Landscape ecology approaches to Eastern Massasauga Rattlesnake conservation

DISSERTATION

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By

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Abstract

The Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) is a rare species across its range and is thought to be experiencing widespread population declines. Application of conservation-oriented management practices to this species is hindered by incomplete knowledge of the spatial distribution of populations and suitable habitat. To address this obstacle to conservation efforts I developed species distribution models (SDMs) for northeastern Ohio and Michigan and incorporated the resulting habitat suitability maps (HSMs) in a range of landscape ecology applications. These models were generated using the software program Maxent and a series of environmental variables that represent different elements of Eastern Massasauga habitat association, including vegetation attributes (Landsat derived vegetation indices; LiDAR) and relative elevation (topographic position index). The Maxent model with the best predictive capacity to identify extant northeastern Ohio populations used location data from across the state. The model selected LiDAR data as the top contributing variable. Northeastern Ohio is a priority for Eastern Massasauga conservation in the state so I also conducted an analysis of historical land use and land cover change to better understand the distribution of populations and habitat in this region. I used object-based classification techniques to analyze historical aerial photographs (covering ~75 years) and found that present day populations and suitable habitat largely coincided with abandoned agricultural fields. In
the absence of natural disturbance agents, agricultural fields that were allowed to go
fallow represented an important source of early successional habitats that are vital to
Massasauga. The early successional, open canopy habitats that Eastern Massasauga rely
on are not permanent fixtures in this landscape making habitat management a necessity.
The Michigan SDM was on a much broader scale than the Ohio modeling effort
incorporating 60 populations distributed across the lower third of Michigan. The
Michigan SDM selected the topographic position index at a 1 km scale as the best
predictor variable. This index uses a digital elevation model to provide information on
relative peaks or valleys depending the scale of analysis. Importantly, this variable
identified the low lying areas more prone to accumulate water and exhibit the moist
conditions Massasauga prefer. The widespread distribution of Massasauga populations in
Michigan also presented the opportunity to assess habitat availability and connectivity.
Using the HSM from the Michigan SDM, I quantified the number of large, contiguous
habitat patches and their protected status. Most were located on private land holdings. I
compared least cost path (LCP) distances and distance-weighted metrics using three
different resistance layers. I found LCPs based on raw HSM values were shorter than
class-weighted HSM or land cover based resistance layers. Therefore conservation
planners need to carefully consider the underlying resistance layers they use for
connectivity based decisions. I also generated a range-wide SDM under different climate
change scenarios to provide a future perspective on Massasauga conservation and
evaluate potential shifts in habitat suitability and identify at-risk populations. The climate
SDM indicated that southern Massasauga populations appear more at risk to changing conditions that may be unfavorable to the species.
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# Table of Contents

Abstract ................................................................................................................................. ii

Acknowledgments ................................................................................................................ v

Vita ........................................................................................................................................ vi

List of Tables ........................................................................................................................ xi

List of Figures ......................................................................................................................... xiv

Chapter 1: Introduction ......................................................................................................... 1

Chapter 2: Application of species distribution modeling to regional conservation efforts:
Utility of models based on local or broad occurrence data ................................................. 6
   Introduction ......................................................................................................................... 6
   Methods ............................................................................................................................... 10
   Results ................................................................................................................................. 17
   Discussion ............................................................................................................................ 19

Chapter 3. Role of historical land use in the distribution of Eastern Massasauga Rattlesnake habitat in northeastern Ohio ................................................................. 25
   Introduction ......................................................................................................................... 25
   Methods ............................................................................................................................... 27
Results .........................................................................................................................31
Discussion....................................................................................................................33

Chapter 4: Application of broad scale species distribution models to conservation
planning for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*)...40

Introduction ..................................................................................................................40
Methods .......................................................................................................................41
Results .........................................................................................................................46
Discussion....................................................................................................................47

Chapter 5: Influence of resistance layer source on estimates of landscape connectivity
using least cost paths ..................................................................................................49

Introduction ..................................................................................................................49
Methods .......................................................................................................................53
Results .........................................................................................................................56
Discussion....................................................................................................................56

Chapter 6: Future impacts of climate change on the distribution of Eastern Massasauga
Rattlesnakes (*Sistrurus catenatus catenatus*) .............................................................60

Introduction ..................................................................................................................60
Methods .......................................................................................................................62
Results .........................................................................................................................64
List of Tables

Table 1. Environmental variables used to create species distribution models for the Eastern Massasauga Rattlesnake in Ohio.

Table 2. Omission rates with the default Maxent regularization setting and in parentheses the average AUC scores across Maxent regularization settings (1.0–5.0) at four feature class combinations: linear (L), quadratic (Q), and hinge (H) for northeastern (NE) Ohio and full Ohio models at 1km and 2km minimum spacing between occurrence points.

Table 3. The state of land cover at ten contemporary Eastern Massasauga localities spanning a historical time frame 1938–2011. Observed land cover classes include agriculture (A), grassland (G), pasture (P), and shrubland (S). The shrubland classification was used for grassland areas consisting of >50% shrub or small trees. Both pasture and shrubland would have been classified as grassland in the historical analysis. They are separated here to provide more detailed information on the conditions present at each site over this historical time scale. The * indicates the land cover information was obtained from 1972 imagery. Sites 8–10 are located in Trumbull County which did not have 1979 imagery available.

Table 4. The proportion (%) of my northeastern Ohio study area occupied by three land cover classes from 1938–2011.
Table 5. Estimated inter-period changes in grassland from 1938–2011. Gains refer to the proportion of grassland added during each time interval and whether those pixels transitioned from agriculture or forest. Losses represent the proportion of the previous grassland total that were a different land cover class by next recorded year.

Table 6. The results from Kruskal-Wallis tests comparing median habitat suitability values from 2,000 random points distributed across three land cover types.

Table 7. The results from Kruskal-Wallis tests comparing median habitat suitability values from 2,000 random points distributed across three land cover types. Agriculture was split into fields still currently being farmed (C) and fields that were abandoned (A) to transition to forest or grassland.

Table 8. Model rankings for the generalized linear model analysis using three land cover classes. The best supported model is shown in bold.

Table 9. Significance values associated with the 1966 and 1979 generalized linear model.

Table 10. Model rankings for the generalized linear model analysis using four land cover classes (agriculture split into two). The best supported model is shown in bold.

Table 11. Significance values associated with the 1966 and 1979 generalized linear model that includes an interaction term.

Table 12. Environmental variables used to create species distribution models for the Eastern Massasauga Rattlesnake in Ohio.

Table 13. Maxent model settings and ranking statistics (top model based on AIC<sub>c</sub> in bold) from the ENMeval R package: Features-linear (L), quadratic (Q), and hinge (H).
RM-regularization multiplier, Mean.AUC-mean Area Under the Curve score across model iterations, Mean.OR10-mean 10% training omission rate across model iterations, AICc-Akaike information criterion corrected for small sample size, delta.AICc-change in AICc from the top ranked model..............................93

Table 14. The predicted change (%) in the Eastern Massasauga’s distribution associated with the average values from three global climate models under less severe (RCP26) or more severe (RCP85) scenarios. The permissive threshold was the minimum training presence from Maxent, which includes more suitable habitat in the binary map for present day and future conditions. The conservative threshold was the maximum sum of sensitivity and specificity which limits the amount of habitat identified as suitable for present day and future conditions.................................................................94

Table 15. Ohio Maxent results showing the distribution of values for both the 1km and 2km filtered points and all regularization values (continued).................................109
List of Figures

Figure 1. Omission rates (ORs) for four feature classes from the four model types representing northeastern Ohio and full Ohio datasets. The ORs were calculated across the range of regularization multipliers employed (1.0-5.0). The box plots show the median, first and third quartiles, and outliers for each feature class across this range. 95

Figure 2. Habitat suitability maps for the top performing model (lowest omission rate) from each of the four model types including: (A) Full Ohio 1km LQ feature classes at the default regularization (LQ:1.0); (B) Full Ohio 2km LQ:1.0; (C) Northeastern Ohio 1km L:2.0; and (D) Northeastern Ohio H:2.0. See text for explanation of model names. 96

Figure 3. Historical land cover composition of present day suitable habitat patches for the Eastern Massasauga in the northeastern Ohio study area. Each year shows the proportional makeup of current habitat patches by the three land cover types. 97

Figure 4. Michigan distribution of Eastern Massasauga. 98

Figure 5. An example of a Massasauga habitat core partially contained within a protected area. Portions of the core within the protected area are blue and portions outside are red. 99

Figure 6. Circuitscape movement corridors between Eastern Massasauga locations (white circles). The two narrower corridors in yellow indicate the location of pinchpoints, where paths for movement are more limited. 100
Figure 7. Circuitscape movement corridors between Eastern Massasauga habitat cores

Figure 8. The topographic position index layer showing relative valleys in blue and peaks in red. The Eastern Massasauga localities represented by the dots are associated with the valley areas.

Figure 9. Pinchpoint located across road showing a narrow corridor for movement across this potential barrier. An Eastern Massasauga location is represented by the white circle.

Figure 10. Illustration of least cost paths (LCPs) based on three resistance layers (blue-CCAP, purple-class weighted HSM, and black-standard HSM). These LCPs connect the snake locality (white circle) to another locality located >1km away. Note the problematic route taken by the standard HSM (black line) across the water body.

Figure 11. The states and province comprising the known distribution of the Eastern Massasauga. Location data used in the species distribution model shown in red.

Figure 12. Suitability maps showing current conditions (A) and future conditions for less severe RCP26 (B) and more severe RCP85 (C) predicted climate change scenarios. Warmer colors indicate higher suitability.

Figure 13. Binary maps of suitable (green) and unsuitable (purple) areas for future conditions from the minimum training presence threshold RCP 26 (A) and RCP 85 (C) and the maximum sum of sensitivity and specificity threshold RCP 26 (B) and RCP 85 (D).

Figure 14. Maps showing changes from the present day for minimum training presence threshold RCP 26 (A) and RCP 85 (C) and the maximum sum of sensitivity and
specificity threshold RCP 26 (B) and RCP 85 (D). The four possible range related changes are: blue - remains suitable, gray - remains unsuitable, red - range contraction, and green - range expansion.
Chapter 1: Introduction

Introduction

The Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) is a rare species across its range in the United States and Canada. It has received some level of protection in every state and province where it resides (Szymanski 1998) and has recently been elevated to Federally Threatened by the U.S. Fish & Wildlife Service. The species ranges from New York and parts of Ontario westward across the Great Lakes region to eastern Iowa (Szymanski 1998). The Eastern Massasauga is typically associated with early successional, open canopy habitats including wet prairie or grassland areas in the vicinity of wetlands where it feeds mostly on small mammals (Szymanski 1998; Durbrian et al. 2008). Snakes hibernate in wetter areas, with a noted preference for abandoned crayfish burrows in many areas (Reinert and Kodrich 1982; Seigel 1986; Marshall et al. 2006; Moore and Gillingham 2006). Conversion of wetlands and grassland habitats to agriculture, indiscriminate killing of snakes and illegal collection for the pet trade are major threats to this species (Szymanski 1998; Bailey et al. 2011). Additionally, a lethal fungal infection has been recently implicated in the deaths of several Massasauga from a population in Illinois, a possible indication of poor immune response related to deleterious genetic effects of small population size (Allender et al. 2011).

With this range of potential threats, population monitoring will be an important component of future conservation efforts. However, comprehensive monitoring is
presently limited by an incomplete knowledge of the distribution of Eastern Massasauga populations. I developed species distribution models (SDMs), in part, to help address our incomplete knowledge of the distribution of Eastern Massasauga populations by providing habitat suitability maps (HSMs) for systematic surveys in both Ohio and Michigan. These two states also presented opportunities for both fine (Ohio) and broad (Michigan) scale landscape ecology conservation applications where I integrated HSMs with other techniques to go beyond basic mapping of suitable habitat. Many management decisions are local, involving one patch of habitat or one wildlife refuge. Increased availability of high resolution data layers has made it possible to create fine scale habitat maps for use in the decision-making process. At a broad scale, HSMs can be used in conjunction with other landscape ecology techniques for status assessments of populations and identify risk factors for persistence. To align with the diverse needs of land managers and conservation planners, my dissertation focused on the development of SDMs and their application as part of a multifaceted approach to Eastern Massasauga conservation efforts involving responses to historical patterns of land use, issues of connectivity, and range shifts due to climate change.

Chapters 2 and 3 primarily focused on Eastern Massasauga populations in northeastern Ohio. The majority of Ohio Massasauga populations appear to be self-contained units that subsist as population islands with little to no probability of either recolonizing sites that historically supported snakes, or being rescued via migration from other extant populations should they disappear. Recent genetic data reinforces the notion that Ohio’s Massasauga populations exist in isolation by showing no evidence of recent
or historical gene flow among six Ohio populations (Chiucchi and Gibbs 2010). Unlike other areas of the state, application of conservation-oriented management practices to this species in northeastern Ohio is hindered by incomplete knowledge of the locations of populations due to lack of survey effort and the cryptic nature of the snakes. The methodological dilemma in developing a HSM for the region was whether to exclusively rely on occurrence data from the area of interest or expand the model training data to include sites from across Ohio. In chapter 2 I developed and compared SDMs based on either local (northeastern Ohio) or broad (statewide Ohio) occurrence data to determine which would be best suited for aiding conservation efforts in northeastern Ohio.

I used the HSM developed in chapter 2 to conduct surveys for Eastern Massasauga across northeastern Ohio for three years. Despite an apparent abundance of suitable habitat, Eastern Massasauga seemed restricted to a few areas. The Eastern Massasauga is typically associated with early successional, open canopy habitats including wet prairie or grassland areas in the vicinity of wetlands (Szymanski 1998; Durbian et al. 2008). As a result, habitat loss for this species can have anthropogenic causes such as conversion of wetlands and grasslands to agriculture and natural drivers as when grasslands are replaced by forest via succession. Information on the impact of historical patterns of landscape change and land use on populations can be important for development of effective conservation measures for threatened species. I track changes in the landscape features that are relevant to massasauga persistence with a series of aerial photographs dating back to 1938 in chapter 3. I demonstrate how land use practices and
forest succession have influenced the distribution of Eastern Massasauga populations and habitats in northeastern Ohio.

