Effects of Climate Change on the Distribution of White-footed mouse (*Peromyscus leucopus)*, an Ecologically and Epidemiologically Important Species

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Abstract

Peromyscus leucopus (White-footed mouse) is a common species found throughout the eastern United States and a key component of midwestern ecosystems. Recently, the species has been expanding its range from the Lower Peninsula of Michigan, to the Upper Peninsula, possibly due to increasing temperatures. Given the shifting environmental conditions, understanding current environmental determinants of current *P. leucopus* distribution can help predict how the species will respond to global climate change. Such insight in turn, is both important for understanding how N. American species communities are likely to be influenced by ongoing climate change and also for applied local conservation efforts. Data on the presence/absence of *P. leucopus* and environmental variables including elevation, land cover, and climate, such as temperature, and precipitation, were used to predict habitat suitability and current distribution in Michigan. We assessed the fit of a model that uses maximum entropy approach (MaxEnt) to relate presence to environmental variables by using a cross-validation process and the receiver operating characteristic. Response curves were used to illustrate the relationship between each of the environmental variables and the probability of presence of *P. leucopus*. And a jackknife test was used to identify those environmental layers that were most important in predicting White-footed mice distribution. Future temperature and precipitation layers were used to predict the possible future distribution of White-footed mice in Michigan and northward. Our analyses indicated that the final model provided a reasonably good fit to the current distribution of the species. Average minimum temperature of April was the environmental layer that contributed most to predicting the current distribution of White-footed mice, whereas, February precipitation reduced the gain of the model most when omitted from the analysis. April average minimum temperature and April precipitation were both positively related to the probability of presence of *P. leucopus*. The importance of temperature and precipitation suggests that the distribution of this ecologically important species is going to change under future climatic regimes. Indeed fitting the present model to future conditions indicates that the species will expand dramatically northward in the next 50-70 years with many Canadian areas north of Michigan becoming suitable habitat for *P. leucopus* by 2050.

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Introduction

The White-footed mouse (*Peromyscus leucopus, Rodentia*) is a widespread and common species found throughout Eastern North America and with a range extending from southern Maine to Alabama and southern Mexico (Lackey et al. 1985). In the northern parts of their range, White-footed mice most often inhabit deciduous forests or mature coniferous forests and shrubby fields (Iverson *et al.* 1967; Lackey *et al*. 1985). In southern localities, the species is found in forested and brush habitats, as well as ravines and riparian areas within drier, desert habitats (Lackey et al. 1985).

Because *Peromyscus leucopus* occurs generally in high population densities, it is an important component of North American forest ecosystems (Marcello *et al.* 2008). Particularly, it plays an essential role as prey for many predators, including other mammals such as raccoons, fox, and mink, (Fanson 2010), and birds such as owls and other raptors (Myers *et al.* 2009a). White-footed mice are influential in high mast years, having a profound effect on forest pests and as seed predators (Clotfelter *et al.* 2007; Kelly *et al.* 2008; Ostfeld *et al.* 1997). As a result, increases in mice densities impact seedling growth at forest edges (Ostfeld *et al.* 1997). Also, during mast years with high acorn production, White-footed mice populations increase dramatically and can effectively control Gypsy moth densities (Clotfelter *et al.* 2007; Kelly *et al.* 2008). This relationship among acorns, White-footed mice, and Gypsy moths has important implications for ticks and the prevalence of Lyme disease (Jones *et al.* 1998; Ostfeld 2009). High acorn densities not only increase *P. leucopus* populations, but also attract deer, which bring ticks. White-footed mice are then important hosts for the tick larvae and infect them with Lyme disease (Jones *et al.* 1998; Ostfeld 2009). Therefore, being able to predict P. leucopus populations may be important in protecting human health and predicting Lyme disease risk (Jones *et al.* 1998; Ostfeld 2009). Furthermore, *Peromyscus* species are also important hosts for Hantaviruses; therefore, changes in distribution of White-footed mice can have epidemiological consequences for humans (Gedeon *et al.* 2009; Ignacio and Abramson 2006).

Climatic changes have a clear effect on White-footed mouse populations. While the empirical field research has suggested links between climate and *P. leucopus* as well as other small mammal populations (Deitloff *et al.* 2010; Iverson et al. 1967; Myers *et al.* 2009b) these relationships have never been modeled. Because field studies typically involve trapping mice over a small area they are can be spatially limited in the scope of predictions they can make.

Modeling that utilizes empirical data can not only make predictions on a larger scale but can also provide information on the relative importance of various environmental variables. As a result, predictive distribution models can help estimate how the occurrence of White-footed mice might change as the result of changes in temperature and precipitation patterns.

The ability to predict species distributions can be vital in wildlife management plans. For instance, wildlife agencies often use potential habitat estimations and distribution data to make decisions about hunting quotas (Baldwin 2009). Predicting locations that fulfill a species' ecological niche is also very useful in conservation decisions, such as where to reintroduce a species or where to locate reserves (Baldwin 2009). Distributional data can also aid in understanding how future conditions will affect organisms (Anciães and Peterson 2001, Cameron and Scheel 2006).

The most common way to predict a species' distribution is to explore its relationship to environmental variables. The use of statistical modeling techniques to predict locations that fulfill the species habitat requirements has become very popular, especially in the context of application of geographic information system (GIS) tools (Guisan and Zimmerman 2000). Predictive distribution modeling or niche modeling has been used in the fields of biogeography, ecology, conservation biology (Guisan and Thuiller 2005; Brito *et al.* 2009; Kumar *et al.* 2009; Suarez-Seoane *et al.* 2008; Wang *et al.* 2010). Distribution point files and environmental layers, such as land-cover type, elevation, and climatic variables that are typically used in the models, are relatively easy to manipulate using GIS software. With a changing climate, these models are beginning to be used not only to predict current distributions of organisms (Brito *et al.* 2009; Kumar *et al.* 2009; Suarez-Seoane *et al.* 2008; Wang *et al.* 2010) but also to predict the impact climate change on future species distributions (Guisan and Theurillat 2000). While the number of species affected by climate change has increased greatly in recent years, there have nonetheless, been very few studies that examine distributional shifts, especially in mammal populations.

