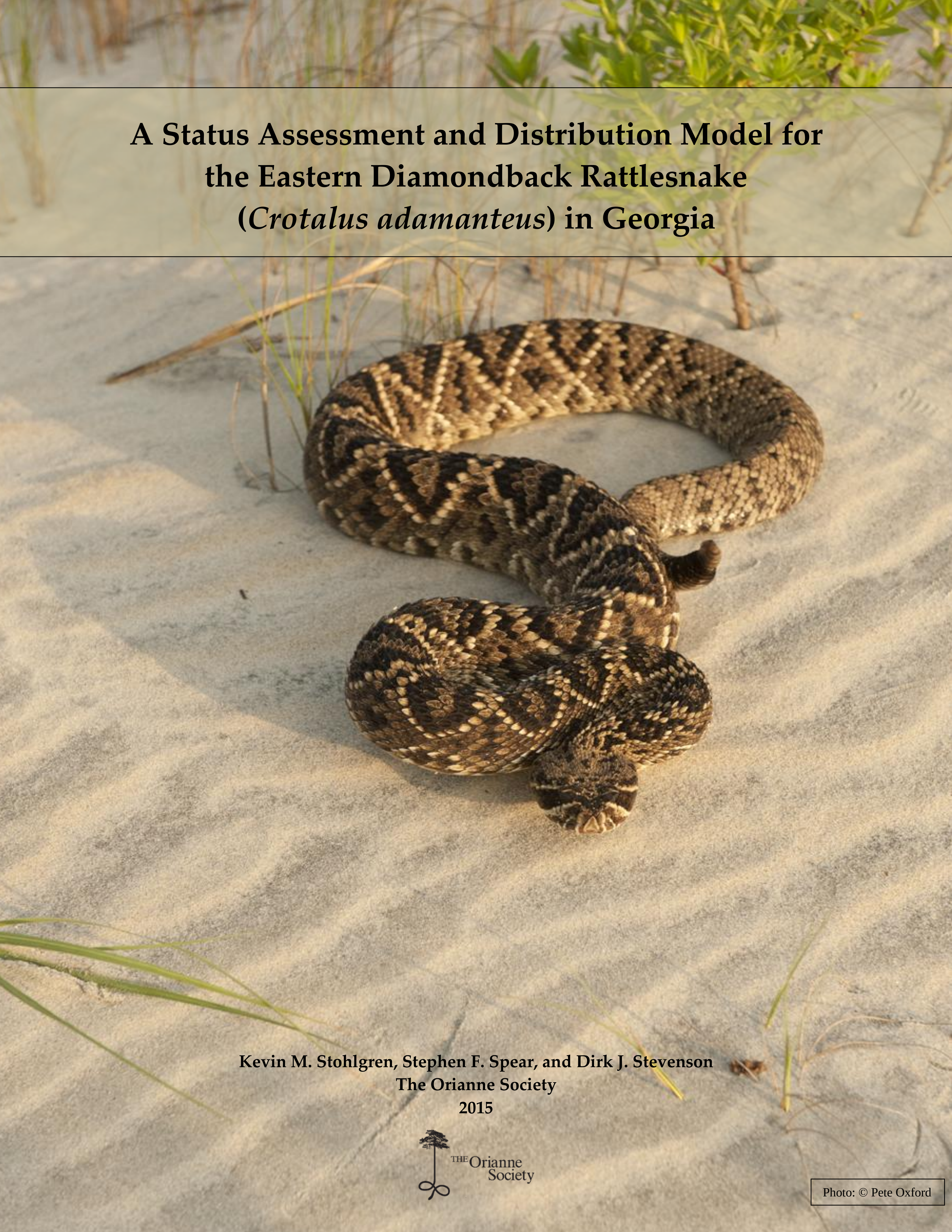
A Status Assessment and Distribution Model for the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) in Georgia



Kevin M. Stohlgren, Stephen F. Spear, and Dirk J. Stevenson
The Orianne Society
2015

THE Orianne Society

Photo: © Pete Oxford

Contents

List of Figures

List of Tables

Executive Summary

Suspected population declines of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) populations led to a petition to list the species under the Endangered Species Act, and the status of the species is currently being reviewed by the U.S. Fish and Wildlife Service. To help address this conservation issue, we collected recent (2000–2015) occurrence records for Georgia, and used these to develop a distribution model for the state. We compiled 381 *C. adamanteus* records for 2000–2015, using 299 of these points to develop a MaxEnt model.

The *C. adamanteus* records that we compiled for 2000-2015 were widely distributed throughout the Coastal Plain, including records for 55 of the 64 counties from which the species has historically been documented. Our model corroborated this, predicting suitable habitat across most of the Coastal Plain. However, predicted suitable habitat was not extensive, indicating that while *C. adamanteus* populations may still be widespread in the state, apparently they are restricted to certain habitat conditions. Our results indicate that the southern third of Georgia remains a notable population stronghold for *C. adamanteus*, with significant, extant rattlesnake populations associated with the quail plantations located in the southcentral and southwestern part of the state, uplands within the Altamaha River Drainage, and the barrier islands and coastal strand regions.

Our descriptive statistics and the jackknife analysis showed that *C. adamanteus* populations are associated with evergreen forest and avoid urban areas and deciduous forests. These results are consistent with habitat descriptions provided in the literature. Less than 14% of the Coastal Plain of Georgia was predicted to have a habitat suitability of 0.5-1.0, but almost 40% of that area occurs on properties that are currently under some level of protection. Conservation efforts for *C. adamanteus* should focus on increasing the amount of suitable habitat available and appropriately managing this habitat (e.g., prescribed fire) to maintain the open-canopied conditions preferred by the species.

Introduction

The Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) is native to the Coastal Plain of the southeastern United States, ranging from eastern Louisiana to southeastern North Carolina, south through all of Florida (Martin and Means 2000). The species occupies open-canopied habitats such as longleaf pine (*Pinus palustris*) ecosystems, which are among the most imperiled habitats globally (Noss et al. 1995; Outcalt and Sheffield 1996; U.S. Fish and Wildlife Service 2003). Loss of habitat, along with the threats of road mortality and human persecution, has led to declines in *C. adamanteus* populations throughout the species' range (Timmerman 1995; Martin and Means 2000; Timmerman and Martin 2003). The declines in *C. adamanteus* populations led to a petition (2011) to list the species under the Endangered Species Act, and the status of the species is currently being reviewed by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2012).

In order to make appropriate conservation decisions, we need the best information available pertaining to the current status of *C. adamanteus*; however, the secretive nature of this species makes it difficult to assess population levels and trends. Species distribution models provide a way to identify suitable areas for a species of interest, and can be developed from a range of data types, such as presence/absence, or presence only data (Anderson and Martinez-Meyer 2004; Phillips et al. 2009; Cianfrani et al. 2010). Species distribution models can be used to initiate status assessments and conservation efforts for rare and declining species, and the ability to use a range of data types makes it useful when other methods of population assessment are not possible (Anderson and Martinez-Meyer 2004; Santos et al. 2009).

One of the most common distribution modeling methods is maximum entropy. Maximum entropy modeling develops spatially explicit models by estimating the probability distribution for a species by finding the distribution that is closest to uniform (Phillips et al. 2004, Phillips et al. 2006). Maximum entropy models utilize presence data and a set of environmental layers to develop a model that reflects the probability that the environmental conditions are suitable to the species to occur there. The output can be used to identify the amount of habitat available to a species and locate sites to conduct targeted surveys (Phillips et al. 2004; Phillips et al. 2006)

The goal of this study is to assess the potential status and distribution of *C. adamanteus* in Georgia by: 1) collecting recent occurrence records for the species, and; 2) using these records to develop a species distribution model. This model output can be used to predicts the current distribution of the snake and identify regions/sites where the species may occur but has not recently or historically been documented.

Methods

Study Area

In Georgia, the historic range of *C. adamanteus* is limited to the Coastal Plain physiographic region. In southwestern Georgia, the known range of *C. adamanteus* essentially includes all of the Coastal Plain, including the Fall Line sandhills region; in southeastern Georgia, the species is known from as far north as Dodge and Burke counties, but has never been documented from the uppermost Coastal Plain counties or the Fall Line in this region. Even so, for the purposes of this assessment, we defined our study area as the entirety of the Georgia Coastal Plain region using a Physiographic Provinces layer in ArcGIS. (Figure 1).