It is important to understand how different resistance layers influence connectivity estimates because one may better reflect actual movement of organisms on the landscape and therefore facilitate the development of corridors to improve connectivity between isolated populations. I focused on Eastern Massasauga conservation efforts in Michigan in chapters 4 and 5. Michigan has more Eastern Massasauga populations than any other state or province making it ideal for understanding broad landscape level patterns in the distribution of Massasauga. Chapter 4 describes the methodology I used to develop a broad scale SDM for the lower half of Michigan and apply it towards assessments of protected status of higher quality habitat patches and estimates of landscape connectivity. I compare the impact of different resistance layers (two forms of the Michigan HSM and a land cover based resistance layer) on population connectivity estimates in chapter 5.

Finally, in chapter 6 I looked at how Eastern Massasauga may be impacted by future climate change by developing a SDM based on precipitation and temperature variables and projecting this model under different predicted scenarios. It is unclear how species will respond to impending climate change. For those tasked with managing the remaining populations of threatened species like the Eastern Massasauga the margin of error is slim. Eastern Massasauga are dispersal-limited and therefore long range movements in response to climate change are unrealistic. Instead, individuals from areas experiencing changes to more unfavorable conditions will need to adapt or be rescued by
human intervention making the identification of the most at-risk populations a high priority.
Chapter 2: Application of species distribution modeling to regional conservation efforts: Utility of models based on local or broad occurrence data

Introduction

Current threats to biodiversity and uncertainty regarding the future impacts of climate change have made identification and mapping of rare habitats and species distributions increasingly important. Geographic Information Systems (GIS) and remote sensing technologies are essential tools in this global effort (Schumaker 1996; Scott et al. 1993). Species distribution modeling (SDM), also known as ecological niche modeling, is an emerging field that has shown great promise for this type of conservation application (Thorn et al. 2009; Williams et al. 2009; Wilting et al. 2010; Zhang et al. 2012).

SDMs are used to generate habitat suitability indices by relating species occurrence data to abiotic and biotic features represented in environmental data layers. The quality of the suitability index largely depends on whether the selected environmental variables are biologically relevant to the focal organism. Climate-derived data layers are commonly used to construct models with temperature and precipitation acting as indicators of specific habitats or vegetation associated with a species (Booth et al. 2014; Hijmans et al. 2005). Geology (Cao et al. 2013), hydrology (Besnard et al. 2013), and land cover (Wilson et al. 2013) can also be represented in SDM data layers to model species-environment relationships.
An obstacle to modeling species-environment relationships of rare or cryptic species is that scarcity or low detectability produces sparse data with which to model distribution or abundance of such species (Bean et al. 2012; Pearson et al. 2007). Small numbers of individuals typically do not provide sufficient information to characterize the range of conditions where a species occurs, thereby limiting the accuracy of any resulting habitat suitability maps (Bean et al. 2012). This is particularly problematic if the intended goal is to model the entire range of an organism with limited occurrence data.

Some of the limitations associated with a small number of occurrences were identified and addressed in previous studies (Bean et al. 2012; Pearson et al. 2007; Shcheglovitova & Anderson 2013; Wisz et al. 2008). Pearson (2007) identified a popular method for constructing SDMs with a small number of occurrences by employing a leave one out cross-validation procedure. This approach circumvents the problem of separating a dataset into testing and training partitions. When there are very few discrete occurrences available, the information associated with each individual occurrence point is critically important for representing the range of conditions in which an organism can be found.

I was interested in examining issues pertaining to construction of SDMs for an endangered species, the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*), in a regional conservation context. Aspects of this species’ conservation status, distribution, and biology make it an ideal subject for exploring alternative methods to create fine scale SDMs with an applied conservation focus. The Eastern Massasauga is listed as threatened in Canada, is a candidate for federal listing under the Endangered
Species Act in the U.S., and is listed as threatened or endangered in every state except Michigan, where they are a species of special concern (Szymanski 1998). Eastern Massasauga are primarily restricted to small, localized populations that require a fine scale habitat modeling approach across their range (Durbian et al. 2008; Moore & Gillingham 2006; Szymanski 1998).

Creating conservation-oriented models for a specific region raises unique challenges. Occupied habitats in the region of interest may be unique and therefore models created with occurrence data from across a species’ range could be too generalized for targeted conservation actions. Conservation efforts are also undermined if too few occurrences from the area of interest underrepresent the range of occupied habitats. Models developed from the sparse data may fail to include patches of suitable habitat and thereby exclude some populations from conservation efforts (Bean et al. 2012).

The Eastern Massasauga distribution in Ohio offers an excellent opportunity to examine how selection of occurrence data influences region-based SDMs. Our focal region for the Eastern Massasauga SDMs was northeastern Ohio, where multiple populations exist in close proximity (<5 km) and the maximum distance between populations is small (39 km). This region is likely one of the last segments of the species’ range where there is a high probability of remnant undocumented populations. Efforts are underway in northeastern Ohio to identify locations to survey for new populations and expand the amount of habitat available to known populations via land acquisition and habitat restoration. Outside of this focal conservation region, Ohio populations are
isolated. Distances between them range from 10–190 km (mean = 94.4 km), and they primarily occur in protected areas.

I aimed to determine the model configuration that would best inform Massasauga conservation efforts in northeastern Ohio by comparing models created exclusively with northeastern Ohio occurrence data with those including occurrence and environmental data from other populations throughout the state. This comparison addressed potential pitfalls associated with fine scale SDMs by directly measuring effects of variation in sample size and in the spatial extent of occurrence data on model performance. These issues are broadly applicable to other regional conservation efforts using SDMs as a conservation tool. Another common obstacle for creating fine scale SDMs is obtaining appropriate environmental data layers that can differentiate suitable habitat from surrounding landscape features. We evaluated an assortment of high resolution, non-climatic environmental data layers and identified a complementary set of variables suitable for fine-scale habitat mapping.

I used the popular SDM software Maxent (Phillips et al. 2006; Phillips & Dudik 2008) for our regional analysis. Maxent does not require true absences and instead uses a presence-background approach, which is ideal for species such as the Eastern Massasauga rattlesnake where detectability is a concern. We tailored our analysis to Maxent by comparing models across a range of user-specified settings because it is one of the most commonly used SDM approaches and has performed well in previous studies with small sample sizes (Pearson et al. 2007; Shcheglovitova & Anderson 2013; Wisz et al. 2008). This allowed us to compare our results with other Maxent based studies using
small sample sizes and provide a framework for future regional conservation SDM projects using Maxent.

Methods
Study species

Eastern Massasauga are found in the Great Lakes region of the United States and Canada, ranging from New York to eastern Iowa (Szymanski 1998). Population declines attributed to habitat loss and human persecution have earned this species considerable attention in recent years (Chiucchi & Gibbs 2010; Dileo et al. 2013; Pomara et al. 2014). Eastern Massasauga habitat in Ohio is characteristic of most of their Midwest distribution, consisting of grasslands in close proximity to wetlands or poorly drained areas (Szymanski 1998). However, there are regional differences in specific habitat types used – predominantly fens and bogs in southwestern Ohio, remnant prairies in northern Ohio, and early successional grasslands in northeastern Ohio.

Environmental variables

There is little variability in climate across Ohio so we assessed environmental data layers that targeted vegetation and hydrology at a resolution of 30 m. We focused primarily on habitat variables derived from Landsat 5 Thematic Mapper (TM) satellite imagery that provided information on vegetation characteristics of Eastern Massasauga habitat. Remote sensing-derived habitat variables are most appropriate for SDMs in areas where there is little variation in climate and the target species is rare or patchily distributed (Bradley et al. 2012), as in our study system.
Use of satellite imagery helps avoid problems related to inconsistencies in the ability of various land cover maps (e.g. National Land Cover Database) to distinguish suitable Massasauga habitat types such as grassland or wet meadow from agricultural areas. Classification errors are common in land cover maps (Langford et al. 2006) and while the consequences may be minor for coarse scale analyses, they have the potential to undermine efforts to develop accurate models representing habitat suitability for Massasauga at local scales (i.e. occurrence sites). Vegetation data from satellite imagery have been successfully used as a predictor variable in a number of SDM studies (Bartel & Sexton 2009; Raxworthy et al. 2003; Zimmermann et al. 2007). We applied a tasseled cap transformation (Crist & Cicone 1984; Kauth & Thomas 1976) to Landsat 5 TM images using ERDAS IMAGINE version 10.1 software to generate three transformed bands that represented brightness (bareness of soil), greenness, and wetness (moisture content of soil and vegetation). Originally developed to examine crop health, the tasseled cap transformation has been successfully integrated into SDM studies (Parviainen et al. 2013; Wilson et al. 2013).

We acquired these data layers from 2010 and 2011 imagery for multiple dates during periods of the year when Massasauga are active (May-October). We used some layers as stand-alone variables (e.g. May greenness) and performed mathematical operations with multiple dates to include phenological properties of vegetation at Massasauga occurrence sites (e.g. mean wetness across May, August, and October; May minus October greenness) using the Raster Calculator in ArcGIS version 10.2. Multi-temporal remote sensing has been proposed as a means to improve predictive
performance of SDMs (Bradley & Fleishman 2008; Bradley et al. 2012) and has only been applied in a handful of studies (Cord & Rodder 2011; Evangelista et al. 2009; Feilhauer et al. 2012; Sheeren et al. 2014). We also used United States Department of Agriculture (USDA) agricultural spatial data from the Cropland Data Layer (CDL) to mask out agricultural areas and prioritize native vegetation for evaluation in the SDM. The CDL is produced annually by the National Agriculture Statistics Service for the USDA.

We supplemented the satellite-derived data layers with LiDAR (Light Detection And Ranging) data obtained from the Ohio Geographically Referenced Information Program (OGRIP) website (http://gis3.oit.ohio.gov/geodatadownload/osip.aspx) to provide detailed profiles of vegetation height and structure. LiDAR data have primarily been used as a predictor variable in avian SDM studies (Ficetola et al. 2014; Sheeren et al. 2014; Tattoni et al. 2012) although Sillero and Gonçalves-Seco (2014) used LiDAR data to determine habitat preferences of a lizard community.

We used the Compound Topographic Index (CTI) and Topographic Position Index (TPI) to supplement the wetness layer from the tasseled cap transformation as additional hydrological variables for assessing soil moisture. The CTI or topographic wetness index is a steady state wetness index calculated using slope and catchment area (Ma et al. 2010). The CTI layer was generated using the Geomorphometry and Gradient Metrics Toolbox for ArcGIS (http://evansmurphy.wix.com/evansspatial#!arcgis-gradient-metrics-toolbox/crro).
The TPI uses elevation data from a digital elevation model to identify slopes and valleys at user-specified spatial scales. We used digital elevation models in conjunction with a TPI extension (http://www.jenessent.com/arcview/tpi.htm) within ArcGIS to generate TPIs at varying spatial scales (500 m–5 km) for use in our SDM.

Occurrence data

We compiled Eastern Massasauga presence data from eight discrete sites in northeastern Ohio and five state wildlife areas throughout the rest of Ohio. The presence data from areas outside northeastern Ohio were combined with the northeastern Ohio data to create our full Ohio dataset. We applied two spatial filters at 1 km and 2 km as a minimum distance between points for the northeast Ohio and full Ohio datasets to reduce the influence of spatial autocorrelation on our models (Boria et al. 2014; Kramer-Schadt et al. 2013). We did not expect to eliminate spatial autocorrelation because our northeastern Ohio study region was fairly small. However, we wanted to minimize the number of occurrences from each individual patch of suitable habitat and the 1 km and 2 km filters accomplished this while retaining sufficient occurrences for our analysis. I included eight snake GPS points for the 1 km filter and six points for the 2 km filter in the northeast Ohio models. I used 15 and 12 points at 1 km and 2 km filters respectively in the full Ohio model. Our limited sample set precluded any spatial filters beyond 2 km, as this would have dropped the sample size for northeastern Ohio below five locations. I used the program ENMTools (Warren et al. 2008; Warren et al. 2010) to visualize the degree of spatial autocorrelation present in our data layers. This program used the input layers to display areas of high or low spatial heterogeneity. I incorporated this
information into our analysis when more then one point satisfied the minimum distance filter. I selected the point that maximized spatial heterogeneity among the points in these cases.

**Experimental design**

I compared northeastern Ohio and full Ohio models across a range of Maxent settings. Numerous studies have demonstrated that the default settings in Maxent do not necessarily produce the best-fit model (Anderson & Gonzalez 2011; Radosavljevic et al. 2014; Shcheglovitova & Anderson 2013; Warren & Seifert 2011). Specifically, I manually adjusted regularization multipliers and feature classes. The regularization multiplier protects against overfitting by relaxing how closely the model matches conditions at training sites. Features such as linear, quadratic, and hinge were the different possible relationships among the variables that can be modeled. I varied the regularization multiplier from its default value (1.0) up to five at increments of one for northeastern Ohio and full Ohio models at both 1 km and 2 km spatial filters. I applied four different feature class combinations including linear (L), quadratic (Q), and hinge (H) features: L, LQ, LQH, and H. I applied two spatial filters at 1 km and 2 km as a minimum distance between points for the northeast Ohio and full Ohio datasets, producing 80 models (Appendix B, Table 15). We report the feature class and regularization multiplier as in the following example. A hinge model at a regularization multiplier of three would be H:3.0.

The sample space considered for the modeling process can contribute to overinflated Maxent model performance (Kramer-Schadt et al. 2013). The area from
which Maxent draws background points should reflect the same biases as surveys used to acquire occurrence data to reduce sampling bias (Kramer-Schadt et al. 2013). I applied a 1 km buffer to serve as an analysis mask around training sites to prevent background points from being drawn from habitats not present in our study area. This is approximately the home range width of Massasauga reported from other studies (Durbián et al. 2008; Szymanski 1998) and should therefore represent areas used by snakes in the model. This area is also sufficiently large to include surrounding land cover types characteristic of the region and not typically associated with Massasauga habitat (e.g. forest, agriculture). I used the projection feature of Maxent following the initial modeling process to visualize the model results across our study area.