MaxEnt (Phillips *et al.* 2006) is a new modeling software and is a general-purpose machine learning method. It uses the maximum entropy principle to predict species distributions and has many advantages. This software accepts continuous and categorical predictor variables and avoids commission errors or predicting a species is present incorrectly (Pearson *et al.* 2007). For species distribution models, data on the presence of an organism is often more accessible than data on its absence, due to the vast occurrence records in museums and herbaria. MaxEnt can build models based on data on presence and absence, or on presence-only. MaxEnt has been shown to create models that better fit available data than previously used techniques such as GARP, GLM, CART (Kumar *et al.* 2009; Wang *et al.* 2010). In addition, MaxEnt results have also been shown to be fairly robust to the existence of spatial errors in location data and MaxEnt requires very few location points to create an accurate model (Baldwin 2009). Therefore, MaxEnt is a good choice to make predictions about the distribution and habitat requirements of species.

Due to the apparent relationship between climate and the occurrences of *P. leucopus* and the importance of understanding species distributions, I used field observation records and environmental layers, including modeled climatic conditions in 2050, to understand the habitat preferences and predict the future distribution of *P. leucopus* using MaxEnt. Variables describing land cover, elevation, precipitation levels, and average minimum temperatures in February, March, and April were used to determine habitat requirements and effects of climate changes on White-footed mice distribution.

Methods

Study area

This study focuses on the Upper Midwest region of N. America. In particular the model was created using data from Michigan's Upper and Lower Peninsula, from around 41°N to 48°N. We trained the MaxEnt software using previously collected presence and absence data of *P. leucopus*. They represented unpublished field records collected by Dr. Philip Myers using standardized sampling methods. To ensure that recorded absences represented true absences of the species rather than inadequate sampling effort, we limited our absence points to those loctions where 1. other common species (*Peromyscus maniculatus*, *Glaucomys volans*, *Glaucomys sabrinus*, *Tamias striatus*, or *Eutamias minimus)* were detected and 2. trapping effort exceeded > 100 trapping nights. By including points of documented absence, instead of allowing MaxEnt to generate background points randomly from the study area, any inherent sampling bias within the points was eliminated. Because all presence and absence points are from Michigan and because range limiting factors may vary regionally, we restricted the predicted current range area to Michigan. However, model predictions were then extended to cover areas north of Michigan, to evaluate the likelihood that habitat conditions favorable for *P. leucopus* like those currently found in Michigan will be extended to locations further north.

Environmental Variables

The environmental variables used represented land cover, topography, and climate, and were chosen based on their likely ecological influence on the distribution of White-footed mice as mentioned in the species relevant literature (Deitloff *et al.* 2010; Myers *et al.* 2009b) (Table 1). All manipulations of environmental layers were done within ArcMap GIS (ESRI version 9.3.1). Both the land-cover grid and the digital elevation model (DEM) have a spatial resolution of 30 meters and were obtained from the National Map Seamless Server on the United States Geological Survey website. We used the NLCD 2001 data (Homer *et al.* 2007) for the land-cover file (Table 2) and NED data (Gesh *et al.* 2002) for the DEM. We obtained average minimum temperature and precipitation levels for February, March, and April from WorldClim.org, a data distribution site maintained by the Museum of Zoology at the University of California, Berkeley, in collaboration with CIAT (the International Center for Tropical Agriculture) and Rainforest CRC (a Cooperative Research Centre for Tropical Rainforest Ecology and Management) (Hijmans *et al.* 2005). Minimum temperature was chosen as an indicator of the length and severity of winter, since areas with pronounced winters are thought to be less suitable for the survival of White-footed mice populations (Myers et al. 2009b) and precipitation was chosen to provide further information on the severity of winter. The climate layers have a resolution of 1 kilometer and cover the entire globe.

All environmental layers were converted into WGS 1984, a standard coordinate frame for the Earth, and then clipped to cover only Michigan using the Raster Calculator in ArcGIS. The land cover and elevation layers were also aggregated to a resolution of 1 kilometer to match the climate layers. We assigned the majority class to each 1km cell on the land-cover file and the average elevation to each 1km cell on the digital elevation file.

To predict the future distribution and potential range expansion of *P. leucopus* under the current trend of a warming climate, land cover and digital elevation models for areas north of Michigan were also used. The present land cover data for Ontario, Canada were obtained from the Institute for Fisheries Research at the University of Michigan Department of Natural Resources and Environment, and the DEM for Ontario was obtained from the GTOPO30 dataset from the USGS Earth Resources Observation Center (eros.usgs.gov) and had a resolution of 30m. The land-cover data used the same classification scheme as the Michigan data, and therefore did not require any reclassifying. Predicted future climatic layers of average minimum temperature and precipitation levels for February, March, and April were obtained from WorldClim.org. The predicted variables were obtained from the Canadian Centre for Climate Modelling and Analysis model (CCCMA), created under a worst-case scenario, in which a heterogeneous world economy has a high rate of population growth, energy use, and land-use change, but slow technological change (referred to as the SRES A2 scenario; IPCC 3rd Assessment Report 2001). Two sets of predicted distributions were created from the MaxEnt model, one using the future climate layer predicted for 2050 and the other for 2080.

