

5-2013

SYSTEMATIC COMPARISON OF TWO HABITAT CONNECTIVITY MODELING APPROACHES: LEAST COST PATH AND CIRCUIT THEORY

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SYSTEMATIC COMPARISON OF TWO HABITAT CONNECTIVITY
MODELING APPROACHES: LEAST COST PATH AND CIRCUIT THEORY

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Forest Resources

by
Adam M. Rose
May 2013

Accepted by:
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ABSTRACT

Intensifying human development requires landscape-level planning to restore connectivity to fragmented and ecologically isolated habitats. The rapidly growing field of conservation planning has produced a variety of approaches to modeling habitat connectivity. The objective of this research is to inform the choice and use of appropriate software packages for connectivity conservation planning. I focused on comparing two prevalent approaches, 1) least cost path, patch-patch modeling using CorridorDesigner software and 2) electrical circuit-theory based approaches for patch-patch and “all points” connectivity using Circuitscape software. Additionally, I compared two dominant connectivity modeling approaches: 1) the focal species approach and 2) a generalized resistance approach using a “naturalness” dataset. When using the same input layers and varying only the software, I found considerable differences in spatial characteristics of outputs, between least cost path (LCP) and circuit theory (CT) approaches including 1) greater specificity of LCP corridors, and 2) spatial disjuncts between LCP corridors and CT areas of high current flow. Mean resistance values for Circuitscape outputs were different than means for CorridorDesigner, suggesting Circuitscape’s different algorithm produces different corridors than CorridorDesigner. As the underlying assumptions of LCP and CT differ, it is not surprising that their outputs would as well, even when using the same input variables. However, conservation planning practitioners need to be aware of these modeling assumptions prior to implementing corridors. The increased specificity of LCP corridors produced by CorridorDesigner and the intuitively accessible LCP concept suggests ease of application but perhaps the risk of bias due to overspecificity. Alternatively, while circuit theory is intuitively appealing because it is a more wholistic landscape-level-analysis, and has useful, spatially-explicit “pinch points”, it may produce output that is too vague for local-land use

planners. Conservation planning webinars and other trainings will help land use planners understand the differences among connectivity modeling assumptions, data structures, and outputs.

DEDICATION

I dedicate this thesis to my family, friends, fellow graduate students, and professors, who helped me get through the hard times and kept me looking towards the future.

TABLE OF CONTENTS

	Page
TITLE PAGE.....	i
ABSTRACT	ii
LIST OF TABLES	iv
LIST OF FIGURES	v
SYSTEMATIC COMPARISON OF TWO HABITAT CONNECTIVITY MODELING APPROACHES: LEAST COST PATH AND CIRCUIT THEORY	1
Introduction and Background.....	1
Materials and Methods	5
Results	17
Discussion	20
Conclusions.....	31
References	64
APPENDICES.....	68
1: Maps Used in the Statistical Analysis	69
2: Maps Used for Visual Comparisons	120
3: Map Results from the Additional Experiments	157

LIST OF TABLES

Table	Page
1 Factors Used to Chose Focal Species	32
2 CN_LEVEL2 Classifications and Species Reclassifications	33
3a Average Pinch Point Capture Per Slice Size	37
3b Results from Tukey Test for Pinch Point Capture	37
4 Significance Results between the Three Methods: Corridor Designer, and Individual and Cumulative Circuitscape	38
5 Differences in Underlying Theories of Corridor Designer and Circuitscape.....	39

LIST OF FIGURES

Figure	Page
1 Level 4 Ecoregions and Random Points	40
2 Workflow Chart for the Extraction of Statistical Values from LCP and CT Output.....	41
3 Means for Black Bear Corridors	42
4 Means for Southern Two-Lined Salamander Corridors	43
5 Means for Eastern Spotted Skunk Corridors	44
6 Means for Pygmy Rattlesnake Corridors	45
7 Ranges for Black Bear Corridors	46
8 Ranges for Southern Two-Lined Salamander Corridors	47
9 Ranges for Eastern Spotted Skunk Corridors.....	48
10 Ranges for Pygmy Rattlesnake Corridors	49
11 Standard deviations for Black Bear Corridors.....	50
12 Standard deviations for Southern Two-Lined Salamander Corridors.....	51
13 Standard deviations for Eastern Spotted Skunk Corridors.....	52
14 Standard Deviations for Pygmy Rattlesnake Corridors	53
15 Means for the Naturalness Dataset Corridors.....	54
16 Ranges for the Naturalness Dataset Corridors	55
17 Standard deviations for the Naturalness Dataset Corridors	56
18 Combined Comparisons of the Means for the Three Methods	57
19 Combined Comparisons of the Ranges for the Three Methods.....	58

List of Figures (Continued)

Figure	Page
20 Combined Comparisons of the Standard Deviations for the Three Methods	59
21 Means of Combined Species Corridors and Naturalness Dataset Corridors	60
22 Example of a Failed Circuitscape Analysis	61
23 Difference Map between Circuitscape and the Habitat Suitability Model	62
24 Example of Output from the Connectivity Analysis Toolkit for the Black Bear	63

SYSTEMATIC COMPARISON OF TWO HABITAT CONNECTIVITY MODELING APPROACHES: LEAST COST PATH AND CIRCUIT THEORY

Introduction and Background

During the past 500 years the pace of landscape change due to interactions with humans through agriculture, road building, industry, and development has rapidly accelerated (Baldwin 2010, pg 18). With increasing human use, habitats have become more fragmented, wildlife and plant populations more isolated, and the need for systematic rather than opportunistic conservation planning more apparent (Hilty et al. 2006, p 21-22). A variety of land uses dissect landscapes (e.g. roads, urban/residential developments, and agricultural monocultures; Hilty et al. 2006, p 17) and can prevent or impair migration or dispersal from one habitat location to another (Beier et al. 2011, Trombulak and Frissell 2000). Due to continuing development, conservation planning is needed to prevent these habitats from becoming more ecologically and evolutionarily isolated.

In efforts to prevent habitat fragmentation and isolation, various conservation efforts can be conducted to improve or maintain habitat quality and connectivity. An improvement to the landscape matrix (i.e. variations in land use/land cover) can come in the form of reserves, buffers, and corridors (Peck 1998, pp 96-103). Reserves are areas of land preserved specifically for the goal of maintaining biodiversity (Peck 1998, pg 89). Buffer regions can be placed within reserves to promote dispersal between core habitat areas, and surrounding reserves to provide a gentler habitat gradient between the reserve and the outside landscape, decreasing edge effects within the reserve (Peck 1998, pg 99). The theory of island biogeography states that the further away viable habitat “islands” are from the “mainland” of viable habitat, the less likely it is for the individuals to move to other populations (Simberloff and Abele 1976). Connecting

habitat “islands” with suitable habitat corridors will allow dispersal between the habitat areas (Peck 1998, pg 96).

An early step in corridor conservation planning (after defining biological goals by determining the landscape(s) and focal species) is modeling selected species use of the landscape in question (Beier et al. 2008). Possible linkage and corridor networks are usually the goal of these analyses and the resulting maps suggest where future conservation efforts should occur (Beier et al. 2008, Beier et al. 2011).

Spatial modeling (i.e., using a geographic information system or GIS) is based on characteristics of the landscape and land uses and, with software advances making complex modeling approaches more accessible, has become a powerful tool for habitat and corridor conservation planning (Woolmer 2010). Modeling habitat connectivity (i.e., “corridors”) has been the focus of much theoretical research and several software development projects (Crooks and Sanjayan 2006). These models can create options for stakeholders by modeling different sized corridors, and potentially multiple corridors, for species movement (Beier et al. 2008). Creating corridor models also puts the modeler in a place to propose other conservation efforts (e.g., wildlife underpasses and overpasses) that supplement the corridor (Beier et al. 2008, Beier et al. 2011).

However, difficulties may occur when choosing among corridor modeling approaches and pieces of software. Different designs and assumptions lead to different algorithms within the modeling software, which can yield different results. An example of this difference is CorridorDesigner (CD) and Circuitscape (CS) (Majka et al. 2007, McRae and Beier 2007). CD assumes the shortest, least cost path is the best (i.e., least-cost path analysis or LCP). CS utilizes circuit theory (CT) and

calculates the current (total movement) through the landscape based on resistance to movement through pixels on a habitat suitability model (McRae and Shah 2009).

CorridorDesigner (<http://www.corridordesign.org/>) is a toolbox for use within ArcGIS (ESRI, <http://www.esri.com>) that uses least-cost path analysis to produce corridor shapefiles of different widths for the most permeable landscapes (i.e. least costly paths within the polygon; Theobald 2006). Multiple corridors are produced during one analysis based on the highest percentages of permeability of the landscape (e.g. 1%, 5%, and 10% most permeable landscapes) between two patches of landscape.

Circuitscape (<http://www.circuitscape.org/Circuitscape/>) is based on the theory that ecological processes such as gene flow might follow a path of least resistance and be analogous to how electrical circuits function. Landscape resistance is a measure of how easily an organism might migrate or disperse through a particular local, based on characteristics of landscape features (e.g., roads and road traffic; Theobald 2010). Like CorridorDesigner, Circuitscape is a Python-based program, but unlike CD, it operates independently of ArcGIS (but is capable of sharing files with it). The basic algorithm for CS follows Ohm's law,

$$I = V/R$$

Where I equates to current or total gene flow, V is the magnitude or force of the flow (i.e. how close to a source/destination), and R is the resistance to flow from the landscape. The values for resistance as pertains to CS are arbitrarily determined during the production of the habitat suitability model (McRae and Shah 2009). The analysis is based on a graph theory framework where each cell in the raster is a node, and the four first-order neighbors or eight first- and

second-order neighbors are connected by edges (McRae et al. 2008). The edges symbolize the analysis of difference between the cell and its neighbor, the total of all the differences is what yields the resistance for the cell (McRae 2006).

CS can yield supplemental data to modeled corridors in pinch points. (McRae and Shah 2009)

Pinch points are areas on a map where a corridor bottlenecks, or for CS, an area of high flow.

Unfortunately for conservation modelers, there are no rules for what thresholds determine a pinch point in CS, and little work that has established a precedent (B. McRae 2011, pers.

Comm.). Therefore, for this study, a threshold of the top 25% of values from the entire map was used, based on Figure 8 in Margules and Pressey (2000). Pinch points can be thought of as a large volume stream travelling through a canal, canyon, or other narrow passage that forces a faster flow to the water. This increase in flow is analogous to increased animal dispersal flow and can be used as a prioritization metric when planning conservation actions.

For this comparative study, CD and CS were chosen because they represent two different and prevalent methods: least-cost path for CD (Beier et al. 2007) and circuit theory for CS (McRae and Shah 2009). Each approach is accompanied by well-documented websites and peer-reviewed articles. Least-cost path analysis has been studied (Theobald 2006) and used in application (Beier et al. 2008, Beier et al 2011, Majka et al. 2007). Circuit theory and to a lesser extent graph theory, (McRae et al. 2008, Urban and Keitt 2001) has been compared to least-cost path analysis (McRae and Beier 2007, Theobald 2006) and used in application as well (McRae and Beier 2007).

In an attempt to reduce confusion that can arise when facing a choice among corridor modeling software, this study will compare and contrast two common tools, least-cost path based

CorridorDesigner (CD) and circuit theory based Circuitscape (CS). The two common tools will be implemented using each of two common methods of deriving landscape resistance surfaces, 1) the focal species approach in which there is the attempt to model a species-specific landscape resistance surface and 2) the generalized approach in which an index of human landscape modification (e.g., Human Footprint, or Naturalness) is used to generate an estimate of structural connectivity. The first objective was to model habitat connectivity using both pieces of software and the same essential input data, for four species within the state of South Carolina [Black Bear (*Ursus americanus* Pallus), Eastern Spotted Sunk (*Spilogale putorius* Linnaeus), Southern Two-Lined Salamander (*Eurycea cirrigera*) and Pygmy Rattlesnake (*Sistrurus miliarius miliarius*)], and compare the outputs (a side by side comparison of these species needs can be seen in Table 1). The second objective was to create connectivity output using both pieces of software, based on a generalized naturalness data set (Theobald 2010), and to compare the outputs. The third and final objective was to compare the results from the focal species output and naturalness output to determine any differences or biases within the software that are not obvious from previous comparisons.

Materials and Methods

Study area

We chose to conduct the modeling comparison within a single, well-defined geographical area that is large enough to encompass considerable habitat heterogeneity, and small enough to allow efficient geoprocessing. South Carolina (82,931 km²) in the eastern United States offers a unique combination of habitats and a high degree of beta diversity from the Atlantic Coastal Plain (subtropical coastline) to the Blue Ridge escarpment (temperate montane), inclusive of 14

level IV ecoregions (Figure 1), with a higher species concentration in the Blue Ridge than in the coastal plain. The land-use patterns of South Carolina range from urban centers with populations > 100,000 to agriculture and managed forest. Elevation ranges from sea level to 1085 m (Sassafras Mountain). Natural corridors potentially exist in streams and rivers running within and between ecoregions from the Blue Ridge to the Coastal Plain. The different types of land cover, the elevation gradient, and the potentially existing corridors make the state of South Carolina a suitable area to compare CD and CS.

Data retrieval

Land Use/Land Cover data for the Southeast Continental US was obtained from the USGS GAP Analysis program at the University of Idaho (<http://www.gap.uidaho.edu/Portal/DataDownload.html>). Road, stream, and elevation data sets were obtained from the SCDNR GIS data clearinghouse (<http://www.dnr.sc.gov/GIS/gisdownload.html>). The naturalness data for the year 2001 used in the non-biased model (i.e., not determined or influenced by any species needs) was obtained from Theobald (2010).

Data Preparation

Before analysis, all data sets were projected to NAD 83 UTM 17N and resampled to 100 m by 100 m (1 ha) cells to keep all data the same resolution, as well as keep the resolution of a fine enough grain for relevance to local-scale planning. All data sets were cropped to the state of South Carolina (or to a 1km buffer around South Carolina for the naturalness dataset obtained from Theobald 2010), based on the need of data preparation.

Landscape resistance models attempt to assign values to rasters representing how difficult or easy it is for dispersal or migration to occur (Baldwin et al. 2010). Given their pervasive ecological effects and function as barriers to gene flow, roads are an important component of all resistance models (Foreman and Deblinger 2000, Theobald et al. 2012). To attempt to model the effect of different sized roads, the roads were differentiated between US, state, and county roads and buffered to 60, 20, and 10 meters, respectively. The buffers were produced in an attempt to model the affect that different traffic volumes and road types (i.e. divided and not divided, with barriers and without, etc.; Trombulak and Frissell 2000) have on species and individual movement. Distance from roads (Euclidean distance) was used to model human extended effects (Woolmer et al 2008).

Habitat types were grouped and reclassified (i.e. the groups were collapsed) based on the perceived needs of the species being modeled (i.e. habitats that would be used similarly by a species, see Table 2). For example, wet deciduous forests, wet coniferous forests, and dry coniferous and deciduous forests were originally independent, but collapsed together for the Southern Two-Lined salamander. The reclassification followed the CN_LEVEL2 classification included in the land cover attribute table, but varied some with the needs of different species (i.e. some CN_LEVEL3 classifications were used to differentiate between similar CN_LEVEL2 classes). This was done for all species used.

Species Selection

Four focal species were chosen to represent a range of taxa and habitat requirements (Table 1) to obtain a varied difference between the different species outputs. Black bear (*Ursus americanus*) was chosen because it is a large mammalian carnivore (Carnivora) with generalist

habitat use patterns and large home ranges (Beier et al. 2008). Eastern Spotted Skunk (*Spilogale putorius*) is a relatively rare mesopredator and was chosen because of its preference for non-disturbed habitats and relatively localized movements (Henderson, 1975). The Southern Two-Lined Salamander (*Eurycea cirrigera*) was chosen because of its widespread distribution and dependence on streams (Guy et al. 2004, Miller et al 2006, Petranka and Smith 2005). Pygmy Rattlesnake (*Sistrurus miliarius miliarius*) was chosen because of the ability to use both moist and xeric habitats, but preference for xeric sites (Ernst and Barbour 1989, pp 205-207; May et al. 1996).

Habitat Suitability Modeling

Habitat suitability modeling is the first step within CorridorDesigner, in making a landscape resistance layer from which to model least cost path corridors. Because our objective was to compare software effects on corridor outputs we opted to use the habitat suitability models produced for focal species within CorridorDesigner as resistance layers for Circuitscape as well. The habitat suitability model tool used was a custom script included in the CorridorDesigner toolbox, and is a combination of the ArcGIS tools Reclass by Table and Weighted Overlay. A geometric mean was used to combine all input factors (e.g., elevation and land cover). The reclass file reclassified the previously grouped habitat types in the land cover dataset to suitability values. Suitability values are not meaningful in an absolute sense. The numeric scale and absolute values are arbitrary yet valuable relative to each other (Beier et al. 2008). For this tool, the total of all the weights for the inputs must equal 100.

Each focal species model was based on perceived habitat needs as derived from literature review. For the Black Bear (Powell et al. 1997, Garshelis and Pelton 1981), land cover was

weighted at 75, both elevation and topographic position (i.e. ridge top, high slope, low slope, and bottoms) were weighted at 10 and the distance from roads was weighted at 5. The Southern Two-Lined Salamander, having much different needs than the black bear had much different weights. The distance from streams was weighted at 30, elevation was weighted at 25, both land cover and topographic position were weighted at 20, and distance from roads was weighted at 5. The distance from roads would have been weighted higher to model the aversion Southern Two-Lined Salamanders have for disturbed and developed areas, but doing so would have lessened the importance of required environmental characteristics (i.e. moist soil as modeled by distance from streams and topographic position, and canopy cover from the land cover layer). Elevation was weighted as much as it was because of maximum and minimum elevations that the salamander is found without crossbreeding (Beachy and Bruce 1992, pp 241-248; Mitchell and Gibbons 2010, pp 137-140). As the Eastern Spotted Skunk prefers non-disturbed sites, the distance from roads was weighted at 50, while the land cover was weighted at 35, and the topographic position was weighted at 15 (Henderson 1975). For the Pygmy Rattlesnake, the land cover was weighted at 45, the topographic position weighted at 35, and the distance from roads was weighted at 20, due to the effect vehicles have on snakes (Ernst and Barbour 1989, May et al 1996). For habitat suitability models that did not have values approaching 100 (the maximum arbitrary value for the HSM), the HSM was normalized to 0-100 using another script in the CorridorDesigner toolbox (the Normalize habitat suitability model tool). This calculation was conducted for the Pygmy Rattlesnake and Eastern Spotted Skunk habitat suitability models.

Habitat suitability modeling is an art and science in and unto itself. The purpose of this study was to compare model effects on corridor outputs. As long as we were using the same inputs in each modeling exercise, and that they were relatively correct and capture taxonomic and habitat use variation, we consider our habitat suitability models to be accurate enough for our purposes.

CorridorDesigner Modeling

CorridorDesigner utilizes an intuitively appealing and for many practical purposes, useful “patch-to-patch” approach, in which least cost path corridors are sought between two core habitat patches, protected areas, or other pre-determined areas of high habitat value (Beier et al 2011). The corridor modeling tool included in CorridorDesigner uses the habitat suitability model previously produced to connect two “wildland blocks” set by the user. A moving window (with a changeable size and shape) is used to analyze the habitat suitability model and determines the least costly, shortest path between the two wildland blocks. A threshold value can be set to limit the inclusiveness of marginal habitat in the corridor model.

If polygons are used for the wildland blocks (as is done for the focal species in this study), the minimum breeding patch size and minimum population patch size (both in hectares) can be set to find where likely sources/destinations are within the wildland block and will initiate/end the corridor model within these habitat patches. Majka et al. (2007) suggest that in the case that either of the minimum patch sizes is not known, set the population patch size to be five times the breeding patch size, or set the breeding patch size at 1/5 the population patch size (which is done for all species except the Black Bear; Majka et al. 2007). It should be noted that the smallest usable patch size is one hectare, any smaller, and the value converts to zero (i.e. the

tool only accepts integer values for the patch size). A zero for patch sizes can be used with points/lines (to indicate where known habitat patches or initial movement locations are) to not find patches and just proceed with the least-cost path analysis.

Wildland blocks were chosen manually based on two criteria. The first criterion was that the wildland blocks be larger areas within the habitat suitability model with high values (i.e. suitability). The second criterion was that the wildland blocks would show potential differences between CD and CS when compared. Beier and others (2007) define wildland blocks as “Large areas of publicly owned or other land expected to remain in a relatively natural condition for at least 50 years.” Protected areas of land were not prioritized in this study to focus on modeled viable habitat regions within the state (protected areas should not be ignored in corridor planning as they can serve as valuable wildland blocks to connect or as refuges within a corridor). In both cases, wildland blocks are areas of land to be connected by corridors and linkages. Approximately five wildland blocks were delineated for each species.

Since the Black bear is a large predator and in the Eastern United States is a habitat generalist, the suitability threshold was set at 60, and the minimum breeding and population patch sizes were set at 1000 and 5000 ha, respectively (Majka et al. 2007). The Southern Two-Lined Salamander is a small animal with small migration and dispersal distances, greatly dependant on the wetness of the habitat for survival; therefore the radius of the circular moving window was set to 70 meters, the habitat suitability threshold was set to 75, the minimum breeding and population patch sizes were set at 1 and 5 ha, respectively. The skunk is a larger animal than the Salamander, but with more localized home ranges than the Black bear. Because of this, the radius of the moving window was set at 60 meters, the suitability threshold set to 80 due to the

specific needs of the species, and the breeding patch size/ population patch size was set to 1/30 ha. The settings used to produce corridor models for the snake were a suitability threshold of 70, a minimum breeding patch size of 2, and a minimum population patch size of 10. All moving windows used a circle with a radius of 200 meters (unless otherwise noted) and the habitat suitability model produced for that species.

Circuitscape Modeling

For this analysis, the graphical user interface was used. To conduct the analysis in CS, the habitat suitability model was converted, as required, to an ASCII file. Wildland blocks (called focal nodes in Circuitscape) for each species were merged to one shapefile, with a new attribute numbered =>1 to match the wildland block number (CS will not read focal nodes with a value of 0), converted to raster, and then ASCII files. Attention was given to insure extent and resolution was the same for focal node files and resistance map files due to CS having (memory intensive) beta code for reprojecting data. The beta code does work, but CS will crash for high numbers of wildland blocks (i.e. more than 50) on low memory computers (i.e. ≤ 4 GB RAM which many personal laptops and desktops have).

The wildland block file was entered as the "Focal node location file" and the data type was set to focal regions (i.e., multiple cells per wildland block). The HSM file was set as the raster habitat map, and set the data type as conductance (inverse of resistance). The connection scheme was set to connect to all eight neighbors, and the connection calculation was set to be the average resistance. Finally, the output file was named, and current and voltage map options were checked to produce current maps. This process was repeated for all species. For easier visualization, the Circuitscape individual and cumulative maps were log-transformed.

In addition to the basic analyses for comparing CD and CS, additional experiments were conducted to find other differences between the two modeling software packages by changing an aspect of either the HSM, the factors creating it, or the wildland blocks for the Black Bear. The changes made include changing the resolution of the HSM, changing urban areas to NODATA value (i.e. a barrier) in the land cover dataset, changing the wildland blocks to their centroid (i.e. a specific point in the landscape and not a region), and attempting to analyze a pair of regions with one outside the HSM. The change in resolution was to determine what effects cell size has on the resulting corridor model, while the changes in the wildland blocks (i.e. using centroids and moving one region outside the HSM, each separate) were an attempt to determine what effects the habitat regions have on corridor models. The barrier experiment was an attempt to determine how to impose a barrier in a landscape, as well as the effect a barrier would have on a possible corridor. The barrier experiment used urban areas as barriers as an example because urban areas are the most changed from the natural landscape and therefore least likely for many species to move through as indicated through initial corridor outputs.

Naturalness data

There are conservation planning situations in which knowing overall levels of connectedness in the landscape may be more important than how best to connect two locales. Without the *a priori* constraint to connect two locations, for example, it may be possible to identify important, as of yet unprotected areas that have high connectivity value. To model this, instead of pre-selected wildland blocks, we used random points distributed through the landscape, including in a buffer zone outside of the state of South Carolina. A buffered area is necessary to prevent

edge effects, in other words current accumulating, along, or increasing near, the state boundaries – an artifact less important when connecting two places within the state.

In the place of wildland blocks, 68 points were randomly placed within a shapefile with an outline 1km beyond the state border for South Carolina. To best capture the diversity of landscapes, the locations were designated through a stratified random design. A minimum of 3 points per level IV ecoregion were selected, and an increasing number of points were created relative to the ecoregion area.

Measures of landscape naturalness are derived from land use/land cover, roads, human settlement, and other data and are widely used as surrogates for the degree of anthropogenic habitat conversion (Woolmer et al 2008, Baldwin et al 2010). We obtained a 2010 naturalness dataset used in recent habitat connectivity modeling for the United States (Theobald 2010). The naturalness data clipped to the buffer of the state was used in place of a habitat suitability model to remove any species bias. All points were connected pairwise in both CD and CS. The naturalness dataset itself was increased by one to allow Circuitscape analysis. CS will not find a complete circuit between two points if one of the points is surrounded by cells with a conductivity value of 0 (Figure 19).

CD used a moving window in the shape of a circle with a radius of 200 meters. Because no individual species was being modeled, no patches were needed (random points were used) so both the minimum breeding and population patch size was set at 0. The suitability threshold was set to 60 to mimic a generalist species. A custom script that utilizes the CorridorDesigner tool was used to iterate through all pairs of points.

Since the focal node file had 68 points, it was important for the HSM and the focal nodes to have the same projection and resolution. One way to do this is to use the “Export to Circuitscape tool” distributed by Jeff Jenness (http://www.jennessent.com/arcgis/arcgis_extensions.htm); this was done for the points and naturalness data. To compare software effects on connectivity models, the settings were kept the same as for the focal species analyses.