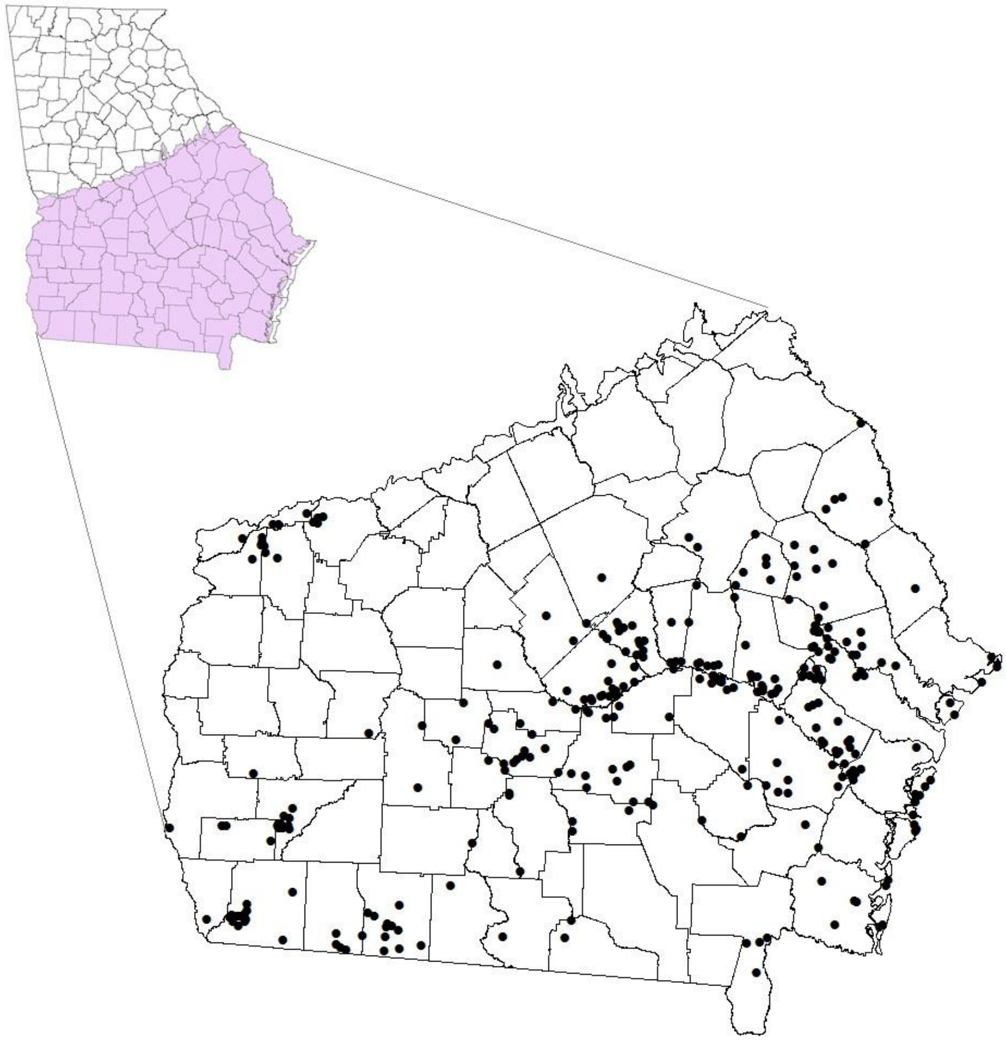


Figure 1: *Crotalus adamanteus* records from 2000-2015 used to generate a MaxEnt habitat suitability model.

Species Occurrence Data

We compiled *C. adamanteus* records for the period 2000-2015 from several sources including: 1) our own records (including incidental field observations and observations from road-cruising and visual encounter surveys); 2) an on-line observation request wherein we solicited records from Orianne Society members and the general public; 3) the Georgia Department of Natural Resources (GADNR) Biotics Database, and; 4-5) from two citizen science databases: HerpMapper and the Herpetological Education and Research Project (HERP). These records included snake sightings supported by photographs, records based on what we determined were credible observations, and records based on museum specimens. For analysis, we only used records that had GPS coordinates or precise locations that allowed us to accurately map the record.

In order to ensure that our models reflected current habitat conditions, we only included records from 2000–2015. Due to a dynamic landscape, using older records may cause the model to identify habitat that in fact is no longer present. To address spatial autocorrelation, we used the program SDMtoolbox (ver1.1c; Brown J. L. 2014) to filter points that were within 1 km of each other so that only 1 of those points remained.

Data Layers

We reviewed the literature and used expert opinion to select habitat variables to develop preliminary descriptive statistics and our MaxEnt model. These variables included land cover, canopy cover, impervious surface, and soils. All environmental layers were resampled to 30 m cell size and clipped to the extent of our study area.

To examine *C. adamanteus* habitat use, we ran a neighborhood analysis using the focal statistics tool in ArcGIS. We used a circular buffer with a radius of 17 cells, an area of approximately 82 ha, which we used to represent an average home range for *C. adamanteus* based on the current literature (Means 1985; Kain 1995; Timmerman 1995; Waldron et al. 2006; Hoss et al. 2010). The resulting habitat variable layers represented the percentage of each variable within the buffer centered on each pixel.

Land Cover

We utilized the 2008 Georgia Land Use Trends (GLUT) land cover map (Figure 2). We reclassified the land cover layer from 13 classes into 8 classes that are biologically relevant to *C. adamanteus*. We combined open water, forested wetland, non-forested salt/brackish wetland, and non-forested freshwater wetland classes into an all water land cover class. We also combined low and high intensity urban into an all urban class, and we combined quarries/strip mines/rock outcrops with the clearcut/sparse land cover class. We then split each land cover type into its own layer where cells of that land cover type equal 1 and all other cells equal 0. This resulted in eight total land cover layers, each representing a single land cover class. This step allowed us to run the neighborhood analysis on each land cover class.

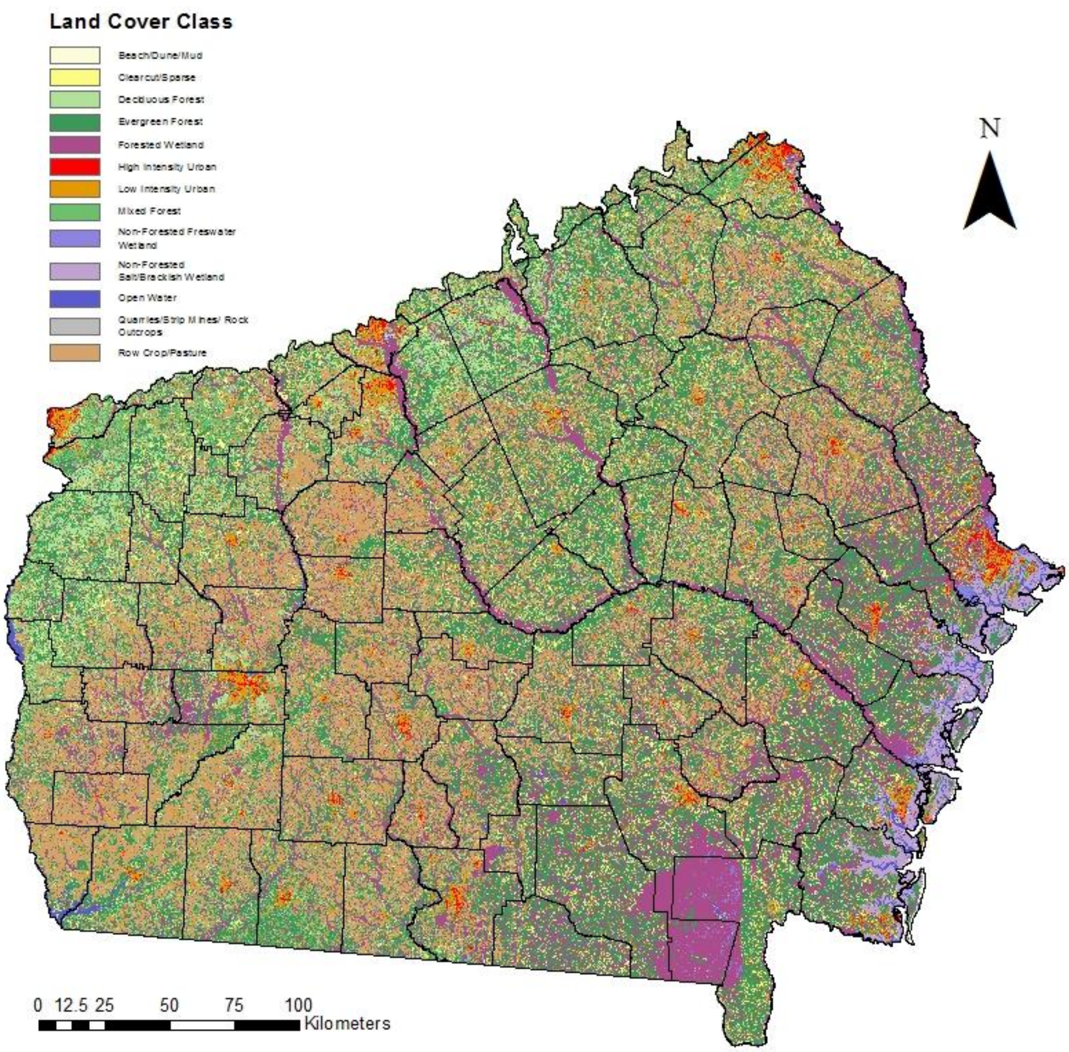


Figure 2: Georgia Land Use Trends (GLUT) land cover classifications (from 2008) for our study area.