**Variable selection and model evaluation**

Our variable selection process involved multiple steps. I used Maxent’s jackknife of variable importance to training gain for our initial assessment. This provides information on how each variable performs by itself and the effect on training gain (a measure of how well the Maxent distribution fits the presence data) when the variable is removed. I removed any variables that had zero or negative training gain. I performed a correlation analysis with the remaining variables to identify correlated variables. When two variables had a correlation above 0.75 (Dormann et al. 2013) the variable that was less important as determined by the jackknife was removed. Finally, any variables with less than 1% contribution to the final model were removed.

A variety of metrics have been proposed for selecting an optimal Maxent model; these include threshold independent and dependent measures. Threshold measures require
converting Maxent’s output to a binary distribution where every cell above a specified
cutoff value is considered suitable habitat. The most commonly used is the area under the
ROC curve (AUC), which is part of the Maxent output. The AUC score is threshold-
independent and represents a model’s ability to accurately rank presence sites above
random background locations. AUC ranges from 0–1.0 with 0.5 indicating no better than
random and 1.0 representing perfect discrimination. Issues with the interpretability and
reliability of AUC have been demonstrated empirically, limiting it’s utility as a
standalone indicator of model performance (Jiménez-Valverde 2014; Lobo et al. 2008).
Maxent also incorporates a threshold dependent measure called the omission rate (OR).
This is the proportion of presence sites that fall below a specified threshold separating
suitable habitat from unsuitable. We chose the OR as our primary measure of model
quality. Rather than select an arbitrary threshold (e.g. 0.5), I used the maximum training
sensitivity plus specificity (MTSS) threshold, which has been shown to be among the top
thresholding options available (Cao et al. 2013; Liu et al. 2013). The MTSS threshold
represents the suitability value that maximizes the sum of sensitivity and specificity. A
threshold-dependent measure should not be the sole criterion for management decisions
but it provides a means to evaluate the conservation potential of different models. An
optimal conservation model will have an OR of zero so no populations are excluded but
not be overly generalized so that marginal habitat is considered suitable. I selected one of
the more conservative thresholds in MTSS and favored models with a lower
regularization multiplier to prevent the optimal model from being too generalized.
Increasing the regularization multiplier may be necessary to reduce the influence of
overfitting; however increasing it too much will reduce a model’s predictive power. I also used AUC as a secondary measure of model quality when comparing among models with different regularization and feature settings from one of our four model types (e.g. full Ohio 1 km). These comparisons all involve the same sample space and thus satisfy requirements for AUC. The AUC and OR scores from the full Ohio models incorporate values from test sites outside northeastern Ohio (Appendix B, Table 15). For model evaluation purposes, I averaged AUC and OR values from model runs using northeastern Ohio points as test sites. This allowed direct comparisons of OR with the northeastern Ohio-specific models.

To compare models with the same OR I calculated the degree of similarity using three overlap metrics from ENMTools including Schoener’s $D$, $I$, and relative rank ($RR$) (Glor & Warren 2011; Warren et al. 2008). These metrics range from 0 (no niche overlap) to 1 (identical niche space).

**Results**

*Variable selection and model evaluation*

Our selection process with the original set of candidate variables yielded seven variables to retain in the final models (Table 1). These were predominantly based on the tasseled cap transformations performed on Landsat 5 satellite imagery. Both wetness and greenness layers were present in the final set of variables. These included individual months (e.g. June greenness) and the difference between months (e.g. May minus October wetness). The LiDAR and CDL layers also were identified as important contributing variables. The jackknife procedure indicated the LiDAR layer contributed
the most unique information not represented by other variables. None of the elevation-based variables we evaluated were selected for the final models.

The expanded Ohio models exhibited lower ORs than the northeastern Ohio models at both 1 km and 2 km spatial filters (Figure 1). The poorest performing models in terms of OR were the 2 km northeastern Ohio models across the range of feature class and regularization combinations examined. The median ORs for 2 km northeastern Ohio models were the highest among the four model types for each feature class (Figure 1).

The 2 km northeastern Ohio models produced a zero OR but not until the regularization multiplier was increased to four at which point the AUC dropped to 0.57 (Appendix B, Table 15). The median ORs for feature classes in the 1 km northeastern Ohio models were both lower than the value for the corresponding 2 km northeastern models and less variable across feature classes (Figure 1). They also equaled the ORs of the 1 km full Ohio models for some feature class regularization combinations (e.g. L:2.0), but importantly never reached zero (Appendix B, Table 15).

The 1 km and 2 km full Ohio models both produced ORs of zero at the default regularization setting. All 2 km full Ohio feature classes had a zero OR while only the LQ feature class produced a zero OR for the 1 km full Ohio model (Table 2). However, the 2 km full Ohio ORs increased at higher regularization multipliers while remaining fairly constant for the 1 km full Ohio models (Appendix B, Table 15). Consequently, the 1 km full Ohio models had lower mean ORs compared to the 2 km full Ohio models across all regularization multipliers for the LQ (0.05 vs. 0.10) and H (0.125 vs. 0.133) feature classes.
Identifying an optimal model among the 2 km full Ohio models was problematic because each feature setting had an associated zero OR at the default regularization multiplier. Moreover, there was little variation in the AUC scores among the four feature classes (0.968-0.974), which made us reluctant to choose one based on this secondary criterion. We selected the 2 km full Ohio LQ:1.0 model for a niche overlap analysis and qualitative comparison with the 1 km full Ohio LQ:1.0 model so I could assess how changes in spatial sorting (1 km vs. 2 km) affected model predictions for the same feature class setting (see section 3.2 below).

The average AUC scores were fairly high, an indication that they were artificially inflated as I expected (Table 2). For each model type, the LQ and LQH features had the highest average AUC scores across all regularization multipliers (Table 2).

*Model overlap:* I found a high degree of similarity between the LQ:1.0 2 km full Ohio model and the LQ:1.0 1 km full Ohio model. The $I$ and $RR$ variables showed little difference ($I = 0.98; RR = 0.93$) between the two models. The $D$ variable was lower for the L:1.0 ($D = 0.78$) and LQ:1.0 ($D = 0.89$) comparison but still indicative of high overlap. The overlap variables also indicate the LQ:1.0 2 km full Ohio shared less similarity with L:1.0 2 km model ($I = 0.96; RR = 0.91; D = 0.80$) than with the LQ:1.0 1 km full Ohio model.

**Discussion**

Our modeling results demonstrated a clear advantage to using a geographically broader set of training data for a targeted regional conservation application. Expanding the modeled environment beyond the region of interest allowed for larger sample sizes
and more diverse representation of occupied habitats producing SDMs with greater
transferability and a broader niche. Both full Ohio model types outperformed the
complementary northeastern Ohio models with lower ORs for all feature classes across
the range of regularization multipliers (Figure 1). More importantly, the full Ohio model
types both produced individual models with ORs of zero at the default 1.0 regularization
setting (Table 1). A number of recent studies that compared a range of regularization
multipliers found multipliers higher than the default setting were required to optimize
model performance (Anderson & Gonzalez 2011; Radosavljevic et al. 2014;
Shcheglovitova & Anderson 2013), but see (Cao et al. 2013). This is due to over-fitting
that occurs when the model output matches the conditions at the training sites too closely
and as a result is not transferable to other locations. Achieving zero OR at the default
regularization setting meant our model predictions were conservative yet transferrable
enough to include all the northeastern Ohio presence sites. This is optimal from a
conservation-planning standpoint because the model did not exclude any known
populations. Rather, it restricted the extent of predicted suitable habitat and thereby
reduced the probability of including marginal habitat in our predictions. Projecting the
optimal models for the four model types across our study area showed that the expanded
Ohio models were more selective in the spatial distribution of predicted suitable habitat
(Figure 2).

I also found that the less complex feature settings, L and LQ, rather than H were
capable of producing low ORs (Table 1). Shcheglovitova and Anderson (2013) found the
opposite in their study of model complexity with small sample sizes. However, their
optimal models were associated with higher regularization values than the default. They proposed that the higher regularization values, which help simplify the model, protected against over-fitting, while allowing for the more varied species-environmental relationships associated with complex features. Our results differed from those of Shcheglovitova and Anderson (2013) in that their environmental variables were exclusively temperature and precipitation layers from the WorldClim database. The indirect relationship between climate variables and a species’ niche may favor more complex features in the Maxent modeling process. Less complex features may have been favored in our models because vegetation indices more directly targeted the structural components of suitable habitat. Additional studies examining a range of environmental variables are necessary to determine what factors may favor certain features over others.

While in our study, the full Ohio datasets using the default settings of Maxent would have produced optimal models; there is still sufficient evidence that a range of Maxent settings should still be compared (Radosavljevic et al. 2014; Shcheglovitova & Anderson 2013).

The impact of increasing the number of presence points on model performance was observed in the differential success of the 1 km and 2 km northeastern Ohio models. A small increase in sample size from six (2 km) to eight (1 km) resulted in lowered ORs (Figure 1). With so few presence sites, the addition of even two locations can help expand the range of suitable conditions considered by the model and lower the OR. Qualitatively, the 1 km northeastern Ohio model also better discriminated suitable from unsuitable than the 2 km model (Figure 2). The full Ohio models further increased the
number of presence points and the range of habitats incorporated into the SDMs, resulting in lower ORs.

Selecting an optimal model for Eastern Massasauga conservation is difficult because both full Ohio model settings produced zero OR models. The 2 km model setting was more consistent with all four feature classes achieving zero OR at the default regularization multiplier while the 1 km model setting reached zero OR only for the LQ feature class. The 1 km model setting includes more presence points than the 2 km model potentially providing it with a broader range of suitable conditions. However, our overlap analysis indicated the 1 km LQ:1.0 model was nearly identical to the 2 km L:1.0 for the I and RR measures and is very similar based on the D measure. I did not observe any major qualitative differences between these two models (Figure 2). This consistency of model predictions indicated that the full Ohio models were not highly sensitive to changes in parameter settings, and as a result, both provide useful habitat suitability maps.

I identified a series of environmental variables that could characterize aspects of Eastern Massasauga habitat at a fine scale. These were predominantly vegetation indices derived from remote sensing. The elevation and hydrology variables did not perform well for our study area. Massasauga habitat patches can be differentiated at the scale of our analyses from surrounding land cover types (forest, agriculture, and riverine) more easily via remotely-sensed surface attributes than underlying geological and hydrological features. Elevation does play an important role in regional distribution of Massasauga as most of the known Massasauga populations in northeastern Ohio were located in the Grand River Valley. The valley environments are more likely to maintain the wet
conditions Massasauga prefer and also were probably subject to less conversion to farmland historically. However, identifying patches of habitat within this valley was only possible by targeting vegetation. LiDAR was identified as the most important variable by the jackknife procedure and in its percent contribution to the final models. Forest was the dominant natural vegetation type in northeastern Ohio and LiDAR’s ability to represent vegetation height better discriminated Massasauga grassland habitat from surrounding forest cover. Our results were consistent with other studies showing how LiDAR can improve habitat suitability models (Tattoni et al. 2012; Vierling et al. 2008). By complementing the spectral qualities of Landsat-derived variables with LiDAR data, I showed that a combination of data types can be used to create accurate fine scale SDMs in areas where climatic variables are not appropriate.

Our results demonstrated that region-specific habitat mapping projects may require including occurrence data from outside the focal area of interest in the SDM process. This is a particularly salient consideration when the focal region is characterized by small sample sizes, clustered observations, and variable habitat types. Region-specific models suffered from a deficiency of ecological information that I mitigated by incorporating additional populations from across Ohio. It would be prudent for future regional mapping projects dealing with rare or endangered species to investigate whether additional presence sites improve model predictions. Future studies are required to determine the scale at which regional models suffer from including additional presence data due to disparate habitat values. Vegetation indices are more likely to be sensitive to large geographic separations between training and testing data than other types of
environmental variables (e.g. climatic and elevation) because they can be influenced by even subtle changes in plant communities or growing season.

Survey results

Survey sites were selected based on Maxent model predictions of suitable habitat. During three years of surveys only one new site was confirmed after I observed a neonate Massasauga under a piece of sheet metal which had been placed to attract snakes. Not all patches of suitable habitat will be occupied for a given species. This is due to barriers that could be physical (e.g. rivers, roads, mountains) or biological (e.g. superior competitors, predators) which prevent dispersal to all available patches. For Massasauga in northeastern Ohio there are likely multiple complementary contributing factors to explain their limited distribution. The seeming abundance of suitable habitat available now does not necessarily reflect historical habitat availability. The early successional habitats that Massasauga reside in are temporary as I describe in Chapter 3. Many of the current suitable habitat patches were previously agricultural fields which are unsuitable for sustaining Massasauga populations. Massasauga can successfully recolonize fallow agricultural fields but this requires some form of refugia from which the snakes can disperse from. In areas with agricultural fields abutting forest with little to no open canopy grassland habitat available, it would be unlikely for Massasauga to persist in this landscape. They also have limited vagility, reducing the probability of dispersers colonizing new habitats unless they are in close proximity to the population of origin.
Chapter 3. Role of historical land use in the distribution of Eastern Massasauga Rattlesnake habitat in northeastern Ohio

Introduction
Conserving biodiversity requires forethought and innovative solutions to abate an anticipated wave of extinctions (Gibbons et al. 2000; Schipper et al. 2008). Successful conservation programs will need to mitigate impacts of anthropogenic habitat loss and climate change on the world’s biota and ecosystems. Mining the past for clues to better understand the current plight of threatened species can help inform and improve these programs.

Understanding how prior anthropogenic activities have influenced wildlife populations can benefit current conservation efforts in various ways. Historical information for exploited marine species has been successfully integrated into studies of genetic diversity (Bonnell & Selander 1974; Hoelzel et al. 1993) and ocean ecosystem function (Lotze & Worm 2009). Species distributions are governed principally by environmental (e.g. habitat) and biological/ecological (e.g. dispersal ability, competition) factors, however in many locations these distributions have invariably been influenced by human activities. Research on populations that have persisted in modified landscapes can provide valuable information if factors related to persistence (e.g., characteristics of refugia) are identified. Moreover, historical factors related to the resilience of populations
can be assessed in areas with varying intensities of land use and used to predict responses to future land modifications.