Large demands for memory can slow conservation planning models and impact the quality of the science (Leonard, et al. 2012). Instead of running Circuitscape for the naturalness dataset on a personal computer (1.30 GHz processor, 64 bit Windows 7, 4 GB RAM; estimated completion time: 700 hours), the analysis was conducted on the Palmetto Cluster, a supercomputer located at Clemson University (information can be located at: <http://citi.clemson.edu/>). This allowed the batch processing of the workload across 201 nodes (CPUs) with eleven connections for each node. Since one processor can run only one connection at a time, running Circuitscape on the Palmetto cluster reduced the run time to five hours, an increase of 139 times.

Statistics

Corridor polygons were used to extract data from the HSM (see Figure 2) for each percent slice of individual corridors using the Zonal Statistics as Table tool. This tool was used to extract statistical information (i.e. mean, standard deviation, minimum, maximum, range, etc) from the HSM (for LCP) as well as the individual and cumulative CS output (for CT) on a scale of 0 - 100 for that species. The extraction was conducted for each pair-wise corridor and the zone specified was the respective LCP corridor model (i.e.: the 0.1, 1.0, 5.0, and 10.0% slices) for each

corridor. Difference maps were produced by subtracting the 1-100 normalized CT outputs from the respective HSM.

The statistical program JMP 9.0 (SAS institute Inc. 2010) was used to describe differences among mean, range, and standard deviations of values extracted from raster (LCP and the CT output) maps with each percent for individual corridors. This analysis was conducted for each species, the different size slices, and the map method (i.e. LCP, individual CT, or cumulative CT). This was done by conducting a Standard Least Squares analysis in the Fit Model tool (JMP). Additionally, an ANOVA followed by Tukey's and LSD post-hoc tests were conducted in SAS 9.3 (2012) to test the differences suggested by the descriptive analysis.

Pinch points arise from a CT analysis and are areas where high current flow encounters moderately constrictive landscape features. In other words these are places where some on the ground conservation action could "unplug" (i.e. remove the resistance in the landscape at that area) and increase flow in a potentially important place for connectivity. In an effort to understand how LCP corridors capture pinch points, corridor polygons derived from LCP were compared to CT pinch points. Pinch points are defined here as the pixels with the top 25% values (e.g., Figure 8, Margules and Pressey 2000) to determine the number of pinch points (i.e., high traffic, high resistance to movement). The CT output raster was reclassified along the quartiles for each pairwise corridor using the Reclass tool. The reclassified datasets CT outputs were clipped to their respective LCP corridors. The percent of pinch points captured in each of the corridors was recorded and used for statistical analyses. Pinch point capture percentage means were computed using JMP 9.0 (SAS Institute Inc. 2010) at a 95% confidence interval. In

addition, t-test and post-hoc Tukey's and LSD test were conducted for the pinch point data in SAS 9.3 (2012) to confirm differences between the means obtained in JMP.

Results

Focal Species

See Figures 2 - 17 for specific trends in focal species and naturalness means, ranges, and standard deviations.

For focal species, means for raster values of the LCP (i.e., the HSM) extracted using corridors (produced by CD) were greater than CT values (Figures 2-5); the individual and cumulative circuit theory means (extracted from the respective Circuitscape outputs using the same corridors as with the HSM extraction) were similar and low. The means for the LCP method decreased as corridor slice size increased. The ranges and standard deviations of the values extracted using the focal species corridors were generally high for both the LCP and the individual CT method, with the cumulative CT method having lower ranges and standard deviations (Figures 7-13). The corridor ranges and standard deviations varied largely on the species for which they were designated. The range values for all datasets were generally constant, with some increase with increasing slice size, as was expected.

Visual comparisons between CorridorDesigner models and Circuitscape output indicate that when the least-cost path corridor is more straight and direct, the circuit theory (i.e.: CS) output has a smoother gradient and is less restricted by high resistance or NODATA areas. This comparison is easily viewable in figures 1-16 in Appendix 2.

Naturalness Dataset

Using the naturalness dataset, means were high for the LCP method, and decreased with increasing slice size (Figure 15). The individual and cumulative CT methods were both low. The range (Figure 12) was fairly consistent for the LCP and individual CT method, but the cumulative CT method had an increasing range with increasing corridor slice size for the naturalness dataset. The standard deviation (Figure 17) for the naturalness dataset increased for the LCP method and both CT methods had similar standard deviations. The individual CT method decreased slightly with increasing corridor slice size.

Using the figures 17-35 in Appendix 2 as a means to compare least-cost path corridors and circuit theory output shows the same trend as the focal species comparisons; the less direct the LCP model, the more flow is restricted by high resistance areas. Some maps show that focal nodes near each other have flows similar in appearance to a magnetic field. For these pairings, at high corridor slice sizes, the corridor becomes less linear, inclusive of more of the study area, and more amorphous.

Comparison

A comparison between the combined species corridors and the naturalness dataset corridors shows that the focal species means are higher for LCP, but lower for both methods derived from CT (Figure 18). Comparisons between the species, map methods, and slice sizes for all means, ranges, and standard deviations can be seen in Figures 18-20. Additionally, the naturalness dataset means decrease for all methods as corridor slice size increases. Table 4 quickly shows statistical significance for each comparison (i.e.: X method minus Y method) between methods. At the 95% confidence level, all comparisons of LCP output or to LCP were statistically significant

for means and standard deviations. For ranges at the same confidence level, both the LCP-Cumulative and the Cumulative-CD comparisons, as well as the Cumulative-CT, and the CT-LCP method comparisons were statistically significant.

Pinch point capture percentages were calculated for each slice size and are reported in Table 3a. The 95% confidence intervals are reported along with the means for each slice size. The mean pinch point capture percentage for each slice size ranges from 12.76% for the 0.1% slice size to 57.20% for the 10% slice size. Table 3b uses the same data as Table 3a and shows which slice sizes are not significantly different using letter designations (i.e.: slice sizes with the same letter are not significantly different).

A difference map is presented (Figure 20) from the naturalness dataset. The map is similar to the HSM in patterns and in value. Negative values are areas where the cumulative CT output has a greater value than the HSM. As there are few areas where the pattern of the map differs from the HSM, therefore an analysis on the difference maps was not conducted.

Maps used in visual comparisons are included in Appendix 1. To assist in the comparison of the two modeling software packages, CT produced maps are presented in log-transformed format to show the differences for all species with slices 0.1, 1.0, 5.0, and 10.0 from LCP. In addition to these comparisons, tests for bear between LCP and CT were conducted. To more easily assist in viewing the difference between LCP and CT pair-wise corridors, an overlay of the 0.1, 1.0, 5.0, and 10.0% slice corridors from LCP were placed on top of the respective individual CT model and presented in Appendix 2. The tests to highlight the differences between LCP and CT through changing the HSM both software packages use to conduct their analysis (Appendix 3). The only result from these tests not presented is the experiment that manipulated the location of the

wildland blocks in which one of the wildland block pairs was placed outside the HSM; LCP attempted to make connections between the two wildland blocks (Figure 8 in Appendix 3), while CT did not include pairings with that core. Note that for the barrier experiment, changes urban areas into NODATA based on initial corridor outputs.

Discussion

Quantitative Data

These analyses suggest that conservation planners who are contemplating either a circuit-theory based or LCP based analysis (e.g., using CorridorDesigner or Circuitscape) should carefully consider differences and how those differences may influence on the ground decisions for habitat connectivity. Even when rescaled to a 0 – 100 range, values for both CT methods (i.e., individual and cumulative CT models) are skewed towards the lower end of the range, when compared to the CD (LCP) method. That is, high areas of current flow (i.e., potential gene flow) do not follow the least-cost path corridor. Instead current flow is dispersed throughout the landscape and accumulates in areas where resistances suddenly increase (e.g., roads). When using the same input values we found substantial spatial differences in output between the methods. This suggests that it may be difficult, and potentially implausible, to use one method to estimate the other. It may be implausible to do so because the programs and methods are, a priori, different. However, many professional land use planners will not have the time to understand these subtleties and may wonder why the outputs for habitat connectivity differ so widely. Thus, better education as to the reasons for these differences and what they might mean for biological connectivity needs to be developed and delivered to end users.

Since the LCP data were extracted from the HSM, it is unsurprising that the values are high, since the theory (Least-Cost analysis) finds the most direct, least costly path between the two locations (Theobald 2006). It is also not surprising that the higher percent slice sizes had slightly lower means than the next largest size. This is due to the inclusion of lower value cells in the expansion of the corridor size.

CS on the other hand, uses circuit theory based on Ohm's law and applies a resistance calculation for each cell based on its 4 or 8 neighboring cells (McRae and Beier 2007, McRae et al. 2008, Shah and McRae 2008), based on user input. This calculation is conducted for every cell in the input habitat suitability model (or unsuitability model if modeled for cost) and then applied to the voltage originating and terminating at two wildland blocks (focal nodes) from the combined focal node file. This allows for a full landscape analysis and the cumulative map for multiple pairings of cores potentially show additional areas in need of conservation (or at least consideration for later projects). Since CS determines flow values through circuit theory, it is not surprising that many of the high value cells do not correspond to the high values selected for use by in the least-cost path analysis. This translates into the values for means extracted using the least-cost path corridor being unpredictable, aside from being lower than the LCP mean values. This also somewhat explains the variations in range and standard deviation values within and between different species.

The effect of species bias varies based slightly on corridor size and mostly on map method (i.e. LCP or CT; Figure 18). For all sizes, LCP values were higher using the naturalness dataset, while CT values, for both cumulative and individual maps, were slightly higher for specific species data. The naturalness dataset LCP values were higher likely due to more areas that contain

higher values in the naturalness dataset as opposed to the more confined areas that are contained in the specific species HSM's. Since the species specific datasets have more isolated high value areas (e.g. Southern Two-Lined Salamander HSM), it is more likely that the CT model follow the LCP model (since the high values in the HSM are surrounded by lower values) However, there are results where this is not the case (i.e. Southern Two-Lined Salamander).

As with means, pinch points do not appear to be a valid metric by which to assess LCP through the use of CT. The highest percentage of captured pinch points was in the 10% slices with 57.20% (Table 3a) of pinch points captured, but the 95% confidence interval points to high variation in the 10% slice capture. Instead of being a worthless metric, pinch points may indicate areas of further consideration for conservation. Since CT does not give indication whether high flow is from high flow and low to average suitability or low suitability and average flow, investigation via HSM values or ground truthing the area is a must if these high flow areas will be included in future conservation planning (i.e.: assessing sufficiency of a model and evaluating additional model areas; Glennon and Didier 2010). Upon confirmation that pinch points are due to higher resistance areas, it can then be assumed that these pinch points indicate areas from the "high risk and high necessity" as quadrant of Figure 8 in Margules and Pressey (2000), and thus should be prioritized accordingly.

Visual Comparisons

Maps presented for visual comparisons are not meant to be used for or to be the basis of conservation plans. These maps were produced from a brief literature review and are by no means definitive. The purpose of these maps is to compare the modeling techniques, and as such, correctness of the maps was not prioritized.

Sample species maps are presented to allow visualization of differences species preference can produce. A large generalist like the Black Bear (Majka et al. 2007) produces a smooth flow with no visible pinch points in Circuitscape analysis. The few high flow areas are directly connected to wildland blocks (increased voltage in the model). The corridor produced from LCP is a relatively straight, path, with few splits. The major split that occurs does so to avoid the less suitable values between the two paths. The Southern Two-Lined Salamander, a small, moisture dependent species (Petranka 1998, pp 241-248; Miller et al. 2006; Mitchell and Gibbons 2010, pp 137-140), has a braided pattern between areas of NODATA from CT with a number of pinch points. The LCP model for the Southern Two-Lined Salamander (Figure 7-9 in Appendix 1, corridor made transparent to view the HSM) travels across large swaths of unsuitable land which CT deems to have no flow through. Other species samples are between these two extremes.

Producing maps from HSMs with highly developed areas reclassified to NODATA cells show what may happen to genetic flow as modeled in CT (Figure 5 in Appendix 3). Not only do the urbanized areas become non-traversable, but the suburban areas are less utilized as well. This can be seen somewhat in LCP as well; the corridor moves away from the more developed areas that it had previously passed through. These results were expected from initial corridor outputs from early in the study. However, that is not to say that urban centers are devoid of wildlife, and should the areas surrounding them should be treated as marginal land. Numerous species live primarily in urbanized areas (e.g. European Starling and Rock Pigeon), and some species will traverse the urban area without difficulty (e.g. Black Bear). This occurred for the Black Bear in the initial data, following a corridor (at multiple places only one cell in width) that ran along the

Congaree River through the center of the city of Columbia, South Carolina (located in the low value areas in the center of the HSM). Corridors such as the Congaree River in Columbia, SC can and are being expanded upon, as well as using unused industrial areas, to form green spaces within cities (De Sousa 2003). These green spaces can be designed to assist the movement of different species through a city, instead of just for human enjoyment; properly designed green spaces would make cities part of viable corridors, instead of obstacles to circumvent.

Maps made with points instead of polygons can have a few benefits. In LCP it allows for a quick analysis before any sort of in-depth analysis (a test run, so to speak). In Circuitscape, there are two ways in which to handle points. The first, and easiest, is to have points corresponding to the wildland blocks (i.e., centroids); these blocks are “burned” into the resistance map with a 0 resistance (100% suitability) value and used as short-circuits to the ground (terminal wildland block; McRae and Shah 2009). The second way is to give the points a buffer so that they have a diameter larger than one cell of the raster. This allows Circuitscape to read the points as a region instead of a single point (as in the case of the naturalness dataset).

Resolution is an important parameter in conservation modeling. For this paper, the resolution for maps (unless otherwise stated) and analyses is 100 meters, the cells covering an area of one hectare. However, maps were produced at 30 meters and 1 kilometer to test the affect resolution has on analyses at a state scale. At thirty meter resolution, Circuitscape could not run on a personal computer (1.30 GHz processor, 64 bit Windows 7, 4 GB RAM) for the extent needed. However, a 1km CS and a 30m CD map are presented. There is little difference between these and a 100m map, most likely due to the scale of the analysis. Corridor and conservation modelers have analyzed multi-state to continental scale extents (McRae and Beier

2007). At a continental scale, a resolution of five kilometers makes sense; at a state or multi-state scale, 100 meters may be too large of a resolution, dependant on the species (Shah and McRae 2008) and how finely detailed the map needs to be for stakeholders (Beier et al. 2011, Glennon and Didier 2010). It is also vital to consider the distance between wildland blocks being connected when selecting a resolution. If a pair of wildland blocks is too close together for a resolution, CD may create a corridor that encompasses both, an unhelpful corridor to say the least (Figures 28-31 and Figure 45 for Circuitscape from Appendix 1).

Comparing the maps in Appendix 2 can show a large difference. For a few maps (e.g. figures 17-20 and 24-31 in Appendix 2) the CT corridor is approximately the same as the corridor from LCP. This is likely from a relatively direct path of high suitability (low cost and resistance) that is contained by lower suitability areas.

The difference map (Figure 20) indicates that attempting to reduce the values of the HSM by a CT output will not alter the pattern of values from the HSM. Small areas, notably low value areas on the HSM may have a negative value (i.e.: the CT output value is greater than the HSM value) when the lower value areas are in either surrounding or surrounded by higher value areas. These areas have relatively high currents, and therefore produce a negative result when subtracted from a low value HSM area.

Theoretical Differences

Many of the theoretical differences in Circuitscape and CorridorDesigner can be seen simply by viewing two maps, one produced by each software package and can easily be identified (Table 5). The main difference between LCP for CorridorDesigner and circuit theory for Circuitscape is

that of directness. CorridorDesigner will prioritize minimizing cost and distance over potentially traversing unsuitable habitat (e.g. drier areas for the Southern Two-Lined Salamander; Figure 9 in Appendix 1) or realistically non-traversable land (e.g. urban areas for the Southern Two-Lined Salamander; data not presented). Circuitscape is a stepwise analysis that will consider each connecting cell to the current cell, allowing for a less direct, more diffuse corridor in an attempt to mimic species dispersal behavior. This also makes the analysis more likely to fail due to a break in the current (the reason the naturalness dataset was transformed by an increase of one; Figure 19).

A philosophy intrinsic to CorridorDesigner is one of choice. Besides the tool that produces the default set of eleven slices, another tool exists that allows the user to set different lowest and highest percent slice sizes, as well as determine the intervals at which the slices are made, giving additional options to stakeholders in this project (Beier et al. 2011, Glennon and Didier 2010). To help in the selection of viable corridors in another tool included in the toolbox. There is a corridor width tool that compares the narrowest width of the corridor to the habitat population/breeding patch size, allowing modelers to determine which corridors are viable. This opens up a number of different choices (in terms of the amount of land to conserve) that Circuitscape does not have readily available. A similar sort of delineation is possible for Circuitscape output, however, the user will manually have to reclassify the dataset and form the corridor polygons within ArcMap. Even then, the cells in the same classification range may not be contiguous (i.e.: connected to produce a corridor; example of contiguous flow can be seen in Figure 8.C. in McRae et al. 2008) as suggested by Table 3a. That is not to say there will not be easily defined corridors (i.e.: Figures 17-20 in Appendix 2).

Connection to Application

It should be noted that the maps and values associated with said maps resulting from this study are not meant to be used as conservation plans or basis for conservation plans. The maps and values are a means to analyze differences between the two methods only.

CorridorDesigner can be viewed as a partial area of interest (AOI) analysis. Not because the method of analysis (a least-cost path analysis on the AOI), but because the result is a portion of the total area. Additionally, multiple analyses must be run and then the results manually combined if multiple pairs of wildland blocks need to be connected with corridors. The fact that the analysis results with a partial AOI suggests that the design philosophy of the toolset is based around giving options to stakeholders (Beier et al. 2007, Beier et al. 2011).

While CorridorDesigner produces partial AOI results, Circuitscape results encompass the whole AOI. The results presented show a gene flow model for the AOI, in this case, the state of South Carolina. Circuitscape produces both individual and cumulative maps, which can be used for corridor design and overall corridor and conservation planning, respectively. Individual corridors can be used between two protected areas, similar to how CorridorDesigner is used, likely with a different path. Since CD utilizes least-cost path analyses, the corridor produced is usually a direct path; direction changes only occur at areas of low suitability (Theobald 2006). CT is not constrained by costs and distances, but by the resistance of the landscape (see s 18-21 for LCP and Figure 22 for CT in Appendix 1) The high flow areas in the cumulative map not captured otherwise by individual corridors can be further considered as conservation projects; not necessarily tied to specific corridors (i.e. not required for specific corridors) but potentially required for overall gene flow.

Three drawbacks should be known about Circuitscape output. Firstly, there is no implied timeframe in the output (McRae et al. 2008, Beier et al. 2008). The gene flow shown may take weeks (i.e. Black Bear movement across the state) or generations (Southern Two-Lined Salamanders dispersing throughout their range) reach the extents shown in the model. While CorridorDesigner treats movement the same as Circuitscape (Beier et al. 2008), CD is assumed to follow areas that are generally high in suitability values (due to attempting to find the least costly path). Because of this generally valid assumption, the corridor can also act as an intermediate habitat area in multigenerational dispersal species, needing minimal extra conservation action within the corridor for intermediate habitat areas. Since Circuitscape doesn't necessarily follow high suitability values, intermediate habitat areas may need to be designed and constructed in addition to other conservation actions. A distance-decay function may be used on Circuitscape inputs to modify the resistance values (i.e. higher resistance from source area) to limit model activity to a single generational timeframe's worth of movement for a given species (Paul Leonard, 2013, pers comm.).

The second drawback from Circuitscape is that high flow values can be a product of 1) proximity to the source/ground focal nodes, 2) proximity to assumed impermeable landscape features (i.e. roads and large streams; seen in Figure 16 in Appendix 1), and 3) high flow due to natural landscape variations. High flow from proximity to focal nodes will be removed with a cumulative map if more than two focal nodes were used (increasing nodes decreases the effect high voltage at the nodes), and through using an analysis window larger than the AOI (allowing the removal of focal node voltage biasing the flow model; Koen et al. 2010). High flow values from proximity to assumed impervious areas such as roads can be changed by increasing the

suitability of roads (decreasing the resistance) and the same for streams since these values are likely an artifact of HSM production (i.e. vector to raster conversion and analysis). However, this can lead to vastly different results, and should not be done to remove the imperviousness of roads completely. If a change in road permeability is decided upon, a sensitivity analysis should be performed to determine the effect such a change will have (Beier et al. 2007). Secondly, for areas that have high flow values from modeled landscape variation, inspection of the landscape (either through the HSM or ground truthing/aerial photography) should be conducted to determine what sort of conservation planning is necessary (e.g. if the habitat is low quality, improve it; if there is just too little quality habitat, expand it) to make sure that the area conserved is sufficient (Glennon and Didier 2010). Pinch points, areas of high flow, can be used as a prioritization metric. Pinch points are located within a corridor (such as within a CD model) would most likely give the most problems to a viable corridor. Conversely, working on the pinch point to increase flow (i.e. promote species dispersal in the areas around the pinch point) will make that corridor a more viable one.

Finally, once the corridor has been created, a transparent method must be used to delineate a corridor. There is no single method which easily defines a Circuitscape corridor like those presented in McRae and others (2008), or an easily visible corridor such as those produced by CorridorDesigner; this is especially true when the output is similar to figure 5 in Appendix 1.

Other methods

In addition to CorridorDesigner and Circuitscape, other methods of corridor planning and conservation modeling have been developed.

The Connectivity Analysis Toolkit (CAT) is a recently released modeling tool that utilizes the centrality metric to analyze connectivity (shortest path analysis output can be seen in Figure 21). Centrality finds the relative importance of each node in the graph (Carroll et al. 2012). CAT is capable of doing this in multiple methods, including a distance/cost method with similar results to a Circuitscape. Linkage Mapper (LM) is another new software package in active development (McRae and Kavanagh 2011). LM is similar to CD in that it uses least-cost path analysis to create corridors, and is a set of tools requiring installation in ArcMap. The tools that are required include Linkage Mapper and Confore Tools (a separate package). The difference is that Linkage Mapper incorporates the idea of resistance (cost) into the corridor produced (McRae and Kavanagh 2011), showing possible corridor sizes, instead of needing multiple polygons. Linkage Mapper mosaics multiple corridors together if applicable, speeding up the process of connecting multiple wildland blocks (McRae and Kavanagh 2011).

Future research

Continuing research in the field of connectivity modeling is important for multiple reasons. The first is that models including more detailed data will give a more realistic picture of viable corridors. One inclusion that may provide a more realistic picture would be a water quality dataset. This would mostly affect the species with a high intolerance for low water quality and those with an aquatic life stage. A second addition to future corridor modeling is the inclusion of generational dispersal distances within the model. This can be modeled through the use of a distance-decay model that increases the resistance the further away from a source habitat area.

Conclusions

The two methods discussed, CorridorDesigner and Circuitscape, are both invaluable tools used to identify areas important for connectivity in conservation modeling. CorridorDesigner uses least-cost path analysis to connect two wildland blocks while making corridors of a range of sizes, allowing options for stakeholders and planners alike. Circuitscape uses circuit theory to analyze a whole landscape and model potential corridors for gene flow; these corridors can be utilized as the basis for further conservation plans or as corridors in and of themselves. In addition to both being valuable tools, they can complement each other.

While easy to use and produces readily understandable corridor models, CorridorDesigner¹ can possibly model a short corridor across realistically non-traversable habitat. Circuitscape however, produces full landscape genetic flow models that may have no transparent, objective method to produce a corridor plan, but rarely has large flow volumes crossing non-traversable habitat. Pinch points from Circuitscape within corridors produced by CorridorDesigner can be used to locate areas that would need additional work when creating the corridor (i.e. prioritized areas). Circuitscape can highlight areas not included in CorridorDesigner's corridor, while CorridorDesigner can be used to come to a compromise between human stakeholders' requirements for animal movement. Using both modeling methods in such a way will promote higher gene flow through corridors by prioritizing areas within the planned corridors.

Table 1. Factors used to choose and used in the habitat suitability modeling for each species. The information was gathered from the respective literature sources.

Species	Size	Habitat Specificity	Habitat requirements	Human disturbance tolerance
Black Bear	Large	Low	General	Medium
Southern Two-Lined Salamander	Small	High	Stream dependence	Low to medium
Eastern Spotted Skunk	Medium	high	Little to no human disturbance	Low
Pygmy Rattlesnake	Small	Medium	Prefers xeric sites	Low to medium

Table 2. CN_LEVEL2 classifications for the landcover dataset with the reclassifications for each species. The value is the number that the raster classifications are labeled with. The reclassification for the different species is based on literature for each species.