Soils

Crotalus adamanteus is associated with sandy, well drained soils. We incorporated the Gridded Soil Survey Geographic Database (gSSURGO) data for the percent of sand (Figure 3) and the percent of clay (Figure 4) for out study area.

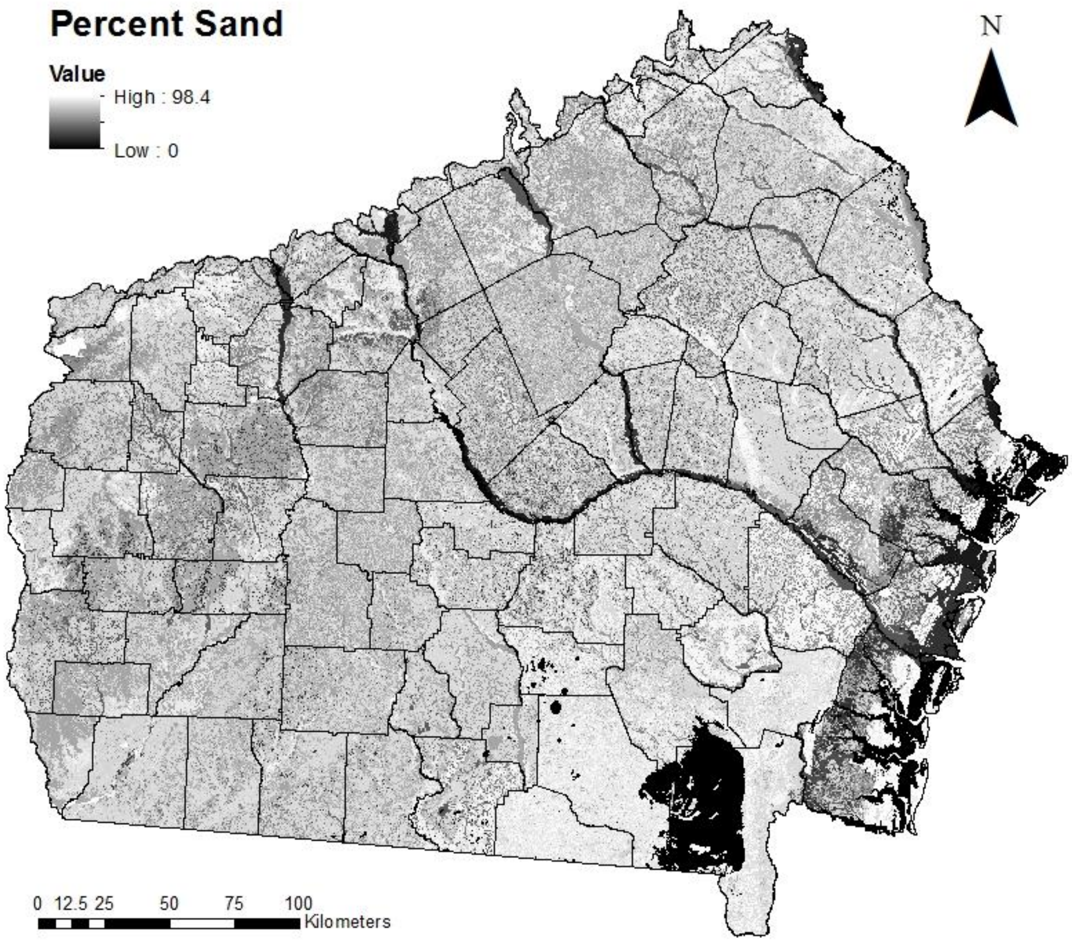


Figure 3: Gridded Soil Survey Geographis (gSSURGO) Database percent sand (from 2014) for our study area.

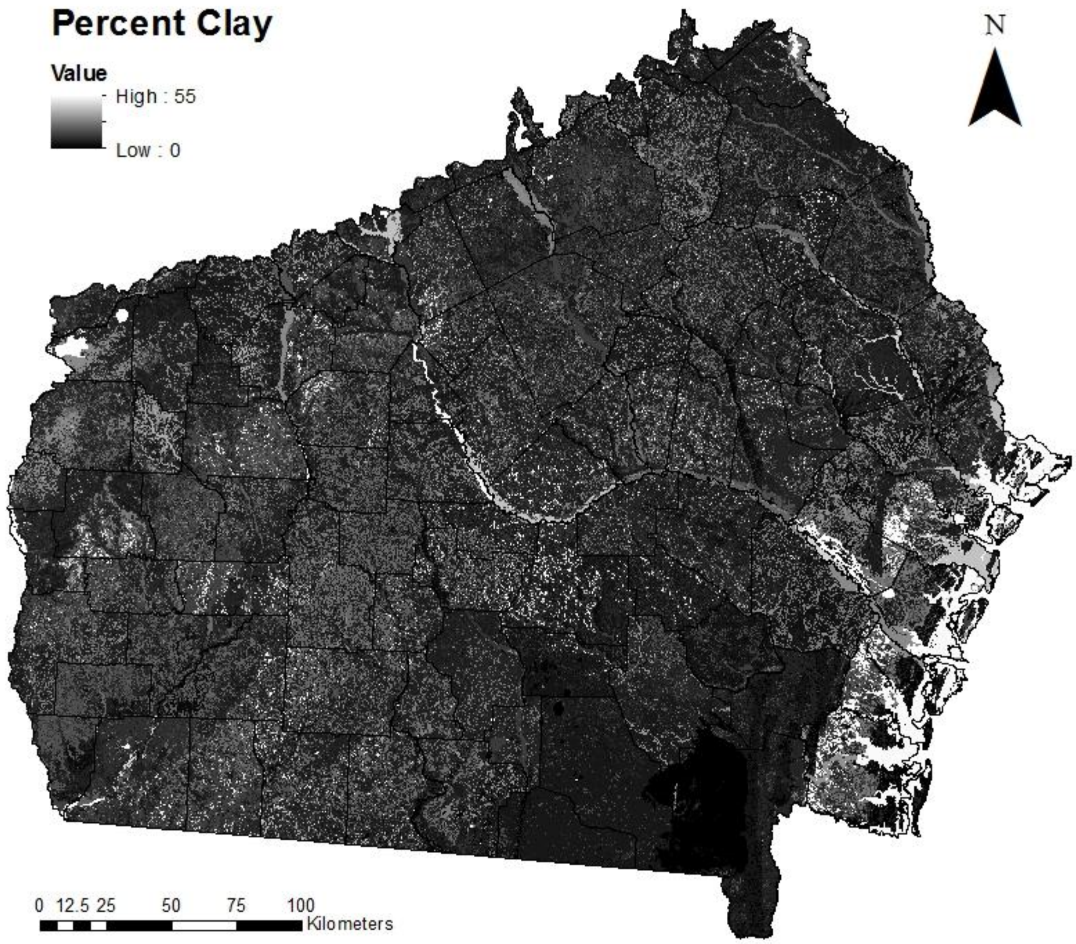


Figure 4: Gridded Soil Survey Geographis (gSSURGO) Database percent clay (from 2014) for our study area.

Canopy Cover

C. adamanteus is typically associated with open-canopied habitats. We utilized the 2008 GLUT canopy cover layer to account for this in our Maxent model (Figure 5).