Occurrence data

A total of 753 points at which *P. leucopus* was either observed (473) or not (259) were used to develop a model of its distribution across the study area. The data were from field observations and collections recorded by Dr. Philip Myers of the University of Michigan. All of the observations are from 1950 to the present, with most of the records occurring from 1980 onwards. All of the points (752) were intersected with the environmental layers to create a table with information representing all of the environmental data to use in the model. A shapefile of the distribution point file was created within ArcMap GIS (version 9.3.1) by displaying the XY data from an Excel sheet of latitude and longitude coordinates of the occurrence points. The datum of the file was then converted from NAD1927 into WGS1984. Any points that were outside the study area (i.e., the State of Michigan) were deleted. Presence points that did not overlay one or more of the environmental layers (due to a recording error), but were within 0.5 kilometers of the nearest environmental data were moved to the closest cell. This file was used to represent the presence points in the model.

MaxEnt Analysis

The MaxEnt software (version 3.2.2) (Phillips *et al.* 2006), which utilizes a maximum entropy approach to species distribution modeling, was used to model the predicted distribution of *P. leucopus*.

The presence and absence points were intersected with the environmental layers (elevation, land cover, temperature, and precipitation) using the sample tool in ArcMap and saved as a comma delimited file representing the environmental data. These two comma delimited files were used to train the model and predict the current distribution pattern. For the future projection model and for validation, the environmental data was used in the form of a table in place of the ascii girds. The future predictions were projected using land-cover, elevation, and climate files with a greater extent than the original model, covering areas north of Michigan in order to predict *P. leucopus'* projected distribution in the face of climate change.

Results were obtained using the logistic output option, which creates a probability map showing the probability of *P. leucopus* occurring in each cell on a scale from 0 to 1. Two types of response curves were created to demonstrate the relationship between each of the environmental variables and the probability of the species occurrence. The first presented are the response of the probabilities to individual variables taken one-by-one in the models. The second, are the marginal response curves, which show the response of each variable in the multi-variate model when all other variables are set to their mean values (Appendix C). The percent contribution of each variable was calculated as the model was generated by showing which variables contributed most to the explanatory gain of the model measured using the path the MaxEnt code uses to achieve the optimal solution. Next, the jackknife feature in MaxEnt was used to measure the importance of each environmental variable to the training of the current model. With the jackknife test, a number of different models were created. Firstly, each variable was excluded, and a model created with the remaining variables. Then a model was created using each of the variables separately and without any other variables. In addition, a model was created using all of the variables. The results are shown in a figure depicting how the model performed with and without each of the variables as compared to with all of the variables.

Evaluation

The model was evaluated using the bootstrap feature within the settings of MaxEnt, where a random selection of 75% of the presence points was used to train the model, leaving the remaining 25% to test the model, with 100 replicates of randomly sampled test points and the presence and absence file as the background points, allowing for the elimination of sampling bias since environmental data around both presence and absence points were used. After an evaluation of model accuracy, all of the presence points (n=493) were used for the final model, in order to include all possible data when creating the probability map of predicted distribution.

The receiver operating curve (ROC) was used to assess the accuracy of the model. The ROC plots the sensitivity values (i.e., the rate of false positive predictions) against specificity values (i.e., the percent of area mapped as presence for a given probability cut-off value). In applying the model to predict current and future patterns with presence and absence points, the ROC was calculated using the presence and absence points as the specified background points.

Table 1. Environmental variables used in MaxEnt models.

Variable Code	Variable Type	Units	Data Source	Mean	Min	Max
tmin2	February average minimum temperature	Degrees C*10	WorldClim	-122.5	-185	-60
tmin3	March average minimum temperature	Degrees C*10	WorldClim	-65.5	-120	-11
tmin4	April average minimum temperature	Degrees C*10	WorldClim	1	-38	40
prec2	February average precipitation	Millimeters	WorldClim	37.8	15	77
prec3	March average precipitation	Millimeters	WorldClim	44.9	25	65
prec4	April average precipitation	Millimeters	WorldClim	61.9	37	105
dem	Elevation	Meters	USGS	300.1	106	676
lc	Land-cover		USGS	-	-	-

Table 2. Definitions and areas of land-cover categories.

Land Cover Category	Definition	Area (km^2)
21	Developed, Open Space	31,584
22	Developed, Low Intensity	52,900
23	Developed, Medium Intensity	7509
24	Developed, High Intensity	4809
31	Barren Land	1913
41	Deciduous Forest	180,254
42	Evergreen Forest	155,662
43	Mixed Forest	132,238
51	Shrub	6558
71	Grassland/Herbaceous	22,625
81	Pasture/Hay	106,954
82	Cultivated Crops	159,209
90	Woody Wetlands	68,634
91	Palustrine Forested Wetland	20,430
95	Emergent Herbaceous Wetland	13,002

Results

Environmental factors related to species occurrence

The environmental variable with the most useful information and with the highest gain in explaining the pattern of *P. leucopus* when used in isolation was minimum temperature of April (Table 2). Therefore, the minimum temperature of April contributed the most to the model; this percent contribution is calculated as the model is being generated and shows which variables were used most or contributed most to the model. Another way to assess the importance of the variables is to look at how well each variable fits the training data. When used in isolation, April minimum temperature fits very well to the training data and can predict much (over 50%) of the distribution of *P. leucopus* without the use of any other variable (Figure 1). Precipitation in February reduced the gain the most when omitted (Figure 1), meaning that this variable contained some information not present in the other variables. However, it did not reduce the gain considerably, so this variable is probably not very important in predicting *P. leucopus* distribution. When variables are highly related, the percent contribution and jackknife procedures may give very different results. When one variable is left out of the model in the jackknife test, if there is second variable that contains similar information, the gain of the model may not be reduced considerably. Therefore, the particular variable may not stand out in the jackknife test. However, the variable may still show up as important in the percent contribution analysis. In this analysis, none of the variables were highly correlated, and the percent contribution and jackknife procedures gave similar results.