VALUE	CN_LEVEL2	Black Bear	Pygmy Rattlesnake	Eastern Spotted Skunk	Southern Two-Lined Salamander
1201	Developed	1	3	1	1
1202	Developed	2	1	2	1
1203	Developed	2	1	2	2
1204	Developed	2	1	2	2
1301	Mining	3	1	2	2
1402	Agriculture	3	3	1	3
1403	Agriculture	4	3	1	3
2102	Open water	4	2	3	4
2103	Open water	4	2	3	4
3105	Beach, shore and sand	5	4	4	5
3110	Beach, shore and sand	5	4	4	5
3119	Beach, shore and sand	5	4	4	5
3120	Beach, shore and sand	5	4	4	5
3210	Cliff, canyon and talus	6	5	5	5
3220	Cliff, canyon and talus	6	5	5	5
3606	Other sparse and barren	6	5	5	5
4106	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	6
4107	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	7
4109	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	6
4125	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	6
4127	Deciduous dominated forest and woodland (xeric-	8	6	6	6

	mesic)				
4130	Deciduous dominated forest and woodland (xeric-mesic)	7	6	6	6
4133	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	6
4146	Deciduous dominated forest and woodland (xeric-mesic)	8	6	6	6
4202	Deciduous dominated forest and woodland (mesic-wet)	9	7	6	7
4206	Deciduous dominated forest and woodland (mesic-wet)	9	7	6	7
4209	Deciduous dominated forest and woodland (mesic-wet)	9	7	6	7
4210	Deciduous dominated forest and woodland (mesic-wet)	9	7	6	6
4212	Deciduous dominated forest and woodland (mesic-wet)	9	7	6	6
4302	Mixed deciduous/coniferous forest and woodland (xeric-mesic)	10	6	6	8
4305	Mixed deciduous/coniferous forest and woodland (xeric-mesic)	10	6	6	8
4308	Mixed deciduous/coniferous forest and woodland (xeric-mesic)	11	6	6	8
4310	Mixed deciduous/coniferous forest and woodland (xeric-mesic)	10	6	6	8
4331	Mixed deciduous/coniferous forest and woodland (xeric-mesic)	11	6	6	8
4401	Mixed deciduous/coniferous forest and woodland (mesic-wet)	12	7	6	9

4403	Mixed deciduous/coniferous forest and woodland (mesic-wet)	12	7	6	9
4504	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4505	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4506	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4536	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4537	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4538	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
4553	Conifer dominated forest and woodland (xeric-mesic)	13	6	6	9
5214	Scrub shrubland	15	8	6	10
5508	Deciduous dominated savanna and glade	15	8	7	10
7503	Sand prairie, coastal grasslands and lomas	15	8	6	10
8102	Harvested forest	16	8	7	10
8103	Harvested forest	16	8	7	10
8107	Harvested forest	16	8	7	10
8108	Harvested forest	16	8	7	10
8201	Managed forest (plantations)	17	8	7	10
8202	Managed forest (plantations)	16	8	6	10
9103	Salt, brackish and estuary wetland	19	9	8	11
9206	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9207	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9208	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9211	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9218	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9232	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9239	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9243	Freshwater herbaceous marsh, swamp, or baygall	20	9	8	11
9301	Freshwater forested marsh, or swamp	20	9	8	12
9302	Freshwater forested marsh, or swamp	21	9	8	12
9303	Freshwater forested marsh, or swamp	20	9	8	12
9703	Depressional wetland	22	9	8	13
9715	Depressional wetland	22	9	8	13

9801	Floodplain and riparian	23	9	9	14
9806	Floodplain and riparian	23	9	9	14
9827	Floodplain and riparian	24	1	8	14
			0		
9838	Floodplain and riparian	24	9	8	14
9841	Floodplain and riparian	23	9	8	14
9842	Floodplain and riparian	23	9	8	14
9843	Floodplain and riparian	23	9	8	14
9845	Floodplain and riparian	23	9	8	14
9850	Floodplain and riparian	24	9	8	14
9903	Flatwood	25	1	8	15
			0		
9906	Flatwood	25	1	6	15
			0		
9907	Flatwood	25	1	6	15
			0		

Table 3a. Means and confidence intervals for the pinch point capture percentage at the four slice sizes with an alpha of 0.05.

Slice Size	Mean (%)	Lower CI	Upper CI
0.1%	12.76	2.56	22.93
1.0%	26.53	13.39	39.68
5.0%	46.52	29.28	63.76
10.0%	57.20	38.23	76.18

Table 3b. Results from post-hoc Tukey test with an alpha of 0.05. Results from a LSD test are statistically the same.

Slice Size	Mean (%)	Grouping
0.1%	12.76	A
1.0%	26.53	AB
5.0%	46.52	BC
10.0%	57.20	C

Table 4. Significance results from Tukey’s post-hoc test at a 95% confidence level for the means, standard deviations, and ranges for each map type. Cells marked with “***” indicate a significant difference in the comparison (i.e.: Method X minus Method Y) for the statistic type.

Map Comparison	Mean	Standard Deviation	Range
LCP – CT	***	***	
LCP– Cumulative	***	***	***
Cumulative – LCP	***	***	***
Cumulative – CT			***
CT – LCP	***	***	***
CT - Cumulative			

Table 5. Differences in results based on the underlying theories of CD and CS.

Difference	CorridorDesigner	Circuitscape
Theory	Least-Cost Path	Circuit Theory (Ohm's Law) Graph Theory
Specificity	High	Low
Inclusivity	Low	High
Determining Corridor	Simple	Potentially complex

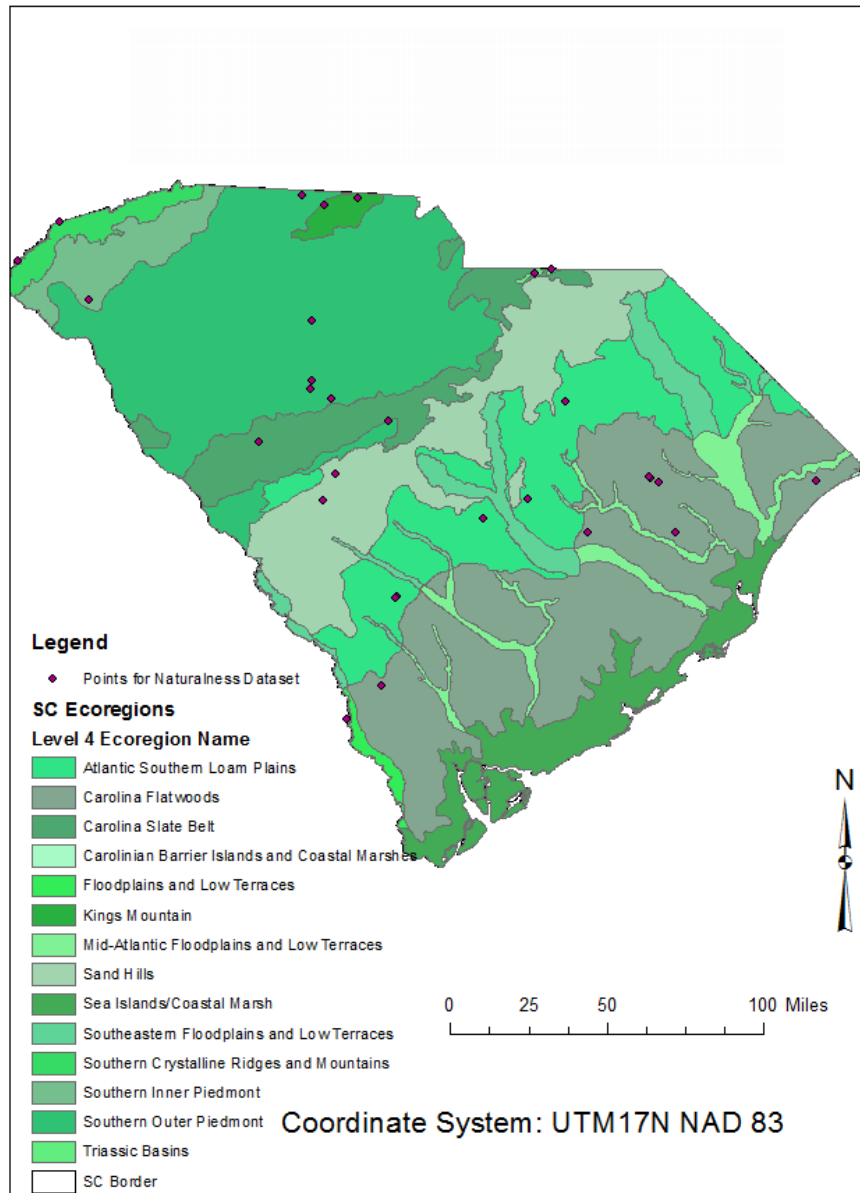


Figure 1. Ecoregions located within South Carolina. The ecoregions were used to prepare a stratified random sampling for the naturalness dataset wildland blocks. The points shown were produced with a minimum of 3 points per ecoregion, and increased with percent of total area of the study area.

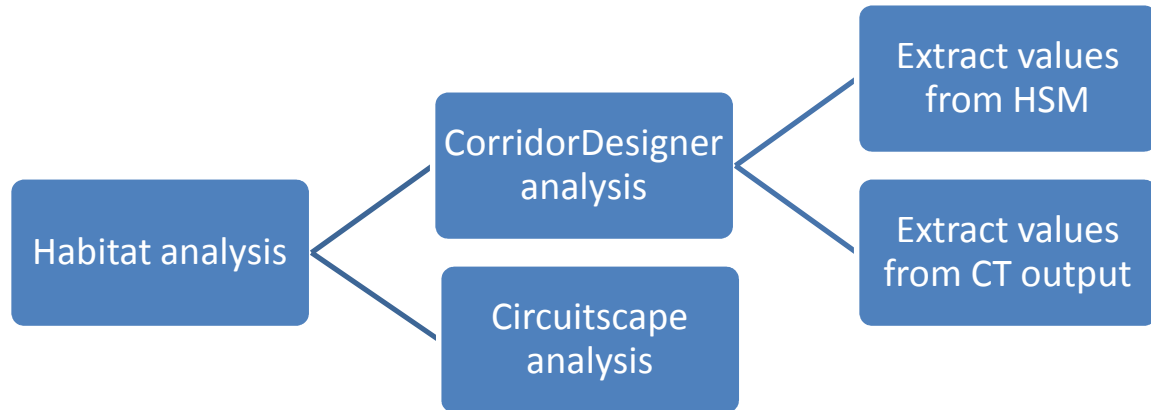


Figure 2. Workflow chart for the extraction from LCP and CT output statistics using the Zonal Statistics tool from ArcMap. The LCP output (corridor shapefiles) was used to extract the value for from the HSM and CT output files (individual and cumulative CT maps).

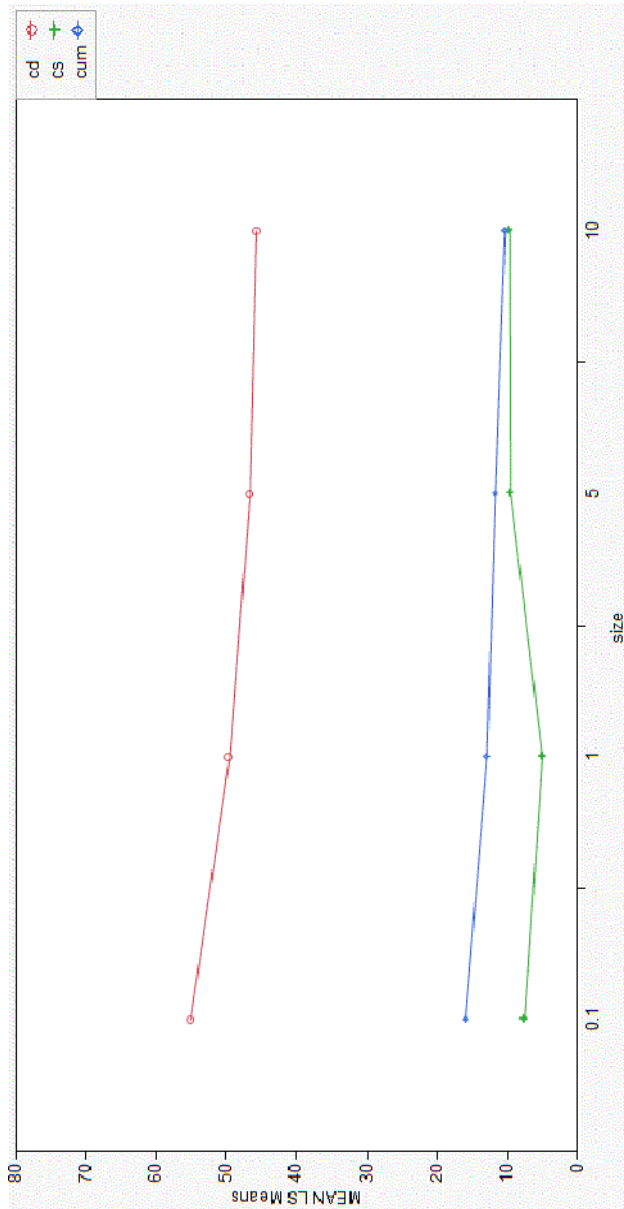


Figure 3. Means for Black Bear corridors. The means for Black Bear extractions generally decrease as size of corridors increase across the three methods. The means were greatest when extracted from the HSM, and least when extracted from the individual CT output.

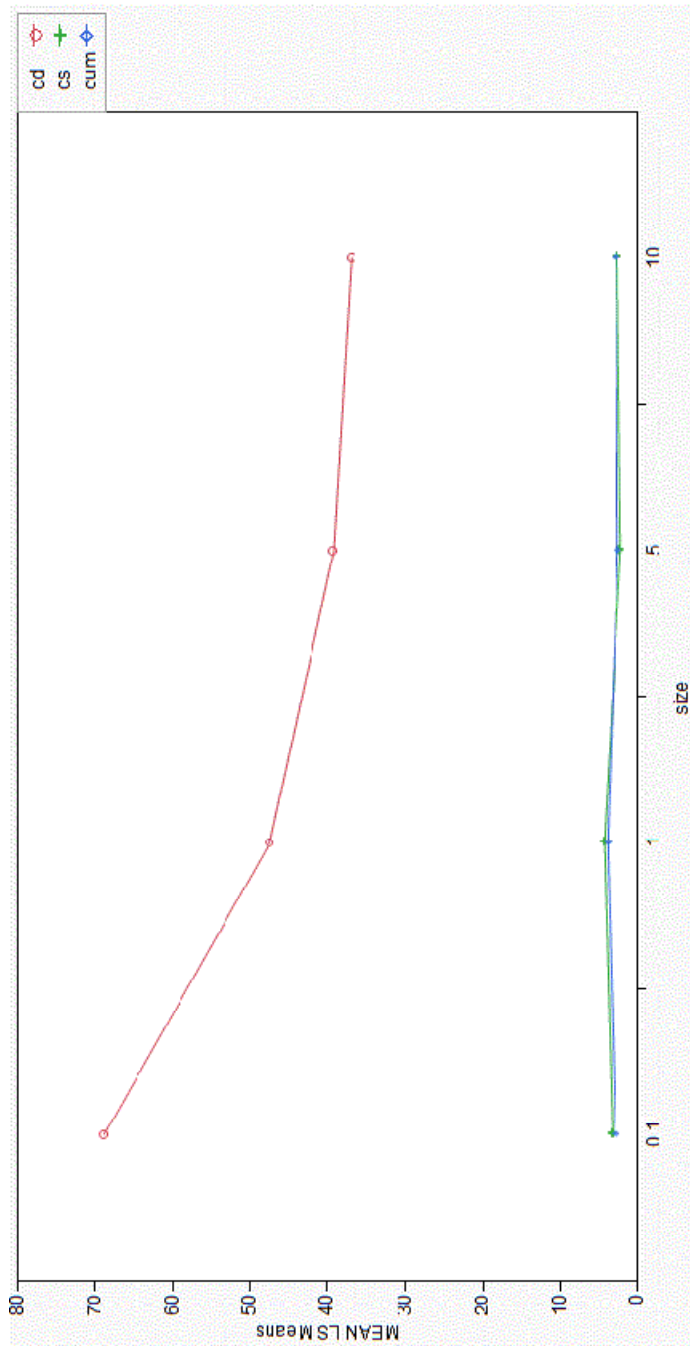


Figure 4. Means for Southern Two-Lined Salamander corridors. The means for Southern Two-Lined Salamander extractions generally decrease as size of corridors increase across the three methods. The means were greatest when extracted from the HSM, and the individual CT and cumulative CT outputs were approximately the same.

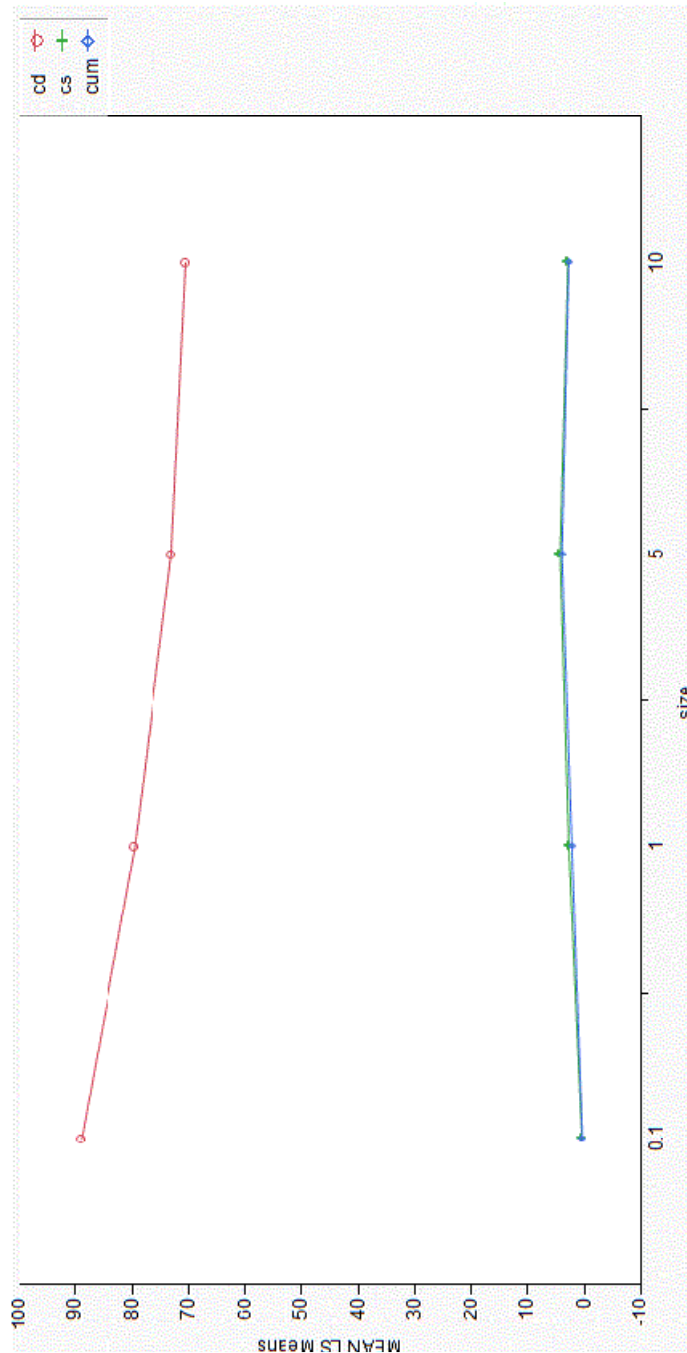


Figure 5. Means for Eastern Spotted Skunk corridors. The means for Eastern Spotted Skunk extractions generally decrease as size of corridors increase across the three methods. The means were greatest when extracted from the HSM, and the individual CT and cumulative CT outputs were approximately the same.

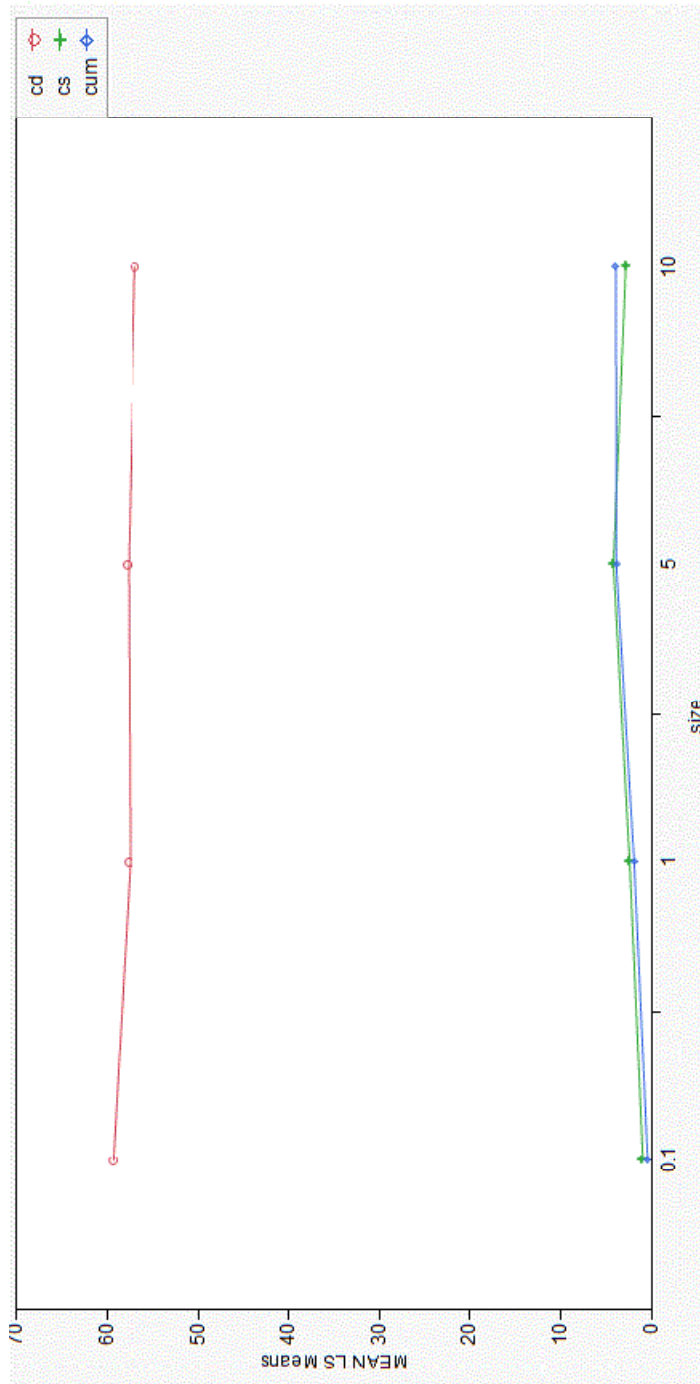


Figure 6. Means for Pygmy Rattlesnake corridors. The means for Pygmy Rattlesnake extractions generally decrease as size of corridors increase across the three methods. The means were greatest when extracted from the HSM, and the individual CT and cumulative CT outputs were approximately the same.

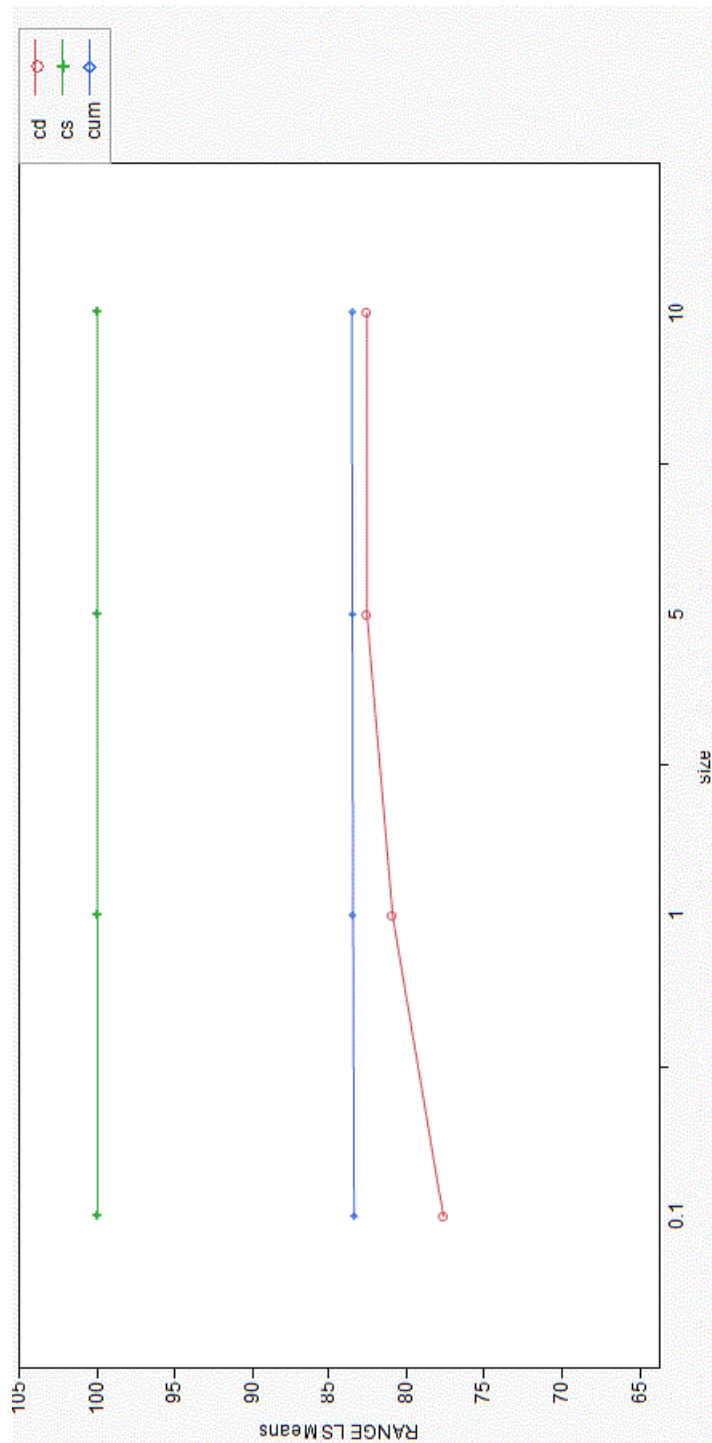


Figure 7. Ranges for Black Bear corridors. The ranges for the Black Bear extraction are constant across all corridor size for but the individual and cumulative CT outputs. The range for the extraction from the HSM increases as slice size increases, but is always the lowest of the ranges.