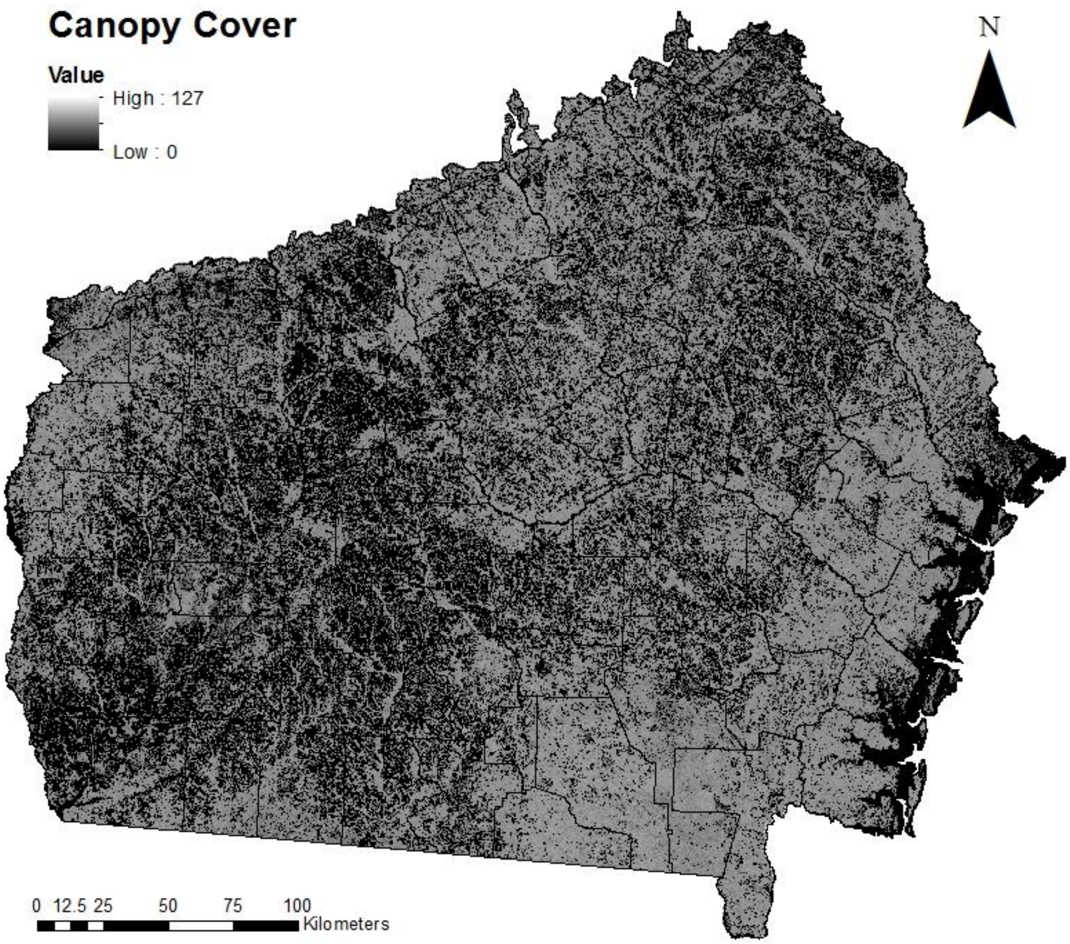


Figure 5: Georgia Land Use Trends (GLUT) canopy cover (from 2008) for our study area.

Impervious Surface

Impervious surface layers indicate areas of development as well as roads which are thought to have negative impacts on *C. adamanteus* populations. We incorporated the 2008 GLUT impervious surface cover layer into our Maxent model (Figure 6).

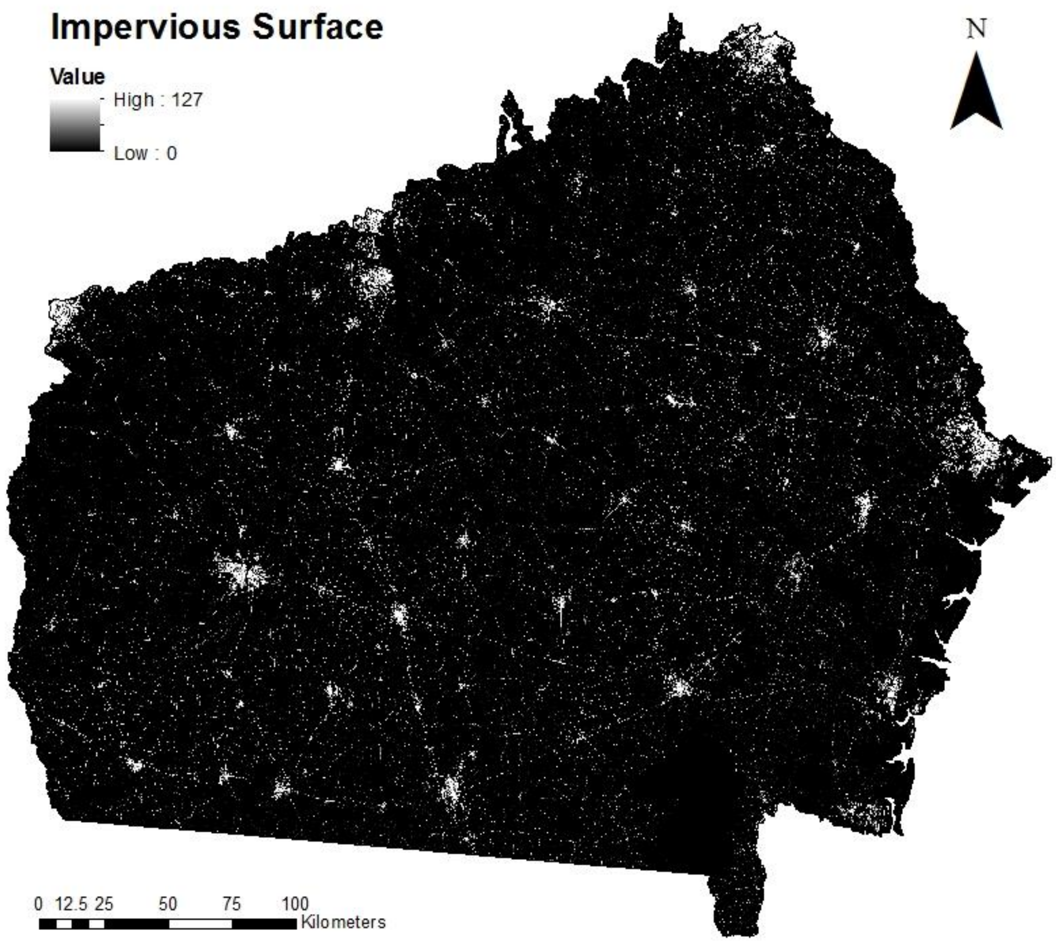


Figure 6: Georgia Land Use Trends (GLUT) impervious surface (from 2008) for our study area.

Descriptive Statistics

Before running our model, we developed descriptive statistics for our data to examine the importance of each land cover class for *C. adamanteus*. We extracted the values of each land cover layer to each record used in our analysis, and plotted them on a graph with confidence intervals. The graphs examine the percentage of each land cover class within an individual snake's home range relative to the availability of each class on the landscape.

Species Distribution Modeling

We used the program MaxEnt (version 3.3.3; Phillips et al. 2004, Phillips et al. 2006) to develop our maximum entropy model of distribution probability for *C. adamanteus* in the Coastal Plain of Georgia. Our occurrence data were input into MaxEnt as training data, along with the associated habitat variables, and 10,000 points randomly generated by MaxEnt to serve as background or pseudo-absence data. We ran a 10-fold cross-validation where the occurrence data are randomly partitioned into subsamples and the model is run 10 times, with each of the partitioned groups being withheld once to be used as validation data. This ensures that all of the occurrence points are used in both training and validation. These results are then averaged to produce a single probability model.

Model Evaluation

We used a jackknife analysis to evaluate the importance of habitat variables in explaining habitat suitability for *C. adamanteus* in the model. A receiver operating characteristic (ROC) plot and the associated area under the curve (AUC) was used to assess the accuracy of the output model.

To quantify the area of the predicted distribution, we reclassified the output based on the maximum training sensitivity plus specificity threshold output by MaxEnt (Lui et al. 2013). We examined the percentage of the predicted distribution on the landscape as well as the amount that is within currently protected areas within the state (categorized as private, federal, or state/local; The University of Georgia Natural Resources Spatial Analysis Lab and the Georgia Department of Natural Resources).

Results

Species Occurrence Data

We compiled a total of 381 records for 2000–2015, including records from 55 Georgia counties (Appendix 1). The spatial filtering process removed 82 records that were within 1 km of the nearest record. This left a total of 299 points that were used in our MaxEnt model (Figure 1).

Descriptive Statistics

The descriptive statistics show that *C. adamanteus* appear to be preferentially using evergreen forest with an average of 36.42% for our *C. adamanteus* records compared to 7.88% available on the landscape (Figure 7). The descriptive statistics also show an avoidance of deciduous forest, urban areas, and clearcut/sparse areas.