Table 3. Estimate of relative contributions of the environmental variables to the MaxEnt model for current distribution, showing that minimum temperature of April contributed the most.

Variable	tmin4	prec4	prec2	tmin2	lc	prec3	dem	tmin3
Percent Contribution	34	30.9	10	9	6.1	5.5	3.1	1

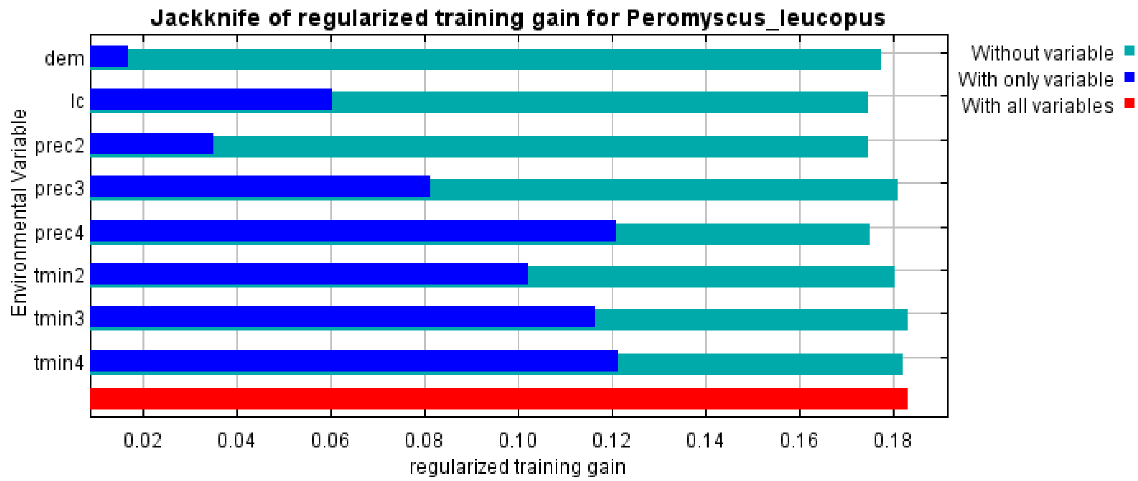

Figure 1. Jackknife test for current prediction showing that minimum temperature of April had the highest gain when used by itself and precipitation in February reduced the gain the most when omitted.

The relationship between each of the environmental variables and the probability of presence of *Peromyscus leucopus* is outlined in the response curves (Figure 2). Minimum temperature for February and March had fairly little effect on the model (Table 3), and therefore, their apparently opposite effect on the probability of presence of P. leucopus (Figure 2) is probably not particularly biologically meaningful. However, April minimum temperature did have a substantial effect on the model (Table 3) and as this variable increases, the probability of *P. leucopus* occurring in that area also increases (Figure 2). The minimum temperature response curves all show a drastic decline in probability at the lowest levels of temperature to a minimum probability, occurring at -140 in February, -90 in March, and -20 in April (Figure 2). However, this is probably due to a small number of locations with these low temperature values. The majority of locations experience higher temperature values and the mean minimum temperature for each month (Table 1) is above the point of rapid decline. Therefore, most localities are probably associated with the remainder of the response curve above this minimum value.

April precipitation has the second largest effect on the model (after April minimum temperature), and has a more linear positive relationship with the probability of presence of *P. leucopus*. As April precipitation increases, the probability of presence of White-footed mice also increases. This positive relationship is particularly strong at the lower values of April precipitation, and can be seen more clearly in the marginal response curve (Appendix C). February and March precipitation do not strongly affect the model, and therefore, their relationships with probability are probably not as biologically meaningful.

Since land cover is categorical, it does not portray a clear linear relationship with probability of presence of *P. leucopus*. The highest probabilities are associated with the developed, forested, cultivated crop, herbaceous/grassland, shrub, and forested wetland land cover categories. White-footed mice typically occur in forested areas (Lackey *et al*. 1985, Myers *et al.* 2009), and therefore the high probability around the forested and forested wetland land cover categories is consistent with the ecology of the species. Most of the elevation in the area is around 100m (Table 2), and up to around 200m, as the elevation increases, the probability of presence of White-footed mice decreases (Figure 2). After about 200m, the probability of presence is more erratic and probably associated with few localities.

