIS (Esri, Redlands, California) to examine the habitat use of evening bat by comparing habitat types, forest management history, and locations of water sources. Habitat data were provided by the U.S. Forest Service. The MaxEnt software package was used for my statistical analyses and to generate figures (version 3.1;http://www.cs.princeton.edu/~schapire/ /maxent/; Phillips et al. 2004, 2006).

Data Analysis

To predict areas of suitable habitat, I used a presence-only species distribution modelling program called MaxEnt (version 3.1; http://www.cs.princeton.edu/~schapire/maxent/; Phillips etal. 2004, 2006). Presence locations were collected in 2013 and 2014 by triangulation (Istvanko et al. 2016). To account for error, I calculated how fast evening bats fly, 19.8 km/h, by averaging the flight speed of two species of similar weight, wingspan, and foraging strategies (*Myotis lucifugus* and *Lasiurus borealis)* as there is no flight speed recorded for the evening bat (Norberg and Rayner 1987). Assuming an average speed of 19.8 km/h, I estimated that evening bats can fly roughly 0.67 kilometers in two minutes. Therefore, I considered two locations recorded at a two-minute interval or longer to be time-independent. Model parameters included land use/land cover classes, stand types, management history, slope, the normalized difference vegetation index (NDVI), and distance water sources. Although Istvanko et al. (2016) studied evening bat's home range, evaluating second-order selection, I compared habitat use with availability at the third order, defined as habitat used within the home range (Johnson 1980).

Maximum Entropy

The MaxEnt software package takes a catalog of presence-only data points from a given species along with environmental predictors of the researcher's choice (such as temperature, land use/land cover, or rainfall) and a landscape divided by grid cells. For my purposes, I assumed that presence-only foraging locations are random samples of individuals rather than the points representing a random sample within the observed range of the study population as they are true presence points (Merow et al. 2013). The presence points were reviewed for duplicates, which were removed. MaxEnt contrasts presences against background locations where presence/absence is unmeasured (Phillips et al. 2009). Background samples are sometimes referred to as pseudo-absences as absence is typically not observed, but rather there is an assumption of absence (Phillips et al. 2009). When selecting environmental variables to include in the model, researchers select ecological gradients predicted to influence a species' presence.

Even though the operator using the program can choose the feature classes that will be used, MaxEnt automatically selects the individual features (per predictor) that contribute the most to the model using the process of regularization while also checking for multicollinearity among predictors (Phillips et al. 2006). Feature classes are chosen a priori based on researchers' general knowledge of the study species. Regularization is used for reducing over-fitting of the model. The first function that regularization performs is to safeguard the empirical constraints from over-fitting the model (Merow et al. 2013).

Sampling bias is a typical concern with any modeling method chosen. Some sampling bias is expected and generally occurs when certain areas are sampled more than others. When sampling is biased, one cannot differentiate whether species are occupying environments because those locations are preferable or because they receive the majority of the sampling (Phillips at al. 2009; Sastre and Lobo 2009; Wisz and Guisan 2009; Newbold. 2010; Chakraborty et al. 2001). When using MaxEnt, the operator assumes that detection probability and sampling probability are consistent across the area and do not factor into the sampling bias. For presence-only data, one must explicitly model the probability of sampling a location because no absence data exist to fully describe which locations were searched (Merow et al. 2013).

To perform model evaluations in MaxEnt, metrics of model fit are needed (Liu et al. 2010). The standard metric used is the area under the receiver-operator curve (AUC). The area under the curve is an arbitrary threshold measuring predictability accuracy based only on location rankings. The metric assumes that a value of 0.5 is the baseline probability of presenceat a random location within the study area. Any value greater than 0.5 denotes predictive capability of a given model while values less than 0.5 demonstrates a lack of predictive capability of a model. The AUC is interpreted as the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point (Merow et al. 2013). Area under the curve values in this range are considered excellent (poor AUC < 0.4; good 0.4< AUC < 0.75 and excellent AUC >0.75, Fielding and Bell 1997) and indicative of good accuracy (Phillips et al. 2009).

Environmental Predictors

The ecological requirements of bats provide substantial evidence that their habitat preferences are determined by resources at the home-range scale. The predictors include 10 land use land cover classes (distance to barren land, distance to developed land, distance to crop land, distance to evergreen stands, distance to deciduous stands, distance to herbaceous land, distance to mixed stands, distance to wetland, distance to pasture, distance to water, and distance to shrub land), slope, distance to stands – managed by prescribed fire, reforestation, silviculture (including release, weeding, and cleaning, pre-commercial thinning, pruning and fertilization), timber harvest–, and the normalized difference vegetation index (NDVI). The predictor "distance to pasture" is labeled as such but is described as a wildlife opening with a water source to create forest discontinuity in mature stands.

The land cover predictors were analyzed as distances from evening bat locations.

Distances were used over proportion of land cover that contained the presence locations to describe evening bat habitat use because telemetry points in real-time showed the bats using their habitat the most accurately. The forest management predictors were also analyzed as distance variables. Management practices were determined at the stand level. The NDVI values reflect the presence of live green vegetation in a given area. Specifically, the higher the NDVI value, the more intense the photosynthetic activity in an area. The land cover map was derived from the United States Department of Agriculture and was categorized into ten classes. Surface bodies of water were provided in an ArcGIS layer format by the United States Forest Service.

Percent Variable Contribution

I used three methods to assess the contributions of environmental predictors to models: 1) percentage contribution, 2) the jackknife test, 3) and the response curves generated per predictor (Phillips et al. 2009). These percent contribution values are only experimentally defined: they depend on the path that the MaxEnt code uses to get to the optimal solution, and a different algorithm could arrive at the same solution via a different path, resulting in different percent contribution values (Phillips et al. 2009). Additionally, when there are highly correlated environmental variables, the percent contributions should be interpreted with caution. Correlations among my variables were weak. The contribution for each variable is determined by randomly permuting the values of the variables in aggregate among the training points (both presence and background) and measuring the resulting decrease in training AUC. Values are normalized to give percentages (Phillips et al. 2009). In my analysis, any values in the original output of less than 5% were not considered important contributions to this output and were not presented.

Jackknife Test of Variable Significance

I also ran a jackknife test to produce different estimates of variable importance. When using this method each variable is tested independently of the others and a model is created with that variable only. Also, each variable is excluded one by one and additional models are created with the remaining variables in aggregate. Additionally, a model was created including all the variables. Finally, this test runs a model with all variables in aggregate. When considering the model with all variables, if none of the models using each variable alone performs better with the aggregate model, this shows that predictive performance improves when the corresponding variables are used (Phillips et al. 2006).

Variable Response Curves

These outputs measure the relationship of the probability of occurrence for the study species and each environmental variable individually. The x-axis shows the range of values for each variable where the y-axis demonstrates the probability of occurrence on a scale from 0 (low probability) to 1 (high probability). Using these curves, a positive or negative response of a species to the environmental variable in question can be inferred.

Additional Modeling Strategies

Other distribution modeling programs have been used to predict habitat suitability. One such program is Ecological Niche Factor Analysis (ENFA), which does not count non-presence points as absences. Instead, ENFA uses presence locations along with the whole study area's environmental variables to predict suitable habitat over a wider range as well as potential distribution (Rebelo and Jones 2010). Environmental Niche Factor Analysis would have been an appropriate modeling program to use with assumed presence points, such as those collected via echolocation calls. As I had true presence points available, MaxEnt was the best choice. In contrast, MaxEnt replaces absence data with background data, which are random samples of the environment. Thus, MaxEnt is more successful at determining a species' realized distribution instead of ENFA as ENFA has the ability to determine a species' potential distribution while failing to extrapolate it (Rebelo and Jones 2010). This failure to make inferences is likely because ENFA only accepts continuous variables whereas MaxEnt also accepts categorical data such as land cover.

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CHAPTER III

RESULTS

Significant Explanatory Variables and Model Performance

The receiver operating characteristic plot (ROC) was high for both the training data and test data from the area under the curve (AUC). The best fit for the training data was for females in 2013 whereas males in 2013 had the lowest AUC. The best fit for the test data was for females in 2013 whereas males in 2013 had the lowest AUC. The AUC values presented in the table below were excellent and indicative of good accuracy.

Table 1: Area under the curve values for test and training data on male and female evening bats. Values generated by MaxEnt.

		TRAINING AUC	*TEST AUC*
FEMALES	2013	0.952	0.949
	2014	0.885	0.871
MALES	2013	0.852	0.814
	2014	0.886	0.887

Females 2013

For females in 2013, “distance to herbaceous land” (18%) had the highest contribution, followed by “distance to shrub land” (17.3%; Fig. 2). Other variables that contributed favorably to the model included “distance to pasture” (13.1%), “distance to harvested stands” (12.2%), “distance to barren land” (11.8%), “distance to burned stands” (11.4%) and “distance to silviculture treated stands” (6.2%).

Females 2014

For female evening bats in 2014 (Fig. 2), the most influential variable was “distance to burned stands” (47.2%) followed by “distance to pasture” (25.4%). Variables that also contributed constructively to the model include “distance to shrub land” (7.9%) and “distance to wetland” (5.4%; Fig. 2).

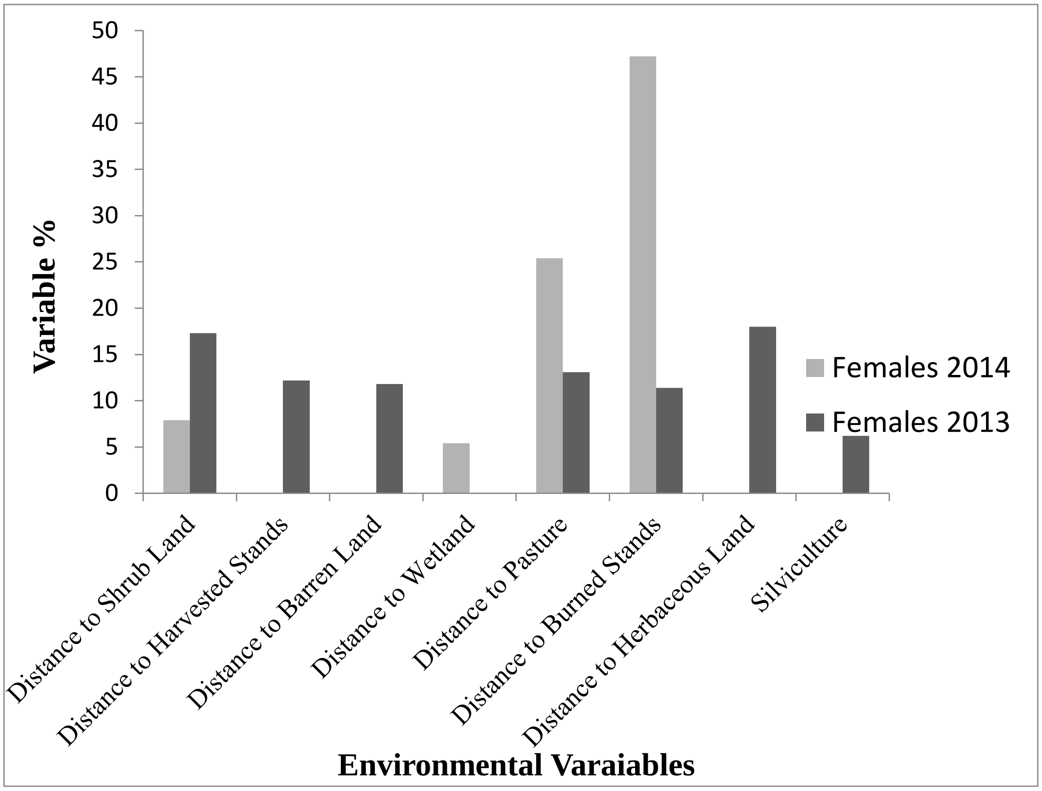

Figure 2: Percent variable contribution of female evening bats in the Sylamore ranger district in 2013 and 2014. Any values in the original output that totaled <5% were omitted as they were not considered important contributions to the model output.

Males 2013

For male evening bats in 2013, "distance to water" was the most influential variable (26.1%), followed closely by "distance to shrub land" (22.6%; Fig. 3). Other variables that positively influenced the model include "distance to harvested stands" (10%), "distance to barren land" (8%), "distance to wetland" (7.7%), "distance to reforested stands" (7.6%), and "distance to cropland" (5%).

Males 2014

With male evening bats in 2014,, the most influential variable was “distance to water” (23.5%) which was succeeded by “distance to pasture” (21.5%; Fig. 3). Other variables that contributed to the model include “distance to harvested stands” (11.9%), “distance to shrub land” (10.4%), “distance to burned stands” (8.5%), “distance to wetland” (6.3%), and “distance to reforested stands” (5.8%).

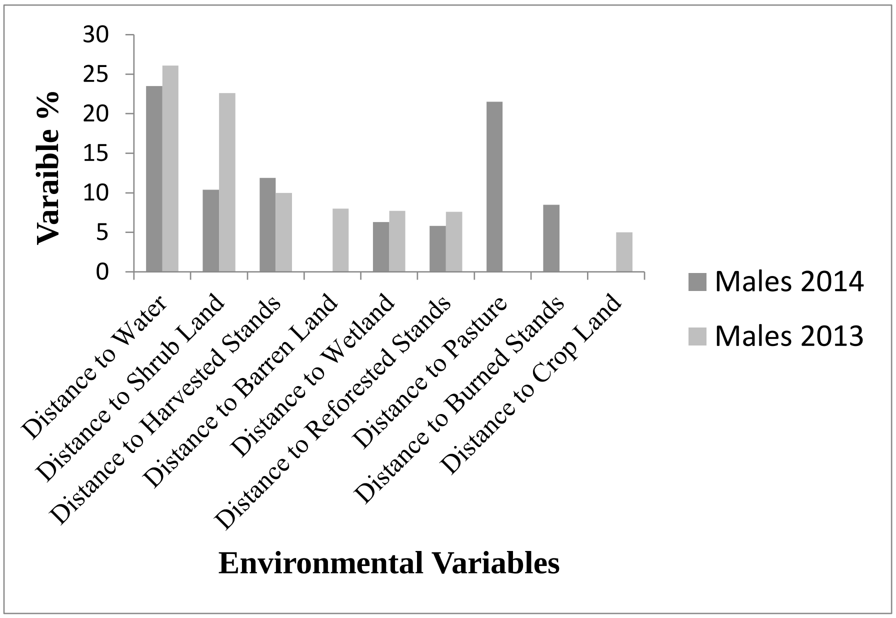

Figure 3: Percent variable contribution of male evening bats in the Sylamore ranger district in 2013 and 2014. Any values in the original output that totaled <5% were omitted as they were not considered important to the model output.