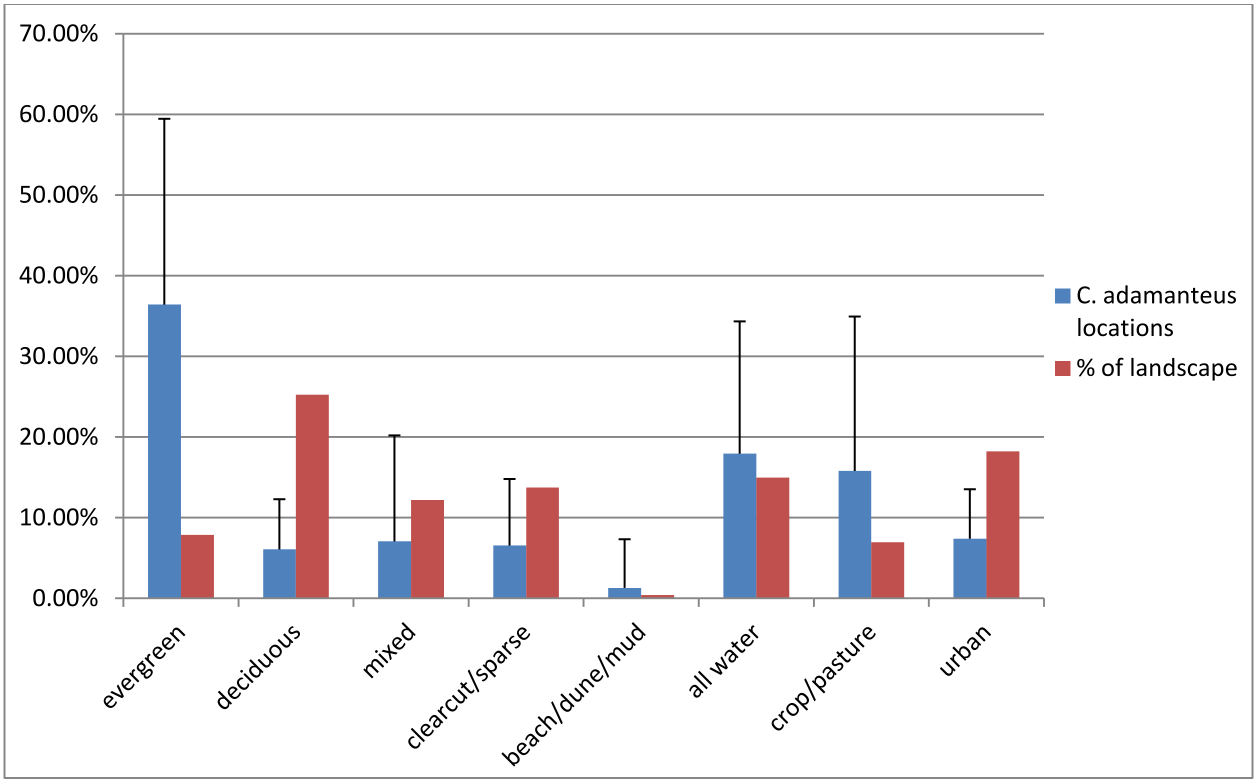


Figure 7: Land cover associations for *Crotalus adamanteus* compared to the availability on the landscape (% of landscape).

Maxent Model

The model had an average AUC value of 0.774 (Figure 8) with probability values ranging from 0.00-0.99 (Figure 9). The reclassified model output (Figure 10) indicated that predicted distribution (0.3789-1.0) comprised 24.51% of the total study area and 9.77% of conservation lands (Table 1).

The jacknife analysis indicated that urban land cover had the highest probability of explaining *C. adamanteus* distribution (Figure 11). Urban land cover also had the highest permutation importance to our model, followed by crop/pasture, and percent sand (Table 2). The response curves indicated the association with urban was positive at low levels, but then becomes negative at higher levels (Figure 12). The association with crop/pasture land cover was also negative (Figure 13) while the association with percent sand was positive (Figure 14).

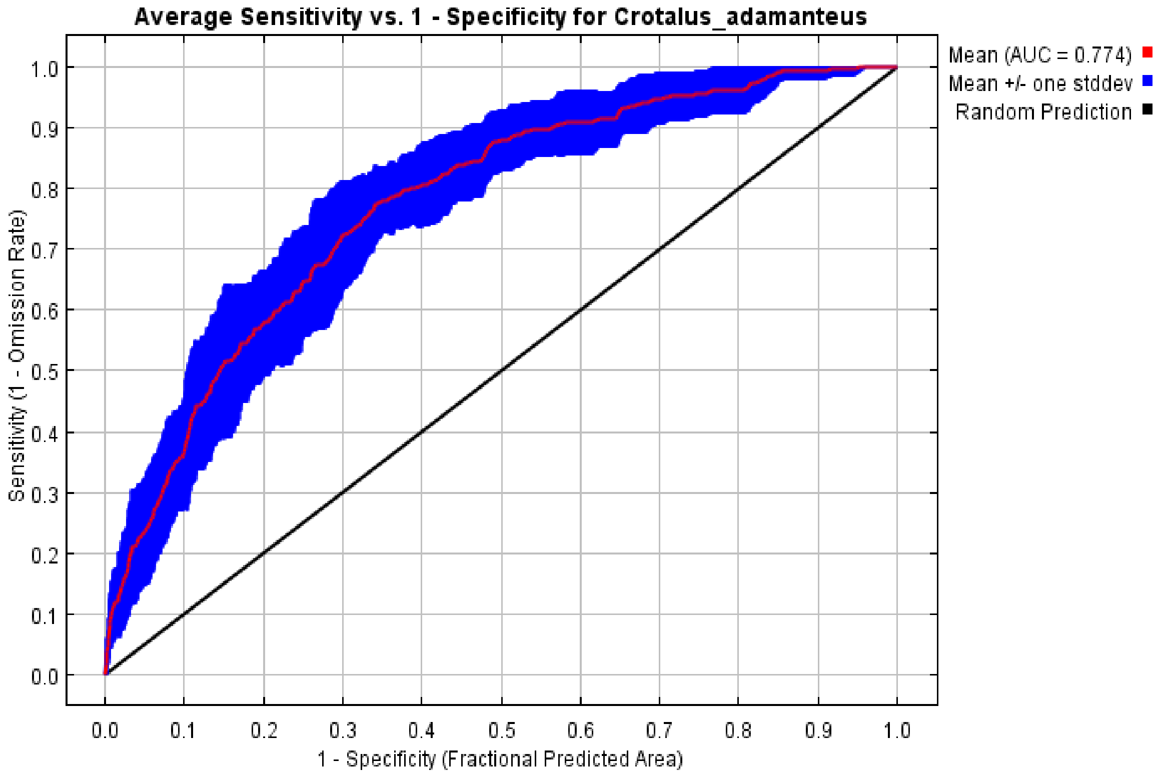


Figure 8: Receiver Operating Characteristic (ROC) plot and the associated Area Under the Curve (AUC) for our 10-fold cross-validation MaxEnt distribution model.