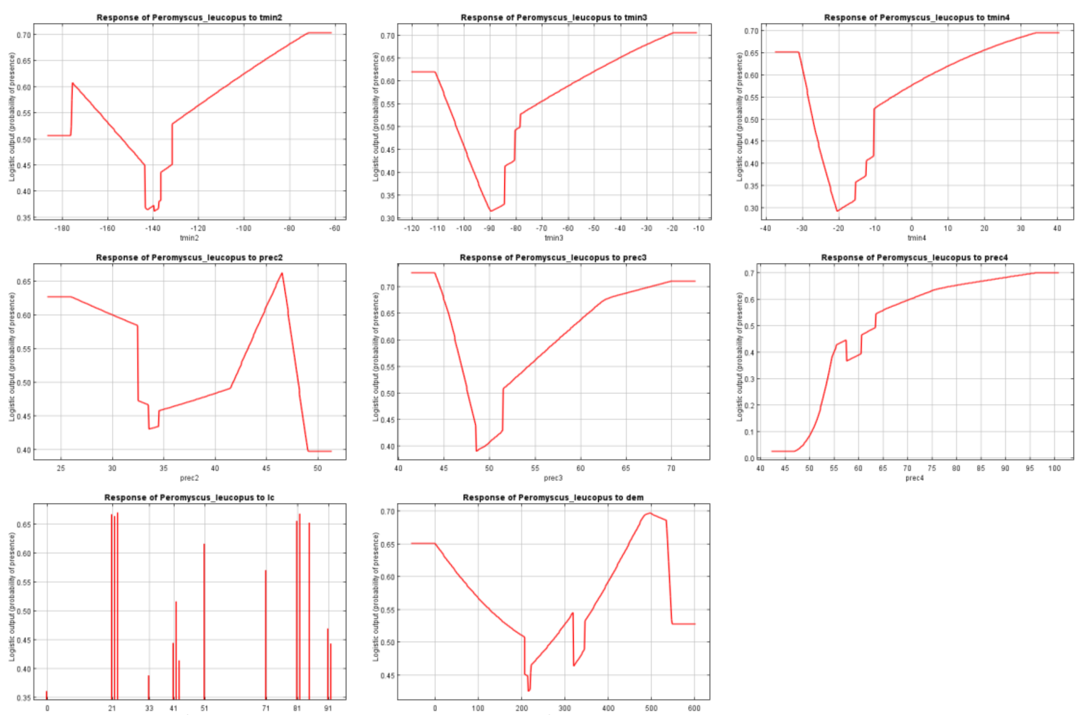

Figure 2. The relationship between individual environmental variables and the probability of presence of *P. leucopus*.

Biogeographic patterns in Michigan

When using all of the points to train the model and Michigan as the study area, the MaxEnt results showed that the model predicts all the Lower Peninsula to be suitable areas for *P. leucopus* (Figure 3). Much of the southern parts of Michigan's Upper Peninsula are also suitable for *P. leucopus*. However, *P. leucopus* is not predicted to occur in the northern tips of the Upper Peninsula; this is consistent with Dr. Philip Myers' field work and the hypothesized ecology and habitat requirements of White-footed mice.

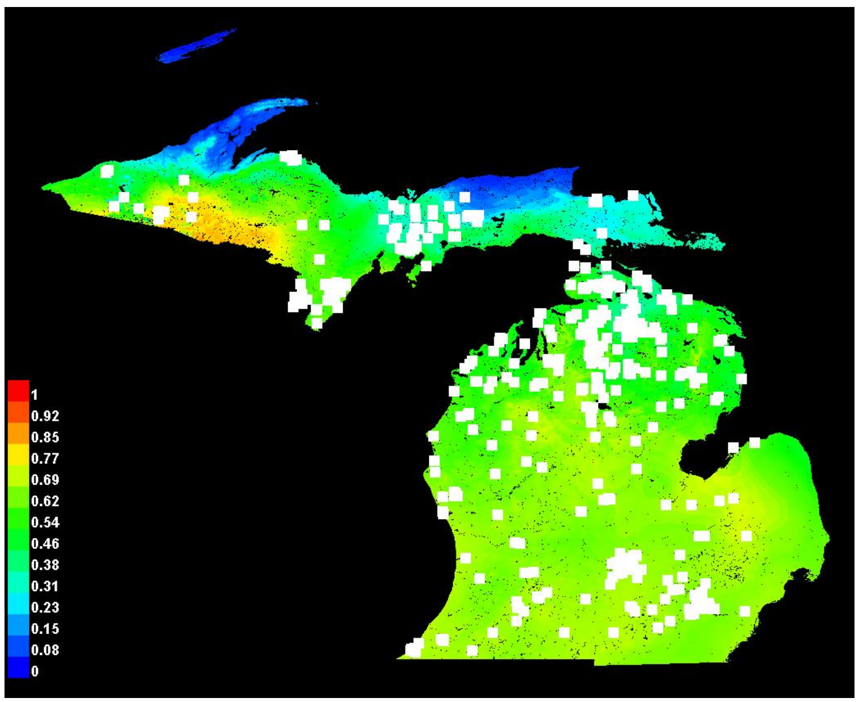

Figure 3. MaxEnt output for current distribution of P. leucopus within Michigan using all presence points and current data to train model; warmer colors show higher probability of occurrence and habitat suitability. White squares represent presence localities.

Evaluation of models

The area under the receiver operating characteristic curve for all of the training data was 0.699 (Figure 4). This shows that the model is fairly accurate with a high probability of correctly predicting presence points within sample.