Jackknife Test Results

Females 2013

The jackknife test of variable significance revealed that “distance to burned stands” had the highest gain to the suitability models when used in isolation, followed by “distance to shrub land” (Fig. 4). “Distance to pasture” decreased the gain the most when it was omitted, followed by “distance to harvested stands” (Fig. 4). Thus, “distance to burned stands” and “distance shrub land” had the highest predictive contribution, but “distance to pasture” and “distance to harvested stands” contain unique predictive information that the other variables lack (Fig. 4).

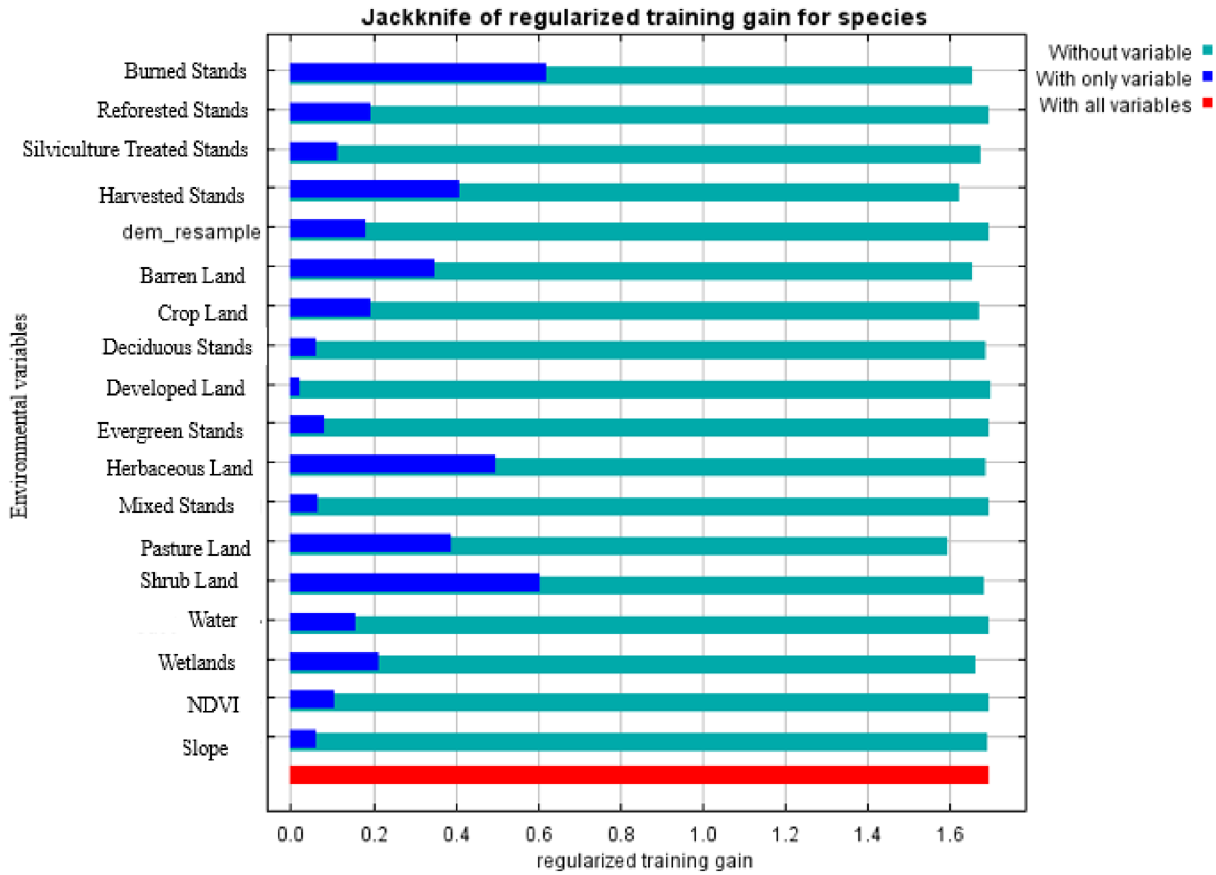

Figure 4: Training gain of the jackknife test of variable significance generated by Maximum Entropy for female evening bats in the Sylamore ranger district for the year 2013. The red bar represents the predictive power of the full model.

Females 2014

For females in 2014, the jackknife test demonstrates that the highest gain was “distance to burned stands” when used in isolation, followed by “distance to crop land” (Fig. 5). This indicates that these variables contain the most useful information when used alone. However, “distance to burned stands” followed by “distance to pasture” decreases the gain the most when they are omitted (Fig. 5). Thus, “distance to burned stands” and “distance to crop land” contain information not present in other variables (Fig. 5).

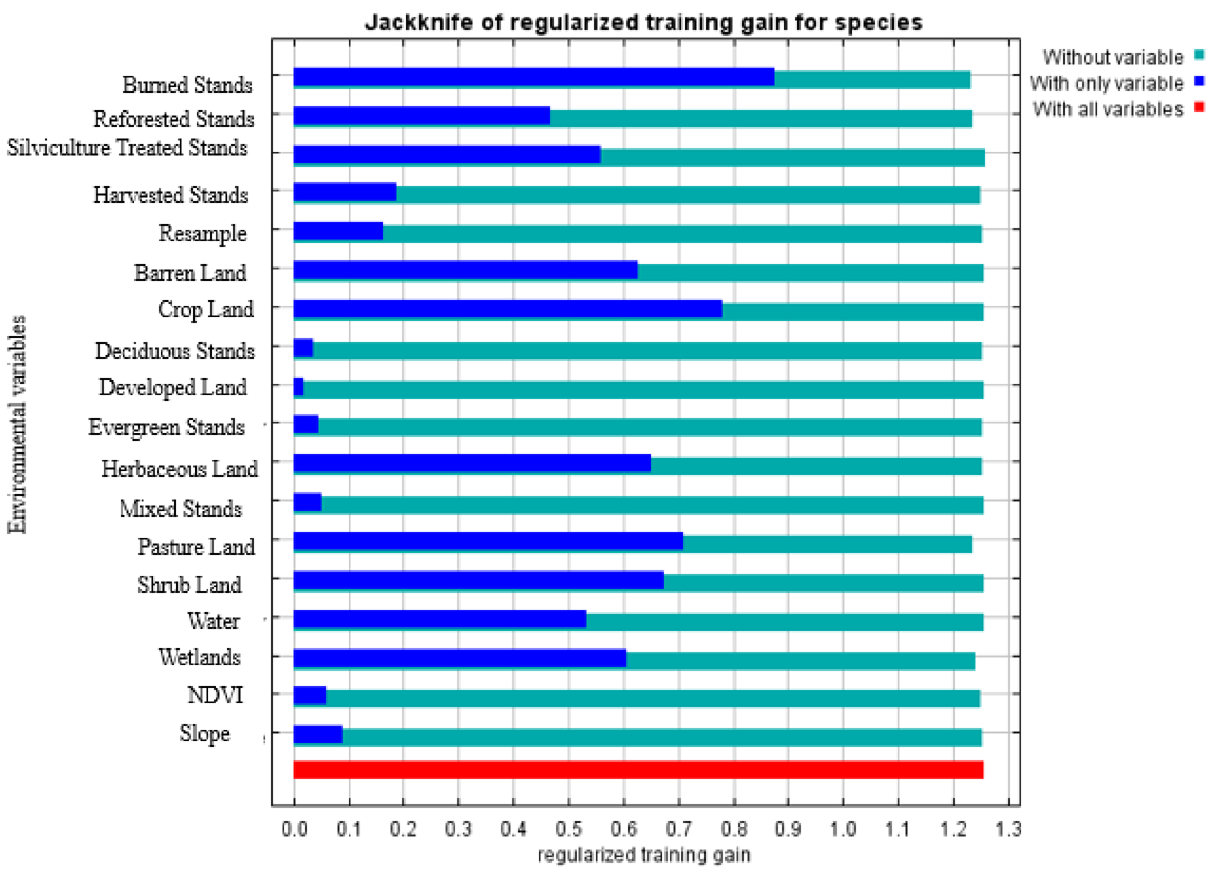

Figure 5: Training gain of the jackknife test of variable significance generated by Maximum Entropy for female evening bats in the Sylamore ranger district for the year 2014. The red bar represents the predictive power of the full model.

Males 2013

For males in 2013, the suitability model that showed the highest gain was “distance to silviculture treated stands” when used in isolation, followed by “distance to reforested stands” (Fig. 6), thus these variables provided the most information when used alone. “Distance to shrub land” decreases the gain the most when it is omitted, followed by “distance to crop land” and therefore appear to have the most information that is not present in the other variables (Fig. 6).

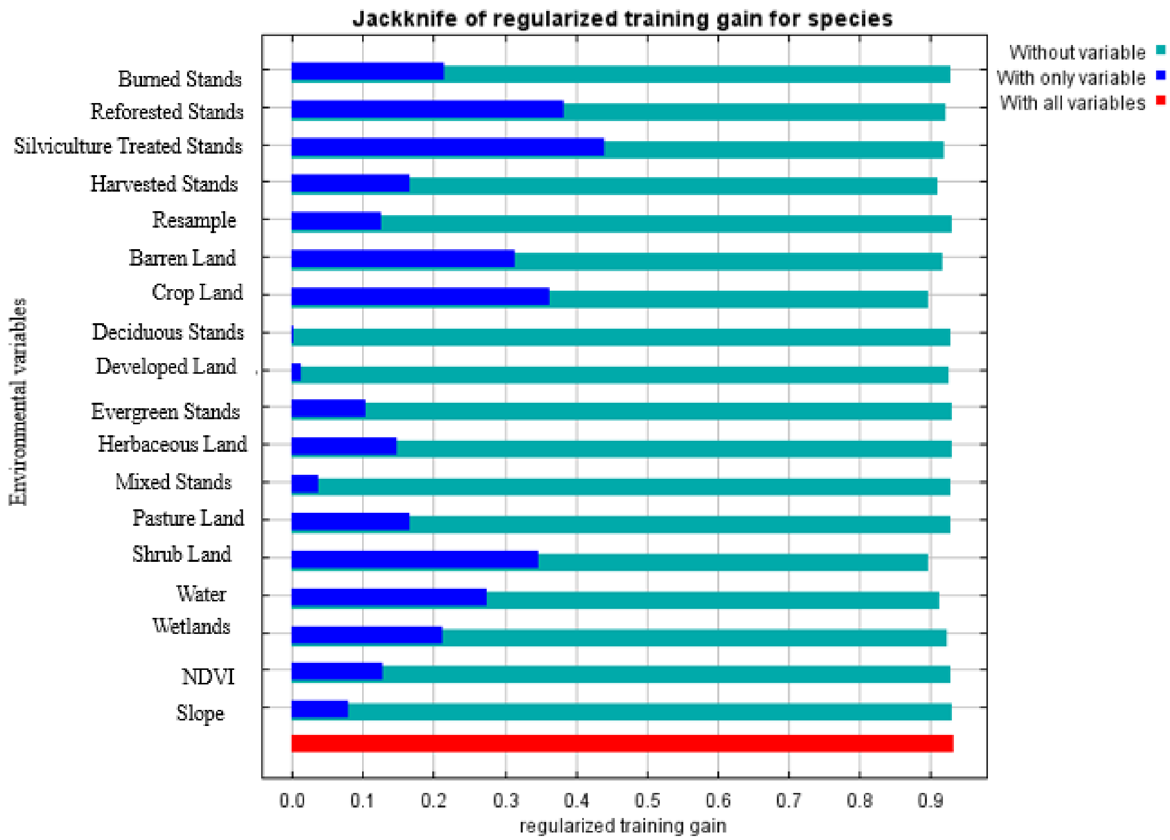

Figure 6: Training gain of the jackknife test of variable significance generated by Maximum Entropy for male evening bats in the Sylamore ranger district for the year 2013. The red bar represents the predictive power of the full model.

Males 2014

With males in 2014, the suitability model that showed the highest gain was “distance to shrub land”, followed closely by “distance to water” and “distance to burned stands” when used in isolation, providing the most information when used alone, whereas “distance to reforested stands” and “distance to burned stands” decreased the gain the most when they are omitted, and therefore appear to have the most information that is not present in the other variables (Fig. 7).