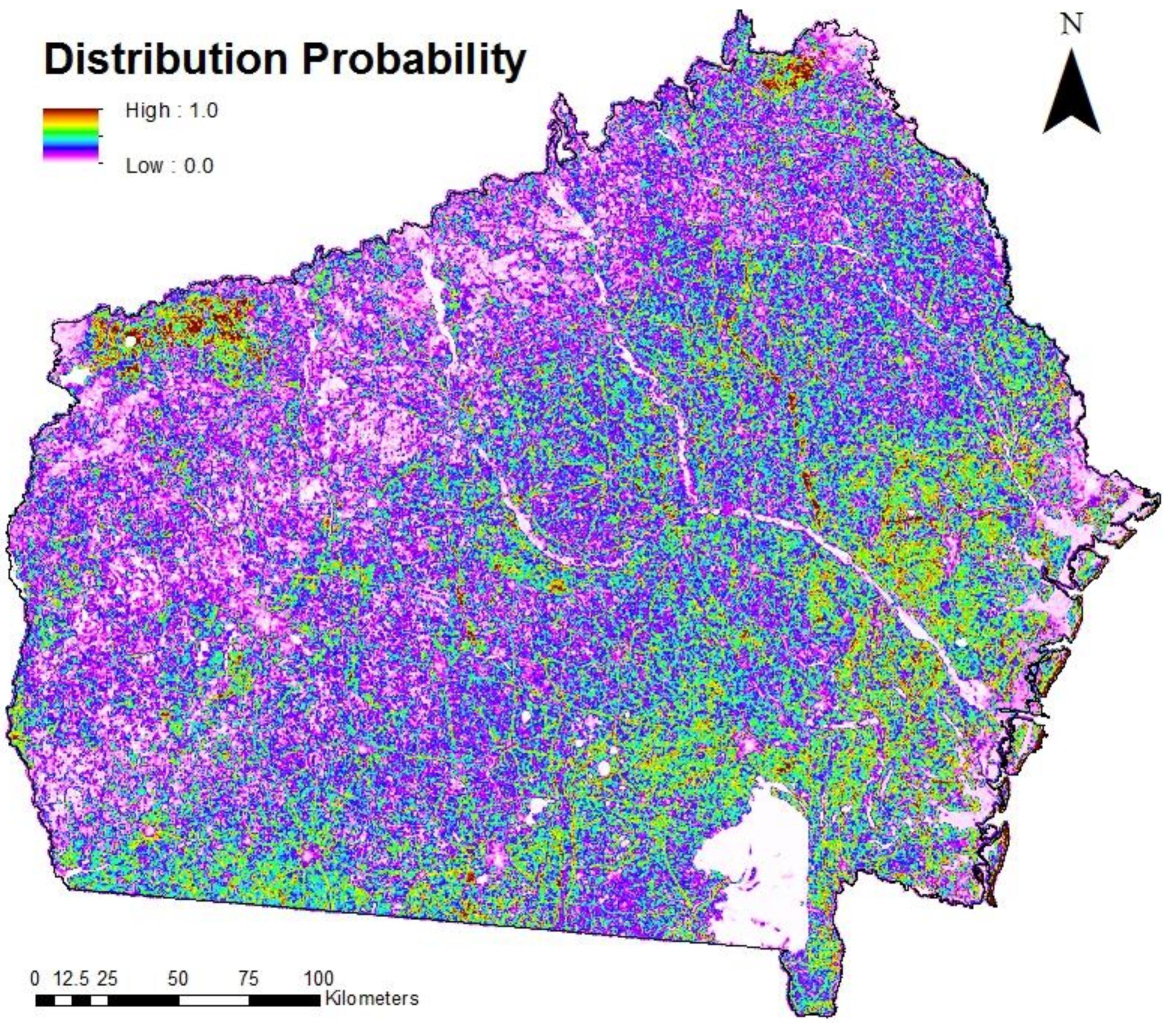


Figure 9: 10-fold cross validation MaxEnt distribution model showing the distribution probability for *Crotalus adamanteus* in our study area.

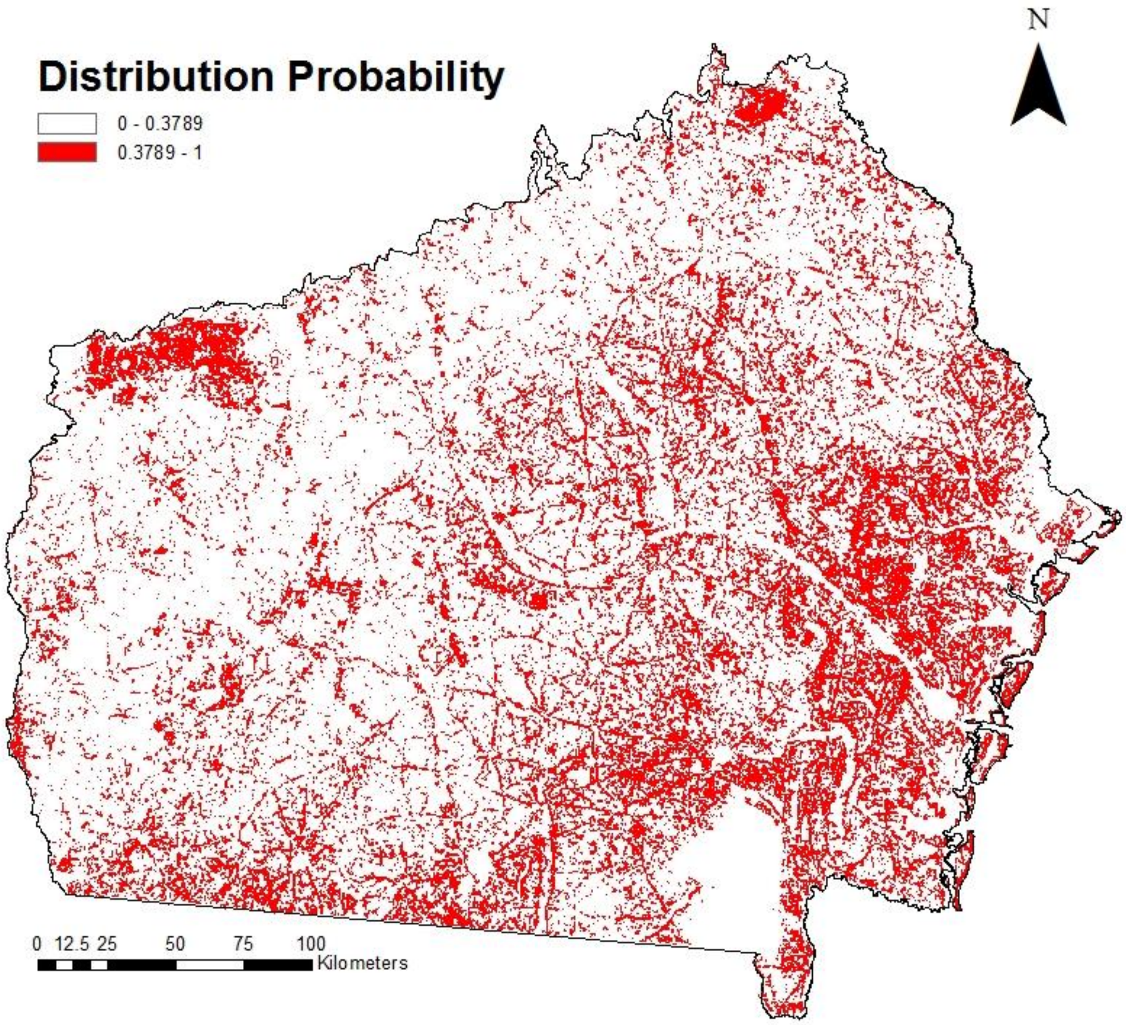


Figure 10: 10-fold cross-validation MaxEnt distribution model showing the distribution probability for *Crotalus adamanteus* in our study area reclassifed based on the maximum training sensitivity plus specificity threshold.

Table 1: Area and percentage of landscape in each of the four prediction classes of relative habitat suitability for *Crotalus adamanteus* in our study area.

Distribution	Area (ha) within Coastal Plain	% of landscape	Area (ha) within conservation lands	% of conservation lands	% of suitable in conservation lands
Not Predicted	7052536	75.49%	546535	70.95%	
Predicted	2289439	24.51%	223779	29.05%	9.77%
Totals	**9,341,974**	**100.00%**	**770,315**	**100.00%**	

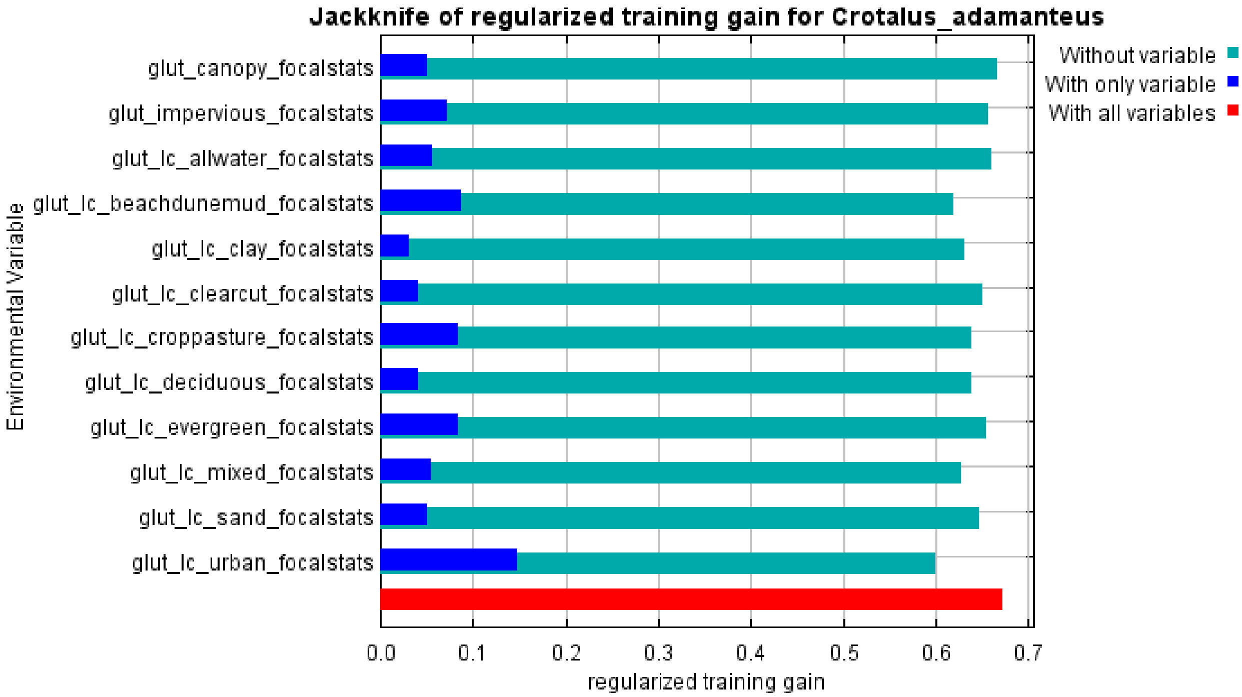


Figure 11: Jackknife analysis of regularized training gain for our 10-fold cross-validation MaxEnt distribution model for *Crotalus adamanteus*.