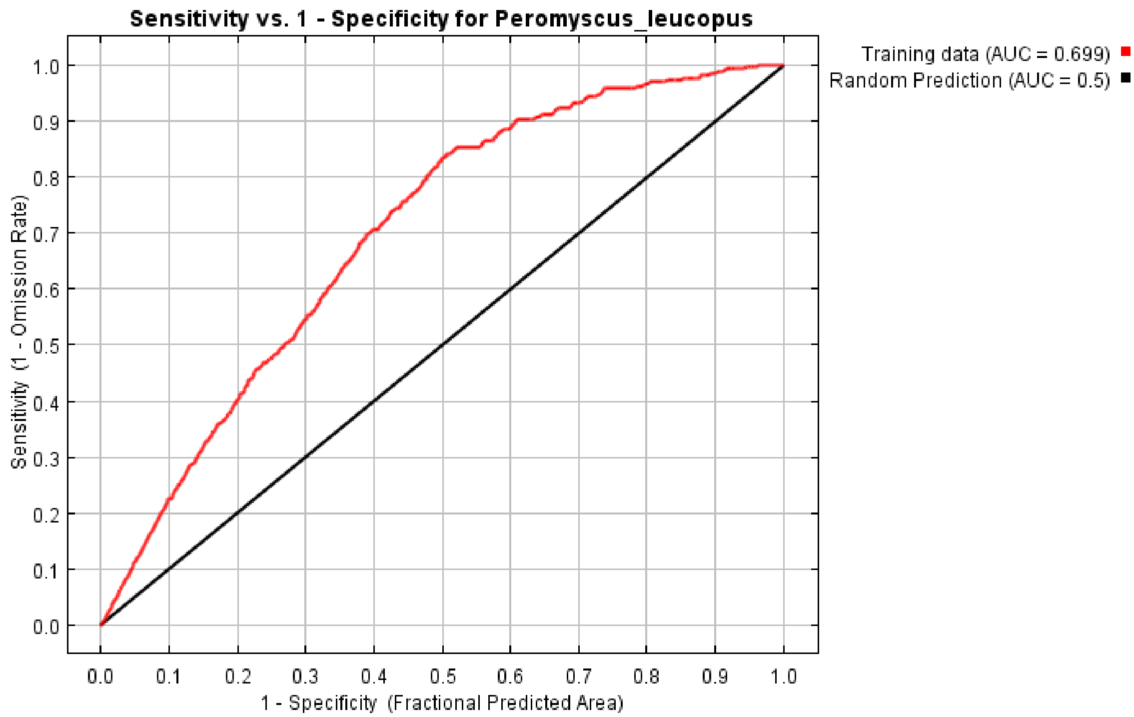

Figure 4. Receiver operating characteristic curve showing the fraction of true positives against the fraction of false positives.

When using the bootstrap validation process (Phillips *et al.* 2006), where 75% of the points were used to train the model and 25% to test the model, and the minimum training presence threshold, the mean test omission was 0.00356 +/- 0.006899, meaning there was a 0.3% omission error. Minimum training presence threshold is set equal to the minimum probability score under any of the training points and represents the minimum suitable environmental conditions for *P. leucopus* (Liu *et al.* 2005).

Projections North of Michigan

Consistent with current field work, when the model was trained using current data layers, MaxEnt predicts that areas north of Michigan are unsuitable habitat for White-footed mice (Figure 5). Using climate layers predicted for 2050 using the CCCMA model, the areas north of Michigan are predicted to be much more suitable for *P. leucopus* (Figure 6). Temperatures and precipitation levels in areas north and west of Michigan are predicted to be outside their current range and will impact habitat suitability for *P. leucopus* (Figure 6), with much of the area predicted to become highly suitable for the species (Figure 6). In 2080, the model predicts all of the area north of Michigan will become habitable for White-footed mice, with no areas showing a probability of occurrence less than around 0.5 (Figure 7).

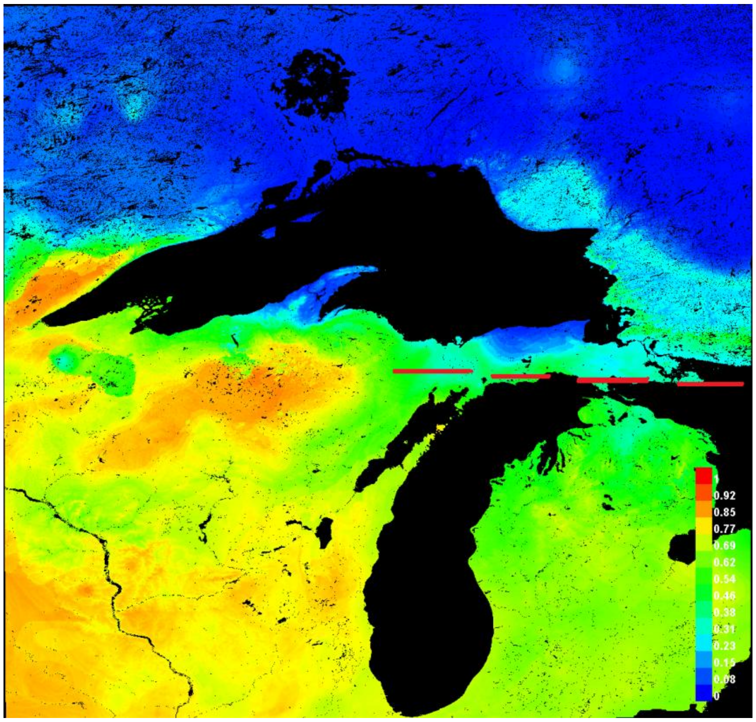

Figure 5. MaxEnt output for current distribution of *P. leucopus* using all presence points and current data to train model, showing predictions north of Michigan. Legend is the same as Figure 3. Red dotted line outlines the predicted current northern limit of the species in Michigan.

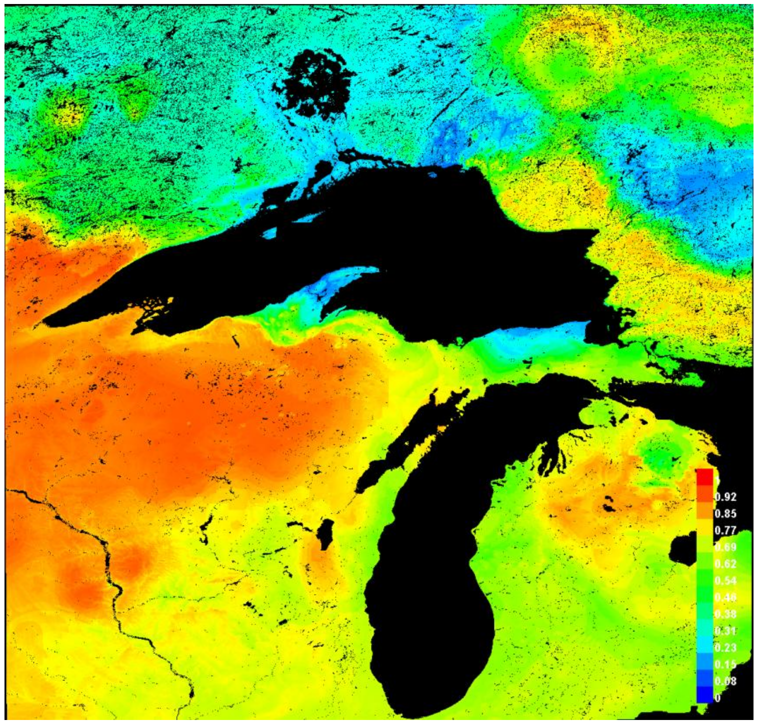

Figure 6. MaxEnt output for predicted distribution of *P. leucopus* in 2050 using the CCCMA model. Legend is the same as Figure 3.