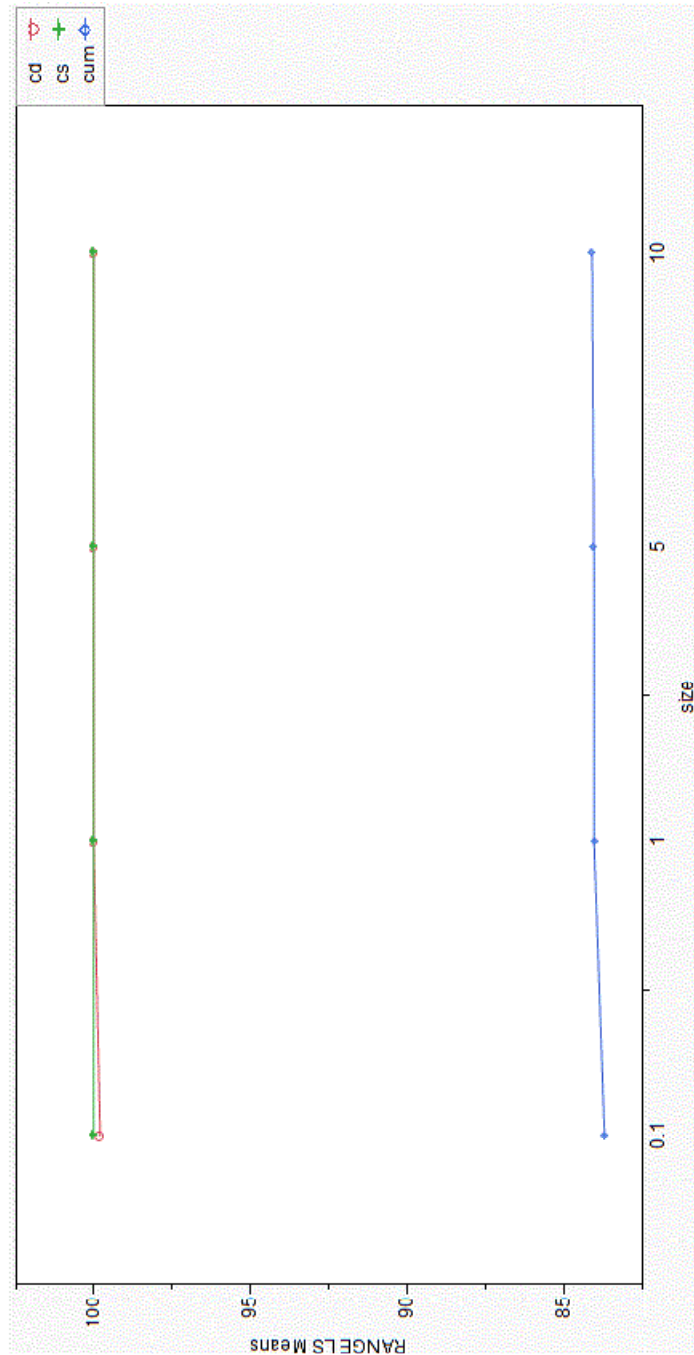


Figure 8. Ranges for Southern Two-Lined Salamander corridors. The CorridorDesigner and the individual CT output extractions are approximately equal except for the 0.1% slice size, where the LCP range is slightly lower. The cumulative CT output is lower, but slightly increases as corridor slice size increases.

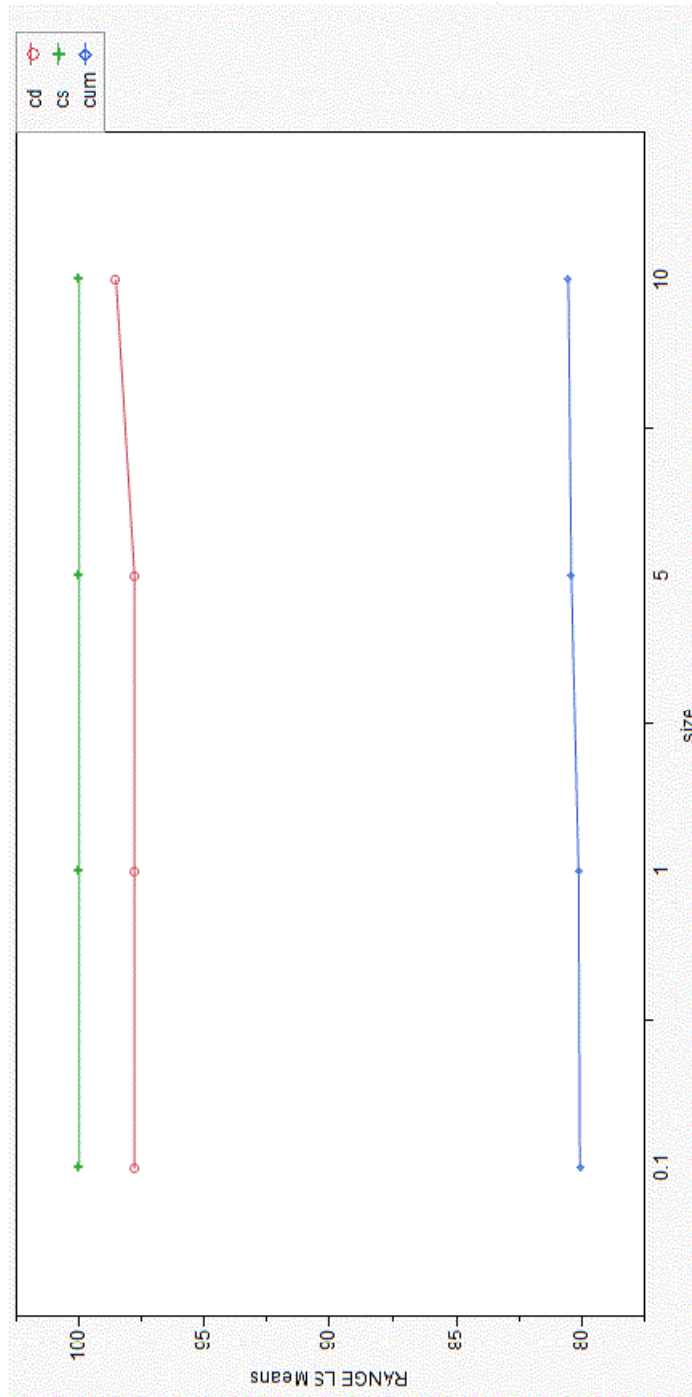


Figure 9. Ranges for Eastern Spotted Skunk corridors. The individual CT range extraction is greatest and constant, while the CorridorDesigner extraction is slightly lower and increases only at the 10.0% slice size. The cumulative CT range extraction is lowest and slightly increases as slice size increases.

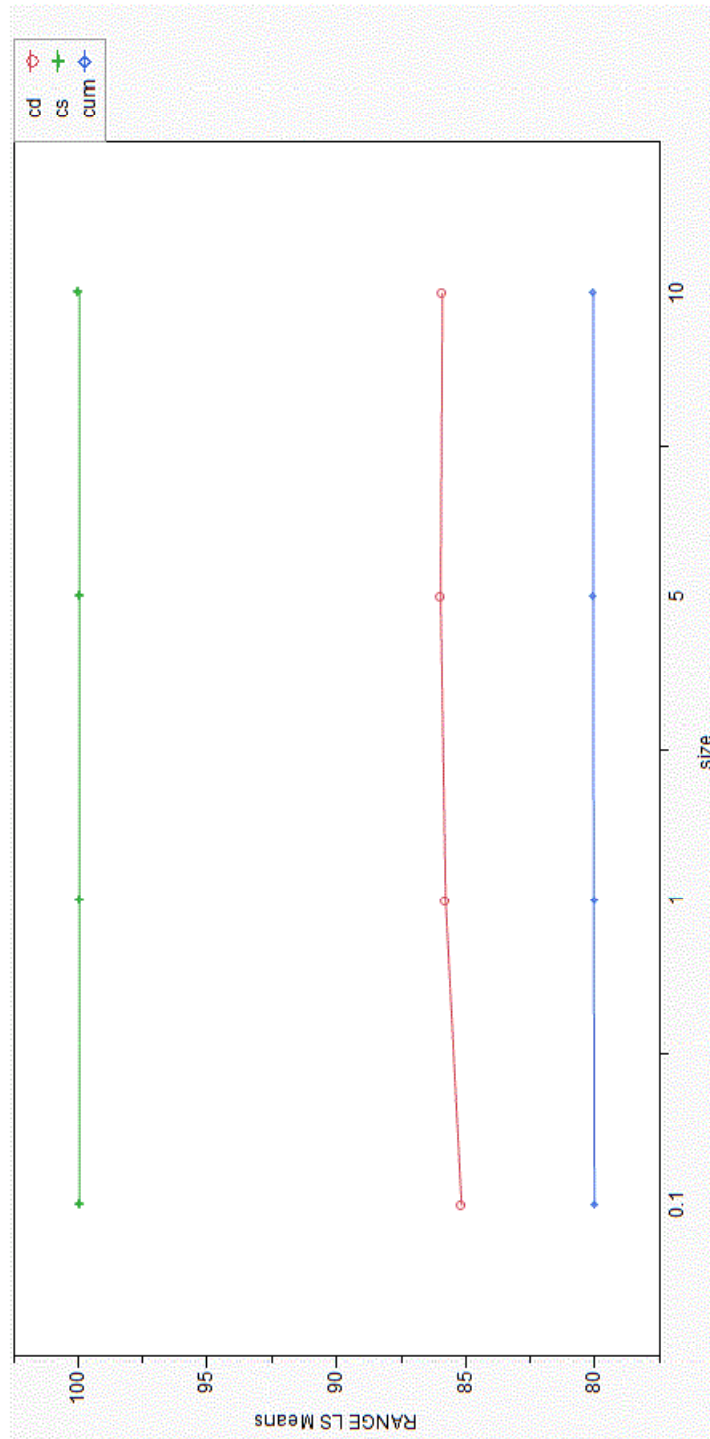


Figure 10. Ranges for Pygmy Rattlesnake corridors. The individual and cumulative CT outputs are constant through all slice sizes, with the individual CT range is the greatest, and the cumulative least of the three methods. The CorridorDesigner range extraction is between the other two methods and increases as slice size increases.

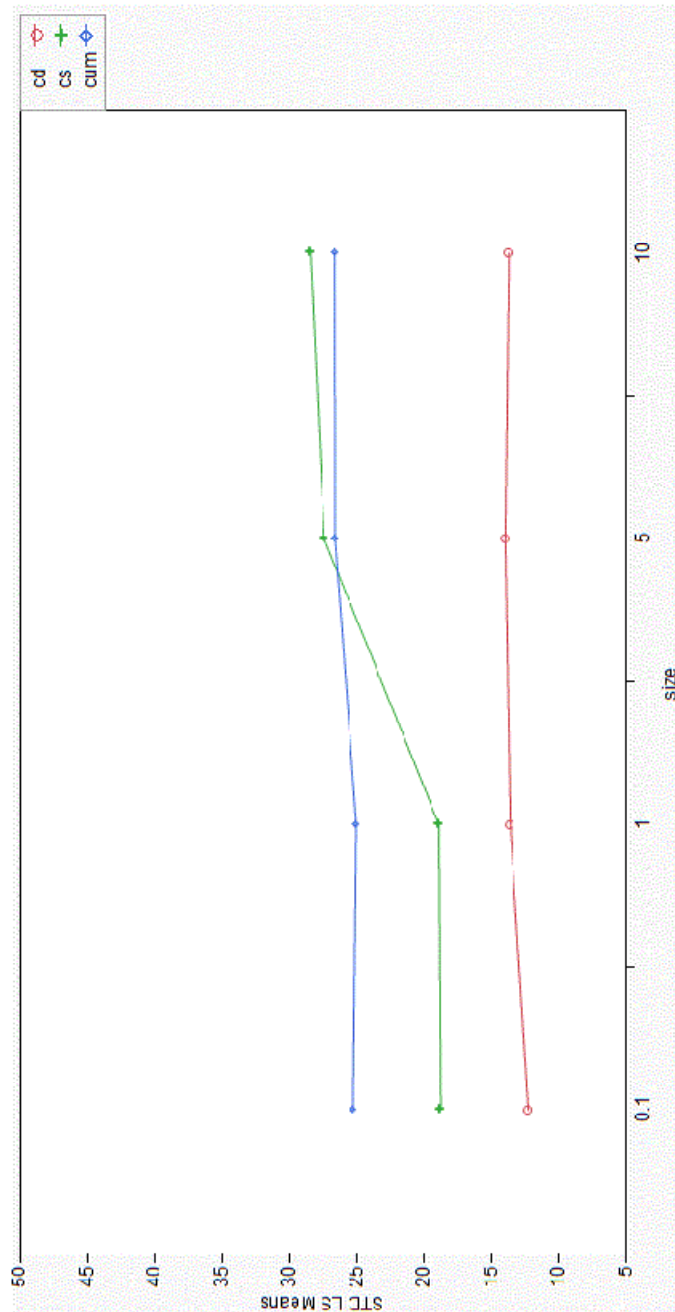


Figure 11. Standard deviations for Black Bear corridors. The standard deviation extractions were greatest in the cumulative CT output for 0.1 and 1.0% slice sizes and in the individual CT output for 5.0 and 10.0% slice sizes. CorridorDesigner standard deviations are the least of the three. The three methods increase as slice size increases, with the individual CT output increasing the most.

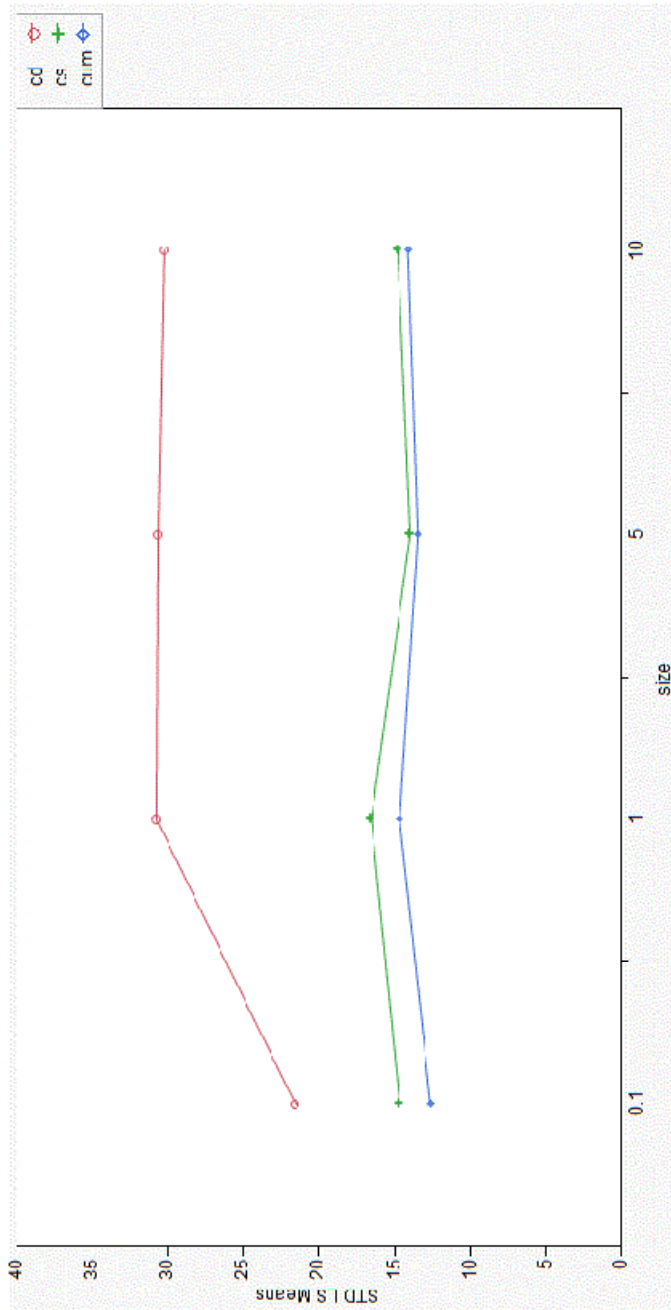


Figure 12. Standard deviations for Southern Two-Lined Salamander corridors. The standard deviation extractions were greatest for CorridorDesigner and the individual CT output standard deviation was slightly higher than the cumulative CT output. All methods increase up to the 1.0% slice size and decreases afterwards. The individual and cumulative CT output increase in the 10.0% slice size.

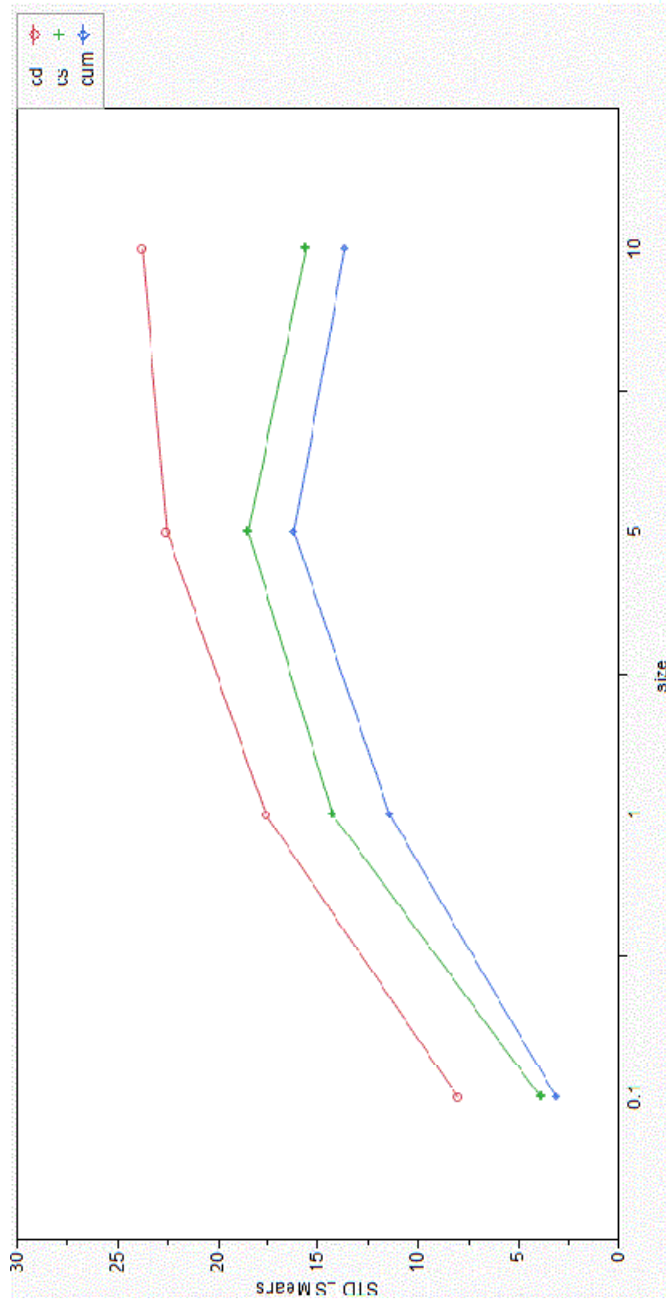


Figure 13. Standard deviations for Eastern Spotted Skunk corridors. The standard deviations for all three methods increase up to the 5.0% slice size, and the CT methods decrease at the 10.0% slice size, while the CorridorDesigner output increases. The LCP output is the greatest and the cumulative CT output is the lowest.

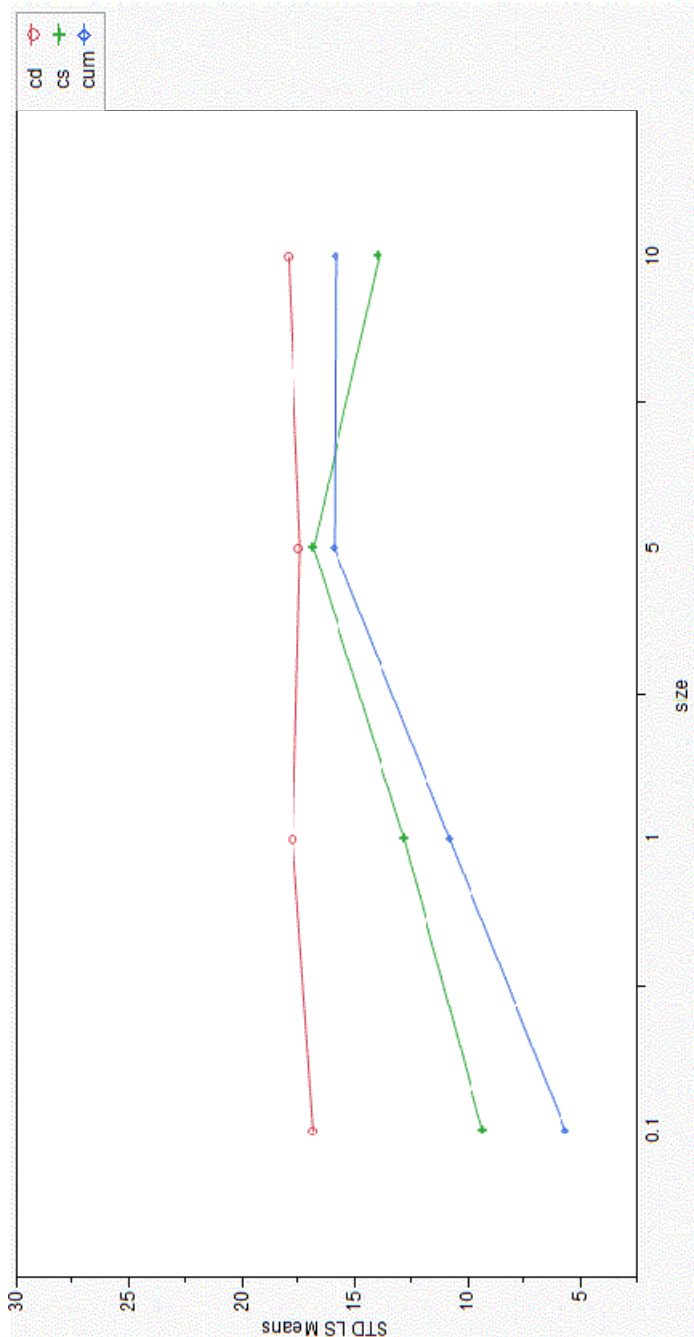


Figure 14. Standard Deviations for Pygmy Rattlesnake corridors. The standard deviation for the CorridorDesigner extraction is the greatest and approximately constant, while both the CT methods increase to the 5.0% slice corridor and decreases slightly for the 10.0% slice size. The cumulative CT output is the least except for the 10.0% slice corridor where the individual CT output is the lowest.

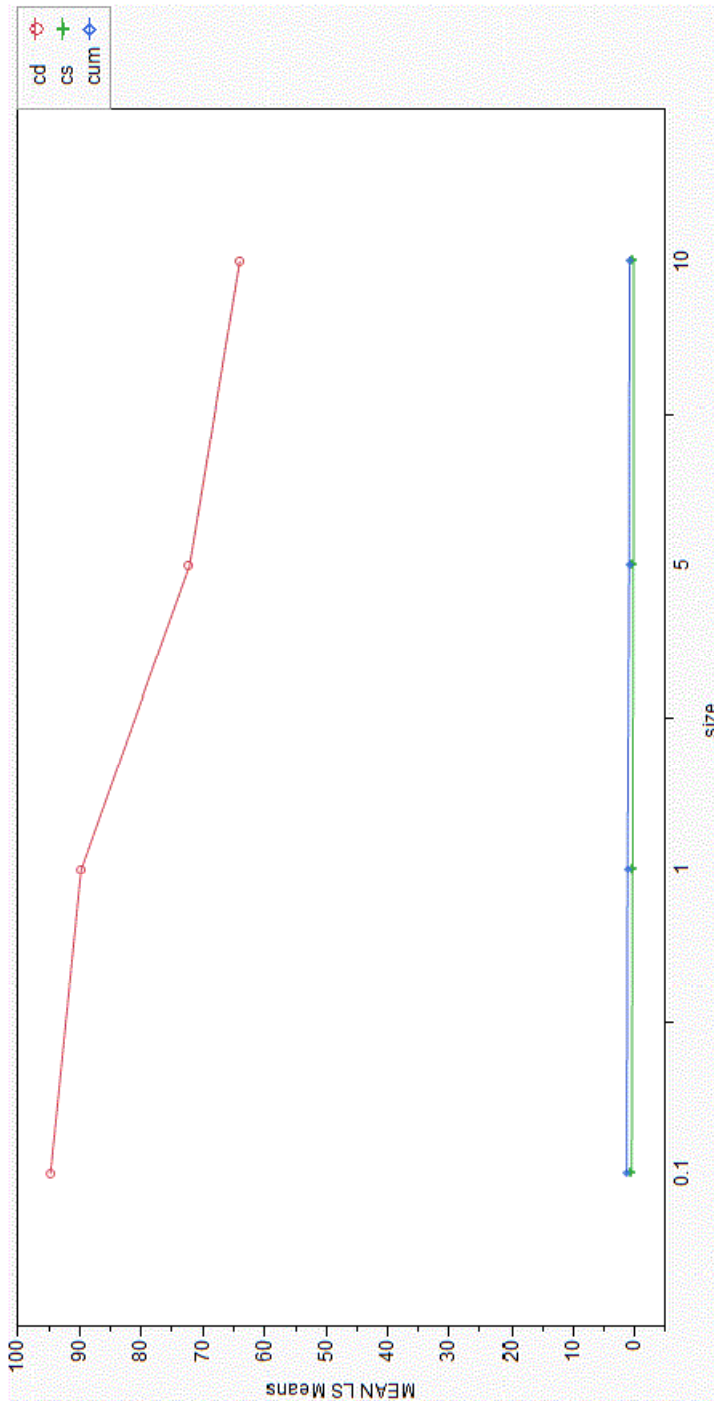


Figure 15. Means for the naturalness dataset corridors. The means for naturalness dataset extractions generally decrease as size of corridors increase across the three methods. The means were greatest when extracted from the HSM, and the individual CT and cumulative CT outputs were approximately the same.