The primary limitation for studying historical activities is a paucity of reliable data. Long-term field studies can provide a wealth of information (Clutton-Brock & Sheldon 2010) but those conducted over historical time scales are limited in number. Historical aerial photograph archives in the U.S. and elsewhere present a unique opportunity for assessing changes in land use and land cover over the past 75 years. Historical aerial photographs have been applied to study trends in land cover (Mast et al. 1997; Morgan et al. 2010), but applications to wildlife research are still sparse (Brambilla et al. 2010; Pringle et al. 2009).

I used historical aerial photographs in conjunction with a recent habitat suitability map to examine how changes in land use and land cover have influenced the current distribution of the Eastern Massasauga (Sistrurus catenatus catenatus), and its habitat in northeastern Ohio. Eastern Massasauga require open canopy habitats that include fens, wet prairies, and coniferous swamps throughout their Great Lakes distribution. In northeastern Ohio they are primarily found in early successional grassland habitats with poorly drained soils. Conversion of these grassland and wetland habitat to agriculture is one of the primary causes for Eastern Massasauga population declines during the last century (Szymanski 1998). An additional threat to snakes in northeastern Ohio is habitat loss due to succession as grasslands are replaced by forest. Increases in forest cover associated with agricultural abandonment have been well documented across the eastern U.S. during the last half-century (Ramankutty & Foley 1999; Ramankutty et al. 2010).
The negative impact of diminishing early successional habitats on biodiversity in the Northeast has started to receive attention from the conservation community (DeGraaf & Yamasaki 2003; Dettmers 2003; Fuller & DeStefano 2003; Litvaitis 2003).

Historical imagery has been incorporated into several species distribution modeling (SDM) studies (Butler et al. 2010; Ficetola et al. 2010; Scozzafava & De Sanctis 2006) but not in the context of assessing the role of historic landscapes in determining the current distribution of suitable habitat. Here, we present a novel approach to shed light on how the historical dynamics of agriculture and forest succession have influenced the present day distribution of an endangered snake and its habitat using object based classification of historical aerial photographs and SDMs. Agriculture and the transition of grassland to forest will continue to impact landscapes inhabited by the remaining Eastern Massasauga populations making it imperative to understand their historical impact now in order to properly integrate this knowledge into future management plans.

Methods
I selected a 7970 ha section of Ashtabula County in northeastern Ohio for the historical analysis. This area has the highest density of known Massasauga sites in northeastern Ohio with seven of the ten confirmed Massasauga localities from the region.

I obtained georeferenced historical aerial photographs from 1938, 1950, 1959, 1966, and 1979 with coverage of Ashtabula County from the Ohio Department of Transportation database. These images were taken during leaf on conditions between April-June. All images with flight information were collected at a 1:20,000 scale. After
resampling all images to the same cell size and clipping to the same extent, I classified each image into three land cover classes: agriculture, forest, and grassland. For agriculture, I visually interpreted and hand digitized all agricultural fields that appeared to be row cropped or barren. Fields that had characteristics of pastureland such as uniform texture and lack of shrubs were not included in the agriculture class as they could be utilized by Massasauga.

I used the object-oriented software program Feature Analyst vers. 5.1 Overwatch Systems to map the forested regions. After masking out the agricultural fields, I selected a sufficient number of forested training locations to cover most of the study area. Varying grayness levels for forested areas made it necessary to get a broad geographic representation of this land cover type to train the supervised classification. I ran multiple passes using the identify correct/incorrect features tool of Feature Analyst. After visually assessing the fit of the forested and agricultural layers I assigned a third category of grassland to any areas not assigned to either of the first two categories. I then ran a low pass filter to smooth the image and remove isolated pixels from contiguous patches of a given land cover type. This procedure was repeated for each of the five independent years. I used multiple iterations of 200 random points to create confusion matrices for classification accuracy assessments.

I used the same hand digitizing procedure to quantify present day agriculture in the study area. Recent aerial photographs were taken during leaf-off conditions making it difficult to apply the object oriented classification technique for mapping forests. I opted to use forest cover estimates from land cover maps to assess long term changes. I
compared the results from two land cover mapping projects, the 2011 National Land Cover Database (NLCD) and 2010 Coastal Change Analysis Program (CCAP) and found the NLCD map was more accurate for forest cover in the study area.

I used the software program Fragstats vers. 4.2 (McGarigal & Marks 1995) to calculate landscape metrics for each individual year assessing the area and proportion of the landscape occupied by each land cover type. I used map algebra in ArcGIS to combine maps from different years and reveal areas where changes in land cover occurred. I used this information to evaluate trends in land cover change over time.

Six of the ten snake locations in northeastern Ohio were agricultural fields in 1938 (Table 3). Though sample size was limited, this observation provides some evidence for the role of agriculture in maintaining early succession habitats. To better understand the role of agriculture in this regard, I used an SDM derived habitat suitability map (HSM-See Chapter 2) to compare suitability scores associated with present day conditions to land cover (agriculture, forest, and grassland) from my five historical images (1938, 1950, 1959, 1966, 1979). I generated 2,000 random points across the study area. After running a cluster analysis in ArcGIS I selected a minimum distance of 40m between points to minimize the influence of spatial autocorrelation in the habitat suitability map. I used the extract multi values tool in ArcGIS to obtain values associated with the land cover class (1=agriculture, 2=forest, 3=grassland) from each year and the HSM (0-100) for every random point. To examine areas that transitioned out of agriculture, I also generated a second set of land cover classes with agriculture split into two separate classes indicating if it is still in use or if it eventually transitioned to either
grassland or forest (1=current agriculture, 2=future abandoned agriculture, 3=forest, 4=grassland). The distribution of HSM scores associated with the random points was right skewed and non-normal. Maxent minimizes the amount of area classified as suitable to avoid over predicting the extent of suitable habitat. I used a non-parametric Kruskal-Wallis test in SPSS vers. 22 to compare present day habitat suitability scores associated with each of the three land cover types from an individual year. When a significant result was identified, I used Mann-Whitney U tests to look at pairwise comparisons between each land cover class. I also used a negative binomial generalized linear model (GLM) to allow for interactions. I used the GLM to compare mean suitability scores from the oldest and most recent images (1938 and 1979) and the two most recent images (1966 and 1979).

The random point approach used in the Kruskal-Wallis and GLM analyses assessed prior land use associations with suitable habitat but the sampled pixels of suitable habitat do not necessarily hold any functional significance for Eastern Massasauga populations because they only represent conditions from a 900 m² cell. Consequently, I complemented the random point sampling method by quantifying how many cells of each land cover type were associated with present day contiguous habitat patches. I used the ArcGIS extension CoreMapper to isolate patches of suitable habitat from the Maxent HSM using a moving window of 100m and minimum habitat suitability values of 0.25 (the value from the maximum training sensitivity plus specificity threshold). I converted these polygons to raster format and used the zonal histogram tool
to extract the land cover type associated with each cell from the classified historical dataset 1938-1979.

I used a chi-square test for each individual year to determine if the pixels that make up the present day habitat patches reflect non-random associations with any of the three land cover classes. My null was set to the overall proportion of each land cover class in the landscape for that particular year.

**Results**

I observed steady shifts in the landscape from 1938–1979 with increasing forest cover and decreasing agricultural areas (Table 4). This trend continued from 1979 to the present day. Despite the observed trends, land use/land cover was dynamic with various shifts occurring between observation years (Table 5). For example, during each time interval some grassland areas were lost via transitions to forest or conversion to agriculture but were replenished by shifts from forest and agriculture. The primary mode of grassland creation was conversion from forest, which exceeded the conversion of agriculture to grassland for every time interval except during 1979–2011. Grassland transitions to forest accounted for most grassland losses, with considerably less conversion of grassland to agriculture (Table 5). Overall classification accuracy was high for all years 1938 (96%), 1950 (94%), 1959 (94%), 1966 (95%), and 1979 (93%) in the analysis with user’s accuracy (commission error) ranging from 89–98% and producer’s accuracy (omission error) ranging from 90–98%.

All of the initial Kruskal-Wallis tests comparing present day habitat suitability scores associated with each of the land cover types from an individual year were
significant (Table 6). Follow up Mann-Whitney $U$ tests identified significant pairwise differences among the three land cover classes for every year in the analysis after Bonferroni correction for multiple comparisons. Significant differences were observed between agriculture and forest as well as grassland and forest during 1938, 1950, and 1959. All pairwise comparisons were significant during 1966 and 1979.

The follow up Kruskal-Wallis tests were significant after subdividing agriculture into two separate classes: agriculture that remained active today and agriculture that was abandoned (Table 7). For all years assessed (1938, 1966, 1979) significant differences were observed between the two agricultural classes and forest as well as grassland and forest. I selected these years to evaluate the oldest image (1938) in addition to the two years (1966 and 1979) where grassland was significantly different from agriculture in the previous Kruskal-Wallis tests.

The best supported model incorporated main effects from 1966 and 1979 followed by the 1966 and 1979 model that added interactions (Tables 8, 9) in the GLM analysis prior to subdividing agriculture. For 1966 highest mean suitability score was associated with grassland locations (mean=14.40 95% CI [13.03, 15.93]) followed by agriculture (mean=12.5 95% CI [11.25, 13.91]) and forest (mean=11.79 95% CI [10.71, 12.98]). A significant difference was observed between forest and grassland locations. I observed the same pattern in 1979 with the highest suitability scores associated with grassland (mean=17.79 95% CI [16.11, 19.65]), agriculture (mean=16.16 95% CI [14.44, 18.08]), and forest (mean=7.39 95% CI [6.75, 8.09]). Both grassland and agriculture were significantly different from forest for 1979.
In the follow up GLM analysis with the two agricultural classes, the 1966 and 1979 model with the interaction term was the most supported (Tables 10, 11). Interactions associated with higher mean suitability scores included locations that were grassland in both 1966 and 1979 (mean=19.14 95% CI [16.67, 21.97]) and locations that shifted from grassland in 1966 to agriculture in 1979 but would eventually be abandoned (mean=24.71 95% CI [18.51, 32.97]) which were not significantly different from each other but were significantly greater than shifts in grassland to forest or permanent agriculture. The highest suitability score was associated with agriculture in 1966 and areas that were still agriculture in 1979 but eventually abandoned (mean=25.87 95% CI [23.20, 28.84]) which was significantly different from shifts in 1966 agriculture to either forest or grassland in 1979.

Agriculture was the predominant land cover type historically associated with the areas that presently constitute habitat patches for the Eastern Massasauga (Figure 3). All chi-square tests comparing the historical land cover composition of present day habitat patches were highly significant (p<0.001).

**Discussion**

The decline in agricultural area and subsequent increase in forest cover in northeastern Ohio from 1938 to the present (Tables 4, 5) were representative of broader trends observed across much of the eastern U.S. during the latter half of the 20th Century (Ramankutty & Foley 1999; Ramankutty et al. 2010). Ohio was among the four states (New York, Pennsylvania, Michigan) that experienced the largest gains in forest cover during the 20th Century (Ramankutty et al. 2010). Conditions in northeastern Ohio were
amenable to reforestation, being predominantly forested before European colonization (Ramankutty & Foley 1999). Northeastern Ohio may have experienced more farm abandonment than other parts of the state (e.g. northwest Ohio) and as these fields were allowed to undergo succession the deciduous forest eventually returned.

Agricultural abandonment and logging became the primary sources of open canopy habitats required by Eastern Massasauga during the period of forest regrowth (Table 5). My historical analysis revealed multiple pieces of evidence that suggest prior agricultural use was an important factor in the current distribution of Massasauga populations. These include the presence of extant Massasauga sites in areas previously used for agriculture (Table 3), higher habitat suitability values associated with prior agricultural areas (Tables 6-11), and agricultural fields disproportionately represented in the land use history of present day suitable habitat patches (Figure 3).

The initial draining of wetlands and conversion of grassland habitats to agriculture undoubtedly had severe negative impacts on Eastern Massasauga populations across its range. However, the gradual abandonment of agricultural fields during the 20th Century likely served as an important source of early successional habitat for Massasauga populations that were able to persist in refugia. This is because grassland habitats are transitory in this landscape, which appears to have required the movement of Eastern Massasauga to track the available habitat. Grassland refugia occupied by snakes in 1938 were unlikely to remain open canopy habitats by 1979 as 63% of 1938 grassland area was a different land cover class in 1979. One of the key findings from the GLM analysis was
that agricultural fields that transitioned after 1979 had higher suitability scores than those that switched to grassland during the 1966-1979 interval.

Three important conclusions from these findings are: 1) Eastern Massasauga can successfully recolonize and persist in former agricultural fields, 2) populations are not spatially static over time and 3) current suitable habitats largely coincide with historic agricultural use. All have important conservation implications.

The presence of Massasauga in prior agricultural fields means extensive restoration efforts to propagate native vegetation may not be necessary to attract snakes to newly acquired properties. This would ease the initial financial burden associated with restoration efforts. What appears to be a biological imperative for movement in this landscape in response to canopy closure is intriguing in light of genetic evidence that suggests a complete absence of gene flow among extant populations across the species’ range (Chiucchi & Gibbs 2010). This would seemingly run counter to the available genetic data for northeastern Ohio. Chiucchi and Gibbs (2010) showed highly structured populations across the Eastern Massasauga’s range, including northeastern Ohio where two of the populations from my study area were included in their analysis. Despite their close proximity (~4 km), the two populations did not appear to have any history of gene flow. Despite the incongruities with the genetic data, the evidence of colonization events is indicative of dispersal in northeastern Ohio, albeit likely on a very local scale.

The two sites sampled by Chiucchi and Gibbs (2010) are presently separated by a road and predominantly forested areas, not principally favored by Massasauga. This separation is visible on a historical time scale as well, with forest and agricultural fields
constituting the majority of the intervening matrix in 1938. Since their study, two new populations have been located between the two sampled sites. There are likely more pockets of snakes as the SDM derived habitat suitability map indicated early successional habitats are widespread throughout this area. If the Eastern Massasauga populations in this region are characterized by small demes moving throughout the landscape on decadal time scales in response to successional transitions it is certainly plausible that two sites could be genetically distinct. The seemingly small Euclidean distance of 4 km can still serve as a functionally significant obstacle to gene flow with the presence of barriers (e.g. roads) and unsuitable habitat (e.g. forest).