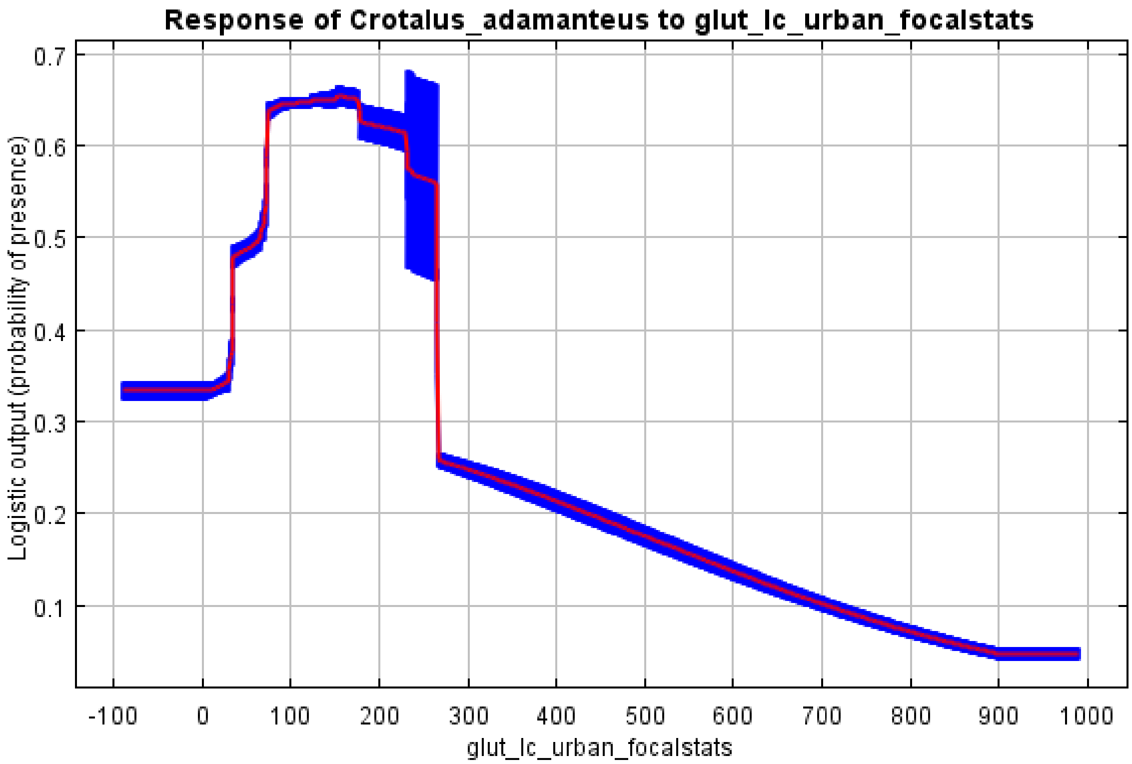


Figure 12: Response curve for Urban land cover in our 10-fold cross-validation MaxEnt model when only that variable was considered.

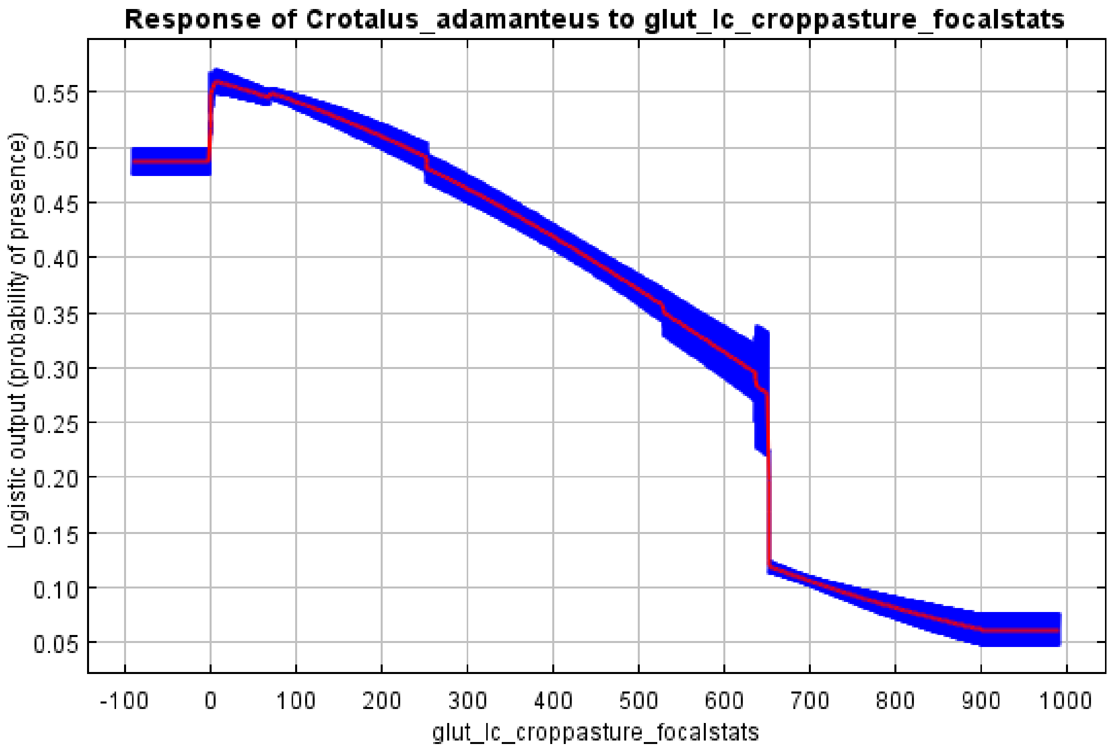


Figure 13: Response curve for crop/pasture land cover in our 10-fold cross-validation MaxEnt model when only that variable was considered.

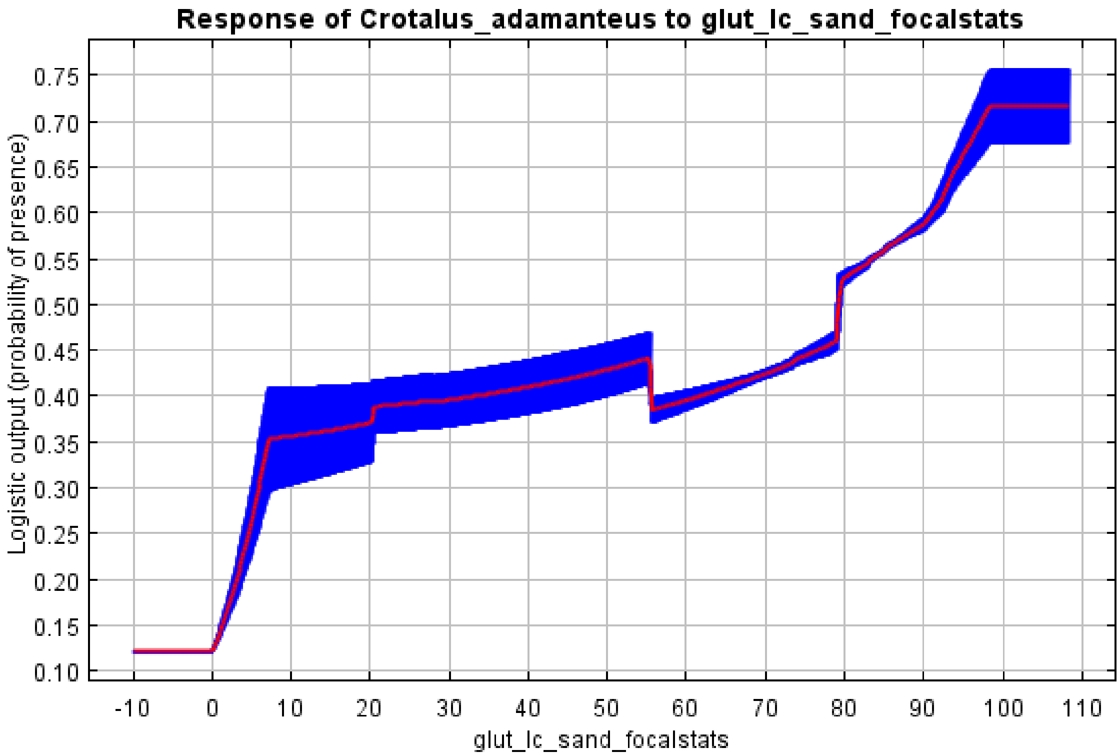


Figure 14: Response curve for the percent sand variable in our 10-fold cross-validation MaxEnt model when only that variable was considered

Table 2: Variable contribution for our 10-fold cross-validation MaxEnt distribution model for *Crotalus adamanteus*. Percent contribution reflects the order in which variables were introduced to the model. Permutation importance reflects the importance of each variable when all permutations are considered.