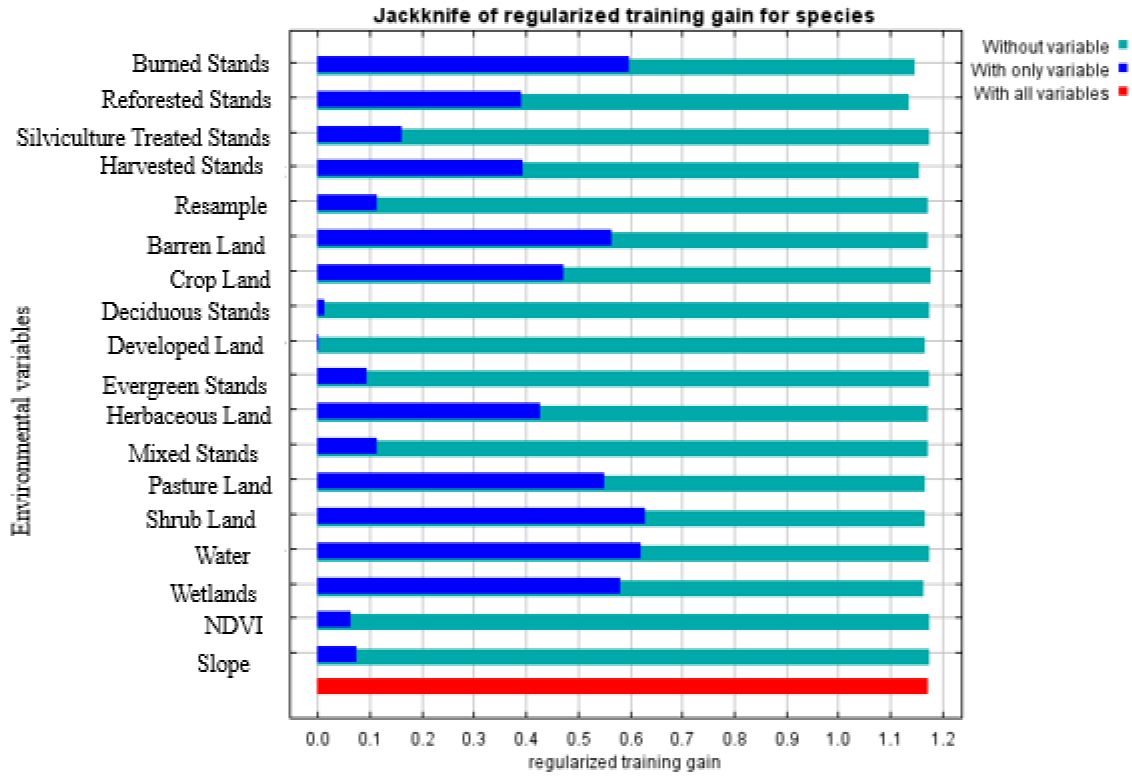

Figure 7: Training gain of the jackknife test of variable significance generated by Maximum Entropy for male evening bats in the Sylamore ranger district for the year 2014. The red bar represents the predictive power of the full model.

Response of Evening Bats to Environmental Predictors

Females 2013

The response curves for “distance to barren land”, “distance to crop land”, “distance to wetlands”, “distance to deciduous stands”, “distance to evergreen stands” and “distance to mixed stands” indicated a higher probability of evening bat presence in proximity of these landscape features (Figs. 8, 9, 14, 18, 19, and 20). The response curves for “distance to burned stands”, “distance to reforested stands", "distance to harvested stands", and "distance to silviculture treated stands" showed a higher probability of occurrence near stands that have been burned, managed, or planted (Figs. 21, 22, 23, and 24). The response curve for "slope" showed a higher probability of occurrence in the less steep areas of my study site (Fig. 16). The response curves for "distance to developed land", "distance to herbaceous land", "distance to water", and "distance to pasture" showed a higher probability of occurrence away from these landscape features (Figs. 10, 11, 12, and 15). The response curve for "NDVI" showed a higher probability of occurrence in areas that have a substantial amount of greenery (Fig. 17). The response curve for "distance to shrub land" showed higher probability of occurrence at a moderate distance from this landscape feature (Fig. 13).

Females 2014

The response curves for "distance to barren land", "distance to evergreen stands", "distance to herbaceous land" (Figs. 8, 19, and 11) and "distance to water" (Fig. 15) indicated a higher probability of evening bat presence close to these landscape features. There is also another peak in probability of evening bat presence >4,000 m from a water source. The response curve for "distance to burned stands" showed a higher probability of occurrence near stands that have been burned (Fig. 21). The response curves for "distance to reforested stands" and "distance to silviculture treated stands" demonstrated a higher probability of presence in stands that have had been managed or had additional trees planted (Figs. 23 and 24). The response curve for "distance to harvested stands" showed a higher probability of occurrence near stands that had not been harvested (Fig. 22). The response curve for “slope” showed a higher probability of occurrence in areas with virtually no slope (Fig. 16). The response curves for “distance to crop land”, “distance to development”, “distance to pasture”, “distance to wetlands”, “distance to deciduous stands”, and “distance to mixed stands” estimated a higher probability of occurrence not in proximity to these landscape features (Figs. 9, 10, 12, 14, 18, and 20). The response curve for “NDVI” indicated a higher probability of occurrence in areas that have a significant amount of greenery (Fig. 17). The response curve for “distance to shrub land” indicated a higher probability of occurrence at a moderate distance from this landscape feature (Fig. 13).

Males in 2013

The response curves for “distance to barren land”, “distance to crop land”, “distance to evergreen stands”, “distance to deciduous land”, “distance to pasture” and “distance to water” (Figs. 8, 9, 12, 15, 18, and 19) suggested a higher probability of evening bat presence in these landscape features. The response curves for “distance to harvested stands” and “distance to silviculture treated stands” demonstrated a higher probability of occurrence in stands that have not been cut or managed (Figs. 22 and 24). The response curves for “distance to developed land”, “distance to herbaceous land”, and “distance to mixed stands” (Figs. 10, 11, and 20) indicated a higher probability of occurrence away from these landscape features. The response curve for “slope” showed a higher probability of occurrence in areas with little to steepness (Fig. 16). The response curve for “NDVI” indicated a higher probability of occurrence in areas that had a substantial amount of greenery (Fig. 17). The response curve for “distance to shrub land” suggested a higher probability of occurrence at a moderate distance from this variable (Fig. 13). The response curve for “distance to burned stands” suggested a higher probability of presence in an area that have not been burned (Fig. 21).

Males in 2014

The response curves for “distance to barren land”, “distance to deciduous stands”, “distance to mixed stands”, and “distance to water” (Figs. 8, 15, 18, and 20) indicated a higher probability evening bat presence in proximity to these landscape features. The response curves for “distance to harvested stands”, “distance to reforested stands”, and “distance to silviculture treated stands” indicates a higher probability of occurrence near stands that have not been cut, had additional trees planted, or been managed (Figs. 22, 23, and 24). The response curves for “distance to development”, “distance to crop land”, “distance to evergreen stands”, “distance to herbaceous land”, “distance to pasture”, and “distance to wetlands” (Figs. 9, 10, 11, 12, 14, and 19) indicated a higher probability of occurrence not in proximity to these landscape features. The response curve for “slope” shows a higher probability of occurrence in areas at little to moderate steepness (Fig. 16). The response curve for “NDVI” illustrates a higher probability of occurrence in areas that have an unsubstantial amount of greenery (Fig. 17). The response curve for “distance to shrub land” shows a higher probability of occurrence at a moderate distance from this variable (Fig. 23). The response curve for “distance to burned stands” illustrates a greater probability of presence in stands that had been burned (Fig. 21).

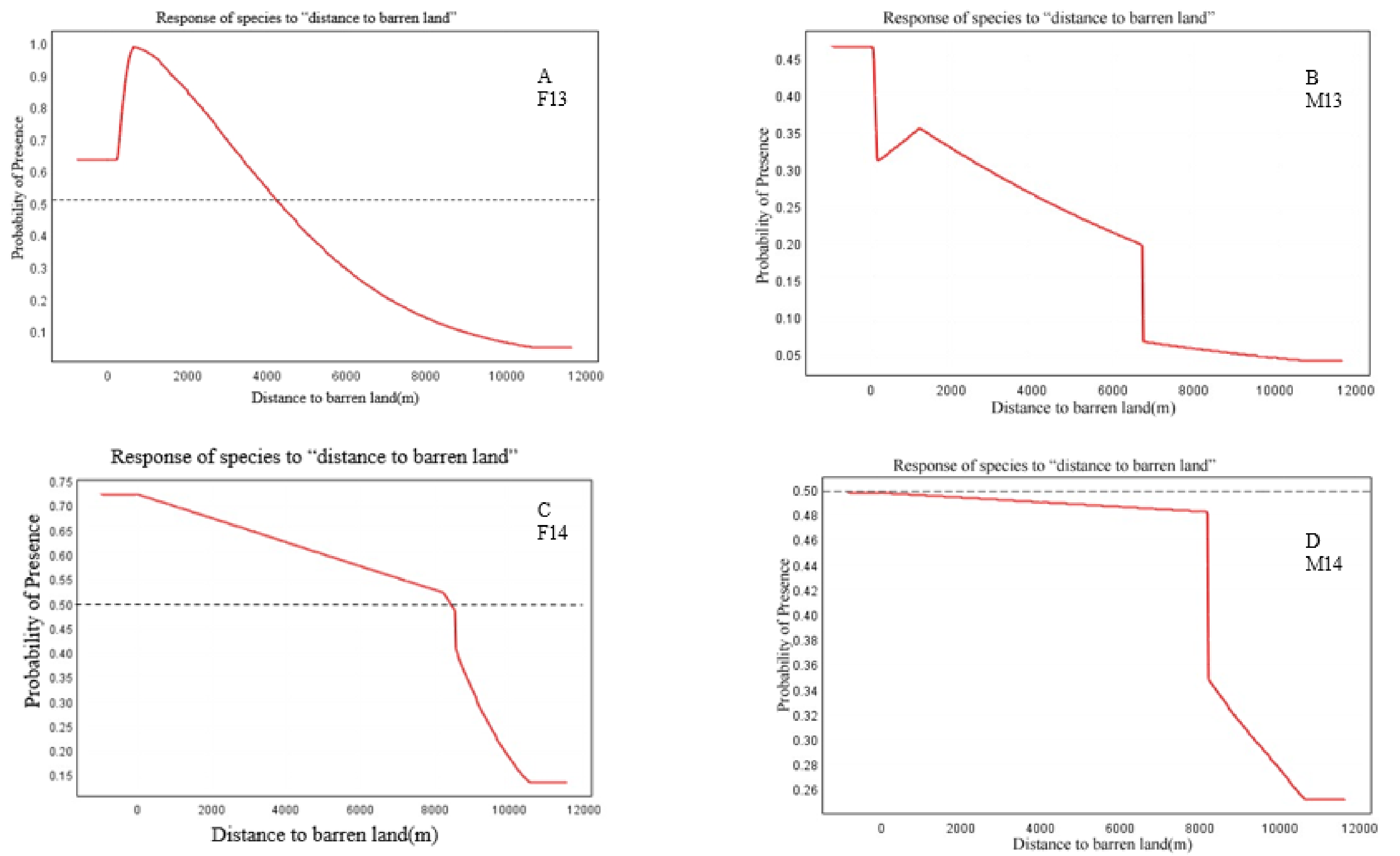

Figure 8: MaxEnt output of response curves for the environmental variable "distance to barren land" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

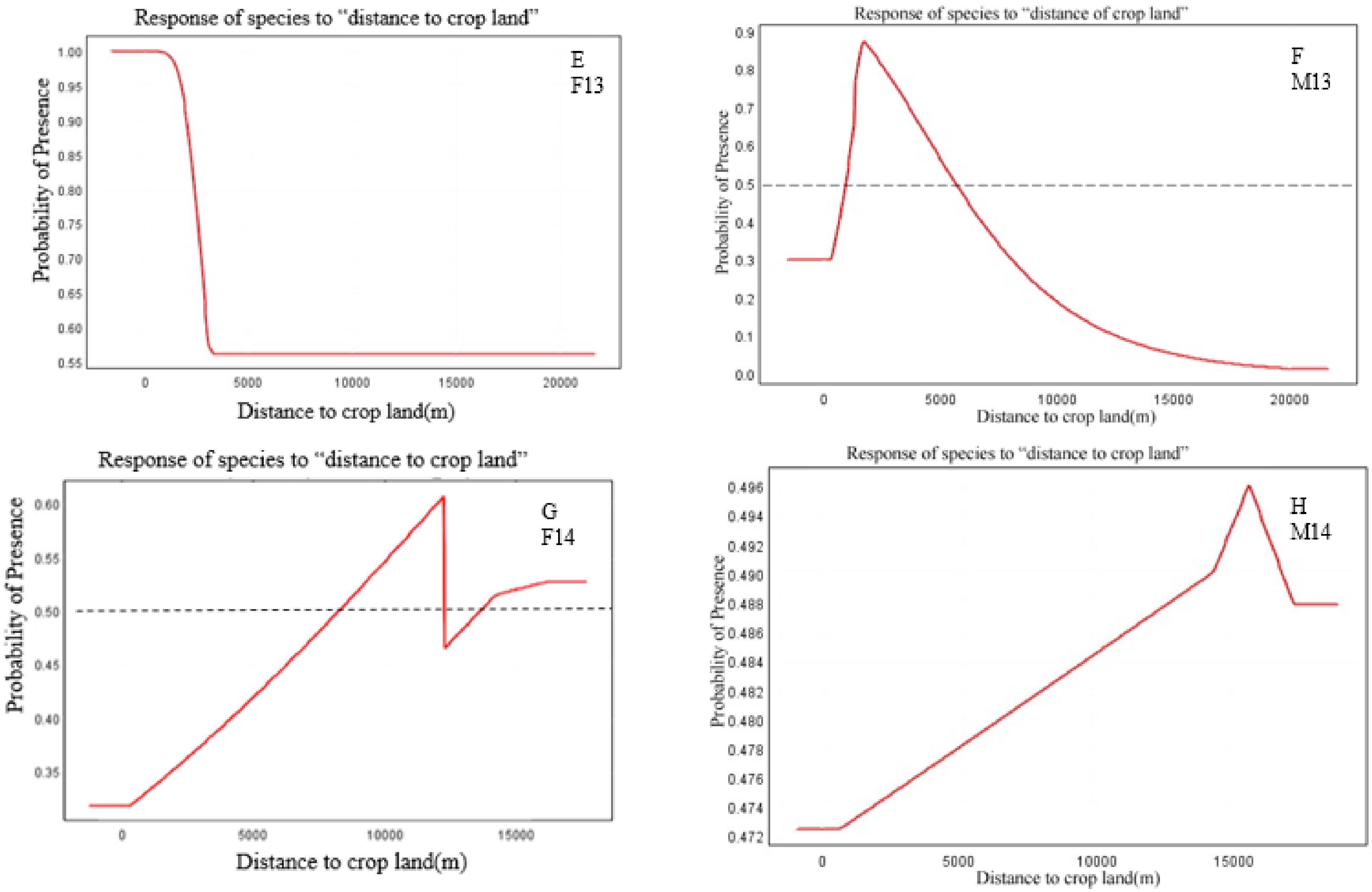

Figure 9: MaxEnt output of response curves for the environmental variable "distance to crop land" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