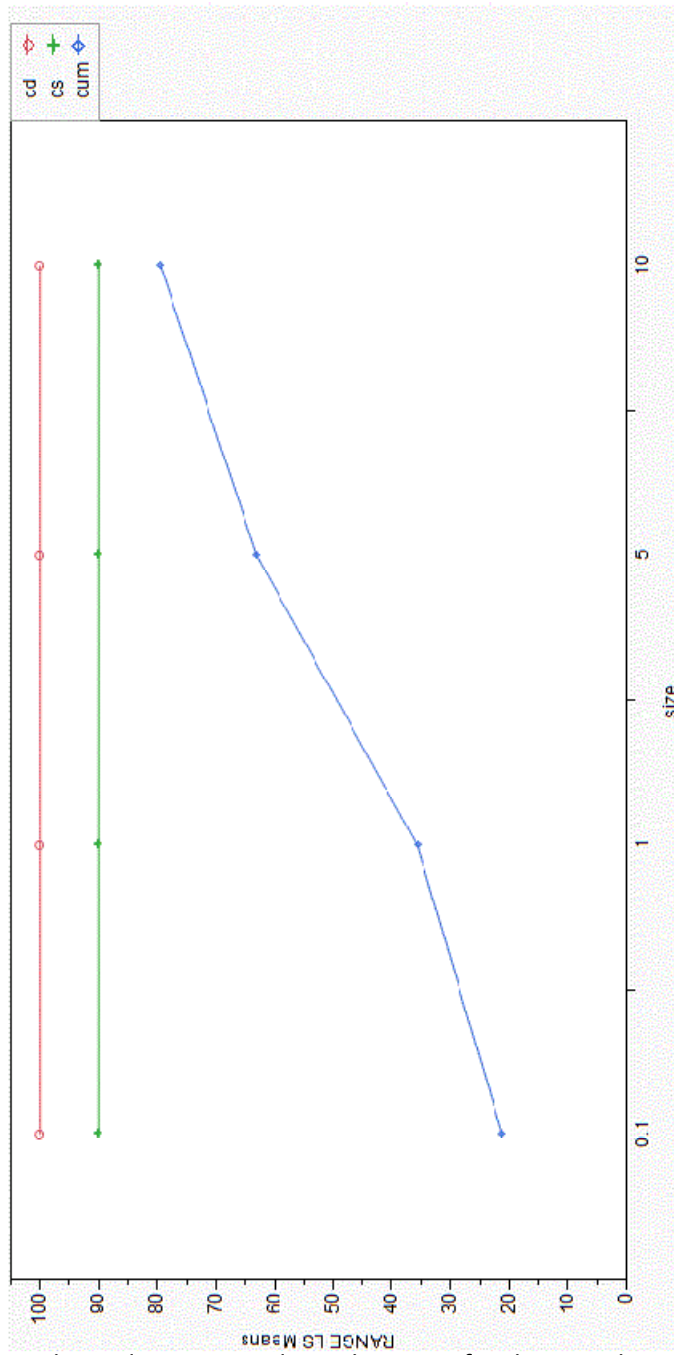


Figure 16. Ranges for the naturalness dataset corridors. The range for the CorridorDesigner extractions was constant through all slice sizes and the highest range of the three methods. The individual CT output was also constant while the cumulative CT output range was the least of the three methods while increasing greatly with the increase of slice size.

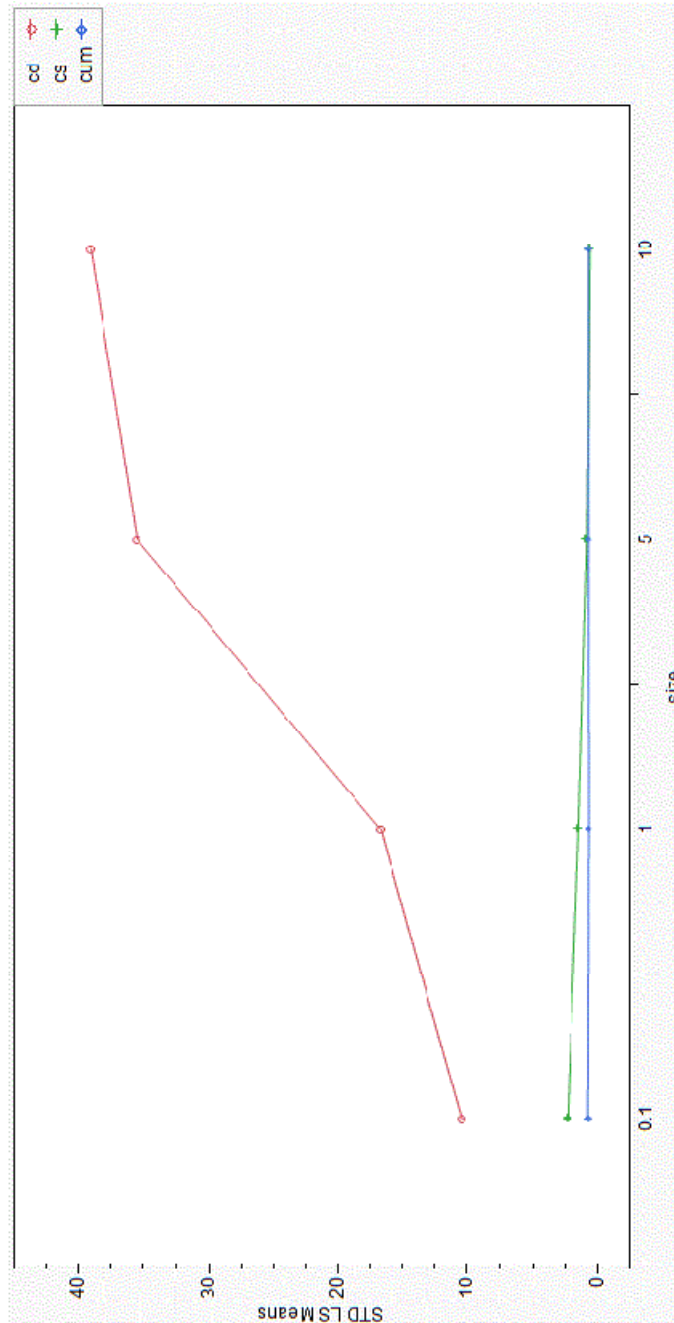


Figure 17. Standard deviations for the naturalness dataset corridors. The standard deviation from the CorridorDesigner extraction is the greatest of the three methods, and increases as the slice size (width of corridor) increases. The cumulative CT output stays constant, and the individual CT output decreases with slice size increase to approximately equal the cumulative CT output.

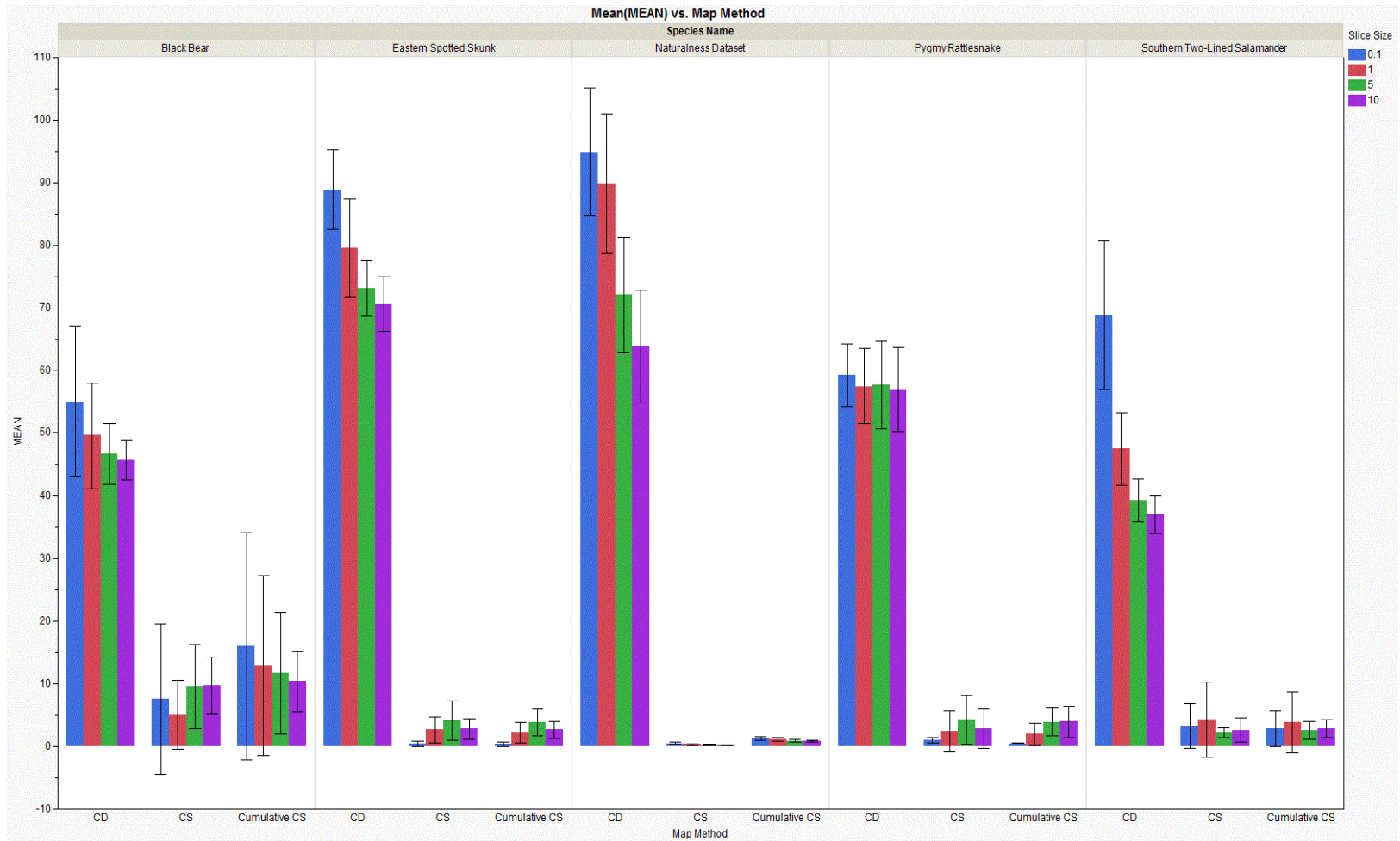


Figure 18. Combined comparisons of the means for the three methods, CD, CS, and cumulative CS, grouped by species and with the slice sizes separated. Blue is 0.1%, red is 1.0% green is 5.0%, and purple is 10% slice size. Error bars are each one standard deviation for the mean of means for the slice size of the species and method type. The species are listed alphabetically.

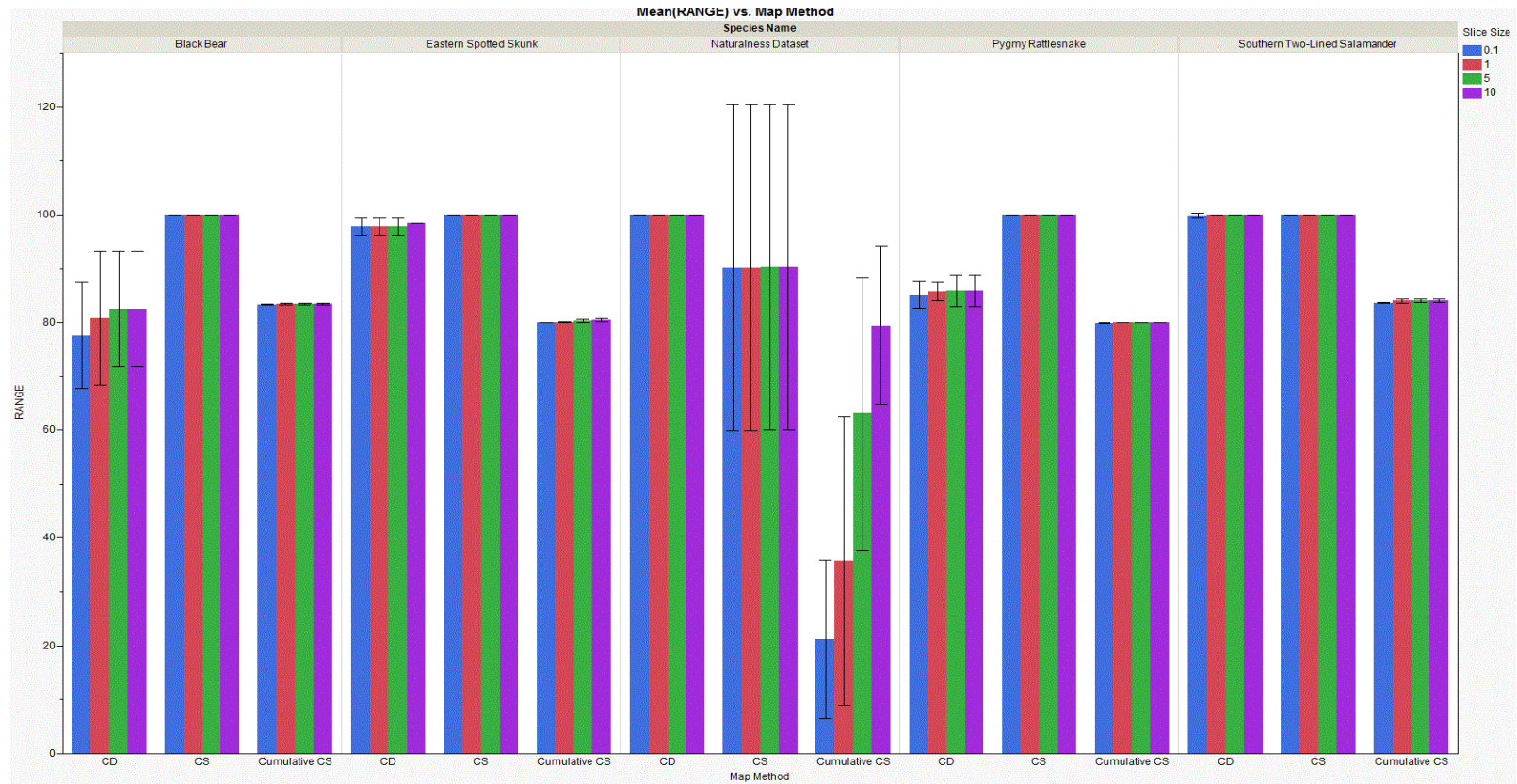


Figure 19. Combined comparisons of the ranges for the three methods, CD, CS, and cumulative CS, grouped by species and with the slice sizes separated. Blue is 0.1%, red is 1.0% green is 5.0%, and purple is 10% slice size. Error bars are each one standard deviation for the mean of ranges for the slice size of the species and method type. The species are listed alphabetically.

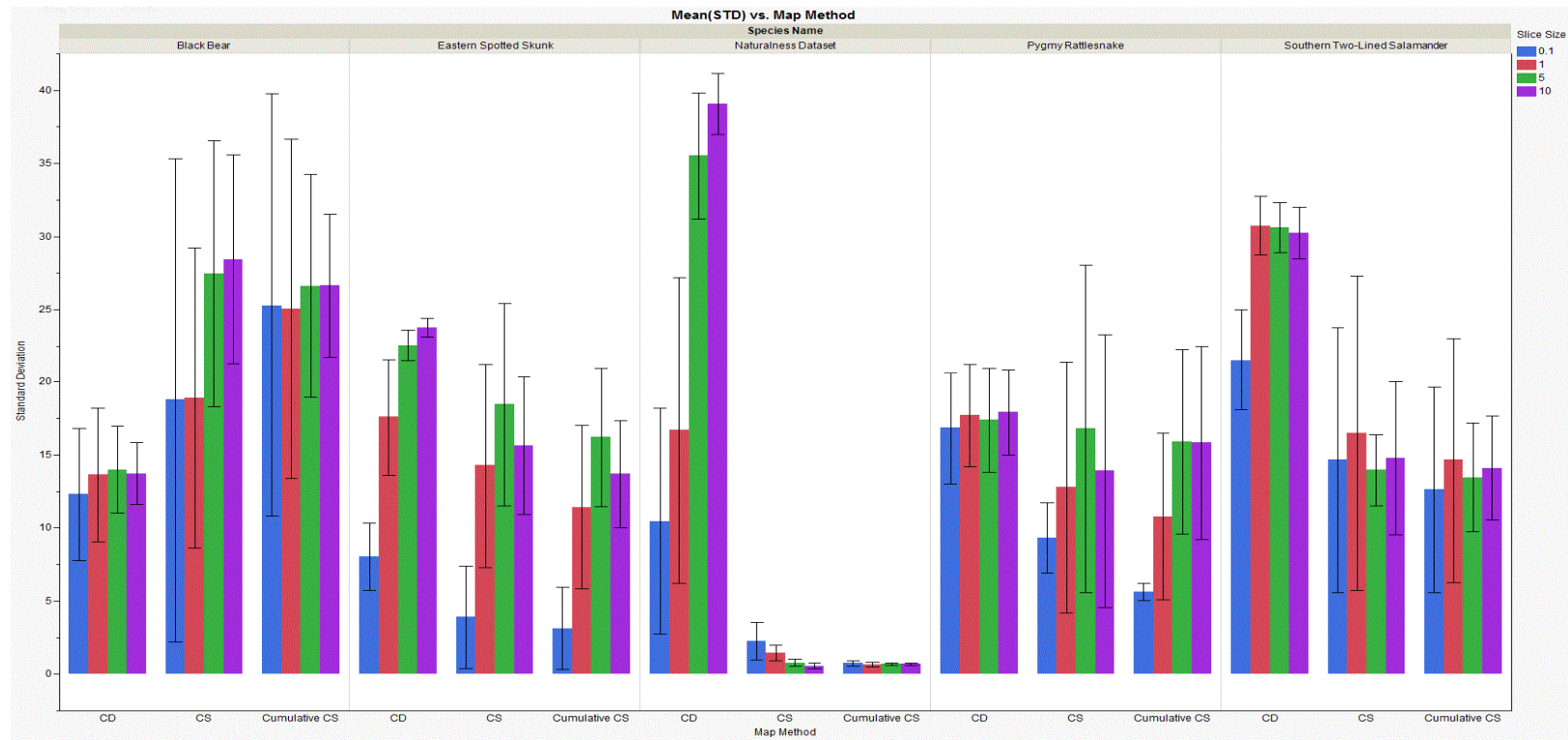


Figure 20. Combined comparisons of the standard deviations for the three methods, CD, CS, and cumulative CS, grouped by species and with the slice sizes separated. Blue is 0.1%, red is 1.0% green is 5.0%, and purple is 10% slice size. Error bars are each one standard deviation for the mean of means for the slice size of the species and method type. The species are listed alphabetically.

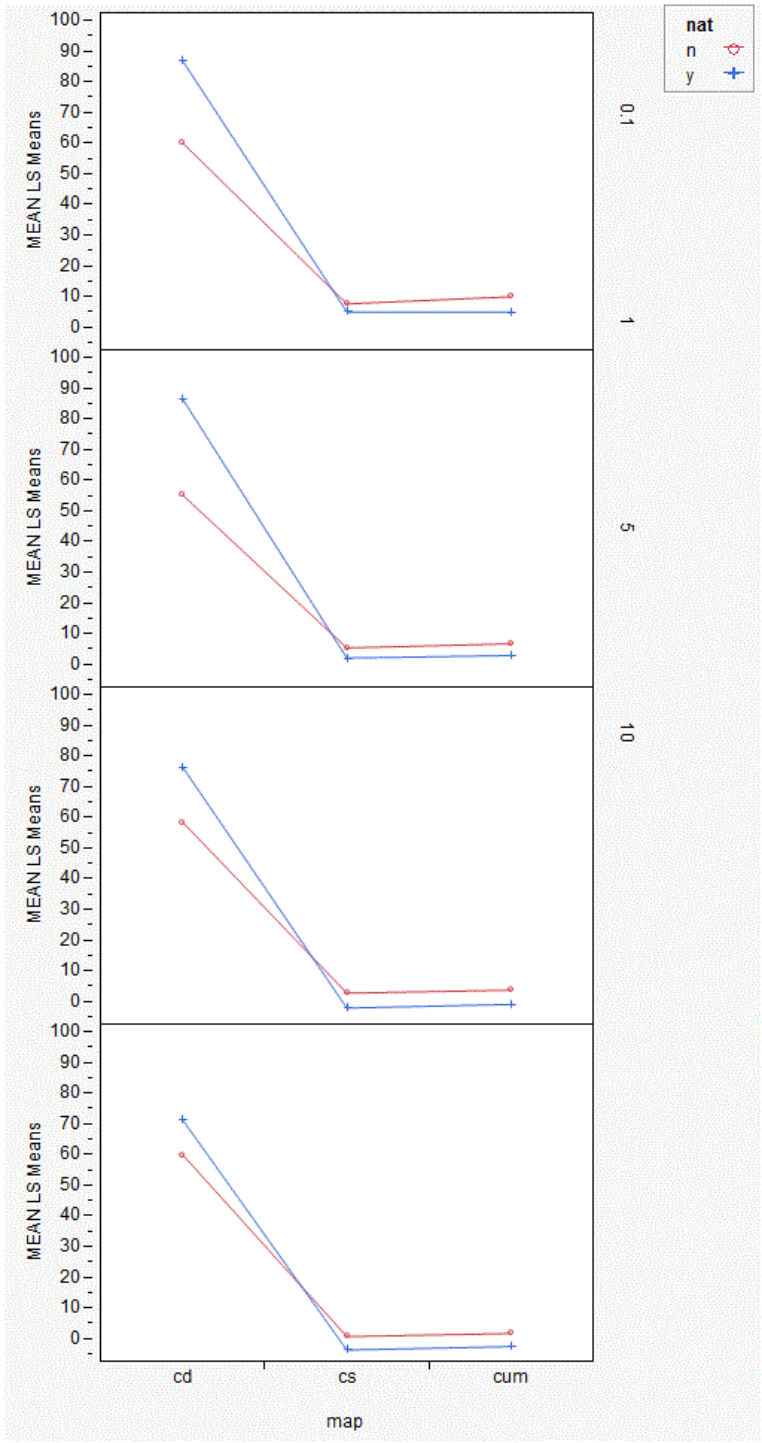


Figure 21. Means of combined species corridors (n) and naturalness dataset corridors (y). The means are highest for CorridorDesigner and lowest for the individual CT method. The highest values are for the naturalness data with the HSM being extracted. The focal species have higher means when either of the CT methods is extracted.

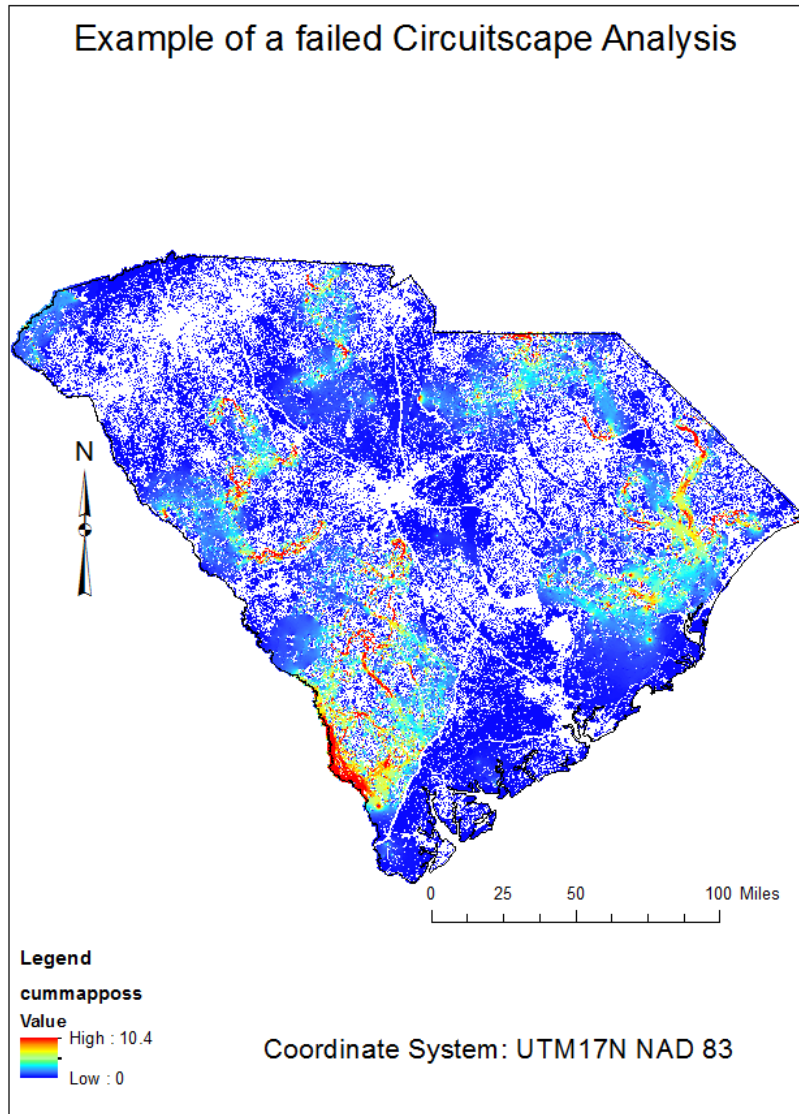


Figure 22. Example of a failed Circuitscape analysis due to zero values present in the landscape map. Circuitscape will not be able to connect two nodes if the path must cross areas of 0 conductances (100% resistance). The cooler (i.e.: blue) areas are areas of lower flow; warm areas (i.e. red) are areas of high flow. Areas in white are NODATA.