Variable	Percent Contribution	Permutation Importance
Urban	27.5	26
Crop/Pasture	13.9	13.1
Beach/Dune/Mud	12.1	3.5
Deciduous	8.6	8.3
Evergreen	8.3	5.1
Mixed	8.3	7.1
All Water	5.8	6.7
Clearcut/Sparse	4	4.6
% Sand	3.3	9.1
% Clay	3.1	8.5
Impervious Surface	3.1	5.8
Canopy Cover	2	2.1

Discussion

The Georgia *Crotalus adamanteus* records that we compiled for 2000-2015 were widely distributed throughout the Coastal Plain, including records for 55 of the 64 counties from which the species has historically been documented (Appendix 1, Figure 1). Essentially, this is corroborated by our MaxEnt model output which predicted rattlesnake populations distributed across most of the Coastal Plain. However, predicted suitable habitat was not extensive, indicating that while *C. adamanteus* populations may still be widespread in the state, apparently they are restricted to certain conditions (e.g., undeveloped or lightly developed regions). The southern third of Georgia has long been considered a notable population stronghold for *C. adamanteus* (see Martin and Means 2000), with significant rattlesnake populations associated with: a) the quail plantations located in the southcentral and southwestern part of the state; b) uplands within the Altamaha River Drainage; c) the barrier islands and coastal strand regions. Our results highlight that these regions still contain large expanses of habitat with environmentally suitable conditions. Considering this and the numerous recent records that we complied for these areas, we believe this area should still be considered a stronghold for the species.

Our descriptive statistics showed that *C. adamanteus* populations are associated with evergreen forest and avoid urban areas and deciduous forests. Our jackknife analysis also indicated a negative association with urban land cover. These results are consistent with habitat descriptions provided in the literature (Martin and Means 2000; Waldron et al. 2006; Waldron et al. 2008; Hoss et al. 2010). It is noteworthy that while many of the inland *C. adamanteus* records compiled by this study are from sites that include intact longleaf pine–wiregrass landscapes, we also obtained a large number of recent sightings from unintact (i.e., no longer a longleaf pine-dominated canopy), disturbed, fragmented, ruderal and/or fire-suppressed sites (e.g., pine plantations, oldfield communities, xeric oak hammocks) where habitat conditions for the species might qualitatively be described as marginal-to-poor. Most of the top variables in our model were also variables that restrict *C. adamanteus*, suggesting that the species may be somewhat of an upland habitat generalist under natural conditions—but a species that does not fare well around human development.

Our distribution model indicated that the Fall Line sandhills area in west central Georgia (Marion, Talbot, and Taylor counties) has a large area of high suitability. This area appears to be disjunct and possibly isolated from other suitable habitat located in this portion of the state. Previous investigators also remarked that this population is essentially disjunct and moreover may have been so historically (Martin and Means 2000). There is an area along the Fall Line in eastern Georgia around Augusta and Fort Gordon that appears to have the environmental conditions associated with occurrence, but *C. adamanteus* has never been known to occur in this part of Georgia. This area is either too isolated for *C. adamanteus* to have established the area, or there is an environmental variable (e.g., temperature) that would exclude them from the area that was not included in our model.

MaxEnt assumes that sampling of presence locations is unbiased and representative of the species distribution as bias in sampling effort can reduce model accuracy (Phillips et al. 2006). We attempted to acquire records throughout the Coastal Plain, but our sampling is likely biased towards areas that biologist frequent, such as state and federal lands, as well as areas along roads. We attempted to reduce clustering of points resulting from increased survey effort by filtering out points that were in close proximity (within 1 km). We recommend future survey efforts in areas where current records (post-2000) for *C. adamanteus* are lacking to ensure that this is not due to a disparity in survey effort.

While approximately 25% of the Coastal Plain of Georgia was identified by our model as potential distribution for *C. adamanteus*, only about 10% of that area occurs on properties that are currently under some level of protection. Conservation efforts for *C. adamanteus* should focus on increasing the amount of suitable habitat available as well as protecting and restoring habitat throughout the Coastal Plain. Upland pine forests and other suitable *C. adamanteus* habitats are maintained through frequent fire and the removal of fire from these communities has resulted in the expansion of hardwood-dominated forests. Habitat management involving prescribed fire, removal of hardwood trees from upland habitats, and the planting of longleaf pine and native ground cover would greatly benefit *C. adamanteus* in Georgia. Proper habitat management offers the possibility of reversing species declines without the need for more expensive measures such as translocations or reintroductions. These management recommendations will also benefit other rare and declining longleaf ecosystem species such as the Eastern Indigo Snake (*Drymarchon couperi*), Gopher Tortoise (*Gopherus polyphemus*), Southern Hognose Snake (*Heterodon simus*), Pine Snake (*Pituophis melanoleucus*), and the Red-Cockaded Woodpecker (*Leuconotopicus borealis*).

Literature Cited

Anderson, R. P., and E. Martinez-Meyer. 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. Biological Conservation. 116:167-179.

Brown J.L. 2014, SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic, and species distribution model analyses. Methods in Ecology and Evolution DOI: 10.1111/2041-210X.12200

Cianfrani, C., G. Le Lay, A. H. Hirzel, and A. Loy. 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? Journal of Applied Ecology. 47:421-430.

Hoss, S. K., C. Guyer, L. L. Smith, and G. W. Schuett. 2010. Multiscale influences of landscape composition and configuration on the spatial ecology of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*). Journal of Herpetology. 44:110-123.

Kain, P. 1995. Home range, seasonal movements, and behavior of the eastern diamondback rattlesnake (*Crotalus adamanteus*). M.S. Thesis. Southeastern Louisiana University.

Lui, C., M. White, and G. Newell. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography. 40:778-789.

Means, D. B. 1985. Radio-tracking the eastern diamondback rattlesnakes. National Geographic Society Research Reports. 18:529-536.

Martin, W. H., and D. B. Means. 2000. Distribution and habitat relationships of the eastern diamondback rattlesnake (*Crotalus adamanteus*). Herpetological Natural History. 7:9-34.

Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Service, Biological Report 28.

Outcalt, K. W., and R. M. Sheffield. 1996. The longleaf pine forest: trends and current conditions. USDA Forest Service Southern Research Station. Resource Bulletin SRS-9.

Phillips, S. J., M. Dudik, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pages 655-662 *in* Twenty-First International Conference on Machine Learning.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling. 190:231-259.

Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications. 19:181-197.

Santos, X., J. C. Brito, J. Caro, A. J. Abril, M. Lorenzo, N. Sillero, and J. M. Pleguezuelos. 2009. Habitat suitability, threats and conservation of isolated populations of the smooth snake (*Coronella austriaca*) in the southern Iberian Peninsula. Biological Conservation. 142:344-352.

Timmerman, W. W. 1995. Home range, habitat use and behavior of the eastern diamondback rattlesnake (*Crotalus adamanteus*) on the Ordway Preserve. Bulletin of Florida Museum of Natural History. 38:127-158.

Timmerman, W. W., and W. H. Martin. 2003. Conservation guide to the eastern diamondback rattlesnake. Herpetological Circular No. 32:53.

U. S. Fish and Wildlife Service. 2003. Longleaf pine ecosystem fact sheet. http://southeast.fws.gov/pfwpine.html.

U. S. Fish and Wildlife Service. 2012. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the eastern diamondback rattlesnake as threatened. http://www.fws.gov/southeast/news/2012/pdf/moresnakeinfo.pdf.

Waldron, J. L., S. H. Bennett, S. M. Welch, M. E. Dorcas, J. D. Lanham, and W. Kalinowsky. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Animal conservation. 9:414-420.

Waldron, J. L., S. M. Welch, and S. H. Bennett. 2008. Vegetation structure and the habitat specificity of a declining North American reptile: A remnant of former landscapes. Biological Conservation. 141:2477-2482.

Appendix 1: County Records for *Crotalus adamanteus* in Georgia

Counties post-2000		Additional Counties pre-2000
Appling	Pierce	Bacon
Atkinson	Screven	Clinch
Baker	Seminole	Dougherty
Ben Hill	Talbot	Jenkins
Berrien	Tattnall	Macon
Brantley	Taylor	Mitchell
Brooks	Telfair	Pulaski
Bryan	Thomas	Sumter
Bulloch	Tift	Treutlen
Burke	Toombs	
Calhoun	Turner	
Camden	Ware	
Candler	Wayne	
Charlton	Wheeler	
Chatham	Wilcox	
Chattahoochee	Worth	
Coffee		
Cook		
Decatur		
Dodge		
Early		
Echols		
Effingham		
Emanuel		
Evans		
Glynn		
Grady		
Irwin		
Jeff Davis		
Laurens		
Lee		
Liberty		
Long		
Lowndes		
Marion		
McIntosh		
Miller		
Montgomery		
Muscogee		