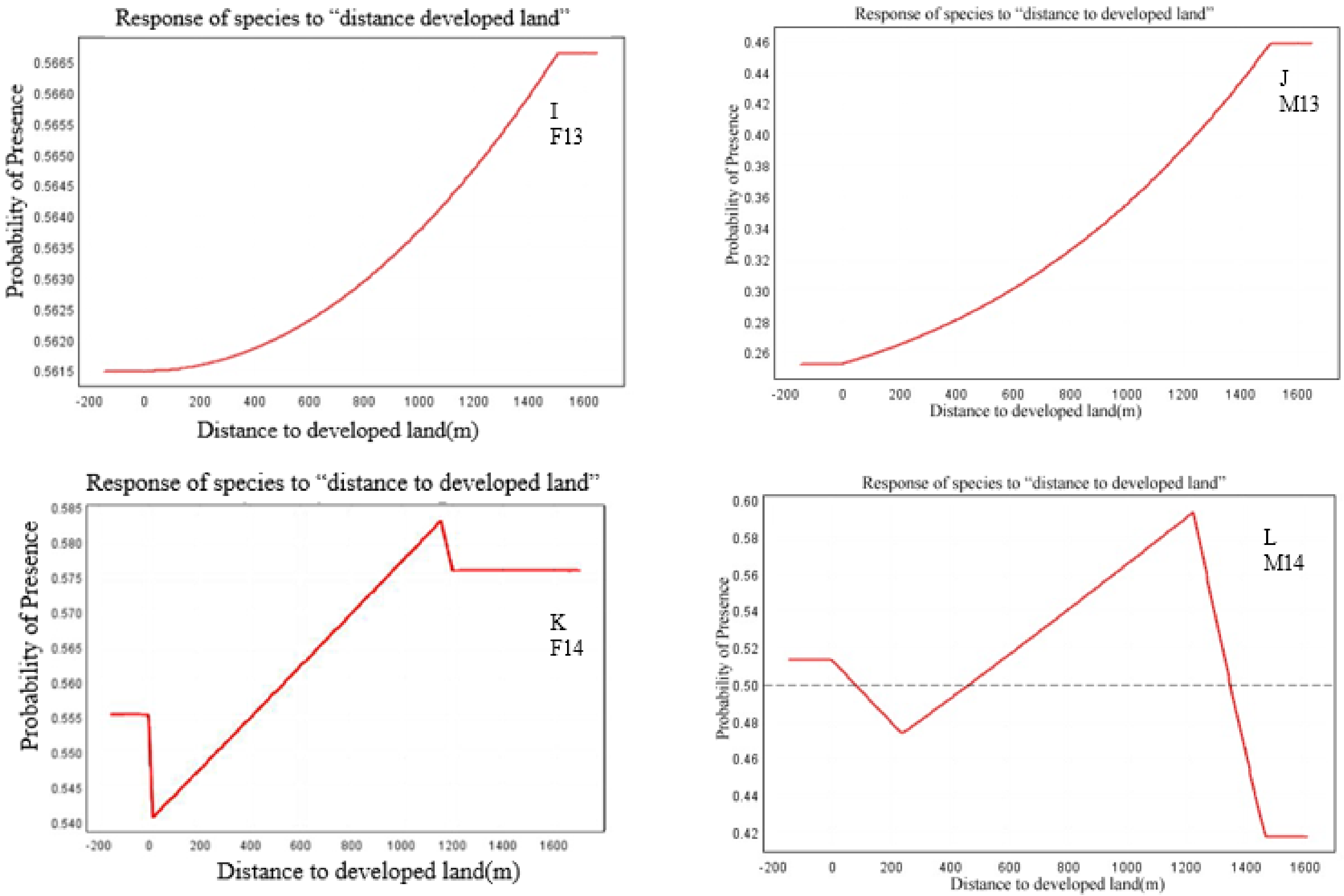

Figure 10: MaxEnt output of response curves for the environmental variable "distance to developed land" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

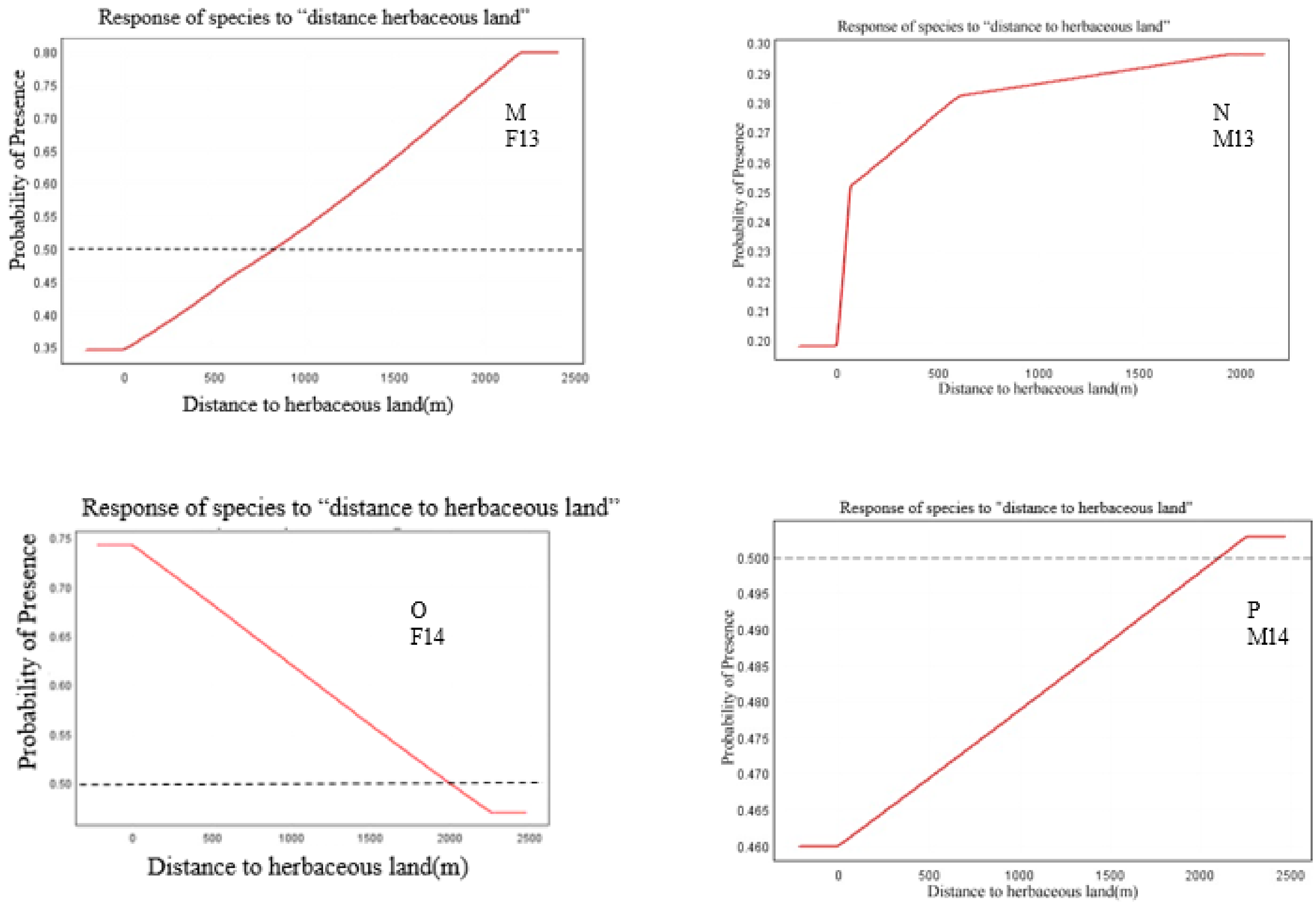

Figure 11: MaxEnt output of response curves for the environmental variable "distance to herbaceous land" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

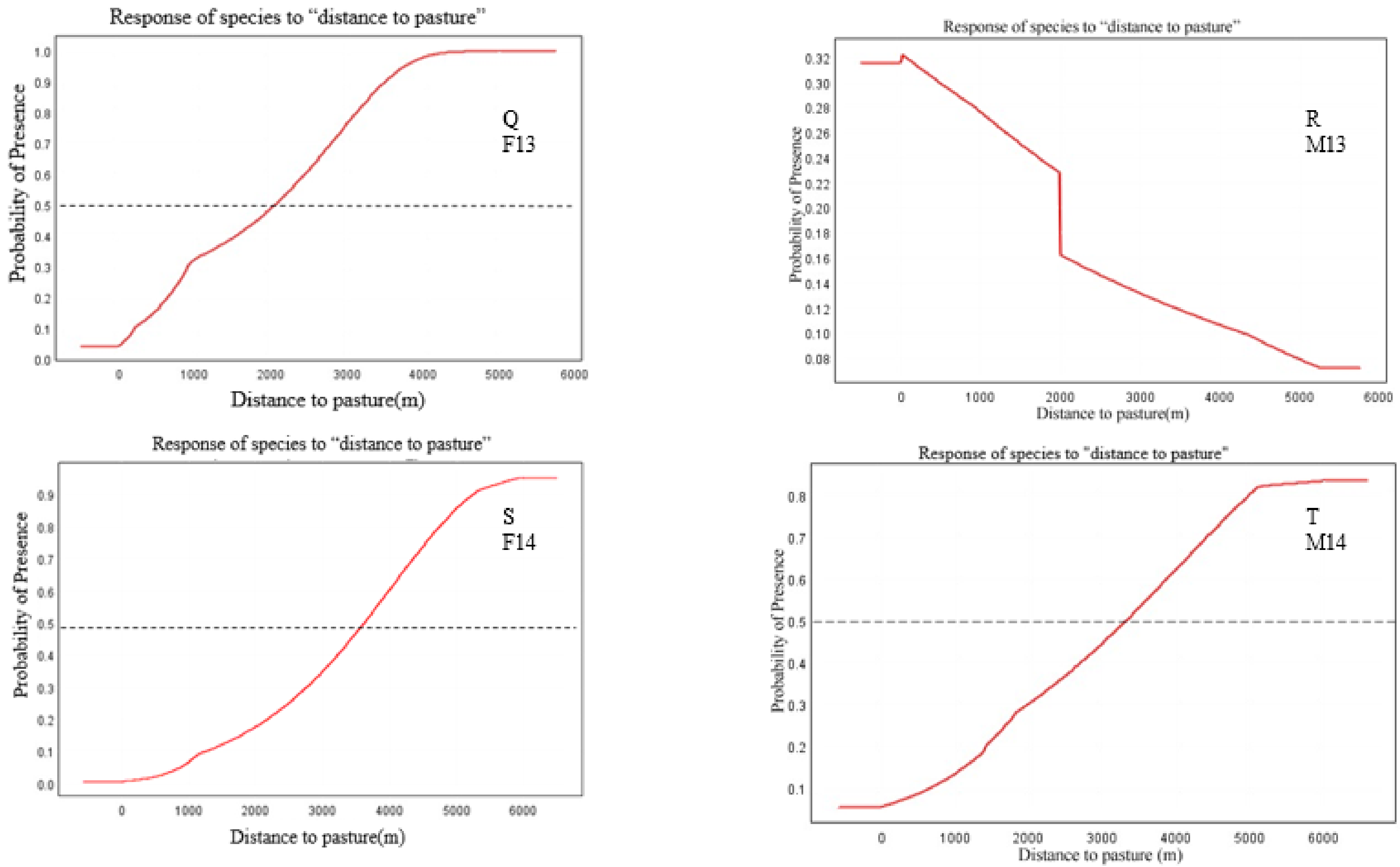

Figure 12: MaxEnt output of response curves for the environmental variable "distance to pasture" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

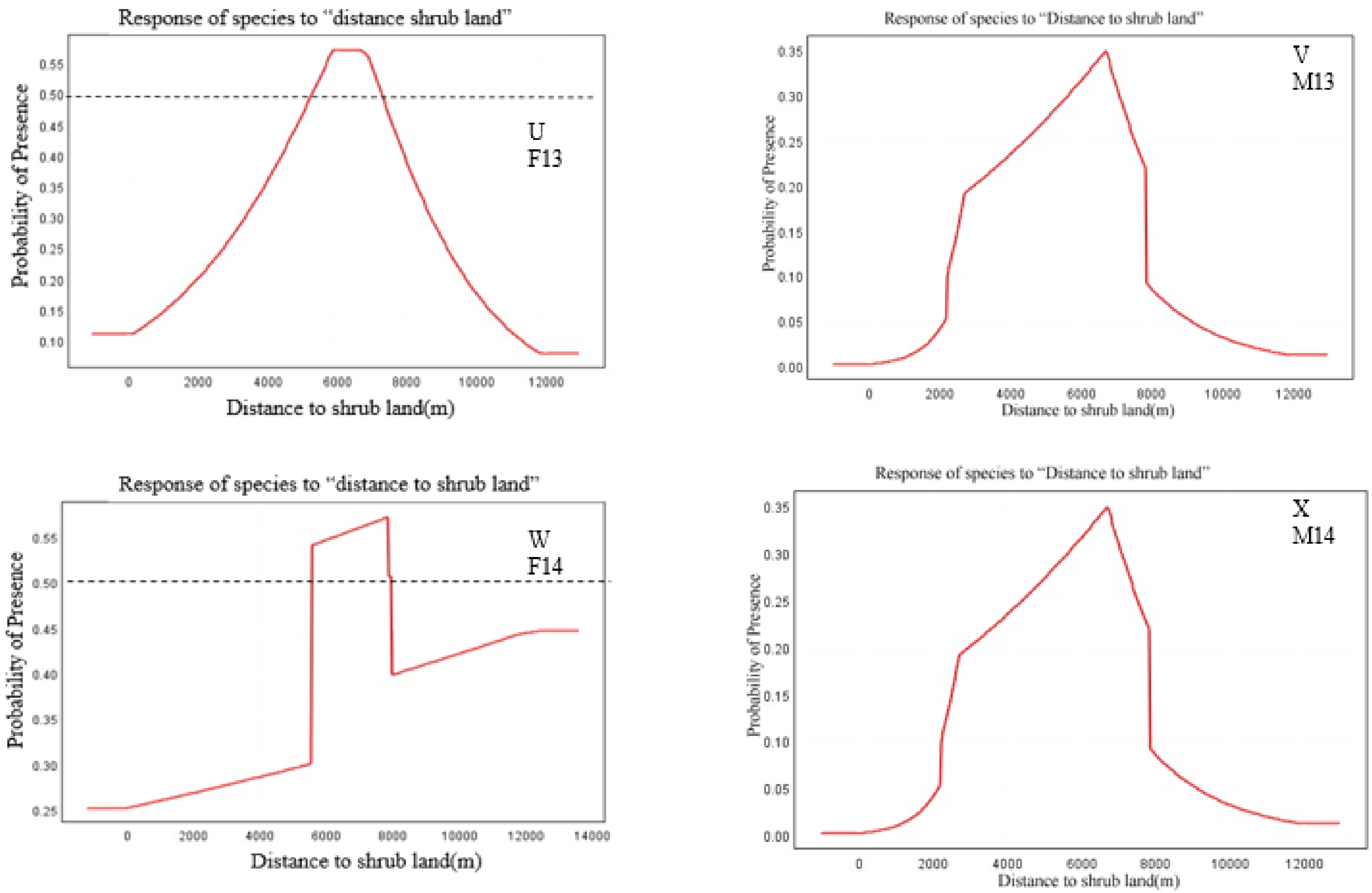

Figure 13: MaxEnt output of response curves for the environmental variable "distance to shrub land" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