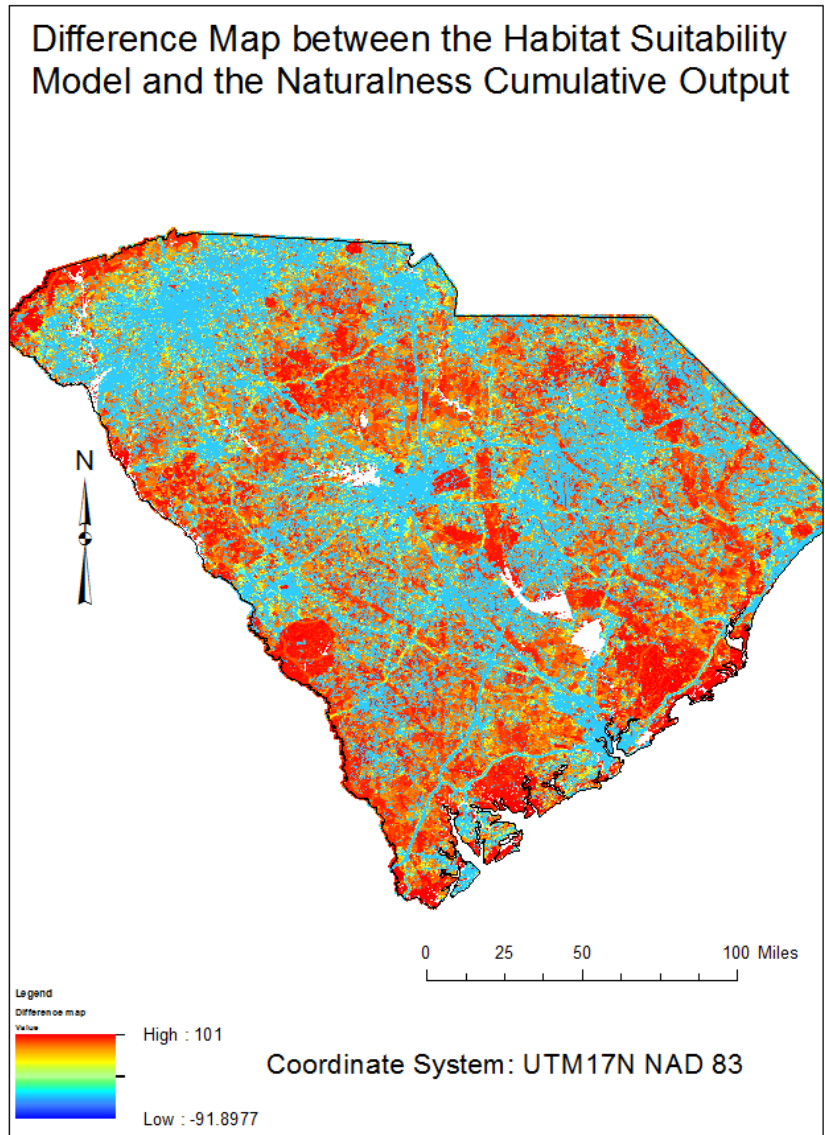


Figure 23. Difference map where the values from the individual Circuitscape output were subtracted from the HSM for the naturalness dataset. The lowest values are 1-2 pixels in size located in the lighter blue areas. The overall pattern of the output follows the HSM. Red areas are positive, meaning the HSM values are greater than the cumulative CS output, while light blue areas are the areas mean no difference between the rasters compared.

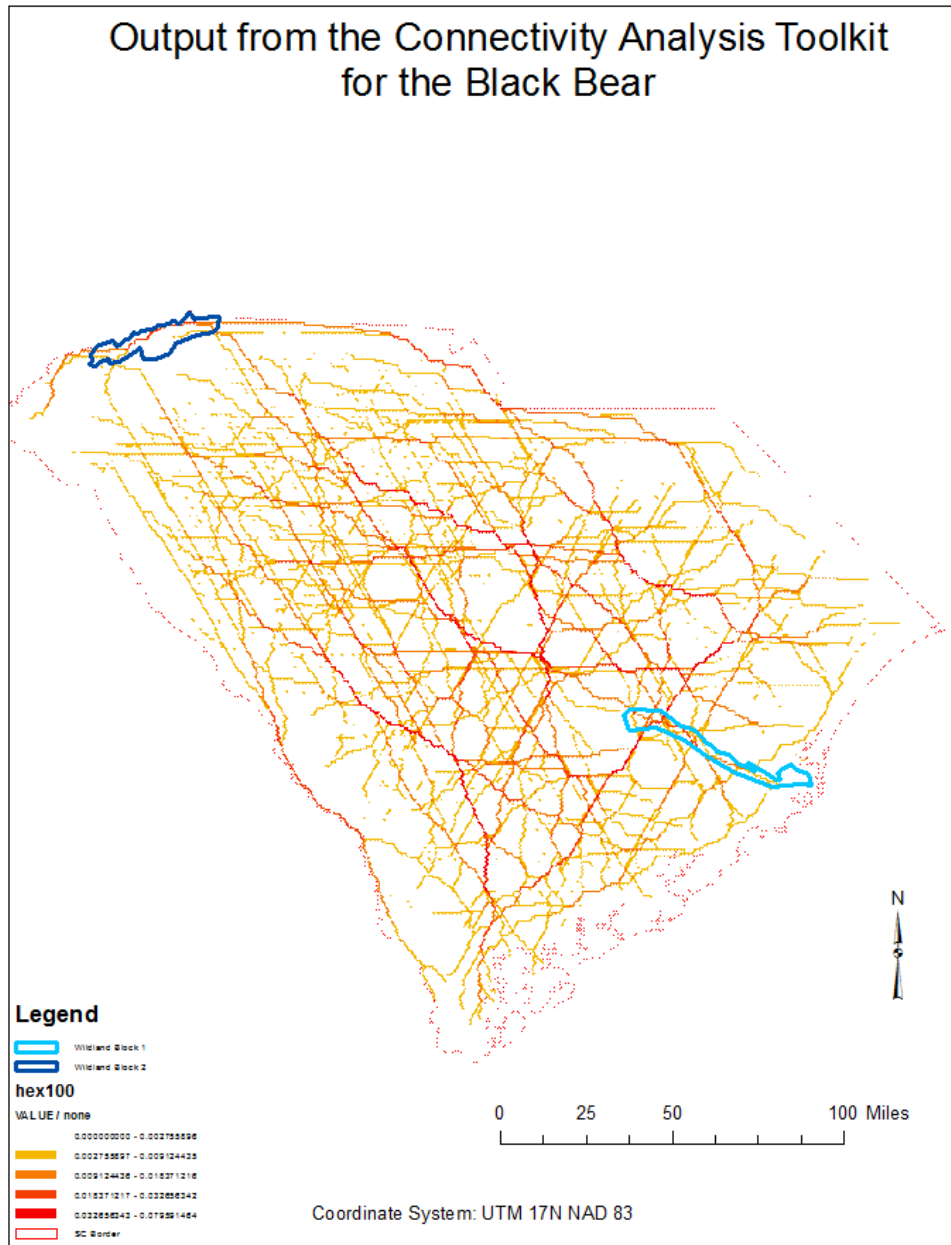


Figure 24. Example of the Connectivity Analysis Toolkit for the Black Bear. The darker red lines are routes of a higher betweenness metric.

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APPENDICES

Appendix 1: Maps Used in the Statistical Analysis

The figures presented in Appendix 1 are the maps and images used in the statistical analysis and visual comparisons discussed above. There is one 0.1, 1.0, 5.0, and 10.0% slice corridor from CD, and the corresponding individual CS and a cumulative CS map for each of the four focal species used in this study. Five each of the above are presented for the naturalness dataset.

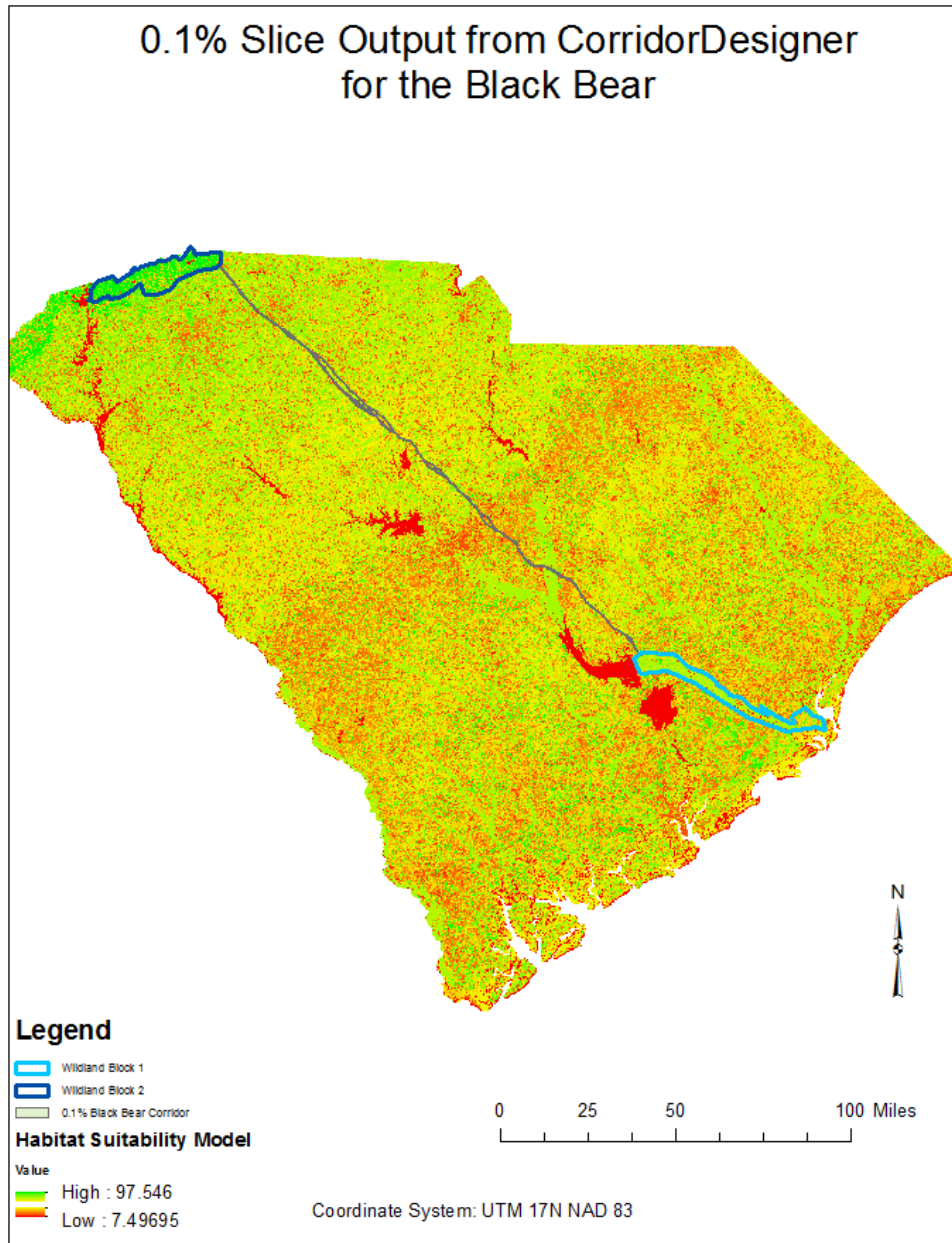


Figure 1.

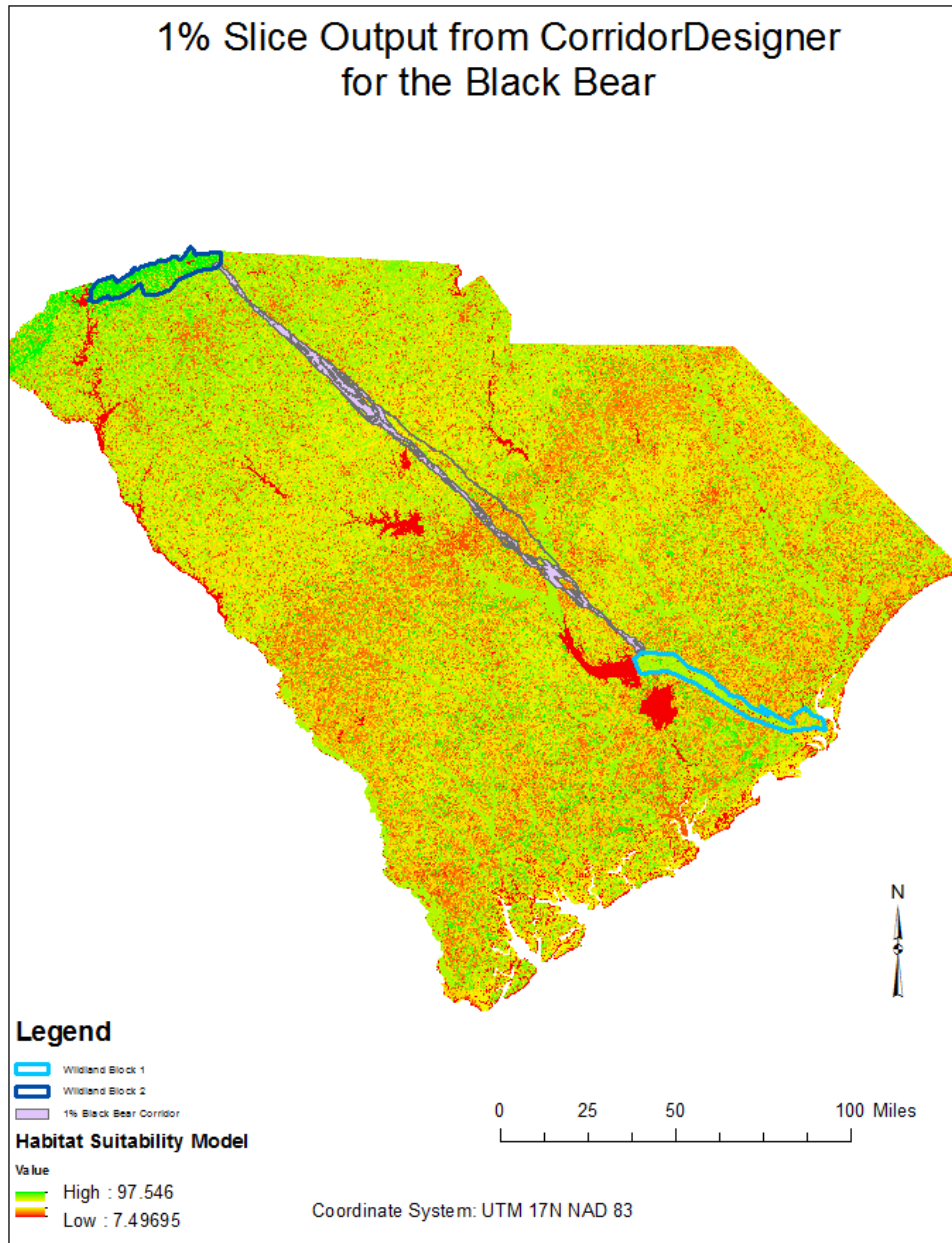


Figure 2.

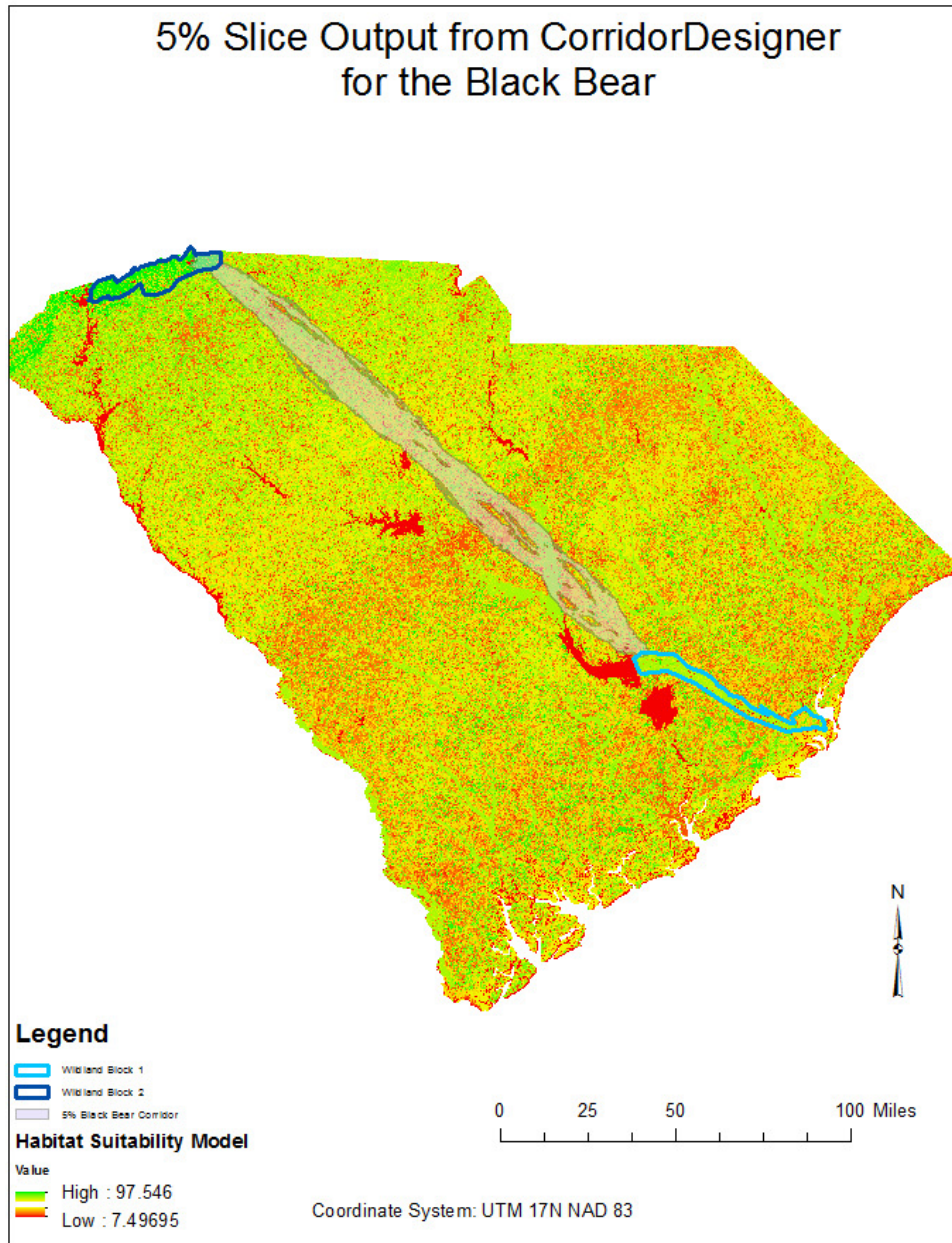


Figure 3.

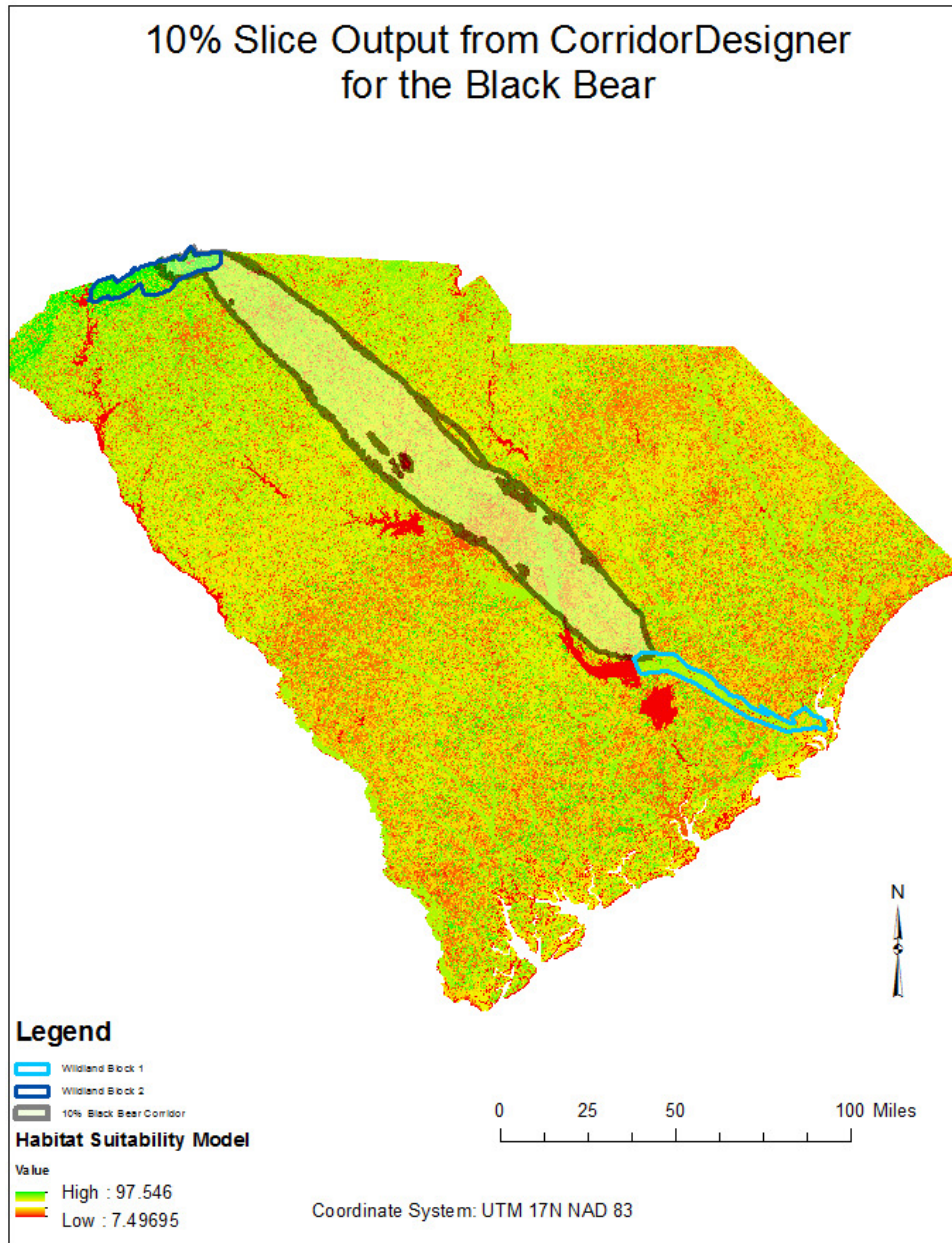


Figure 4.

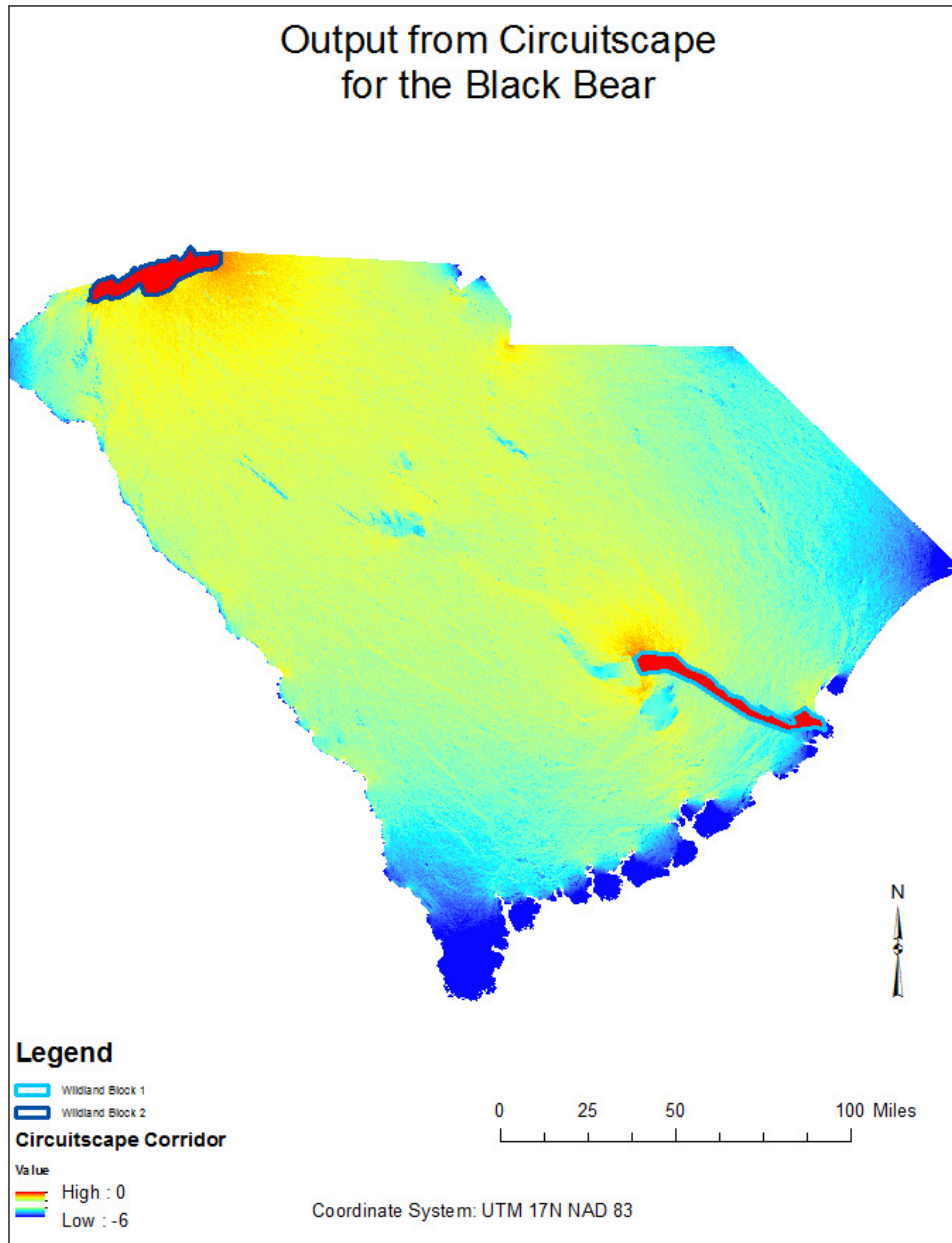


Figure 5.