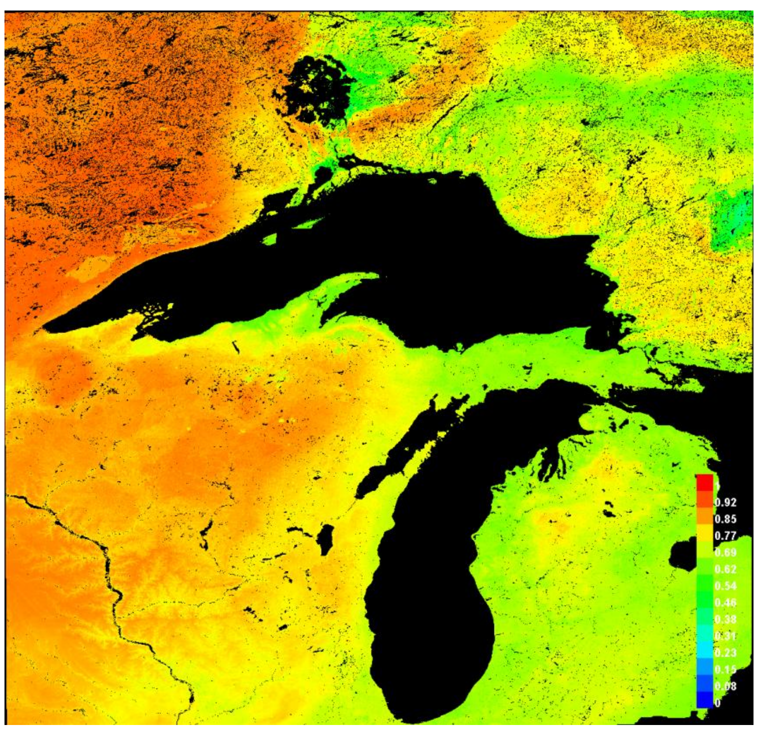

Figure 7. MaxEnt output for predicted distribution of *P. leucopus* in 2080 using the CCCMA model. Legend is the same as Figure 3.

Discussion

MaxEnt output showed that climate, particularly the conditions towards the end of winter, is critical in predicting the spatial distribution of *P. leucopus*. The minimum temperature of April was the most important variable in predicting current White-footed mice distribution and produced the highest gain in prediction in the model when used alone. Also, the response curve showed that as the minimum temperature in April increased above zero, so did the probability of *P. leucopus.* This makes biological sense, since as the temperatures warm at the end of winter, White-footed mice are better able to survive. Therefore, minimum temperature towards the end of winter is probably very useful in predicting *P. leucopus* occurrence. Without any other information, this variable will still produce fairly accurate results. Amounts of precipitation in April was the second most important variable, showing that climatic conditions at the end of the winter season are useful in predicting White-footed mice distribution, and further suggesting that the end of winter climate conditions are critical in determining *P. leucopus* survival.

Precipitation in February reduced the gain of the model most, meaning that when this variable was removed, the model performed less accurately than when any other variable was removed. This suggests that February precipitation holds some information not present in any other variable, which is important in predicting the distribution of *P. leucopus*. The relationship between February precipitation and the probability of *P. leucopus* occurrence is not linear (Figure 2). When February precipitation is fairly low, *P. leucopus* probability of occurrence was fairly high, and then decreases as precipitation levels increase. However, at fairly high levels of February precipitation, the probability of occurrence increases drastically and then drops again (Figure 2). February precipitation consists mostly of snow and might be important as an insulator for *P. leucopus* during this cold part of the year when precipitation levels are fairly low. During this period the species forages under the snowcover, insulated from extreme temperatures and many predators (Lackey *et al.* 1985). As the precipitation levels increase and snow begins to accumulate, it may become more difficult for White-footed mice to survive. However, these high levels of February precipitation are not common in the study area (Table 1).

Various recent empirical studies examined the relationship between White-footed mice and climate. For instance, shifts in climate are thought to be the drivers behind recent changes in the abundance and range of *P. leucopus* in Wisconsin (Long 1996), Minnesota (Deitloff *et al.* 2010), and Michigan (Myers *et al.* 2009b). The range of White-footed mice expanded northward in Wisconsin during the 1970's (Long 1996). While *P. leucopus* displays biennial population density cycles in Minnesota, it has shown an overall increase in population size since 1978 (Deitloff *et al.* 2010). Since 1980 in Michigan, warming temperatures are thought to have been responsible for *P. leucopus* extending its range over 200 kilometers northwards, and moving from occurring almost solely in the southern Lower Peninsula into the more northern Upper Peninsula (Myers *et al.* 2009b). Before around 1980, White-footed mice were only found in the southern most parts of the Upper Peninsula in Menominee County (Myers *et al*. 2009b). By the early 1990s, field notes and specimens from the University of Michigan Museum of Zoology recorded trappings of *P. leucopus* 70km northeast of Menominee localities (S. Meagher in Myers *et al.* 2009b). Trapping records document a small population of *P. leucopus* northeast of Menominee County, near Seney National Wildlife Refuge in 1999 and populations continue to move eastward over the next few years (Myers *et al.* 2009b). By 2006, White-footed mice were the most commonly found small mammal in some eastern Upper Peninsula locations, with some populations found in central and westward Upper Peninsula (Myers *et al.* 2009b). Similar patterns in abundance of *P. leucopus* have also been observed in northern parts of Lower Peninsula where densities have increased greatly since 1981 (Myers *et al.* 2009b). This expansion in range and increase in abundance of the White-footed mice coincided with an increase in temperatures, most significantly an increase in average minimum temperature. Because the rise in minimum was most pronounced in winter months (Myers *et al.* 2009b), this is suggestive that warmer winter temperatures and possibly shorter winters are important environmental determinants for White-footed mice.