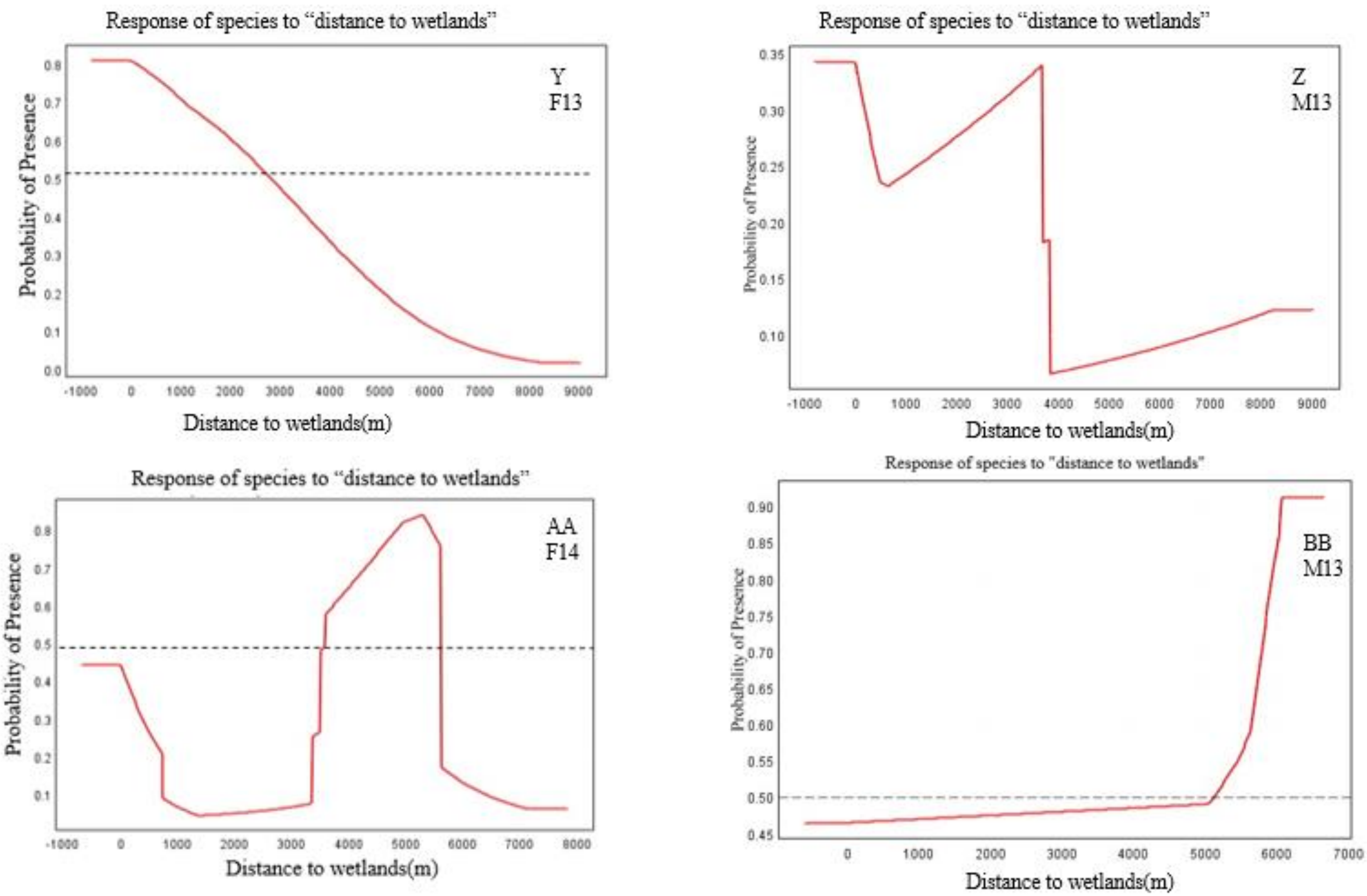

Figure 14: MaxEnt output of response curves for the environmental variable "distance to wetlands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

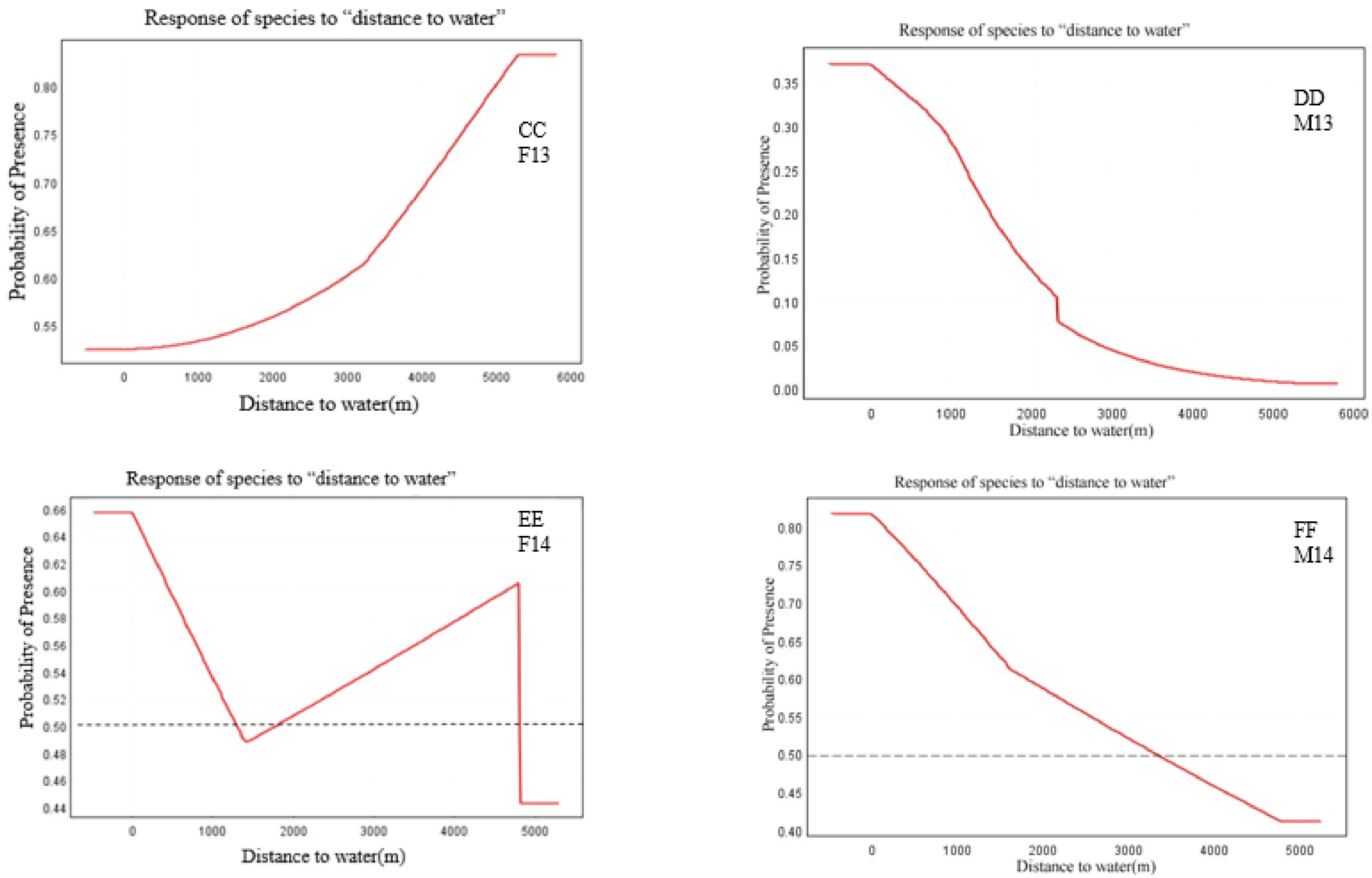

Figure 15: MaxEnt output of response curves for the environmental variable "distance to water" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

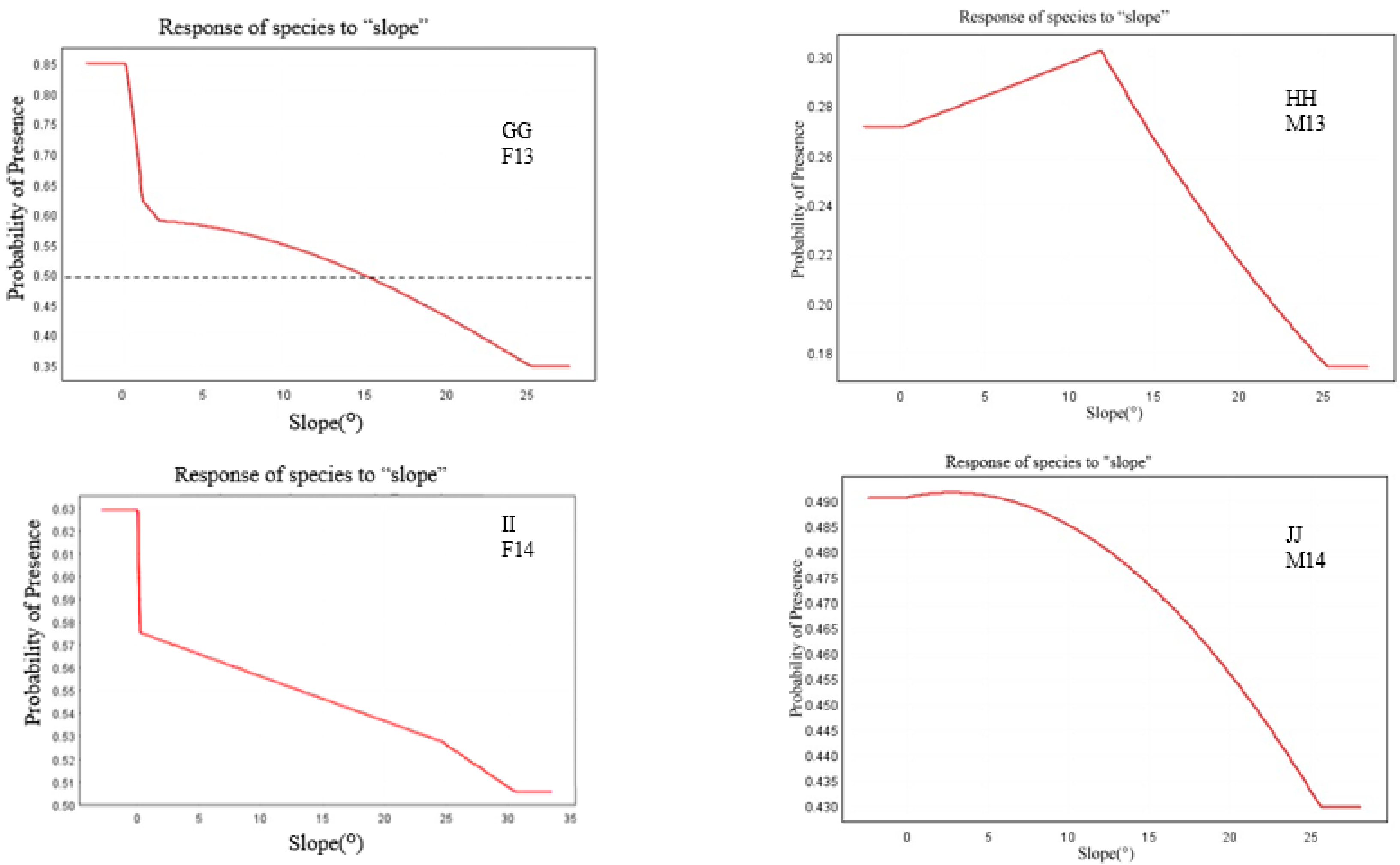

Figure 16: MaxEnt output of response curves for the environmental variable "slope" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