Massasauga dispersal is poorly understood, in part because population genetic studies have repeatedly found highly structured populations (Chiucchi & Gibbs 2010; Dileo et al. 2013; Gibbs et al. 1997). Chiucchi and Gibbs (2010) showed that Eastern Massasauga populations have existed in genetic isolation over historic time scales that predate any European influence on the landscape and therefore selection for dispersal as a mechanism for inbreeding avoidance may not be as strong. Eastern Massasauga radiotelemetry studies have also noted small home ranges and low levels of dispersal, though exceptions exist, particularly in areas where critical resources (e.g. hibernacula; bask sites) are more dispersed (Durbian et al. 2008; Szymanski 1998). Therefore, selection for dispersal may be habitat-dependent (e.g. fens vs. early successional grassland) and differ across the range. The ecological and evolutionary consequences for organisms associated with ephemeral habitats are well documented (Travis & Dytham
1999) and Eastern Massasauga occupying early successional habitats may share some of these traits.

Historically, northeastern Ohio has not been subject to regular fire regimes (Nowacki & Abrams 2008). Rather, beaver (*Castor canadensis*) have been suggested as the primary natural disturbance agent and source of open canopy habitat in the region. Beaver activity has previously been demonstrated to be a useful indicator for the presence of other species (Bartel & Sexton 2009; Cunningham et al. 2007; Suzuki & McComb 2004). For example, the endangered St. Francis’ satyr butterfly (*Neonympha mitchelli francisci*) utilizes habitat similar to the Eastern Massasauga and is associated with early successional riparian vegetation resulting from beaver activity (Bartel & Sexton 2009).

Declared extirpated from Ohio by 1830, it took just over a century for beaver to re-establish colonies in Ohio with the first recorded sighting occurring in Ashtabula County in 1936 (Chapman 1949). This time period where beaver were absent from the region may have been particularly difficult for Eastern Massasauga populations as it coincided with historical peaks in cropland area (Ramankutty & Foley 1999).

Today, beaver are commonly viewed as a nuisance animal as the flooding associated with their damming activities can cause property damage and private landowners may be reluctant to lose trees on their property. This can lead to lethal control options, even in protected areas within the region (pers. obs.) and underscores the need to formally investigate the role of beaver activity in Massasauga habitat use and dispersal within the region.
River corridors have been proposed as a possible conduit for massasauga dispersal and future genetic studies could focus on parts of the Massasauga’s range where multiple populations exist in close proximity to one another and riverine systems. If beaver activity has been the primary natural disturbance agent in northeastern Ohio, then Massasauga spatial distribution should be associated with the clearing and flooding activities of beaver along a river corridor. Experimental manipulations involving forest clearing in northeastern Ohio could evaluate Massasauga dispersal and the colonization potential of newly created habitats by varying the distances and types of land cover (forest vs. agriculture vs. grassland) separating these patches from occupied sites.

Direct management activities to maintain open canopy habitats via mechanical removal of trees and prescribed burns have been in place in northeastern Ohio and are being applied elsewhere in the Massasauga’s range (Bailey et al. 2012; Cross et al. 2015; Steen et al. 2015). However, these are primarily restricted to known Massasauga sites. Early successional habitats can transition to closed canopy habitats in short time spans (<10–20 years) as I observed in some areas within the historical time series and it is unlikely another wave of agricultural abandonment will take place in northeastern Ohio to provide a source of new habitat. My study area experienced a 55% decrease in agricultural land from 1938 to 2011 and 81% of the current agricultural land was being farmed in 1938, so most of the remaining active agriculture is associated with long term operations. Therefore it is vitally important to identify as many remaining populations as possible to allow for habitat management to prevent the loss of populations as their habitats transition to forest.
The historical perspective enabled by the aerial photographs illuminated several important aspects of Eastern Massasauga habitat use/availability in northeastern Ohio that will apply to other sections of their range where early successional habitats are involved. Paradoxically, the presence of agricultural fields appears to have benefited Eastern Massasauga in northeastern Ohio as they were abandoned and allowed to transition to a more natural state. Sustained habitat management will be required to maintain the remaining Eastern Massasauga populations and their early successional habitats for the foreseeable future.
Chapter 4: Application of broad scale species distribution models to conservation planning for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*)

**Introduction**

The development of species distribution models (SDM) for the Eastern Massasauga rattlesnake (*Sistrurus catenatus catenatus*) in Ohio (Chapter 2), with relatively few remaining populations statewide, has the promise to help guide regional survey efforts to identify undocumented populations in northeastern Ohio and inform land purchasing decisions intended to expand the amount of area available to support current and future populations. However, the recent decision by the USFWS to elevate the Eastern Massasauga to Federally Threatened underscores the immediate need for information with more tangible applications to broadly assess threats and aid recovery efforts across the species’ range.

I generated a broad scale SDM for Michigan in order to make a habitat suitability map (HSM) available for comprehensive evaluations of the remaining Eastern Massasauga populations and habitats within the southern half of the state. Michigan, compared to other states, has roughly 100 populations of Eastern Massasauga (Szymanski 1998) and therefore is essential for the long-term persistence of the species. The Eastern Massasauga Michigan distribution is bimodal with clusters of northern and southern populations and a clear gap in the central part of the state (Figure 4). Most populations occur in the southern half of Michigan. The large number of populations in Michigan has
the potential to supply a wealth of information that is not available or more difficult to obtain elsewhere in the species’ range, such as fine scale gene flow and commonalities in habitat attributes shared among populations. Both of these questions can be addressed with a broad scale HSM.

The presence of more populations distributed across a broader area in Michigan requires a model to be more transferrable across space than the Ohio-based model that was primarily intended for regional predictions in northeastern Ohio. A broad scale SDM has the potential to identify important factors related to the distribution of Eastern Massasauga populations that would not appear in individual site-based habitat assessments currently taking place in Ohio and Michigan. Both are necessary to inform future management of Eastern Massasauga populations by identifying the environmental or climatic factors operating at broad scales that shape the distribution of populations and the fine scale habitat attributes that are important for individual survival and fecundity (Cross et al. 2015; Pomara et al. 2014).

In this chapter, after the SDM creation and selection process, I use the resulting HSM for several Eastern Massasauga conservation mapping applications in Michigan to illustrate its utility as a multi-purpose conservation tool. These include identifying common habitat features shared among Michigan populations, mapping the location and discerning the protected status of large, contiguous habitat patches, and assessing population connectivity (See also Chapter 4).

**Methods**

*Species distribution model*
I used the SDM software program, Maxent vers. 3.3.3 (Phillips et al. 2006) to create the Michigan HSM. I acquired statewide Eastern Massasauga location data from the Michigan Natural Features Inventory (MNFI). Locations are stored in the MNFI database as shapefile objects, a buffered circle with increasing buffer lengths associated with greater uncertainty in the exact location. I limited point selection to 200 m buffers and used the centroid of these objects. Points were then filtered so that no points less than 5 km apart were used. This ensured that each point was drawn from a separate population and reduced the influence of spatial autocorrelation. Eastern Massasauga home ranges are typically 1-2 km in diameter (Durbin et al. 2008; Szymanski 1998).

**Data layers**

Vegetation indices were derived from Landsat 5 satellite imagery using a Tasseled Cap Transformation (Kauth & Thomas 1976). I selected scenes from the Massasauga active period (April-October) that minimized cloud cover for the lower third of Michigan. All scenes were downloaded using the USGS GLOVIS interface (http://glov.is.usgs.gov). I performed the Tasseled Cap Transformations in Erdas Imagine vers. 9.2. I also used digital elevation model (DEM) derived variables including Roughness, which is a terrain ruggedness index from a 3x3 30m cell moving window produced from the Geomorphometry toolbox in ArcGIS vers 10.2 and a Topographic Position Index (TPI) implemented in the Land Facet Corridor Designer ArcGIS extension. The TPI identifies relative peaks and valleys in the landscape based on a user defined comparative distance. Finally, I used the percent canopy cover layer associated with the 2011 National Land Cover Database (NLCD) (Homer et al. 2015).
performing variable from the Ohio Maxent model (Chapter 2) was LiDAR data, which introduced vegetation height information. There was no statewide LiDAR data available for Michigan so I used the canopy cover layer to help the model focus on open canopy habitats where most Massasauga in southern Michigan are found. The populations in northern Michigan occur in coniferous swamps and some shoreline habitats (Degregorio et al. 2011), which contrast with the fens and wet prairie habitats predominantly used by Massasauga in southern Michigan. At this fine a scale, models trained with environmental information from forest (northern MI) and non-forest (southern MI) populations did not generate models with strong predictive power in my preliminary analysis.

**Maxent**

Maxent runs were implemented in ENMeval, an R package that can compare models across a range of user customized settings (Muscarella et al. 2014). I split the 60 locations into four “bins” of 15 points each based on geographic proximity. This allowed me to use the \( k \)-fold cross validation method wherein models are generated using \((k – 1)\) bins as training data for model calibration and the withheld bin as test data for model evaluation. This is repeated until all \( k \) bins have been used for testing purposes. The bins were created using a geographically structured approach that spatially separates the points so each bin contains points from the same general region (Radosavljevic et al. 2014). This method allows for the test data to be spatially independent of the training data. In order to be completely spatially independent, the background points selected by Maxent to compare to the presence data should not come from the areas occupied by the
test data (Radosavljevic et al. 2014). Therefore, I generated 10,000 random background points within 1 km buffers around all presence points. For each of the $k$ runs I only applied the background points associated with the $(k - 1)$ bins being used for training data. ENMeval provides both threshold dependent (omission rate) and threshold independent (AUC) measures of model quality. It also ranks models using the AICC$_C$ approach developed by Warren et al. (2010). I used the AICC$_C$ rank as my primary selection criterion for determining the optimal model setting.

**Habitat Analysis**

I processed the HSM using the Core Mapper tool from the Gnarly Landscape Utilities ArcGIS toolbox (Shirk and McRae 2013) to quantify the extent of Eastern Massasauga habitat across southern Michigan. I restricted the analysis to patches meeting the minimum target size of 100ha suggested by Durbian et al. (2008) for management and restoration efforts. The minimum suitability value for a pixel to be included was set to the maximum sum of sensitivity and specificity threshold (0.28) from the Maxent output. This is one of the more conservative thresholding options available. Once the habitat cores were isolated, I used ArcGIS proximity tools to calculate the nearest neighbor for all cores. I used the intersect tool in ArcGIS to determine how many cores were located in protected areas using shapefiles representing federal, state, county and NGO land holdings to assess the protected status for all habitat cores. I also used the MNFI Massasauga database to determine how many cores were associated with known snake locations.
To estimate connectivity I used the Linkage Mapper toolbox in ArcGIS to generate least cost paths (LCP) and cost weighted distances (CWD) among habitat cores separated by less than 5 km. I restricted the analysis to distances less than 5 km due to the limited dispersal capabilities of Massasauga. I also used Linkage Mapper to run Circuitscape, which generated movement corridors and associated effective resistance distances as a complementary approach to the LCP analysis (See Chapter 5 for a more thorough review). I compared LCP distances and CWD/effective resistance ratios between habitat cores for three different resistance layers. One based on the standard values from the HSM, a modified HSM to include class weights and finally a land cover based resistance layer from the MNFI (See Chapter 5 for additional information).

I then used the Pinchpoint Mapper option in Linkage Mapper to identify bottlenecks in the corridors. Pinchpoints indicate narrow sections of the corridor where paths for movement are more limited and therefore more important to be monitored and maintained. These Circuitscape corridors and pinchpoints were also generated for a subset of Massasauga locations used for the Chapter 5 analysis. This allowed for qualitative comparisons of the patterns and potential vulnerabilities of linkages located between habitat cores and between confirmed presence localities. Three separate resistance layers were used for the LCP and Circuitscape analysis involving the standard HSM, a class weighted HSM, and a land cover based layer (See Chapter 5 for description).
Results

Six variables were selected for the final Maxent model representing both elevation and land cover attributes (Table 12). The two DEM derived layers (TPI and roughness) were the top contributing variables to the final Maxent model. The preferred model settings based on AICc were linear and quadratic features at the default regularization setting (Table 13).

CoreMapper identified 86 core areas that satisfied the 100ha minimum area requirement. Eight of these were located <30m from adjacent cores due to thin bands of unsuitable habitat (e.g. dirt roads, river), so I excluded these from the average nearest neighbor calculation. The average nearest neighbor distance for the remaining 78 cores >30m from the closest adjacent core was 5744m. Only 25 (29%) of the 86 habitat cores were at least partially located within state (17), NGO (5), or county (3) protected areas (Figure 5). Twenty-six (30%) of the habitat cores were associated with a shapefile object from the MNFI. This did not necessarily mean that a snake population existed inside the core. Six of the 60 Massasauga localities used for the Michigan SDM were found within habitat cores.

Forty-two LCPs among habitat cores present in all three resistance layers were identified and used for comparisons among the layers. The mean LCP distances for the standard HSM resistance layer were the shortest (mean=2396 m) and closest to the Euclidean mean (1919 m) followed by the class-weighted HSM (3027 m) and land cover layer (3589 m). The same pattern was observed for CWD/effective resistance ratios with the small mean associated with the standard HSM layer (32.81) followed by the class weighted HSM (32.18) and land cover layer (36.39). Many potentially important
pinchpoints were identified in corridors connecting habitat cores and Massasauga localities (Figure 6, 7).