When considering projected climate change, the model predicts that future climate conditions in the Upper Peninsula and in Canada will be more suitable for *P. leucopus* than at present. Currently, the model indicates that areas to the north of Michigan's Lower Peninsula are mostly unsuitable for White-footed mice, with the probability of occurrence ranging from 0 to around 0.4 (Figure 5). However, utilizing the future climate layers from the CCCMA model, our analysis predicts that the areas north of Michigan will become much more favorable for *P. leucopus* by 2050 and 2080 with probabilities of occurrence ranging from typical habitat (0.5-0.65) to highly suitable habitat (0.65-0.9) (Figures 6 and 7).

The northward expansion of White-footed mice is likely to have important ecological implications for these newly colonized regions. *P. leucopus* is the critical reservoir species for Lyme disease, a pathogen that infects of broad range of vertebrate hosts including humans (Ostfeld 2009). Currently, Lyme disease is prevalent and is rapidly expanding in parts of the eastern United States, posing a significant public health threat (Diuk-Wasser *et al.* 2010). While the epidemiological dynamics of this pathogen are likely to be dependent on a variety of other, not yet well understood, ecological processes, the northward expansion of White-footed mice portents of a likely expansion of the disease into regions where it used to be absent.

In addition to these epidemiological implications, the predicted northward range expansion of White-footed mice could have ecological effects in forests. White-footed mice are important prey items, and changes in their occurrence have likely implications on the abundance of diverse mammals and bird predator species such as raccoons, foxes, and raptors (Fanson 2010; Myers *et al.* 2009a). In addition, through competition, *P. leucopus* can impact the population dynamics of other small mammals such as deer mice (*Peromyscus maniculatus*). While *P. leucopus* is slightly larger than *P. maniculatus*, the two species overlap in many areas of the northeastern United States (Wolff 1996) and likely compete in some areas of habitat overlap (Deitloff *et al.* 2010; Wolff 1996). *P. maniculatus* is typically a more northern species; it has more adaptations for winter survival and is a stronger competitor in colder climates than *P. leucopus* (Pierce and Vogt 1993; Wolff 1996). In years with low mast production and especially harsh winters*, P. leucopus* populations decline more drastically than *P. maniculatus* populations (Wolff 1996), further demonstrating the importance of winter conditions in affecting *P. leucopus* occurrence. *P. leucopus* is impacted more by fluctuating environmental conditions such as food availability and climate than *P. maniculatus* (Wolff 1996); therefore, predicted future climate changes may drastically increase the availability of suitable habitat for the species and give them an advantage over *Peromyscus maniculatus*.

All of the factors mentioned above, including competition, predations and parasitism have the potential to further influence the distribution and occurrence of P*. leucopus* beyond climatic conditions *per se*. These factors are notoriously difficult to predict and have not been taken into account in this study. Thus the MaxEnt model cannot such biological processes into account, and only predicts the differences in climate and the probability of habitat suitability for *P. leucopus*.

Despite the limitations of modeling, this study shows that climate conditions, particularly temperature and precipitation towards the end of winter, are extremely important in predicting current *Peromyscus leucopus* distribution. With the current climate changing across the world, modeling studies are likely to play an important role in complementing field studies and making large-scale predictions about current distributions and future range shifts. With models such as those from MaxEnt, we can identify the suitability of habitats and then make predictions needed to foreshadow the movement of ecologically and epidemiologically important species, such as *Peromyscus leucopus*. This model predicts that as soon as by the year 2050 climate change will allow large regions of northern Michigan and Canada to be invaded by White-footed mice as the species moves northward, they are likely to affect both forest dynamics as well as the prevalence of emerging infectious diseases.

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Appendix A

Manipulations on Environmental Layers

Land cover and DEM layers were downloaded as multiple files from USGS (seamless.usgs.gov). Within ArcMap, each file was re-projected into WGS1984 using the Project Raster function under Projections and Transformations in Data Management Tools. Once each file had been re-projected, they were combined into one file using the Mosaic to New Raster function, under Data Management Tools. The last step required re-sizing the files to fit the study area (Michigan) and re-sampling the files to a cell size of 1 kilometer to match the files with the largest resolution, the climate layers. These last steps were performed by evaluating the files using a file with the desired cell size and extent within Raster Calculator in Spatial Analyst Tools.

Landcover and DEM files for Ontario, Canada were also re-projected into WGS1984 and cut down to fit the study area using Raster Calculator. The US landcover and DEM were subsequently combined with the Ontario data using the Mosaic to New Raster function.

Appendix B

Manipulations of files for use in MaxEnt

Each of the input variables had to be converted into the file types required by MaxEnt (comma delimited file for distribution points and ASCII grids for environmental layers). The attribute table of the points file was exported as a dBASE table and converted to a comma delimited (.csv) file. The environmental layers were converted to ASCII grids (.asc) within ArcMap using the Raster to ASCII function under Conversion Tools. Prior to converting the landcover file to an ASCII grid, land type values 11 (open water) and 127 (non-classified areas) were reclassified as NoData to remove any areas that are not potential *P. leucopus* habitat using the Set Null function in ArcMap. This step prevents these areas from unnecessarily interfering with the training of the model in MaxEnt.

The table containing the information from each of the environmental layers was created using the Sample Function under the Spatial Analyst Tools within ArcMap. The distribution file and the environmental layers were saved as a dBASE table using the Sample function and then converted to a .csv file to be used in MaxEnt to represent the environmental data.

Appendix C

Marginal Response Curves

The following set of response curves illustrates the relationship between each of the environmental variables at the probability of presence of *Peromyscus leucopus* while the values of all other variables are held constant at their mean value.