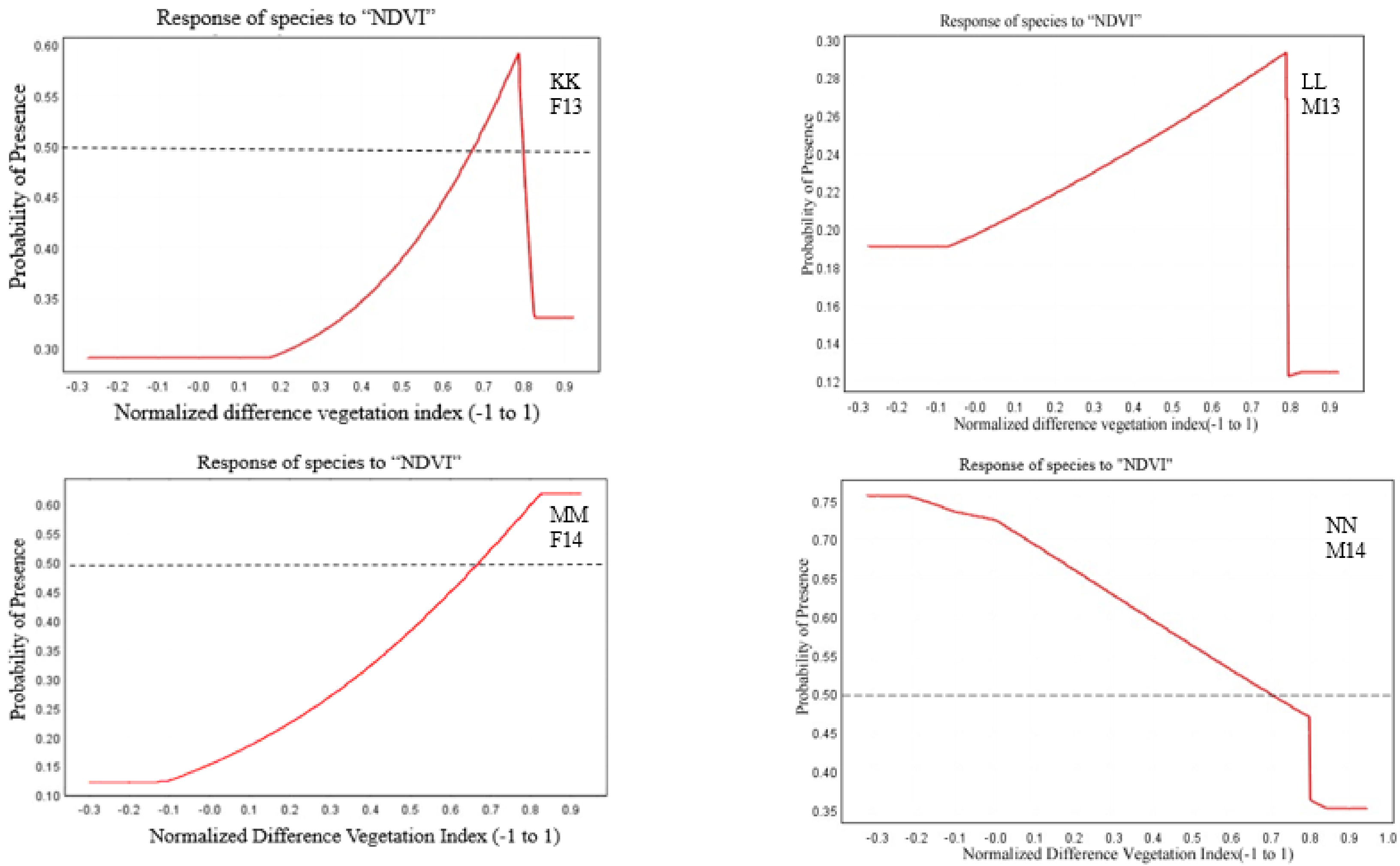

Figure 17: MaxEnt output of response curves for the environmental variable “NDVI” for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

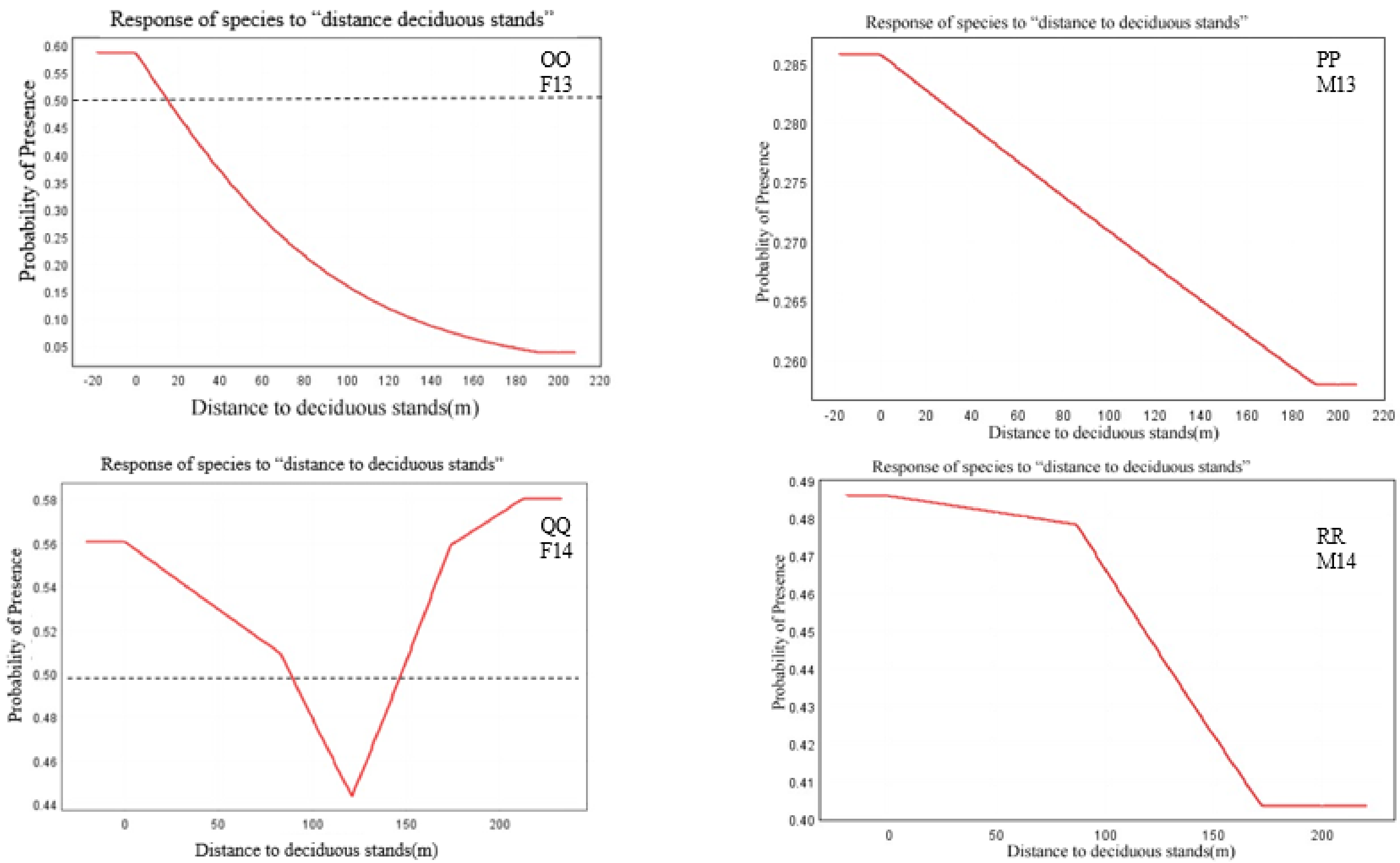

Figure 18: MaxEnt output of response curves for the environmental variable "distance to deciduous stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

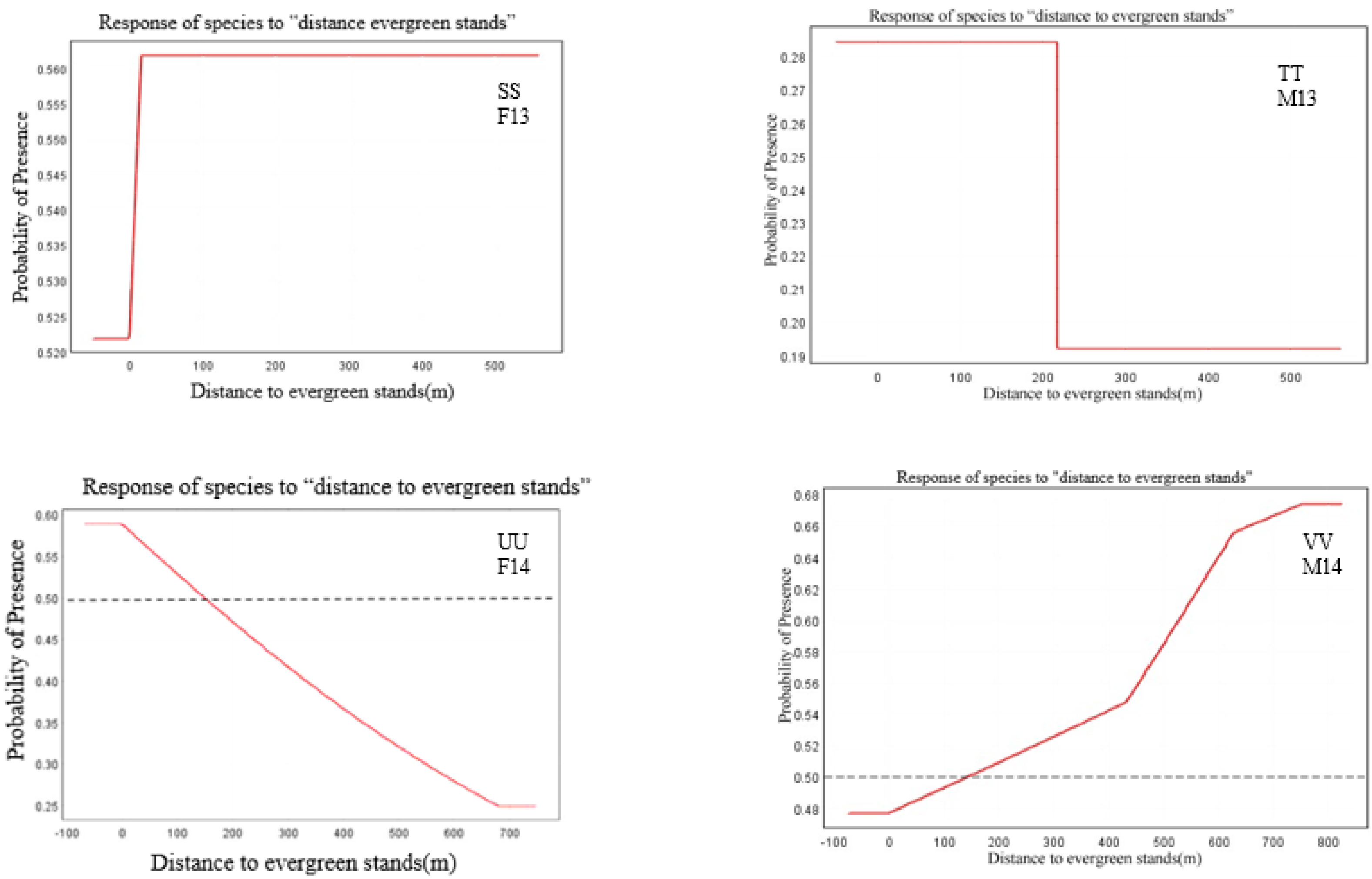

Figure 19: MaxEnt output of response curves for the environmental variable "distance to evergreen stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

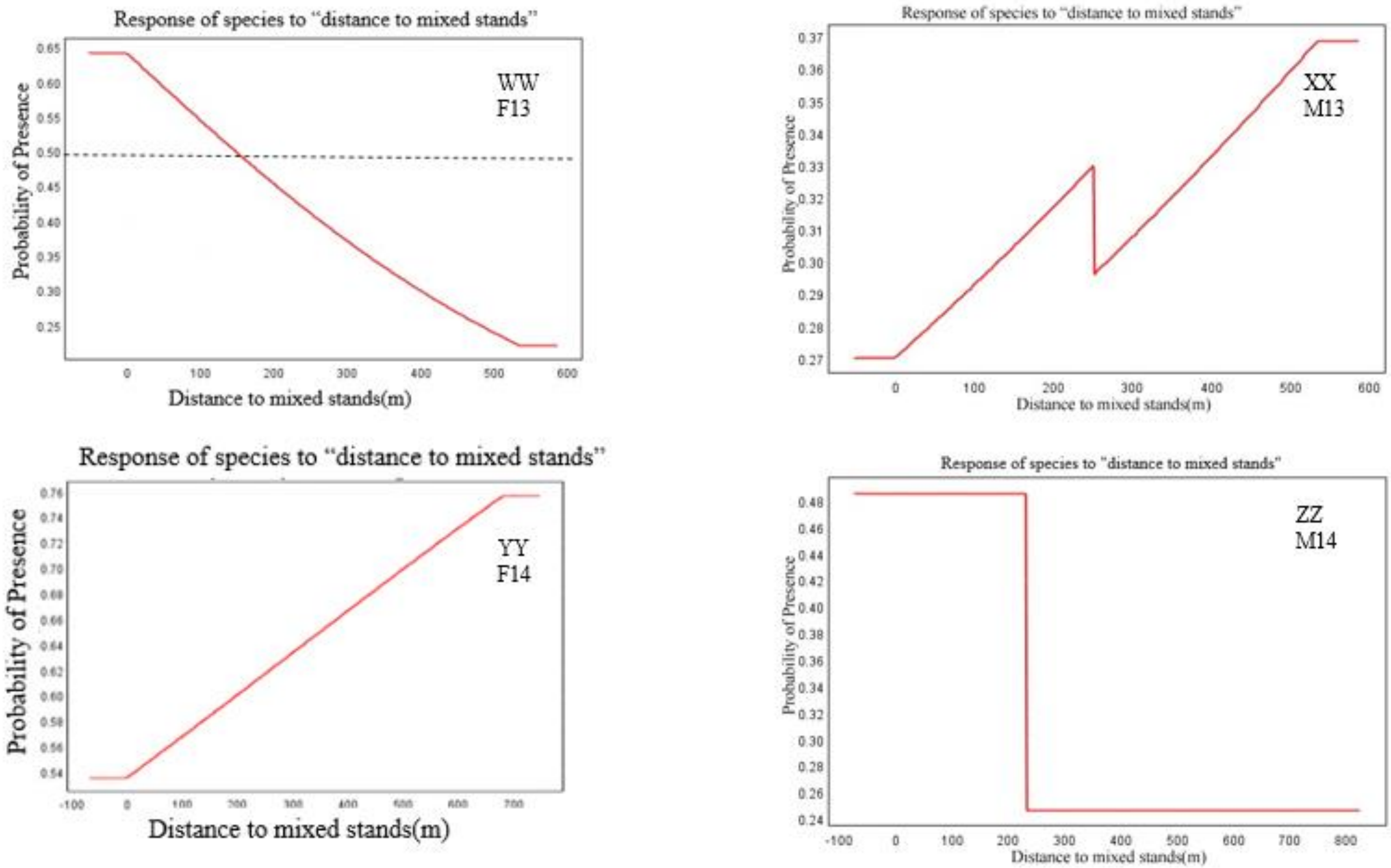

Figure 20: MaxEnt output of response curves for the environmental variable "distance to mixed stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