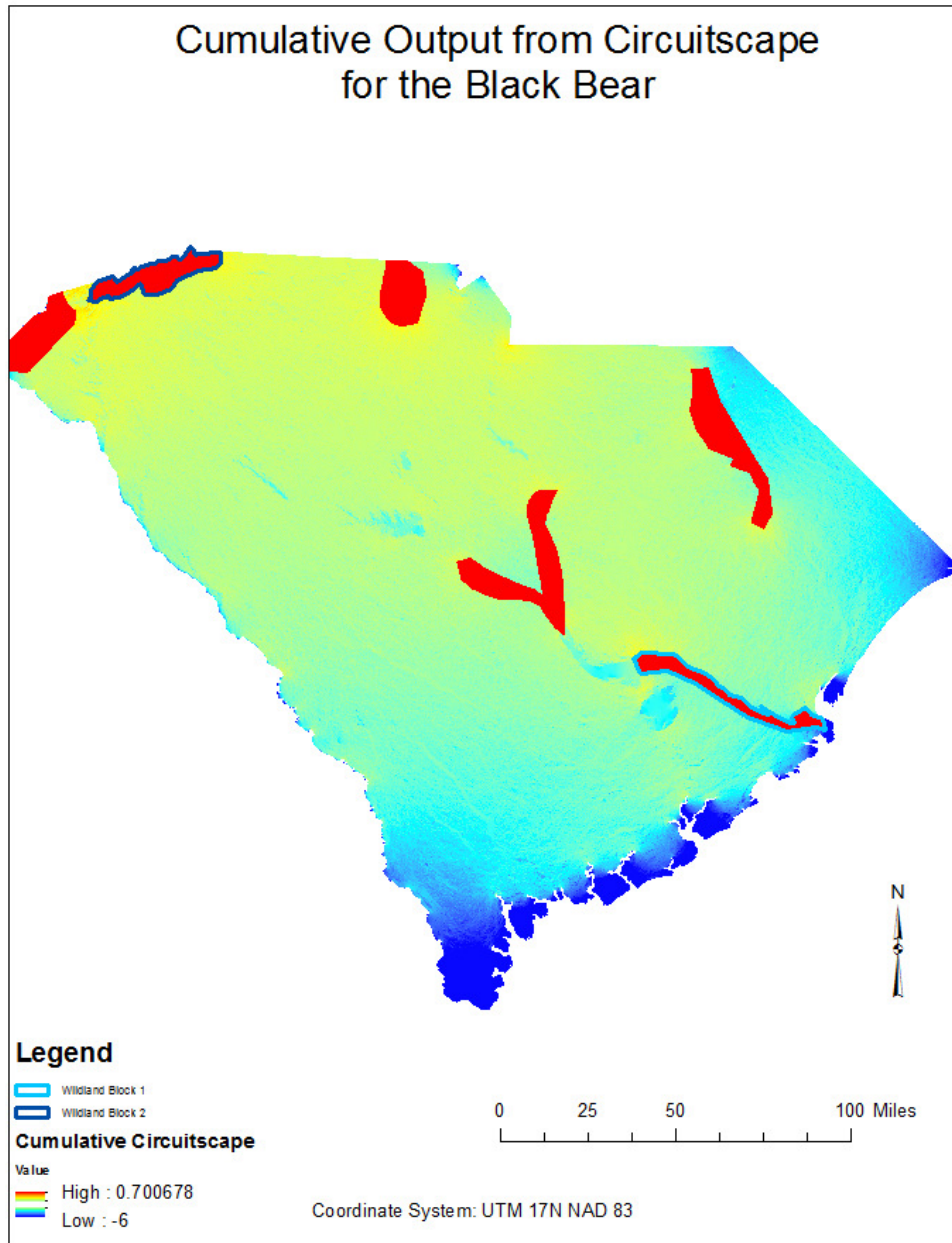


Figure 6

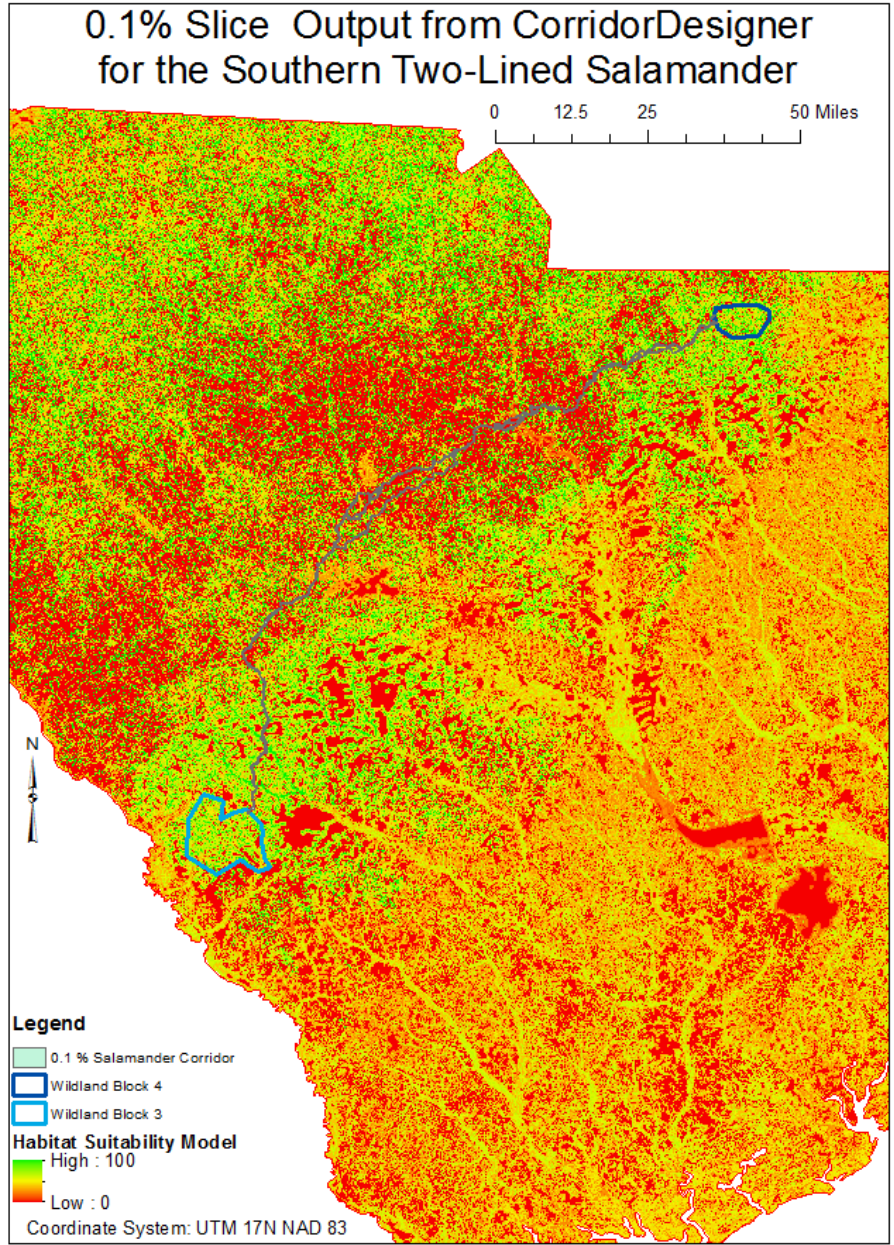


Figure 7.

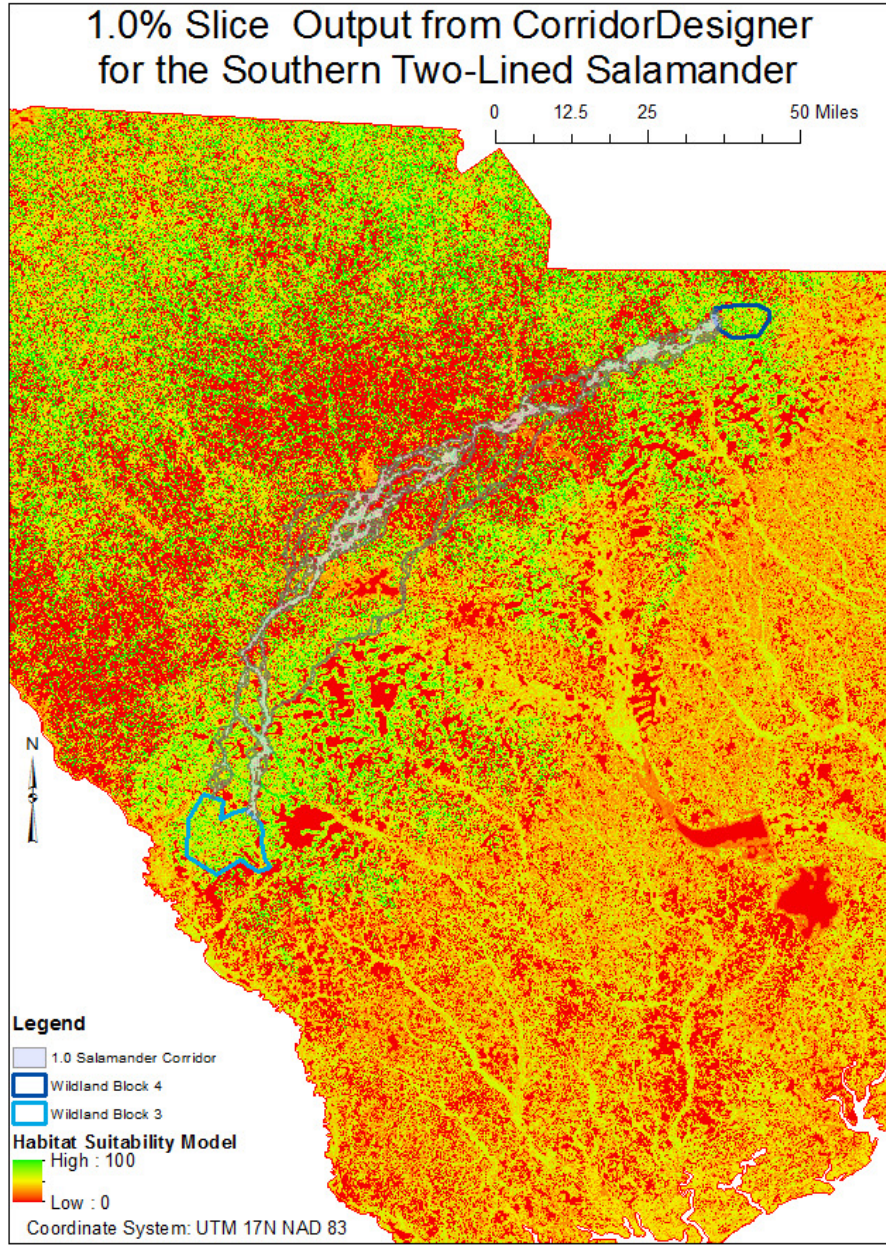


Figure 8.

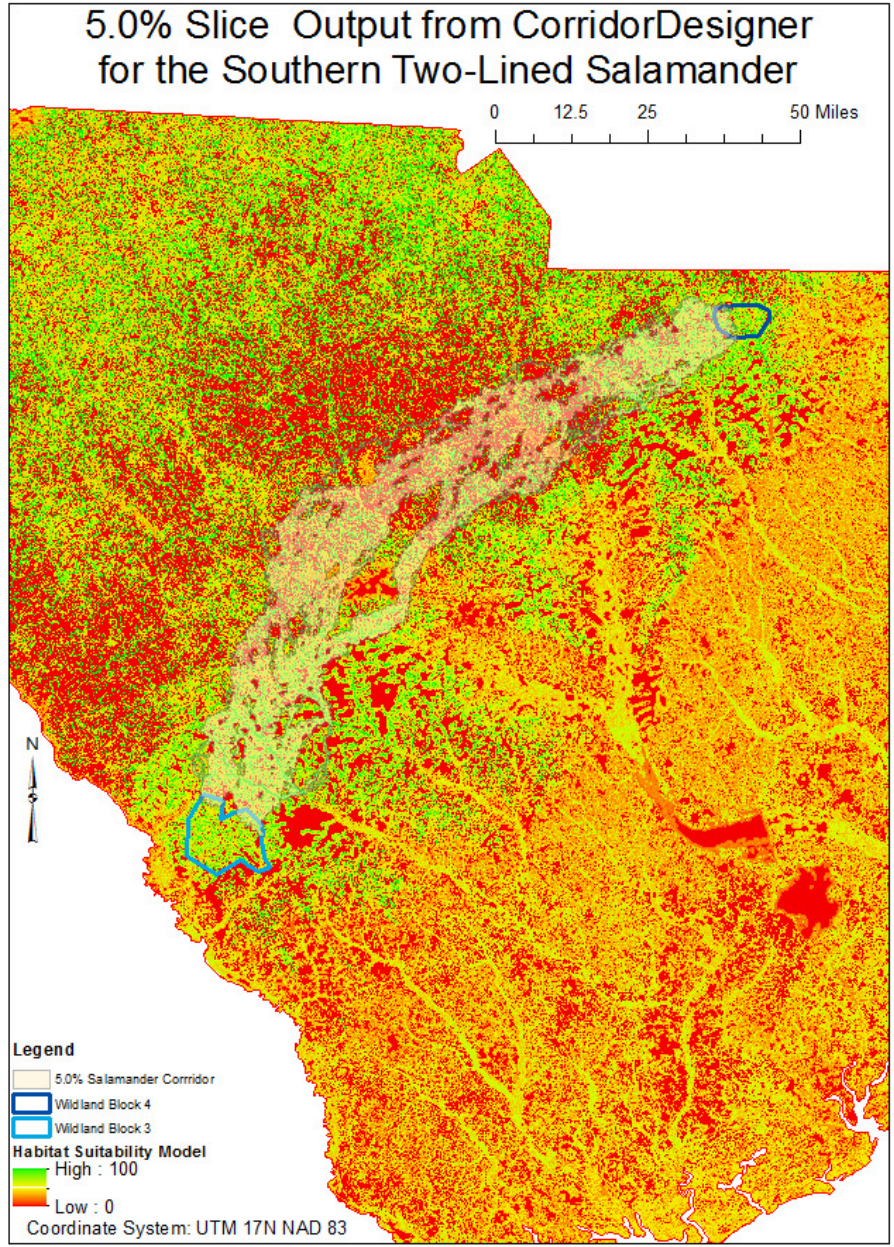


Figure 9.

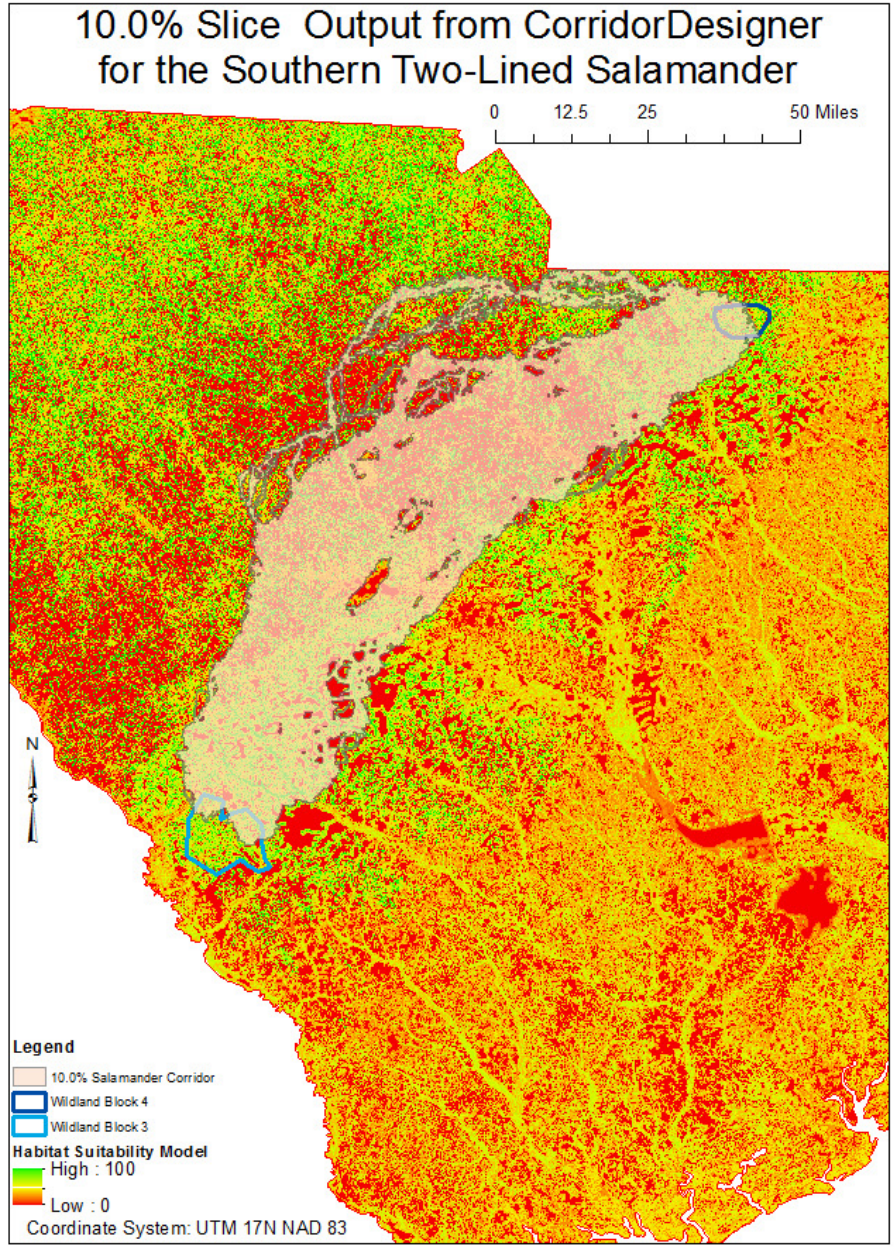


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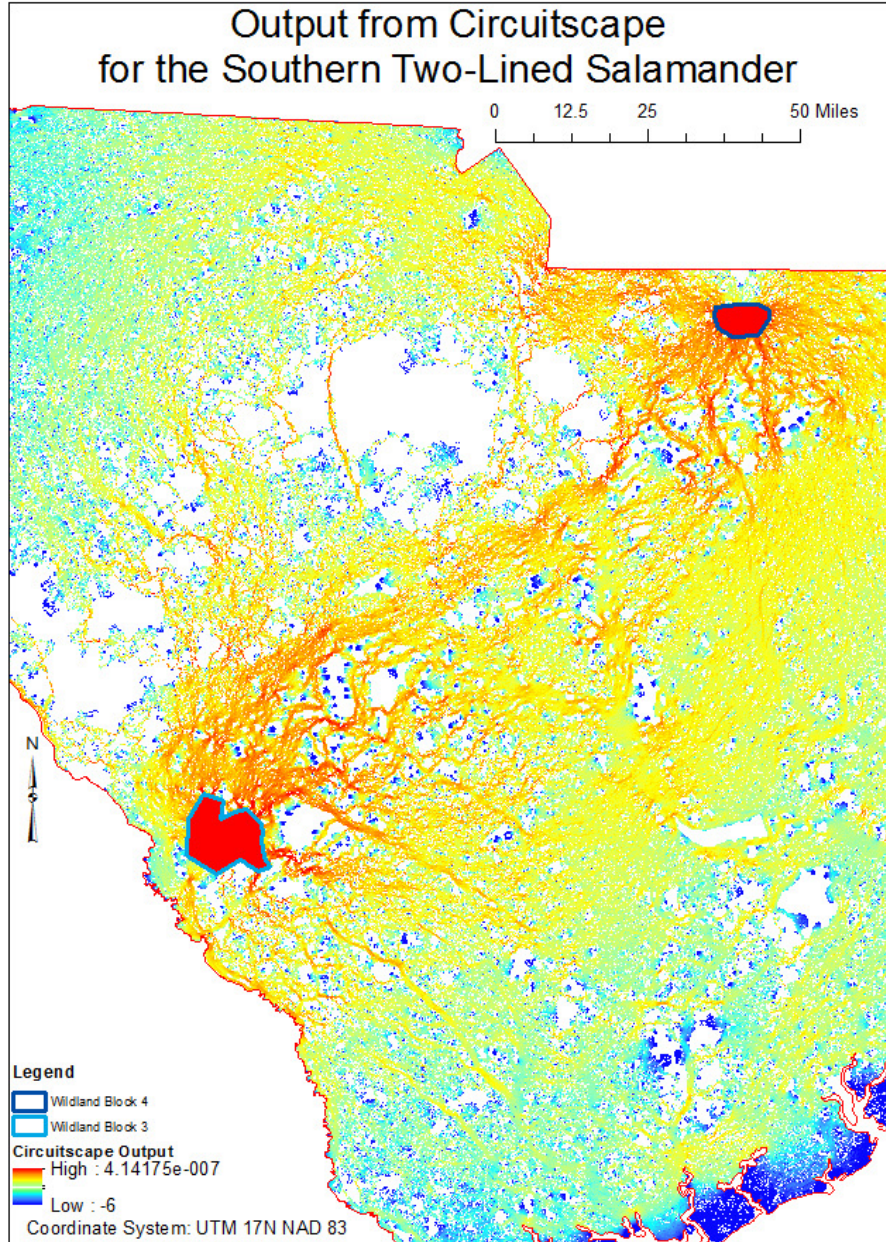


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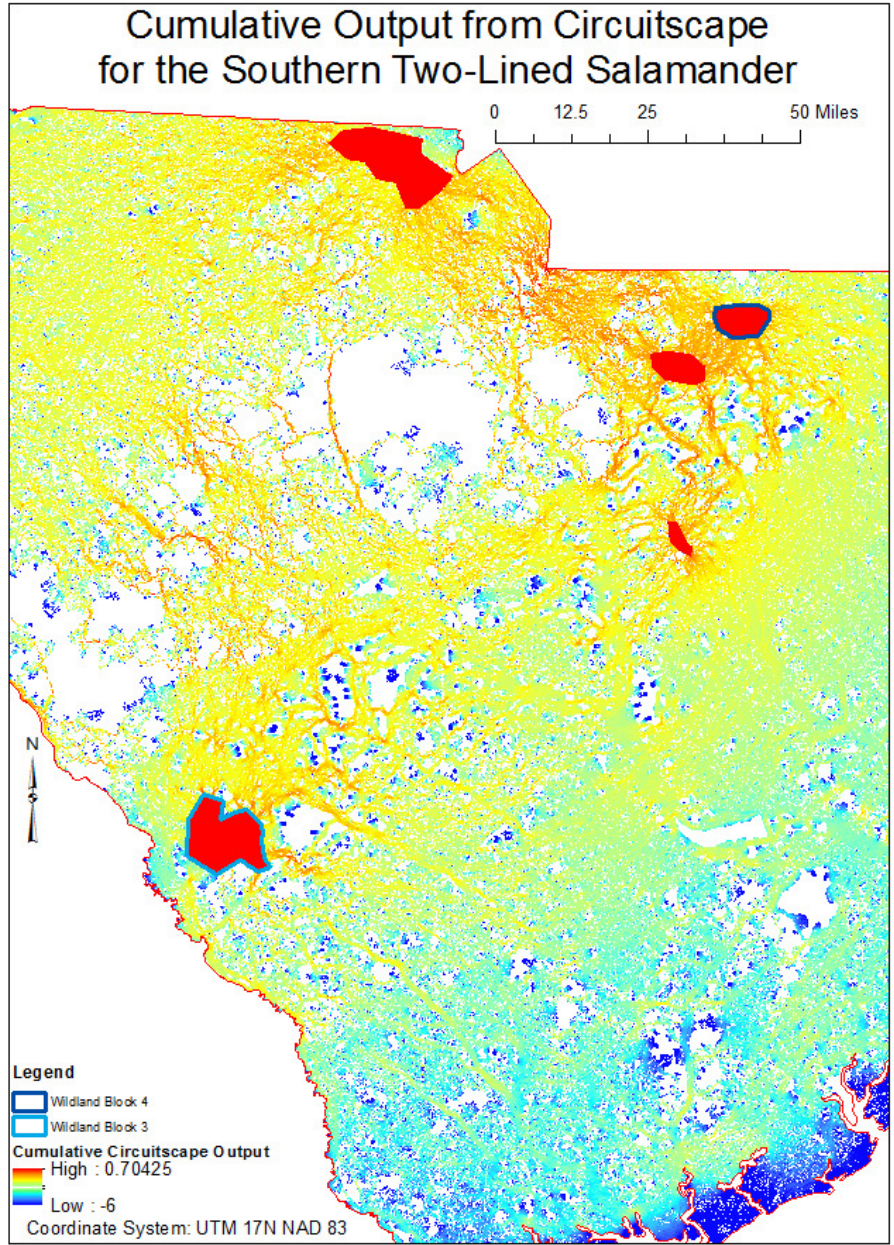


Figure 12.

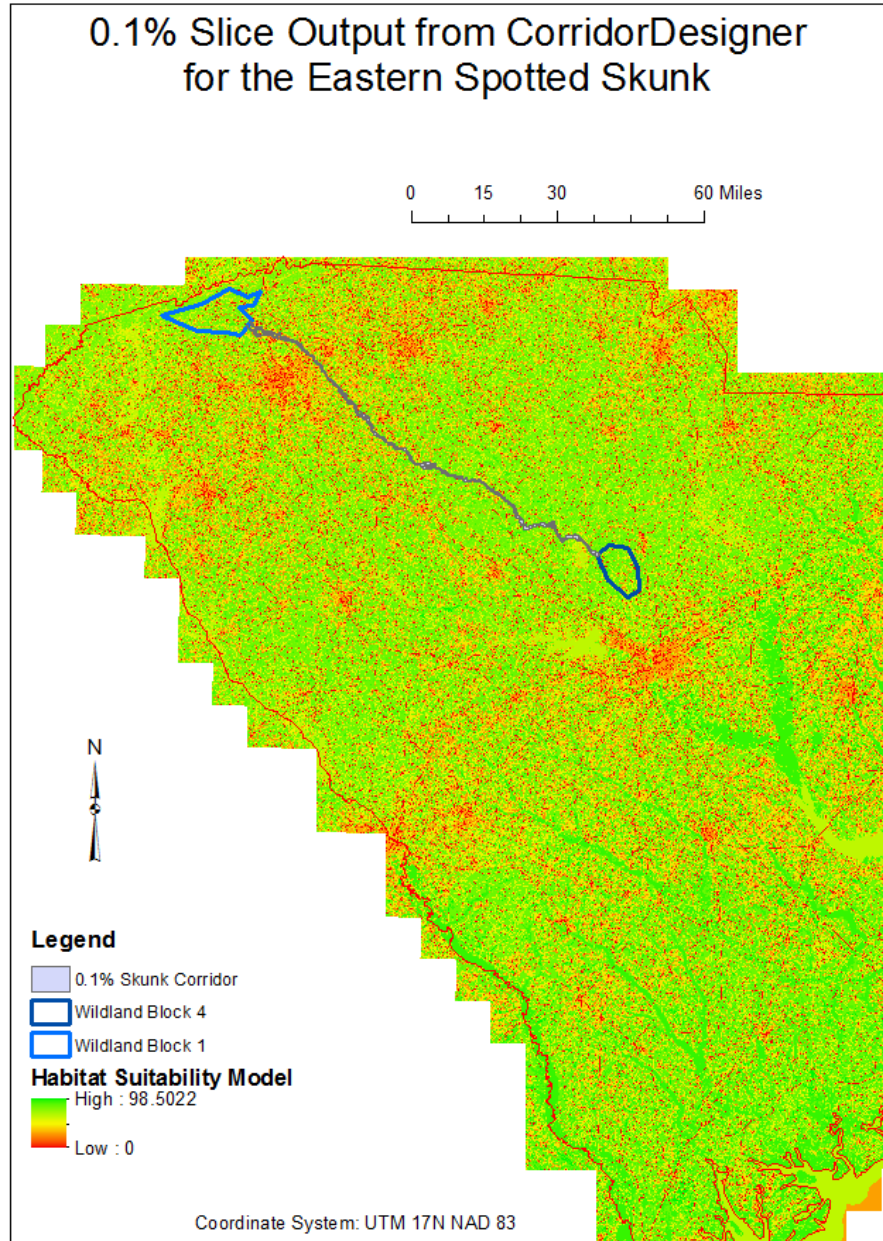


Figure 13.