**Discussion**

A broad array of variables was retained for the final Maxent model with the elevation-based variables (TPI and roughness) contributing the most to the final HSM (Table 12). Elevation-based variables were not informative for the Ohio based HSM because the majority of the northeastern Ohio points were located within a single river valley. Therefore, the predictive qualities of the model were focused on discerning suitable conditions within the valley with variables such as LiDAR data. In contrast, the Michigan based model was broader in scope involving many more populations across a wider area. At this scale, broad geographic trends in the Massasauga’s distribution could be detected by the model. Most evident was the strong association of Massasauga points with valleys as shown in the 1 km TPI (Figure 8). The use of a TPI in SDMs has more commonly been applied to environments with significant topographic relief (Braunisch et al. 2013; Nielsen et al. 2010; Olson et al. 2014) including several snake habitat models (Guisan & Hofer 2003; Lyet et al. 2013). A small number of studies on salamander distributions have employed TPIs in wildlife habitat models on a fine scale (Peterman et al. 2013; Peterman & Semlitsch 2013). Although the Eastern Massasauga does not require moist microhabitats on par with amphibians, poorly drained conditions are one of the more consistent habitat attributes found across the species’ range, as long as these areas include sufficient open canopy. It is not surprising then that the TPI has been extensively used in hydrological studies for delineating saturated areas (Grabs et al. 2009;
Merot et al. 2003; Rodhe & Seibert 1999). This study represents the first application of a TPI to model habitat for a wetland associated snake.

It is promising that 86 habitat cores were identified and only 30% were associated with confirmed Massasauga observations, suggesting there are likely additional Massasauga populations not yet in the state’s database. However, less than a third of these cores are currently located in protected areas. This is an example of how SDM results can be used for longer term planning, prioritizing which areas should be purchased.

Pinchpoints were located in both the HSM and CCAP resistance layers (Figures 6, 7). These narrowed linkages were generally associated with common barriers on the landscape such as water bodies or roads. Pinchpoints located at road crossings could be used as target locations for the installation of road mitigating structures (Figure 9). Drift fences and road culverts have reduced road mortality for other species (Dodd et al. 2004; Glista et al. 2009) and are presently being studied with Massasauga in Ontario.
Chapter 5: Influence of resistance layer source on estimates of landscape connectivity using least cost paths

Introduction
Understanding how animals traverse their environment is central to maintaining populations in fragmented landscapes (Taylor et al. 1993). With increasing demands being placed on natural systems, identifying and protecting landscape linkages to promote dispersal and gene flow is critically important to avoid loss of genetic diversity and local extinctions (Manel et al. 2003; Storfer et al. 2007). Widespread adoption of remote sensing and Geographic Information System (GIS) technologies have greatly facilitated a better understanding of landscape connectivity (Menon & Bawa 1997; Osborne et al. 2001). One of the more common approaches for assessing landscape connectivity has been through the use of least cost path (LCP) analysis. LCPs involve the use of a resistance or cost surface to estimate connectivity between habitat patches and have been widely used to identify important corridors for gene flow (Wang et al. 2009). The accuracy of LCP for inferring corridor use and gene flow has been called into question because it is based on the assumption that organisms have knowledge of the optimal path of lowest resistance (Koen et al. 2012; Pinto & Keitt 2009; Sawyer et al. 2011).

An alternative method for assessing landscape connectivity has come from an application of circuit theory. The software program Circuitscape applies circuit theory to
infer landscape connectivity (McRae et al. 2008). Rather than identify a single path that minimizes costs to movement, Circuitscape treats an animal’s movement as a random walk through the landscape without detailed knowledge of the best possible route thereby representing connectivity as a range of alternative pathways. The effective resistance (in ohms) calculated by Circuitscape is a more holistic characterization of landscape permeability to movement than the LCP making it an ideal complementary measure.

Another important aspect of assessing landscape connectivity are the cost or resistance surfaces underlying the connectivity measures. Parameterizing the cost surface is the most critical step in the process and different cost assignments can produce drastically different estimates of connectivity (Spear et al. 2010). A range of environmental factors have been incorporated into LCP studies to create the resistance surface (Etherington et al. 2014; Zancolli et al. 2014) but many studies rely solely on land cover for assigning cost values. In some cases it may be the only environmental layer available or is simply the best single representation of animal habitat. A potential drawback of using land cover maps is misrepresentation of the landscape due to misclassification errors (DeFries & Los 1999; Langford et al. 2006). A separate issue lies in the makeup of land cover maps. As categorical representations of the landscape, every patch of habitat has to be lumped into a class. The classes associated with land cover maps are often fairly general meaning that unique habitat types (e.g. cypress swamp) are given the same label (e.g. wetlands). For some species in some environments, this distinction may not negatively alter connectivity estimates but it has the potential to overestimate connectivity for species that have more specialized dispersal requirements.
(Goodwin & Fahrig 2002; Kindlmann & Burel 2008; Tiebout & Anderson 1997). The all or nothing nature of categorical maps could also serve to overestimate distances if traversable gaps exist in contiguous blocks of what is considered unsuitable or marginal habitat.

Species distribution modeling (SDM) or environmental niche modeling presents a possible alternative to land cover maps as the basis for a resistance surface. SDMs have been used for conservation applications such as reserve design (Carroll et al. 2010) and guiding survey efforts for endangered species (Wilting et al. 2010). SDM derived habitat suitability maps (HSM) are now being applied to LCP analyses (Milanesi et al. 2015; Wang et al. 2008). HSMs can incorporate a range of environmental variables associated with species presence data and display more subtle variation in landscape features than categorical land cover maps. Previous studies have successfully used HSMs to explain patterns of gene flow (Milanesi et al. 2015; Wang et al. 2008), although they have not been applied to as wide a range of organisms or landscapes as land cover based LCPs or Circuitscape analyses. The difference in connectivity estimates produced by HSM or land cover based cost surfaces have not been explicitly examined. I used HSM and land cover based cost surfaces to compare LCP and Circuitscape connectivity estimates for a threatened rattlesnake species to address this gap in knowledge.

The Eastern Massasauga Rattlesnake (Sistrurus catenatus catenatus) has been proposed for listing as Threatened under the Endangered Species Act and could greatly benefit from landscape connectivity analysis. The environmental or population characteristics responsible for promoting gene flow are unclear due to high levels of
structure observed in multiple genetic studies (Chiucchi & Gibbs 2010; Dileo et al. 2013) and fine scale investigations are limited to a few pairs of populations from these studies. It is possible that Massasauga dispersal requires adjacent patches in close proximity and specific environmental attributes for a corridor to be viable. Along these lines, identifying habitat linkages could help direct habitat management activities to remove barriers separating patches.

I developed a HSM with the popular SDM software program Maxent to complement a land cover based resistance surface created by the Michigan Natural Features Inventory (MNFI). Michigan has more Eastern Massasauga populations than any other state or province and therefore provides the best opportunity for investigating fine scale gene flow. There is also a greater need to assess connectivity as multiple clusters of sites exist in close proximity to one another (<5-10 km) contrasting with other states where populations primarily exist in complete isolation.

The aim of this study was to determine if the HSM and land cover based cost surfaces would result in significantly different LCP and Circuitscape based measures of connectivity. I expected the HSM to be associated with higher connectivity estimates (i.e. shorter distances) because it better captures subtle variation in the environment. No genetic data were available to assess either cost surfaces ability to predict gene flow, consequently the connectivity estimates were used to identify areas with differences in predicted connectivity that can serve as potential sampling sites for future population genetic research in Michigan.
Methods
Locations

I selected a subset of locations from the Michigan Massasauga database for the connectivity analysis. Locations were selected based on their level of precision (<200 m diameter associated object file) and proximity to other points (<5 km). These included pairs of locations as well as clusters of points where individual pairs still satisfied the 5km cutoff. I selected 5km as the maximum distance between pairs of points as a realistic estimate of how close populations would have to be for successful gene flow given home range diameters are typically small, ranging from 1–2 km (Durbin et al. 2008; Szymanski 1998). After the filtering process I selected 44 points representing clusters ranging in size from 2–6 points.

Layers

The two resistance surfaces were the Maxent derived HSM and the layer supplied by the MNFI. The MNFI resistance surface was based on 2006 Coastal Change Analysis Program (CCAP) land cover data produced by NOAA. It consisted of four class weights (1, 20, 30, 100) with 1 assigned to land cover classes considered suitable habitat for Eastern Massasauga. The suitability values of the Michigan HSM ranged from 1–90 with larger values indicating higher quality habitat. I inverted the values in the HSM to use it as a resistance surface where lower values were associated with higher quality habitat and therefore assumed to be more traversable. I then rescaled the original MNFI layer to align with the range of values in the HSM so that the most costly category was reduced from 100 to 90. For an additional comparison, I modified the standard HSM resistance surface by converting the unique integer distribution into four classes to more resemble the
structure of the MNFI CCAP resistance surface. I converted the continuous Maxent output values 1–90 into four equal intervals. These classes were assigned values of 1, 20, 30, and 90 respectively to complete the class weighted HSM. Finally, as roads were not explicitly incorporated into either resistance surface I included them as a final cost class. I obtained a Michigan roads shapefile then added a 30 m buffer for all roads. This was intended to eliminate “cracks” from the resulting cost surface where optimal paths may incorrectly pass through seams in the roads layer (Rothley 2005). I then assigned a resistance value of 100 to all roads. I assigned the highest resistance value to roads because the areas surrounding the snake sites are predominantly natural vegetation making roads the primary modified landscape feature with known negative consequences for Eastern Massasauga in terms of deterring movement and road mortality (Dileo et al. 2013; Shepard et al. 2008).

Connectivity measures

I evaluated connectivity by estimating LCP and effective resistance distances among pairs of snake points using the standard and class weighted HSM and CCAP resistance surfaces. I used Linkage Mapper vers. 1.0.9 in ArcGIS vers. 10.2 to calculate LCP and cost-weighted distance (CWD) among all pairs of points. Linkage Mapper also calls Circuitscape vers. 4.0 to calculate effective resistance among pairs of points. The LCP lengths provide a general estimate of connectivity between populations but assume an organism has complete knowledge of their environment in order to select the least costly path. The CWD metric provides information on the accumulated cost associated with a LCP based on the values derived from each cell of the resistance layer. The
effective resistance estimate produced by Circuitscape evaluates connectivity by assuming a random walk approach where each of four or eight paths (user option) from a point of origin are equally likely to be taken. The effective resistance value describes the permeability of the landscape across a number of possible paths thereby characterizing the width of movement corridors and availability of alternate routes (McRae 2008). Direct comparisons of the CWD or effective resistance between the standard HSM and CCAP resistance surfaces are complicated by the different weighting schemes. The standard HSM accumulates more cost values because suitable habitat can be a range of values in the standard HSM compared to a static value of one in the CCAP layer. To allow for a comparison using a measure of connectivity that accumulates cost I used Linkage Mapper output of the ratio of CWD/effective resistance. Using the ratio value instead of either cost weighted measure by itself allowed me to compare the standard HSM and CCAP layers. Increasing values of the CWD/effective resistance ratio indicate increasing corridor width and more quality pathways.

Calculations were limited to 10 km buffers around points, and all pairwise calculations were limited to points <5 km apart as Eastern Massasauga migration beyond this distance is unlikely given their limited dispersal ability (Durbian et al. 2008; Szymanski 1998).

I also evaluated key areas within corridors called pinchpoints. Circuitscape was run through Linkage Mapper to identify sections of corridors where the path narrows. These pinchpoints represented key locations to be maintained in order to maintain connectivity among populations.
**Statistical analysis**

I used a paired t-test to compare LCP lengths for both the standard and class weighted HSM with the CCAP resistance layer in SPSS vers. 22. The LCP data were square root transformed prior to the analysis. To compare the CWD/effective resistance ratios I first log transformed the values then applied a paired t-test as with the LCP comparison.

**Results**

The standard HSM LCPs were the shortest (mean=1609 m) followed by the class weighted HSM LCPs (mean=1781 m) and CCAP LCPs (mean=2222 m). The average Euclidean distance between locations was 1295 m. After square root transforming the LCP distances there were significant differences between standard HSM (mean=36.25, SD=17.38) and CCAP (mean=40.89, SD=21.02); t(43)= 4.74, p<0.001) as well as standard HSM and class weighted HSM (mean=37.99, SD=18.60); t(43)= 5.16, p<0.001. The difference between CCAP and class weighted HSM was significant t(43)= 3.24, p=0.002, though marginally insignificant after the conservative Bonferonni correction. The CWD/effective resistance ratios were not significantly different for the standard HSM (mean=16.61, SD=5.11) and CCAP (mean=17.85, SD=7.67); t(46)= -0.264, p=0.793.

**Discussion**

The choice of underlying resistance surface, whether land cover or HSM based, does appear to have a significant influence on LCP length and therefore on estimates of
connectivity. In this study both the standard HSM and class weighted HSM LCPs were shorter than the land cover LCPs, although only the differences between the standard HSM LCPs and land cover LCPs were significantly different. However, no significant difference was observed in CWD/effective resistance ratios between the standard HSM and CCAP resistance layers so this did not apply to all connectivity measures. Milanesi et al. (2015) conducted the first study quantifying the effects of using different HSM methods to estimate LCP distances and predict genetic distance. They found significant variation among HSMs in terms of both LCP distances and correlations with genetic distance. However, comparisons between HSM and land cover based resistance surfaces for landscape genetics applications are still lacking.

The lack of these comparisons may be partly due to the nature of the available environmental data in the regions being studied. Many HSM are based on bioclimatic variables, in part because land cover data may not be available for remote or tropical areas. In these cases, no comparison is possible. However, when land cover data are readily available and HSMs are used, the land cover data may be incorporated as a predictor variable in the HSM with other environmental variables (e.g. elevation). This will produce a more variable resistance surface than the land cover data alone but the analysis will still be influenced by the categorical makeup of the land cover data. My results demonstrate that there are consequences for how connectivity is measured based on selection of resistance layer despite the lack of significant differences in the layers themselves. The vegetation indices present in the HSM are related to the satellite imagery used to classify the land cover map. There is a high degree of overlap between areas
predicted to be suitable by the HSM and the various palustrine wetland classes present in the CCAP land cover map. However, not all palustrine wetlands are also predicted to be suitable by the HSM.