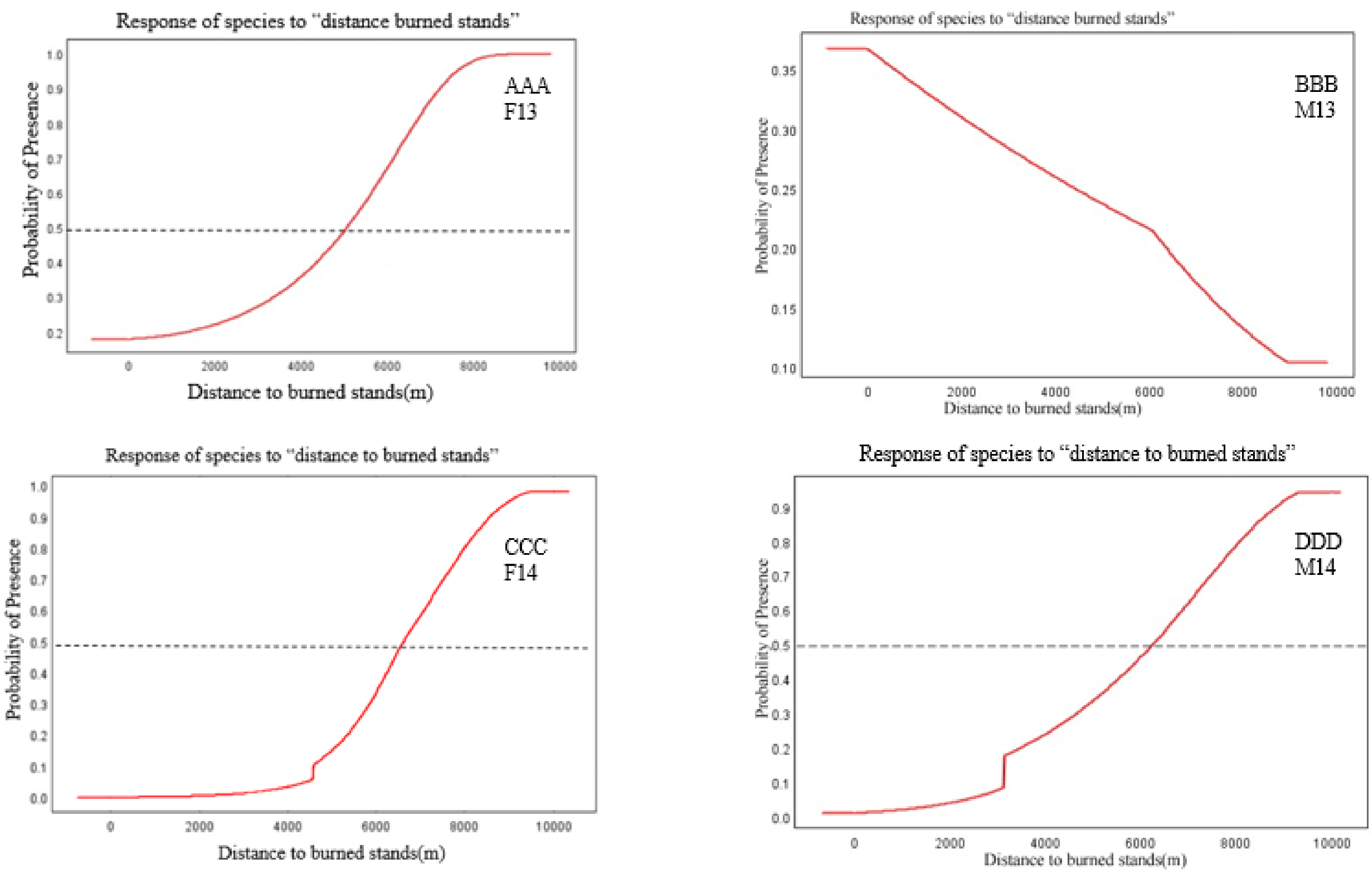

Figure 21: MaxEnt output of response curves for the environmental variable "distance to burned stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

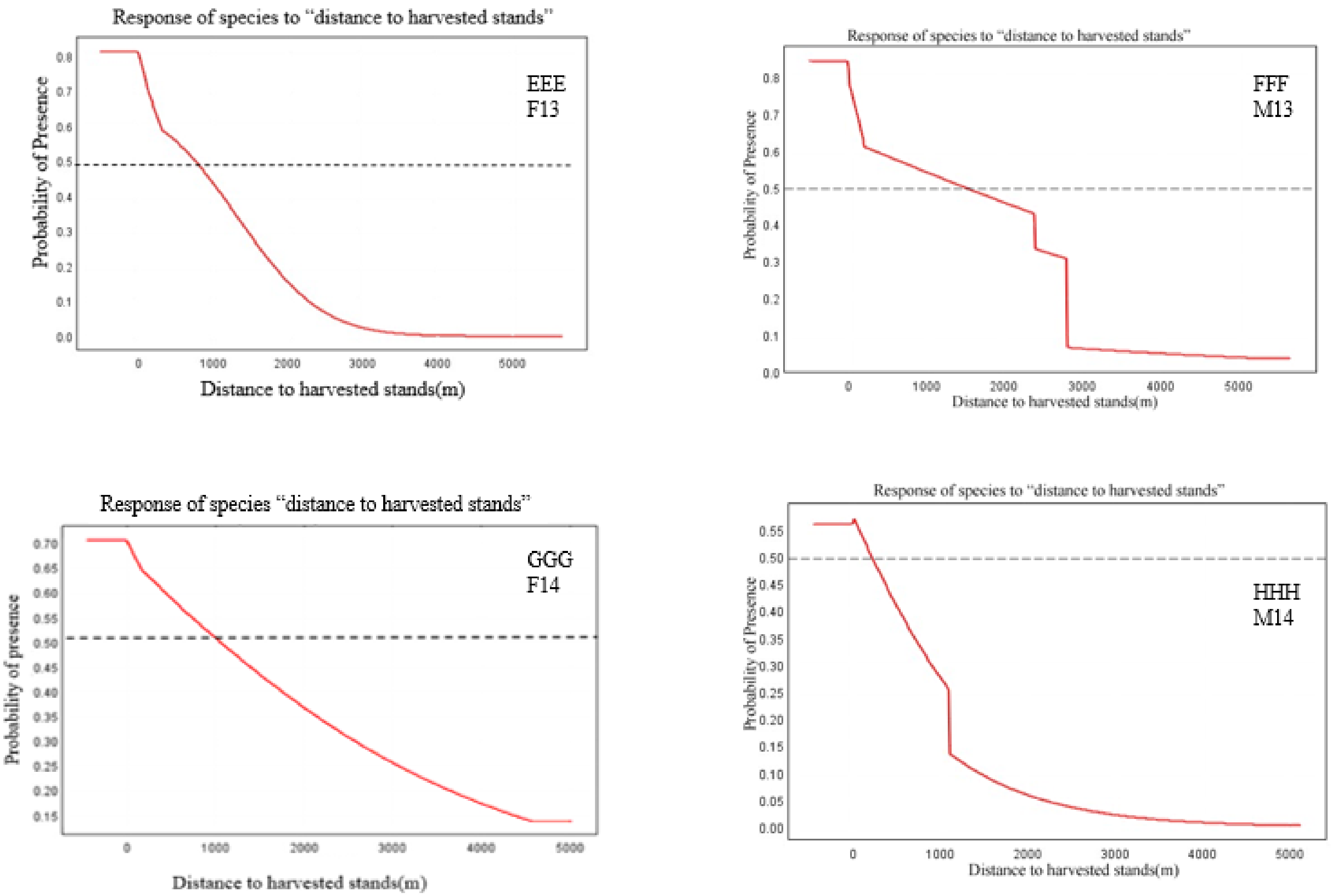

Figure 22: MaxEnt output of response curves for the environmental variable "distance to harvested stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

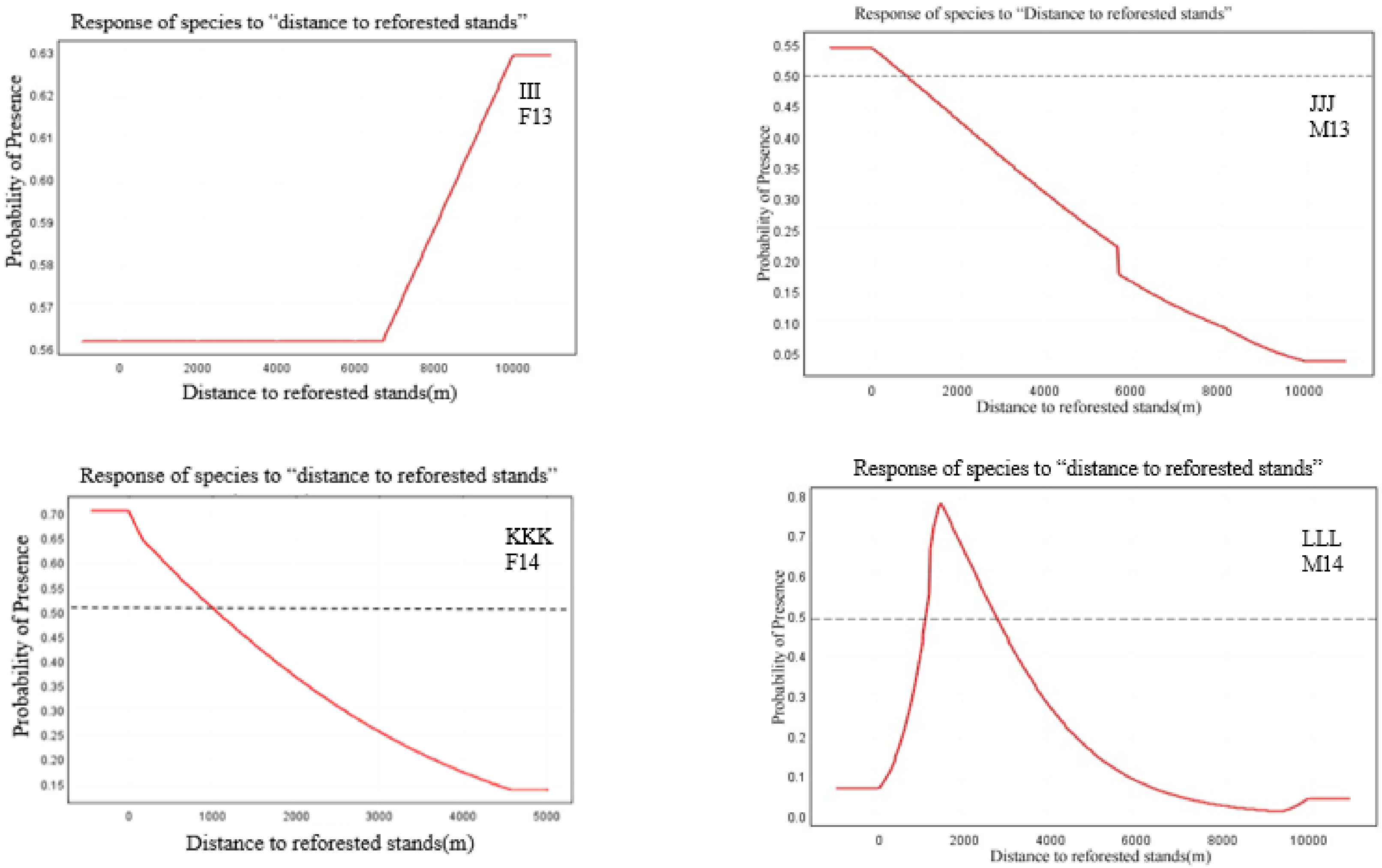

Figure 23: MaxEnt output of response curves for the environmental variable "distance to reforested stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

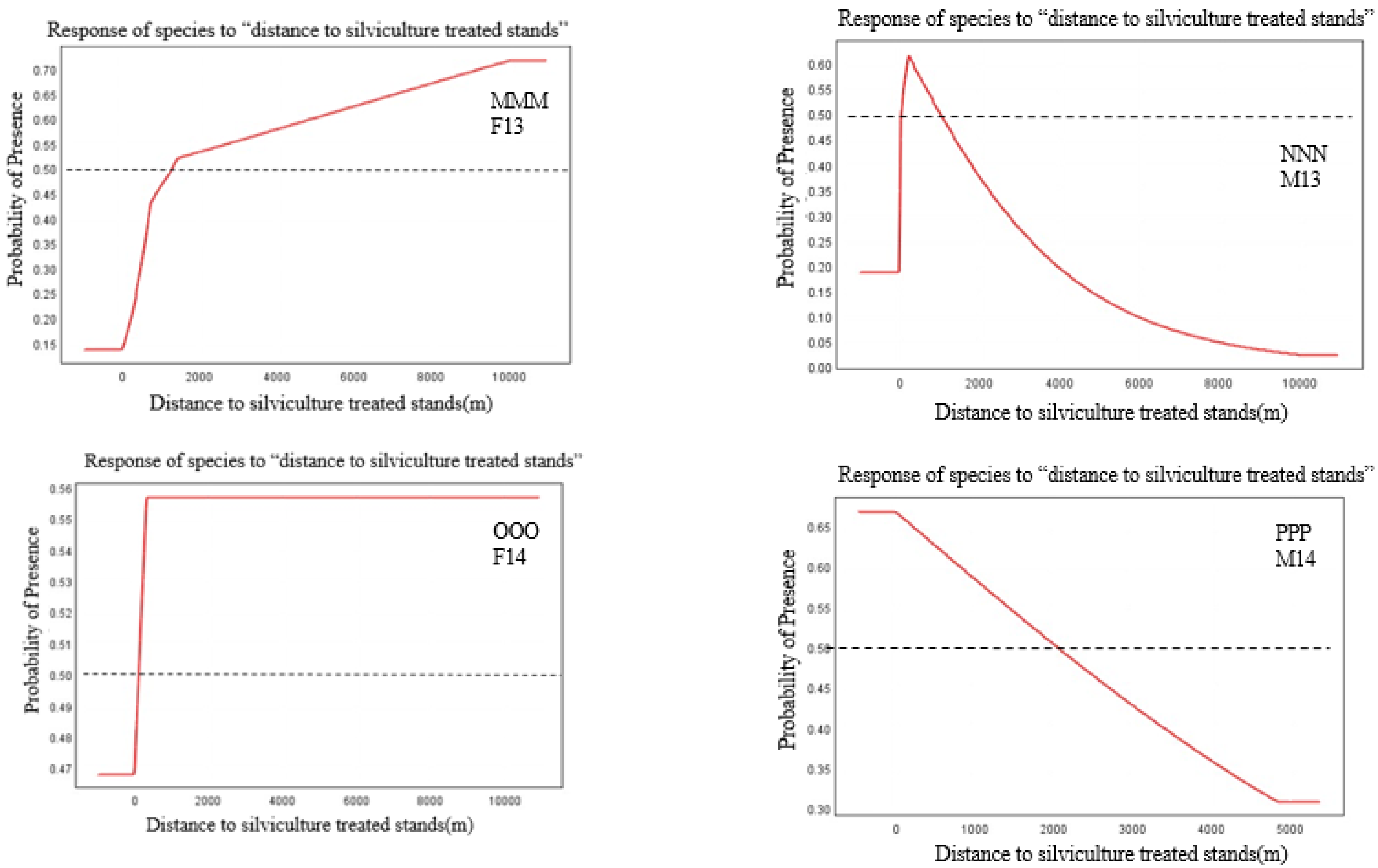

Figure 24: MaxEnt output of response curves for the environmental variable "distance to silviculture treated stands" for female and male evening bats in the Sylamore Ranger District in 2013 and 2014.

Sex-Specific Habitat Suitablity Maps

Habitat suitability maps were generated by MaxEnt models for both sexes in both years. Manipulation of the raster layers allowed me to combine the maps between years to give maps for the sexes in both years.

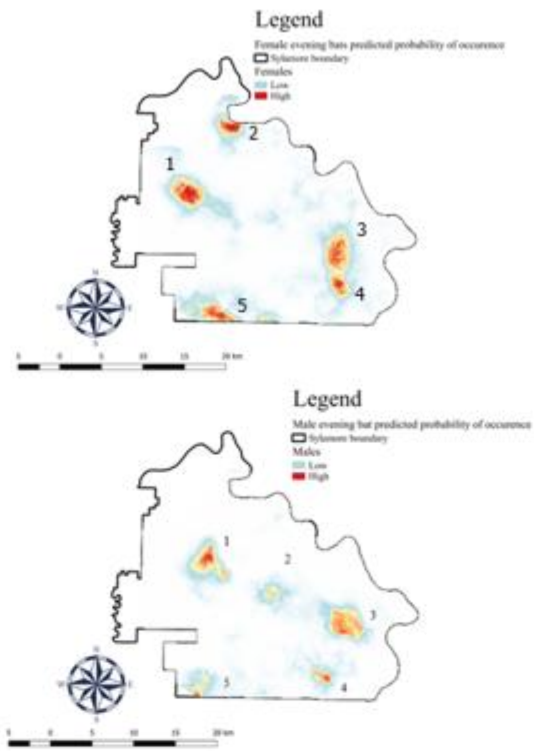

Figure 25: Habitat suitability map generated by my MaxEnt models for female and male evening bats illustrate the probabilities of occurrence in the Sylamore Ranger District. The light colors represent low probability of presence whereas the dark colors represent high probability of presence. On each prediction map, core foraging areas are noted with a number. The areas numbered two through five are areas of recorded presence via telemetry methods. However, on both maps the core foraging areas numbered one were predicted by the software program alone.

CHAPTER IV

DISCUSSION

My study demonstrates that evening bats in the Sylamore Ranger District forage in areas where forest management methods have created less under-story and mid-story in forests and soft edge habitat. Interest in forest use by bats and the effects of forest management on their populations has been sparked by greater awareness of bats' ecological role in maintaining forest health (Marcot 1996) as well as concern about the conservation status of many species of forest bats, especially as bats face decline from White-Nose syndrome and other threats (Pierson 1998). Evening bats specifically tend to show foraging site fidelity and demonstrate flexibility in foraging behavior relative to structural complexity and composition of forest stands. Similarly, other studies have demonstrated that evening bats forage (Istvanko et al. 2016) and roost (Menzel et al. 1998, Istvanko et al. 2016) primarily in oak and pine-dominated stands and open areas created by prescribed fire and timber harvests (Clem 1993, Carter et al. 2004). Distance to burned stands was a consistent influential variable in explaining the foraging selection of evening bats throughout my study with the exception of males in 2013, distance to burned stands negatively impacted habitat use. Evening bats also forage along forest edges such as those created by proximity to agriculture land such as along row crop fields (Duchamp et al. 2004), pasture, and shrub land as determined by the short distance between foraging locations and these landscape features. Evening bats foraged along forest edges in the Sylamore as expected from other studies (Carter 1998). A noted exception was the response to pasture edges. While proximity to pasture was an important landscape feature in all but one year (males 2013), the response was that evening bats select foraging habitats away from these edges.

Variation Between the Sexes

Sex-specific differences in the foraging habitats of bats have rarely been addressed (but see Mata et al. 2016), although differences in home range size and roost sites have been addressed specifically in evening bats (Istvanko et al. 2016). In my study, male and female bats used various parts of the forest for foraging and the structures of their foraging habitat were associated with forest management practices. The results were consistent between years for females while males in 2013 showed a difference in habitat selection than the males in 2014. Males showed a proclivity for edge habitat and water resources while females selected for edge habitat and stands managed by prescribed fire. Overall, the probability of occurrence is lower for males than for females when considering each variable. This supports the idea that males have more flexibility in their habitat selection than females, likely due to lower energetic demands.

Field technicians working on the data collection stated that radio-tagged bats were tracked to roost trees near these locations but no foraging locations could be gathered by telemetry due to the topography of the region. Therefore, the MaxEnt software correctly predicted habitat suitability in an area where no telemetry data were collected. This demonstrates the predictive power of the MaxEnt software based on the weighted importance of certain landscape characteristics that are entered into the models. Evening bats in general showed a strong selection for forests managed with prescribed burns as documented elsewhere (Boyles and Aubrey 2006). Prescribed burns result in managed stands having greater canopy light penetration than unburned stands, which provides warmer roost and foraging sites that benefit from increased solar exposure, less navigable clutter, and a higher prey density (Perry et al. 2007). For female evening bats, proximity to burned stands and edge habitat were the greatest factors that determined presence. The positive responses to environmental predictors such proximity to barren land, at a moderate distance to shrub land, and proximity to evergreen stands with high probability of presence in stands managed by prescribed fire and silviculture work as well as areas with a high NDVI value supports habitat associations known from data collected. This result indicates that they select foraging habitat in pine-dominated stands near edge habitat that maintains its upper story while not exhibiting a dense under or mid-story. The negative response to factors such as close proximity to developed land, proximity of pasture, and steepness suggest that they select foraging habitat in flat, relatively undisturbed areas. These responses are likely because the energetic demands of females during reproduction exceed those of males and likely require females to select roosts favorable for rearing pups (Istvanko et al. 2016).

In contrast, proximity to water and edge habitat were the greatest factors that determined presence of male evening bats, followed closely by timber harvests. The positive response to environmental predictors such as proximity to barren land and deciduous stands, the moderate distance from shrub land, relatively flat areas, and areas away from reforestation efforts, silviculture work, and timber harvest support associations with those specific habitat types. This pattern indicates that males, like females, also foraging near water and edge habitat that maintains its under and mid-story, lending some consistency across the species. The negative response to proximity to developed areas and herbaceous land suggest that males select foraging areas that are rarely disturbed. Although differences between the sexes were detected, some consistent patterns were found for the species. For example, edges produced by proximity to burned stands and shrub land and crops were preferentially selected (Figures 18 and 21). These differences point to aggressiveness toward conspecifics (Ancillotto and Russo 2014) in regards to males and females competing for the same prey (Mata et al. 2016).

Rainfall may, in part, explain the variation of responses among the sexes between years. During the months of April-August, the area received about 50 cm of rain in 2013, and 66 cm in 2014. Specifically, the positive response to wetlands by males and females in 2013 and their negative response in 2014 may be explained by this difference as wetland habitat tends to have more permanent water features rather than ephemeral ones. It follows that ephemeral waters were comparatively more abundant in 2014. It can also explain why females showed a negative response to water in 2013, but a positive response in 2014. With 15 more cm of rain in 2014, there would be more ephemeral water sources available for selection.

Comparison of Foraging Habitats and Roost Sites

Appropriate roost sites and their availability are likely the limiting factor in determining habitat choice by bats (Kunz 1982). Roost availability may influence where bats can forage, resulting in some bats foraging in lower-quality habitat (Geggie & Fenton 1985). This is especially true if commuting to those foraging locations is costly. However, some bats can travel long distances from roosts to foraging grounds (Brigham 1991; de Jong 1994), conceivably to take advantage of both prime roosting and foraging sites (Crampton and Barclay 1998). Comparing the two facets of habitat use could assist managers in making management decisions that best benefit bats at a home range level and a habitat use level. Istvanko et al. (2016) found that male and female evening bats select roosts primarily in the genus *Quercus* with little variation in characteristics such as height, diameter at breast height (DBH), and decay stage. In terms of foraging habitat, I found that both males and females used different stand types regularly (evergreen, deciduous, or mixed). Istvanko et al. (2016) also reported that greater basal area and larger canopy coverage was a consistent feature in male roosts at the plot level. My results, specifically in response to forest management techniques, further demonstrated that female and male evening bats had a positive response to proximity to timber harvests and prescribed fire, both of which result in a decrease in basal area. Interestingly, female evening bats exhibited positive responses to proximity to stands that have been reforested or managed by silviculture in both years as both of these management strategies increase basal area. Conversely, males showed a negative response to proximity to stands that have been reforested or managed by silviculture. These patterns could be due to competition between the sexes for optimal habitat as females require roosts with specific parameters for ideal reproduction (Wilkinson and Barclay 1997). Thus, males roost in areas of high basal area while their foraging areas were associated with management practices that produce lower basal area. In opposition, females roost in areas with lower basal area relative to males while foraging in areas with management practices that increase basal area.

Canopy cover is an important component of foraging habitat as it provides protection from predators in species, such as evening bats, that emerge to feed before or near sunset. Normalized difference vegetation index values that are high (values approaching one) are considered to be a good indicator of substantial canopy cover (Trout et al. 2008). Male evening bats demonstrated a positive response to high NDVI values (highest probability of presence at ~0.8) in 2013, indicating that they were foraging in areas with considerable canopy cover. However, the response curve for male evening bats in 2014 indicated a negative response to high NDVI values (lowest probability of presence at values ~ 0.8-0.9). The difference in rainfall between the years could explain this variance, as areas with considerable canopy cover were further available in 2014 and thus less important in terms of habitat use. Istvanko et al. (2016) also found males roosted in un-thinned areas more than thinned areas containing trees with small diameters (Istvanko et al. 2016). Roost site selection may be the limiting factor when determining foraging habitat (Kunz 1982; Furlonger et al. 1987). If this is the case, bat presence would likely decrease as timber harvest increases, which is predicted by my study population showing a negative response to proximity to stands that have been harvested.

Management Recommendations

An important finding in this research is that forest management practices influence foraging site selection in evening bats and roosting and foraging habitat can vary greatly in their landscape characteristics. For example, when male evening bats are roosting and foraging, they select foraging habitat for areas of high canopy cover. However, females are more flexible in the percent canopy cover they select when roosting but show a preference for foraging in areas with substantial canopy cover. Also, when considering basal area, I found that males roost in stands managed with techniques that result in high basal areas but forage in areas that have been managed to decrease basal area. Managers who focus on one order of habitat selection and use rather than looking at multiple orders would miss critical aspects of this species ecology. Therefore, managers should consider factors that affect both foraging and roosting habitat selection when managing for this and similar species.

Conclusions and Future Direction

My methodology evaluated habitat suitability models for evening bats providing new, critical information on how forest management techniques influence the habitat use of the evening bat. The predicted habitat suitability maps can be used to predict areas of occupancy for future conservation planning. The modeling results were congruent with my understanding of evening bat habitat use and illuminates the sex-specific habitat use during foraging observed in this species. These models depict patterns of habitat use and provide an understanding of the relevant landscape characteristics, both natural and human-influenced that have a relationship with the ecology of the evening bat. Forest management regimes are important to consider depending on their positive or negative impact on all species in a management area. My study site in particular was a management area for Indiana bats (*Myotis sodalis*) during the active season. Capture records of Indiana bats have been and continue to be historically low in this area (Risch unpublished). Thus, Indiana bats' response to these management practices is hard to quantify. However, evening bats may be good proxies to evaluate the effects of these management strategies on other bat species. Future research should apply these analytical approaches to other bat species.

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