The lack of distinct classes in the standard HSM resulted in more straight-line segments of each respective LCP that lead to the shorter overall distances. The CCAP LCPs were more prone to circuitous routes tracking the suitable habitat classes of the land cover map that were assigned a cost of one. The class weighted HSM LCP distances were intermediate because although this resistance layer had the same cost values as the CCAP, the suitable habitat patches with a cost of one were determined by the MTSS threshold from Maxent, which is one of the more conservative thresholding options. Therefore the permeable areas with a cost of one were smaller and more fragmented than in the CCAP layer, which assigned this cost to multiple land cover types. This is a potential advantage of the class weighted HSM over the CCAP land cover resistance layer. Assigning entire land cover classes a cost of one in the CCAP layer resulted in longer observed LCP distances and almost complete avoidance of shorter routes through lower quality habitat. The cost weighted HSM LCPs passed through suitable habitat patches if available but also utilized marginal habitat when suitable patches were absent.

The standard HSM was much more permissive in terms of LCP routes. Without blocks of habitat receiving a cost of one, the standard HSM LCPs were less tied to patches of suitable habitat. Whereas the CCAP method resulted in a near complete avoidance of marginal habitat, the standard HSM LCPs incorporated frequent paths through marginal habitat. Mateo-Sánchez et al. (2015) found movement through marginal
habitat was an important component of brown bear gene flow that their habitat model resistance layer did not predict. However, this finding was demonstrated for a highly mobile species, one with obvious dispersal advantages over a low vagility species such as the Eastern Massasauga. An example of problematic shortcuts through unsuitable habitat with the standard HSM LCPs occurred when paths cut across water bodies while the class weighted HSM and CCAP LCPs followed a land based route along the edge of the water body, a more likely path of movement for this species (Figure 10).

Thus the class weighted HSM produced the most balanced LCPs of the three resistance layers in terms of tradeoffs between maintaining connections through suitable habitat and traversing marginal habitat to shorten the route. Wang et al. (2008) determined class weighted HSM resistance layers were better predictors of genetic distance than the standard HSM though their analysis did not include any land cover based resistance surfaces.

Importantly, together these LCPs represent different hypotheses that will require Eastern Massasauga genetic data to determine their functional significance. Fine scale genetic work on the Michigan populations is planned that will allow for evaluations of LCPs, CWDs, and effective resistances from these three resistance layers.
Chapter 6: Future impacts of climate change on the distribution of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*)

**Introduction**

The future biodiversity of many regions may largely depend on the adaptability of the resident organisms to climate change (Sala et al. 2000; Thomas et al. 2004). Conservation policy and practice will have to adapt as well (Markham 1996). As the more severe impacts of climate change are still decades away, the response from the conservation community has primarily focused on planning/preparing for various predicted scenarios (Araujo et al. 2004; Heller & Zavaleta 2009; Pressey et al. 2007). These efforts have taken various forms from identifying sensitive habitats or species vulnerable to sea level changes (Gilman et al. 2008) to assessing species vulnerability based on physiological tolerances (Hoffmann & Sgro 2011). However, detailed information on physiological tolerances are lacking for most species.

One method for overcoming this obstacle is the application of species distribution models (SDM) that model an organism’s niche associated with present day precipitation and temperature patterns (Guisan & Zimmermann 2000; Phillips et al. 2006). The resulting suitable conditions can be then projected across the landscape under different climate change scenarios to identify where potential range expansions or contractions may occur (Rehfeldt et al. 2015; Schneiderman et al. 2015). This correlative approach has drawbacks. The lack of physiological data for species means these models may
underestimate the physiological tolerances of organisms as well as any behavioral responses that may mitigate the impacts of changing climate (Kearney et al. 2009). Care must also be taken to sample across a species’ range so that the model incorporates the full range of occupied conditions.

Despite some limitations, these predictive models are still an important tool for making broad geographic assessments for at-risk species and habitats (Peterson et al. 2002). Examples include areas expected to undergo profound changes (e.g. Florida Everglades), species that are unlikely to be able to respond due to low vagility and/or restricted range (Milanovich et al. 2010), and species requiring specific environmental conditions for egg development or sex determination (Pike 2013).

I evaluated the potential impacts of climate change on a threatened rattlesnake, Eastern Massasauga (Sistrurus catenatus catenatus). Pomara et al. (2014) identified environmental changes associated with Eastern Massasauga population declines across their range over the last half century. Winter drought was the primary predictor of population declines followed by the proportion of the landscape used for agriculture. A high water table is important for successful overwintering by Eastern Massasauga. Many populations make use of abandoned crayfish burrows and spend the winter partially submerged (Szymanski 1998).

Given that some environmental changes are already affecting Massasauga populations (Pomara et al. 2014) it is important to identify the most at-risk populations for future, more extensive shifts in climate. As a temperate species, the most vulnerable Eastern Massasauga populations to climate change are likely to be located along the
southern extent of their range in portions of Illinois and Ohio (Figure 11). Eastern Massasauga are not well adapted to dispersing long distances and most populations throughout the range are highly fragmented (Szymanski 1998). As a result, human intervention may be required to prevent local extinctions and predictive models will be an essential part of the planning process for prioritizing locations for rescue efforts and selecting potential repatriation sites if it was deemed necessary.

Methods

I used a large portion of the Michigan locations used for the SDM in Chapter 4 and several Ohio populations from Chapter 2 in tandem with several points obtained through VertNet (http://vertnet.org) to represent other sections of the Eastern Massasauga’s range (Wisconsin, Illinois, Indiana, Pennsylvania, New York, and Ontario, Canada (Figure 11). In total, I used 56 localities with a minimum distance of 20 km between locations.

I obtained 19 bioclimatic variables (Hijmans et al. 2005) at ~1 km² spatial resolution (http://www.worldclim.org/bioclim) and removed variables that were highly correlated (>0.75) for the Eastern Massasauga’s range. I then used the jackknife of individual importance and percent contribution values from Maxent to make final variable selections. I created 100 km overlapping buffers around each point from which background points were drawn although I masked out the Great Lakes so background point selection was restricted to terrestrial habitats.

The future climate data were obtained for three separate global climate models (GCMs) HadGEM2_AO (HD), MIROC5 (MC), and MRI-CGCM3 (MG) at the 2070
average (2061–2080). I selected bioclimatic values from two representative concentration pathways (RCPs) for each of the three GCMs representing the least severe (RCP26) and most severe (RCP85) scenarios for each respective model (HD; MC; MG). I selected these three GCMs because they spanned the range of low to high predicted impacts on the future distribution of reptiles and amphibians across California (Wright et al. 2015).

I used the SDM software program Maxent to generate the climate models. I evaluated a range of Maxent settings and selected the LQ feature sets with a regularization value of two for the final model. Two separate model projections were created for each of the three GCMs representing the RCP 26 and RCP 85 scenarios for a total of six models. I then used Raster Calculator in ArcGIS to average the three GCM models for each RCP to create average RCP 26 and average RCP 85 rasters.

Quantifying potential changes in an organism’s distribution due to climate change requires converting the Maxent continuous habitat suitability map (HSM) to a binary map of suitable and unsuitable habitat. To represent a range of potential outcomes I used two different thresholds for the creation of the binary habitat maps. I used the minimum training presence (MTP) threshold from the Maxent output (0.17) for a more permissive representation of the extent of suitable habitat. The MTP threshold uses the lowest suitability value associated with a presence location as the cutoff between suitable and unsuitable habitat. For a more conservative representation of suitable areas I used the maximum training sensitivity plus specificity (MTSS) threshold (0.48). This threshold operates as a tradeoff between errors of commission and omission. Therefore each average RCP (26 and 85) was mapped at a relaxed and conservative threshold value.
I used Raster Calculator to subtract the four thresholded average rasters from the present day threshold maps to determine the potential proportional changes to suitable habitat across the Eastern Massasauga’s range with special attention to changes predicted to occur in Ohio and Michigan.

**Results**

The bioclimatic variables 9 (mean temperature of driest quarter), 14 (precipitation of driest month), and 16 (precipitation of the wettest quarter) were retained for the final model. The precipitation variables 16 and 14 were the greatest contributors in that order to the final model.

All models show shifts in suitable habitat with more habitat contraction associated with the averaged RCP 85 map (Figure 12). The two thresholds show a wide range of possible changes (Figure 13). Areas along the southern portion of the Eastern Massasauga’s range (Illinois, Indiana, Ohio) experience the most dramatic change, generally becoming less suitable.

I observed similar trends for both MTP and MTSS thresholds on the resulting range changes (Table 14; Figure 14). There is more present day habitat considered suitable with the MTP threshold so less proportional range “expansion” is possible under future climate scenarios. There is more unsuitable habitat associated with the present day MTSS threshold, which resulted in some range expansion, more so under the RCP 26 scenario. The RCP85 emission scenarios were associated with more range contraction than the RCP26 scenarios (Table 14; Figure 14).
Discussion
These models demonstrated how conditions in the southern portion of the Eastern Massasauga’s range may become increasingly unfavorable regardless of the severity (RCP26 vs. RCP85) of climate change (Figure 12). Climate change has the potential to enhance the suitability of some sections of the Midwest already predicted to be suitable (Minnesota and Wisconsin; Figure 12) and transition additional areas from unsuitable to suitable under the conservative threshold for RCP26 (Figure 14). Generally, temperate reptiles and amphibians may experience range expansions associated with warmer climates when dispersal limitations are not implicitly considered (Araújo et al. 2006). However, the predicted impacts on Eastern Massasauga appear to be mainly detrimental, and realistically it is highly unlikely Eastern Massasauga are capable of dispersal into new areas such as Minnesota (previously extirpated). Therefore, the more southerly populations throughout Illinois, Indiana, Ohio and Pennsylvania may require more intensive monitoring of demography and population health indicators than populations farther north. One potential adaptive advantage Eastern Massasauga may have over other sympatric ectotherms such as the threatened Blanding’s turtle (*Emydoidea blandingii*) is that it has been considered part of a species complex with the Western (*S. c. tergeminus*) and Desert Massasauga (*S. c. edwardsii*) that live in more arid environments. However, more recent genetic data suggest the Eastern Massasauga belongs in a separate clade by itself (Kubatko et al. 2011).

Broad scale applicability of this bioclimatic model may be limited because the data are likely biased towards conditions in Michigan where most populations occurred. Also, some parts of the range (e.g. western Pennsylvania) were not included in predicted
suitable areas for the present day model (Figure 12). As discussed in Chapters 2 and 4, environmental processes related to specific habitats (e.g. early successional grassland, fens, wet prairie) are the best predictors for delineating suitable habitat on a fine scale and optimal habitat structure and hydrological conditions likely trump climate for areas such as western Pennsylvania.

Despite a bias towards Michigan sites, the top predictor variables (precipitation of wettest and driest quarters) identified by the model corresponds well to the findings by Pomara et al. (2014) showing decreased adult survival associated with high drought risk in the winter and high flood risk in the summer. The model was based on average conditions associated with these two precipitation variables while Pomara et al. (2014) evaluated inter-annual variability to ascertain drought and flood risk. The precipitation means from the snake locations that inform the model reflect conditions amenable to snake persistence and increased fluctuations from these normal conditions year to year brought on by climate change are reducing survival rates.

Incorporating the predictions of climate change models into SDMs helped identify the most at risk populations of Eastern Massasauga. The southern populations are expected to experience the most drastic changes with important precipitation conditions shifting to levels outside what is observed throughout their range. The adaptive capacity of Eastern Massasauga to respond to these changes is unknown, underscoring the need for a formal monitoring program as climate change progresses.
References


Scozzafava, S., and A. De Sanctis. 2006. Exploring the effects of land abandonment on habitat structures and on habitat suitability for three passerine species in a highland area of Central Italy. Landscape and Urban Planning 75:23-33.


Appendix A: Tables and Figures

<table>
<thead>
<tr>
<th>Variable</th>
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</thead>
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<tr>
<td><strong>LiDAR</strong></td>
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<td><strong>Cropland Data Layer</strong></td>
<td>U.S. Department of Agriculture, National Agricultural Statistics Service</td>
</tr>
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</tr>
<tr>
<td><strong>June Greenness</strong></td>
<td>Derived from Landsat 5 <a href="http://glovis.usgs.gov">http://glovis.usgs.gov</a></td>
</tr>
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<td><strong>August Wetness</strong></td>
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</tr>
<tr>
<td><strong>May – October</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Wetness</strong></td>
<td></td>
</tr>
<tr>
<td><strong>May – October</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Greenness</strong></td>
<td></td>
</tr>
<tr>
<td><strong>May – August</strong></td>
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</tr>
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<td><strong>Greenness</strong></td>
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Table 1. Environmental variables used to create species distribution models for the Eastern Massasauga Rattlesnake in Ohio.
Table 2. Omission rates with the default Maxent regularization setting and in parentheses the average AUC scores across Maxent regularization settings (1.0–5.0) at four feature class combinations: linear (L), quadratic (Q), and hinge (H) for northeastern (NE) Ohio and full Ohio models at 1 km and 2 km minimum spacing between occurrence points.

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>LQ</th>
<th>H</th>
<th>LQH</th>
</tr>
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<td>1km NE OH</td>
<td>0.25</td>
<td>0.375</td>
<td>0.375</td>
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<tr>
<td>1km Full OH</td>
<td>0.125</td>
<td>0</td>
<td>0.125</td>
<td>0.25</td>
</tr>
<tr>
<td>2km NE OH</td>
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<td>0.5</td>
<td>0.667</td>
<td>0.667</td>
</tr>
<tr>
<td>2km Full OH</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 2. Omission rates with the default Maxent regularization setting and in parentheses the average AUC scores across Maxent regularization settings (1.0–5.0) at four feature class combinations: linear (L), quadratic (Q), and hinge (H) for northeastern (NE) Ohio and full Ohio models at 1 km and 2 km minimum spacing between occurrence points.
<table>
<thead>
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<td>S</td>
<td>S</td>
<td>G</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>G</td>
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<tr>
<td>Site 4</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>G</td>
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<tr>
<td>Site 5</td>
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<td>Site 6</td>
<td>P</td>
<td>P</td>
<td>G</td>
<td>G</td>
<td>P</td>
<td>G</td>
</tr>
<tr>
<td>Site 7</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td>Site 8</td>
<td>P</td>
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<td>A</td>
<td>A</td>
<td>A*</td>
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<td>G</td>
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<td>Site 10</td>
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<td>A</td>
<td>P</td>
<td>A</td>
<td>P*</td>
<td>S</td>
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</table>

Table 3. The state of land cover at ten contemporary Eastern Massasauga localities spanning 1938–2011. Observed land cover classes include agriculture (A), grassland (G), pasture (P), and shrubland (S). The shrubland classification was used for grassland areas consisting of >50% shrub or small trees. Both pasture and shrubland would have been classified as grassland in the historical analysis. They are separated here to provide more detailed information on the conditions present at each site over this historical time scale. The * indicates the land cover information was obtained from 1972 imagery. Sites 8–10 are located in Trumbull County which did not have 1979 imagery available.
<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>25.86</td>
<td>24.71</td>
<td>25.91</td>
<td>22.40</td>
<td>21.00</td>
<td>24.52</td>
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<tr>
<td>Agriculture</td>
<td>41.87</td>
<td>38.91</td>
<td>39.58</td>
<td>38.80</td>
<td>36.42</td>
<td>18.75</td>
</tr>
<tr>
<td>Forest</td>
<td>32.27</td>
<td>36.38</td>
<td>34.51</td>
<td>38.80</td>
<td>42.57</td>
<td>53.60</td>
</tr>
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</table>

Table 4. The proportion (%) of northeastern Ohio study area occupied by three land cover classes from 1938–2011.
<table>
<thead>
<tr>
<th>Time Period</th>
<th>Gains (% of total)</th>
<th>Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>From agriculture</td>
<td>From Forest</td>
</tr>
<tr>
<td>1938_50</td>
<td>11.30%</td>
<td>14.60%</td>
</tr>
<tr>
<td>1950_59</td>
<td>5.60%</td>
<td>22.20%</td>
</tr>
<tr>
<td>1959_66</td>
<td>13.60%</td>
<td>15.50%</td>
</tr>
<tr>
<td>1966_79</td>
<td>15.40%</td>
<td>30.80%</td>
</tr>
<tr>
<td>1979_2011</td>
<td>53.80%</td>
<td>18.80%</td>
</tr>
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</table>

Table 5. Estimated inter-period changes in grassland from 1938–2011. Gains refer to the proportion of grassland added during each time interval and whether those pixels transitioned from agriculture or forest. Losses represent the proportion of the previous grassland total that were a different land cover class by next recorded year.
<table>
<thead>
<tr>
<th>Year</th>
<th>Agriculture</th>
<th>Forest</th>
<th>Grassland</th>
<th>N</th>
<th>df</th>
<th>Kruskal-Wallis $\chi^2$</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>1,048</td>
<td>904</td>
<td>1,053</td>
<td>2000</td>
<td>2</td>
<td>30.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1950</td>
<td>1,040</td>
<td>893</td>
<td>1,101</td>
<td>2000</td>
<td>2</td>
<td>46.89</td>
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</tr>
<tr>
<td>1959</td>
<td>1,049</td>
<td>888</td>
<td>1,082</td>
<td>2000</td>
<td>2</td>
<td>46.46</td>
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</tr>
<tr>
<td>1966</td>
<td>1,033</td>
<td>881</td>
<td>1,159</td>
<td>2000</td>
<td>2</td>
<td>74.21</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1979</td>
<td>1,042</td>
<td>846</td>
<td>1,227</td>
<td>2000</td>
<td>2</td>
<td>138.7</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 6. Results from Kruskal-Wallis tests comparing median habitat suitability values from 2,000 random points distributed across three land cover types.
<table>
<thead>
<tr>
<th>Year</th>
<th>Agriculture (C)</th>
<th>Mean Rank</th>
<th>Agriculture (A)</th>
<th>Forest</th>
<th>Grassland</th>
<th>N</th>
<th>df</th>
<th>Kruskal-Wallis $\chi^2$</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>599</td>
<td>1,300</td>
<td>904</td>
<td>1,053</td>
<td>2000</td>
<td>3</td>
<td>321.4</td>
<td>&lt;0.001</td>
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<tr>
<td>1966</td>
<td>610</td>
<td>1,341</td>
<td>881</td>
<td>1,159</td>
<td>2000</td>
<td>3</td>
<td>389.7</td>
<td>&lt;0.001</td>
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<tr>
<td>1979</td>
<td>618</td>
<td>1,380</td>
<td>847</td>
<td>1,227</td>
<td>2000</td>
<td>3</td>
<td>465.4</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

Table 7. The results from Kruskal-Wallis tests comparing median habitat suitability values from 2,000 random points distributed across three land cover types. Agriculture was split into fields still currently being farmed (C) and fields that were abandoned (A) to transition to forest or grassland.
<table>
<thead>
<tr>
<th>Model</th>
<th>Log-likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ωAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>1966 + 1979</td>
<td>-6999.38</td>
<td>14008.79</td>
<td>0.00</td>
<td>0.53</td>
</tr>
<tr>
<td>1966 + 1979 1966*1979</td>
<td>-6995.56</td>
<td>14009.21</td>
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<td>0.43</td>
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<tr>
<td>1979</td>
<td>-7004.21</td>
<td>14014.43</td>
<td>5.65</td>
<td>0.03</td>
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<tr>
<td>1938 + 1979</td>
<td>-7004.08</td>
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<td>9.41</td>
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</tr>
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<td>1938 + 1979 1938*1979</td>
<td>-7003.44</td>
<td>14024.97</td>
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<tr>
<td>1966</td>
<td>-7097.94</td>
<td>14201.90</td>
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<td>1938</td>
<td>-7122.92</td>
<td>14251.85</td>
<td>243.07</td>
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Table 8. Model rankings for the generalized linear model analysis using three land cover classes (agriculture, forest, and grassland). Random points were generated across the study area and the associated land cover information from each point was extracted for each year (1938, 1966, and 1979) in addition to the current habitat suitability value and used to develop the model. The best supported model is shown in bold.
<table>
<thead>
<tr>
<th>Source</th>
<th>Wald chi-square</th>
<th>df</th>
<th>P value</th>
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<tr>
<td>(Intercept)</td>
<td>10788.28</td>
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<td>&lt;0.001</td>
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<tr>
<td>1966</td>
<td>9.49</td>
<td>2</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1979</td>
<td>194.25</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
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</table>

Table 9. Significance values associated with the 1966 and 1979 generalized linear model.
<table>
<thead>
<tr>
<th>Model</th>
<th>Log-likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ωAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>1966 + 1979 1966*1979</td>
<td>-6769.01</td>
<td>13564.20</td>
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<tr>
<td>1966 + 1979</td>
<td>-6776.85</td>
<td>13567.75</td>
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<td>1938 + 1979</td>
<td>-6779.37</td>
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<tr>
<td>1938 + 1979 1938*1979</td>
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<td>13576.80</td>
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<td>1966</td>
<td>-6885.25</td>
<td>13778.52</td>
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<td>1938</td>
<td>-6922.78</td>
<td>13853.59</td>
<td>289.39</td>
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Table 10. Model rankings for the generalized linear model analysis using four land cover classes (agriculture split into two, forest, and grassland). Random points were generated across the study area and the associated land cover information from each point was extracted for each year (1938, 1966, and 1979) in addition to the current habitat suitability value and used to develop the model. The best supported model is shown in bold.
<table>
<thead>
<tr>
<th>Source</th>
<th>Wald chi-square</th>
<th>df</th>
<th>P value</th>
</tr>
</thead>
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<td>(Intercept)</td>
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<td>&lt;0.001</td>
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<tr>
<td>1979</td>
<td>33.09</td>
<td>3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1966*1979</td>
<td>17.41</td>
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<td>&lt;0.01</td>
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Table 11. Significance values associated with the 1966 and 1979 generalized linear model that includes an interaction term.
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<tr>
<td><strong>Roughness</strong></td>
<td>DEM; Geomorphometry and Gradient Metrics Toolbox</td>
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<tr>
<td><strong>Canopy Cover (%)</strong></td>
<td>2011 National Land Cover Database</td>
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<td><strong>June Wetness</strong></td>
<td>Landsat 5</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td><strong>October Wetness</strong></td>
<td>Landsat 5</td>
</tr>
<tr>
<td></td>
<td><a href="http://glovis.usgs.gov">http://glovis.usgs.gov</a></td>
</tr>
</tbody>
</table>

Table 12. Environmental data layers used to create species distribution models for the Eastern Massasauga Rattlesnake in Ohio.
<table>
<thead>
<tr>
<th>Features</th>
<th>RM</th>
<th>Mean.AUC</th>
<th>Mean.OR10</th>
<th>AIC&lt;sub&gt;C&lt;/sub&gt;</th>
<th>delta.AIC&lt;sub&gt;C&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>1</td>
<td>0.83</td>
<td>0.15</td>
<td>1390.31</td>
<td>25.48</td>
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<td>LQ</td>
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<td>0.86</td>
<td>0.17</td>
<td>1364.82</td>
<td>0.00</td>
</tr>
<tr>
<td>H</td>
<td>1</td>
<td>0.84</td>
<td>0.25</td>
<td>1512.01</td>
<td>147.19</td>
</tr>
<tr>
<td>L</td>
<td>2</td>
<td>0.82</td>
<td>0.15</td>
<td>1390.66</td>
<td>25.83</td>
</tr>
<tr>
<td>LQ</td>
<td>2</td>
<td>0.86</td>
<td>0.15</td>
<td>1370.49</td>
<td>5.67</td>
</tr>
<tr>
<td>H</td>
<td>2</td>
<td>0.83</td>
<td>0.22</td>
<td>1401.19</td>
<td>36.37</td>
</tr>
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Table 13. Maxent model settings and ranking statistics (top model based on AIC<sub>C</sub> in bold) from the ENMeval R package: Features-linear (L), quadratic (Q), and hinge (H), RM-regularization multiplier, Mean.AUC-mean Area Under the Curve score across model iterations, Mean.OR10-mean 10% training omission rate across model iterations, AIC<sub>C</sub>-Akaike information criterion corrected for small sample size, delta.AIC<sub>C</sub>-change in AIC<sub>C</sub> from the top ranked model.
<table>
<thead>
<tr>
<th>Distribution Change</th>
<th>Proportion of Eastern Massasauga’s Range</th>
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<tr>
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<tr>
<td>Contraction</td>
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Table 14. The predicted change (%) in the Eastern Massasauga’s distribution associated with the average values from three global climate models under less severe (RCP26) or more severe (RCP85) scenarios. The permissive threshold was the minimum training presence from Maxent, which includes more suitable habitat in the binary map for present day and future conditions. The conservative threshold was the maximum sum of sensitivity and specificity which limits the amount of habitat identified as suitable for present day and future conditions.
Figure 1. Omission rates (ORs) for four feature classes from the four model types representing northeastern Ohio and full Ohio datasets. The ORs were calculated across the range of regularization multipliers employed (1.0-5.0). The box plots show the median, first and third quartiles, and outliers for each feature class across this range.
Figure 2. Habitat suitability maps for the top performing model (lowest omission rate) from each of the four model types including: (A) Full Ohio 1km LQ feature classes at the default regularization (LQ:1.0); (B) Full Ohio 2km LQ:1.0; (C) Northeastern Ohio 1km L:2.0; and (D) Northeastern Ohio H:2.0. See text for explanation of model names.
Figure 3. Historical land cover composition of present day suitable habitat patches for the Eastern Massasauga in the northeastern Ohio study area. Each year shows the proportional makeup of current habitat patches by the three land cover types.
Figure 4. Michigan distribution of Eastern Massasauga.
Figure 5. An example of a Massasauga habitat core partially contained within a protected area. Portions of the core within the protected area are blue and portions outside are red.
Figure 6. Circuitscape movement corridors between Eastern Massasauga locations (white circles). The two narrower corridors in yellow indicate the location of pinchpoints, where paths for movement are more limited.
Figure 7. Circuitscape movement corridors between Eastern Massasauga habitat cores (black areas). The two narrower corridors in yellow indicate the location of pinchpoints, where paths for movement are more limited.
Figure 8. The topographic position index layer showing relative valleys in blue and peaks in red. The Eastern Massasauga locations represented by the dots are associated with the valley areas.
Figure 9. Pinchpoint located across road showing a narrow corridor for movement across this potential barrier. An Eastern Massasauga location is represented by the white circle.
Figure 10. Illustration of least cost paths (LCPs) based on three resistance layers (blue-CCAP, purple-class weighted HSM, and black-standard HSM). These LCPs connect the snake locality (white circle) to another locality located >1 km away. Note the problematic route taken by the standard HSM (black line) across the water body.
Figure 11. The states and province comprising the known distribution of the Eastern Massasauga. Approximate location data used in the species distribution model shown in red. Actual location data are not shown due to concerns over illegal collecting.
Figure 12. Suitability maps showing current conditions (A) and future conditions for less severe RCP26 (B) and more severe RCP85 (C) predicted climate change scenarios. Warmer colors indicate higher suitability.
Figure 13. Binary maps of suitable (green) and unsuitable (purple) areas for future conditions from the minimum training presence threshold RCP 26 (A) and RCP 85 (C) and the maximum sum of sensitivity and specificity threshold RCP 26 (B) and RCP 85 (D).
Figure 14. Maps showing changes from the present day for minimum training presence threshold RCP 26 (A) and RCP 85 (C) and the maximum sum of sensitivity and specificity threshold RCP 26 (B) and RCP 85 (D). The four possible range related changes are: blue - remains suitable, gray - remains unsuitable, red - range contraction, and green - range expansion.
## Appendix B: Ohio Species Distribution Model Maxent Output

<table>
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<tr>
<th></th>
<th>NE Reg 1 L</th>
<th>NE Reg 1 LQ</th>
<th>NE Reg 1 LQH</th>
<th>NE Reg 1 H</th>
<th>NE Reg 2 L</th>
<th>NE Reg 2 LQ</th>
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</thead>
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<td>0.93</td>
<td>0.93</td>
<td>0.94</td>
<td>0.91</td>
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<tr>
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<tr>
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Table 15. Ohio Maxent results showing the distribution of values (AUC-area under the ROC curve; OR-omission rate) for both the 1 km and 2 km filtered points and all regularization values (continued).
Table 15: Continued

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(Continued)
Table 15: Continued

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