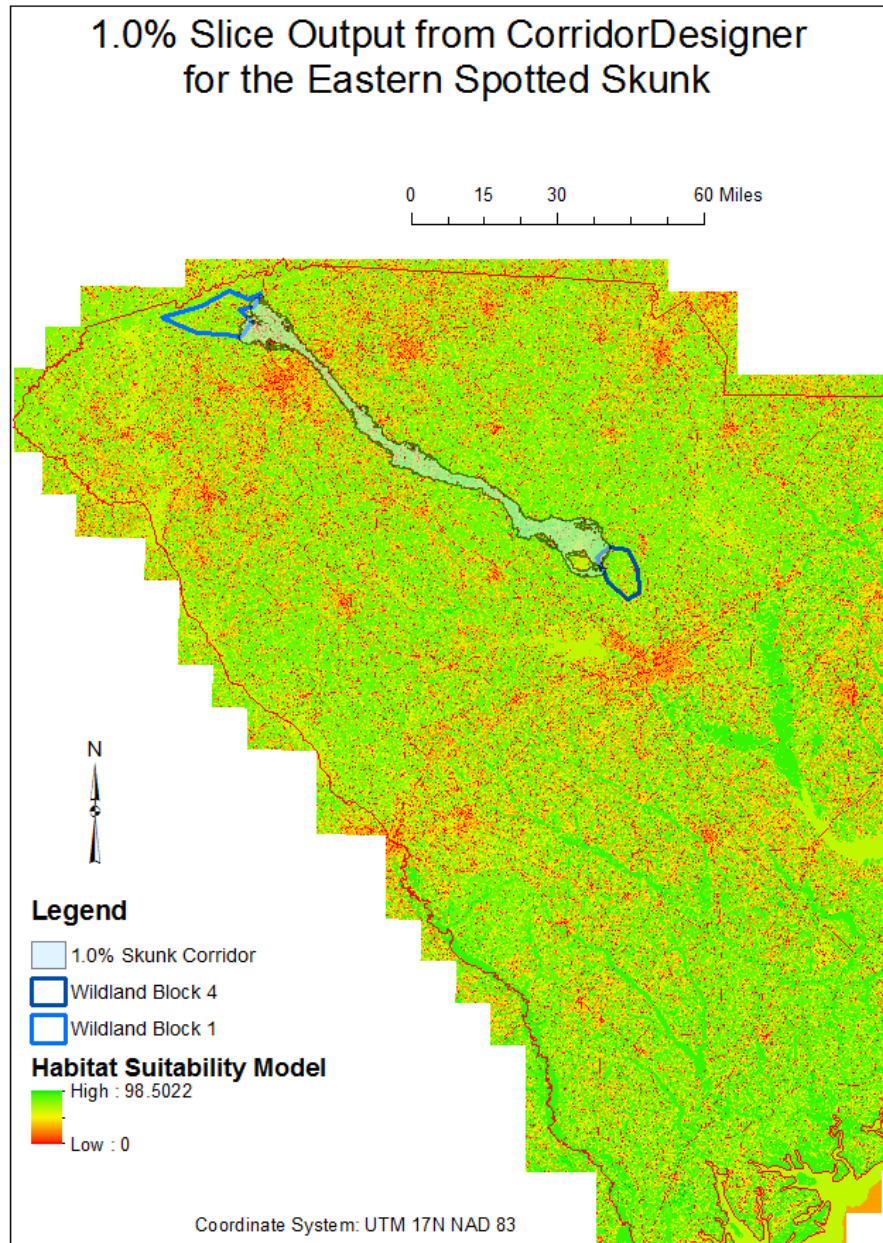


Figure 14.

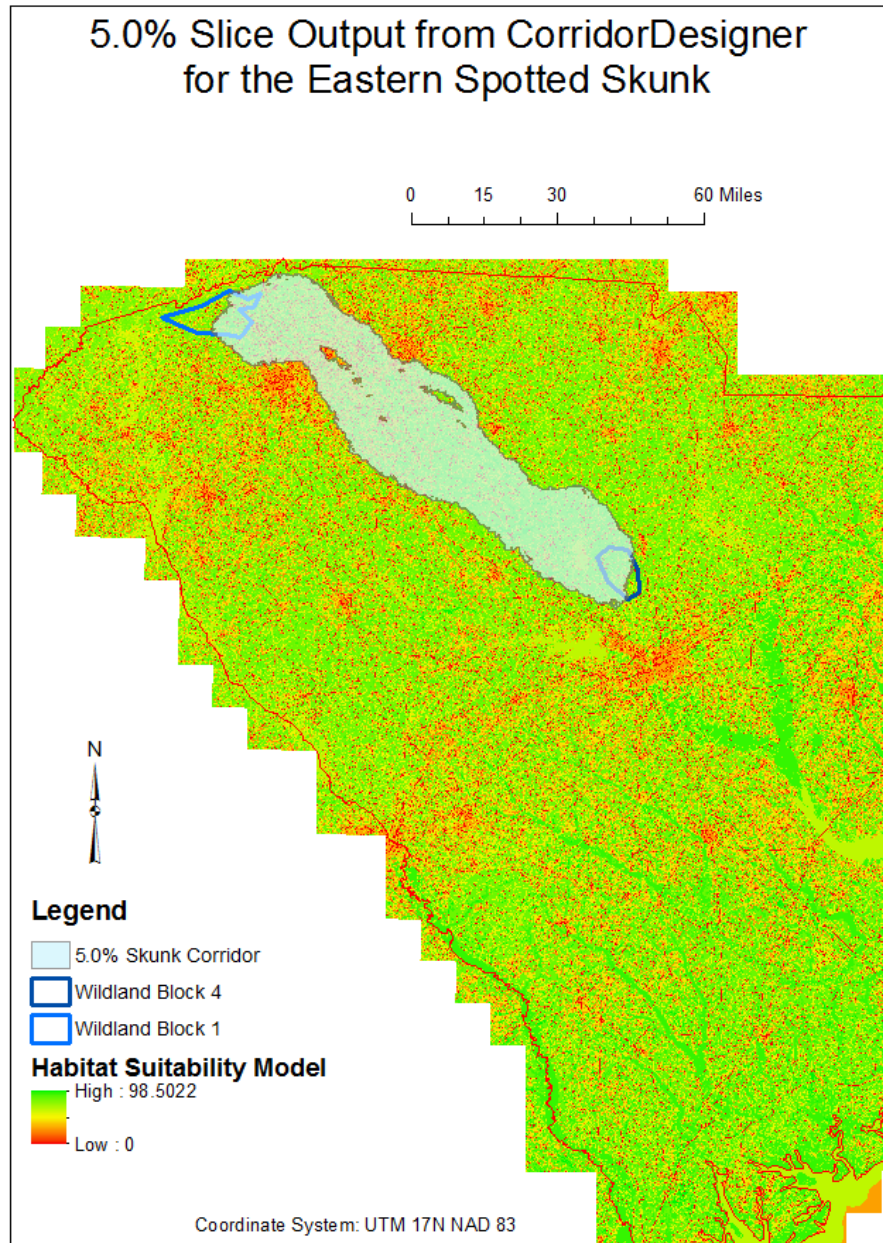


Figure 15.

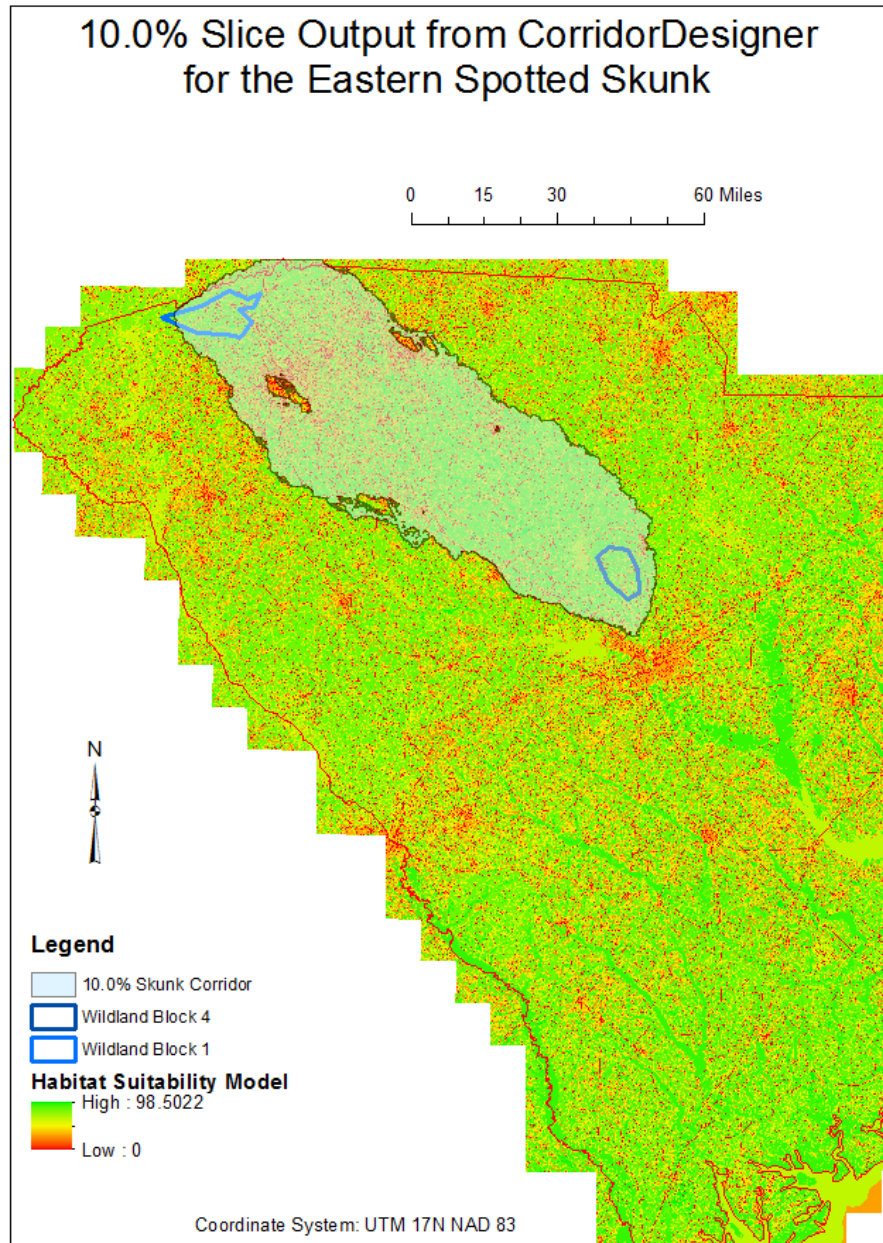


Figure 16.

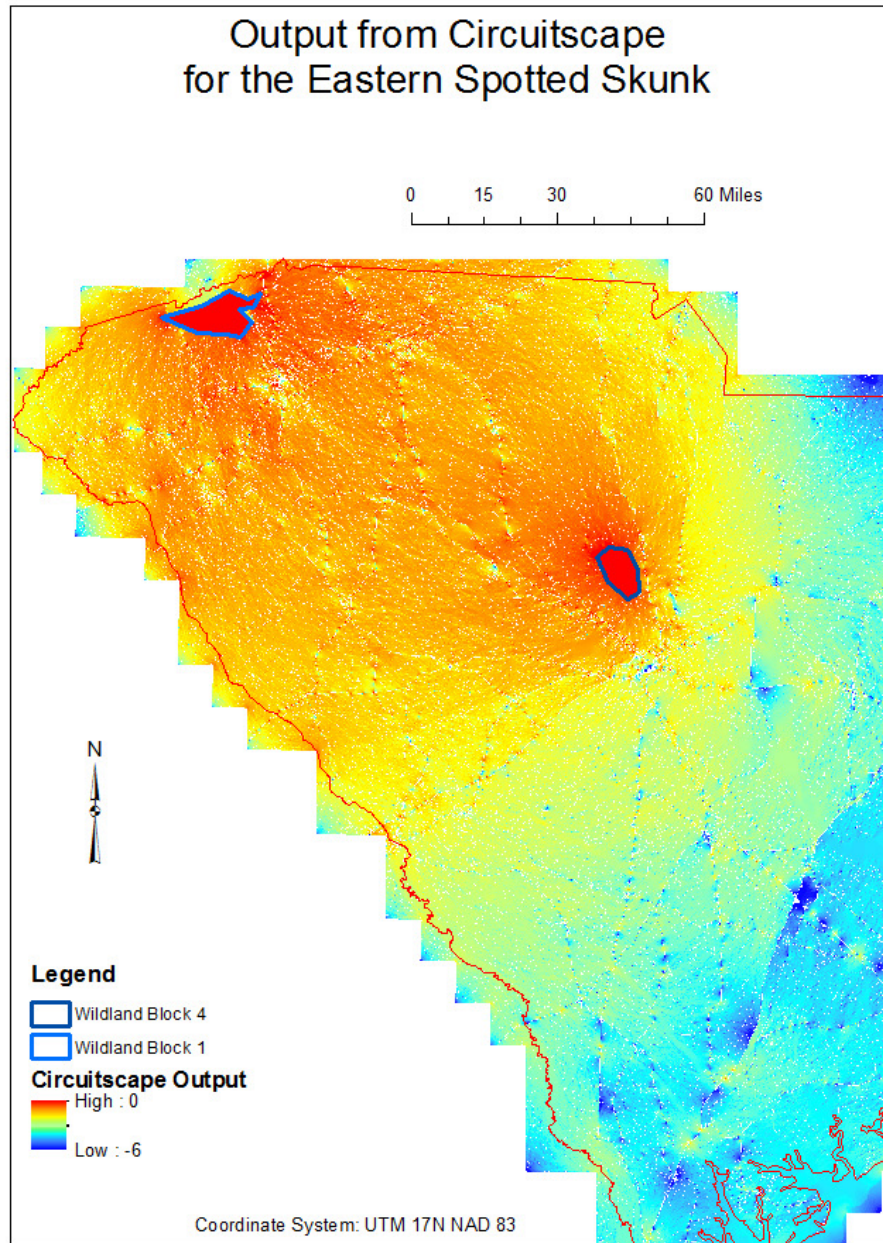


Figure 17.

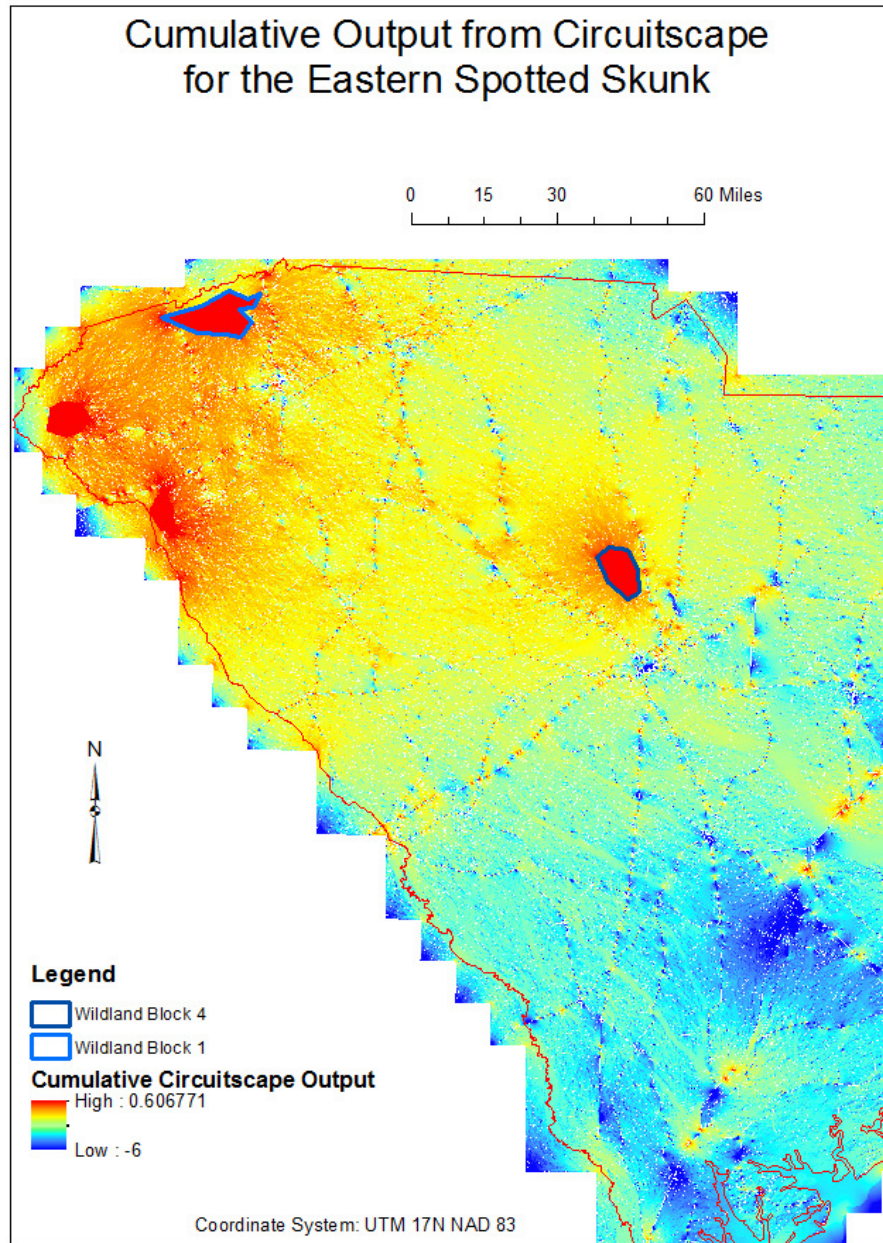


Figure 18.

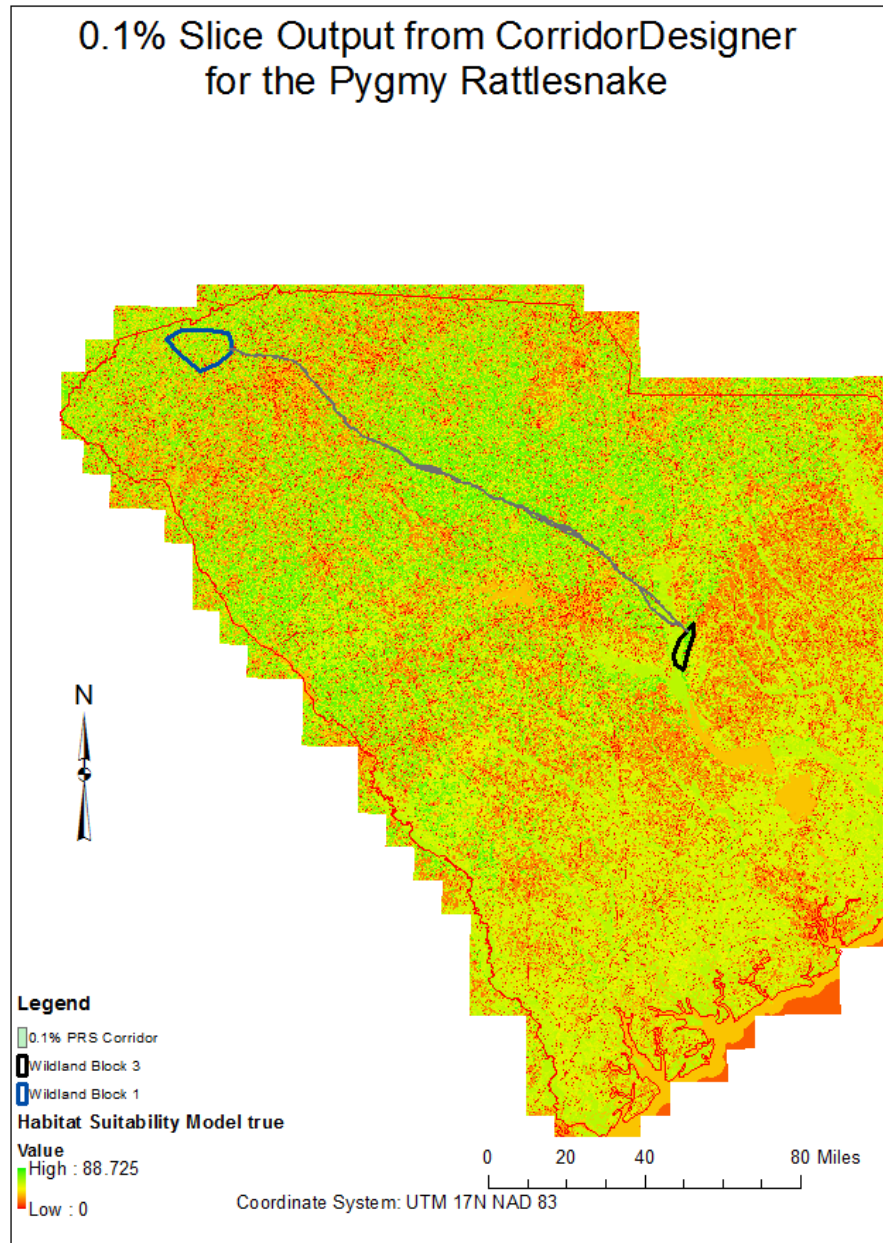


Figure 19.

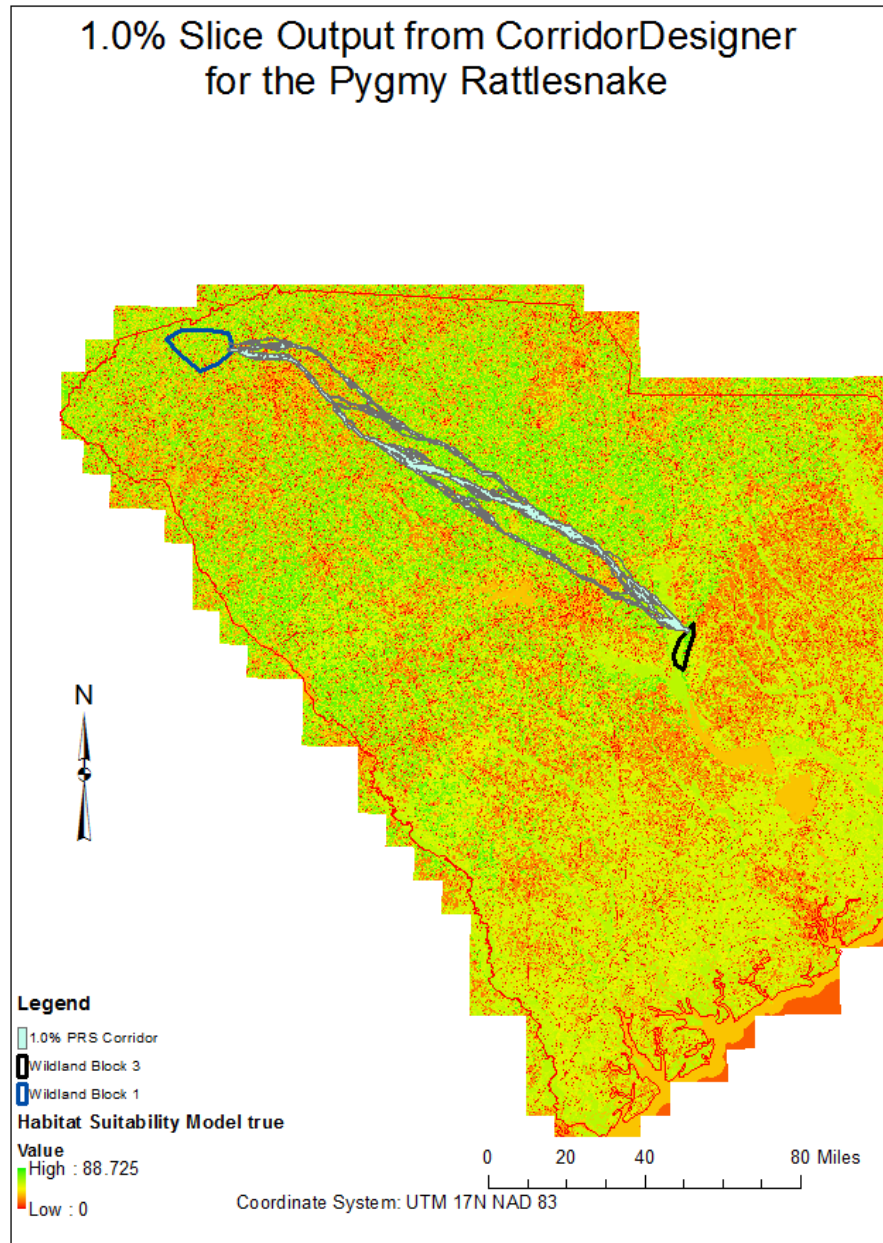


Figure 20.

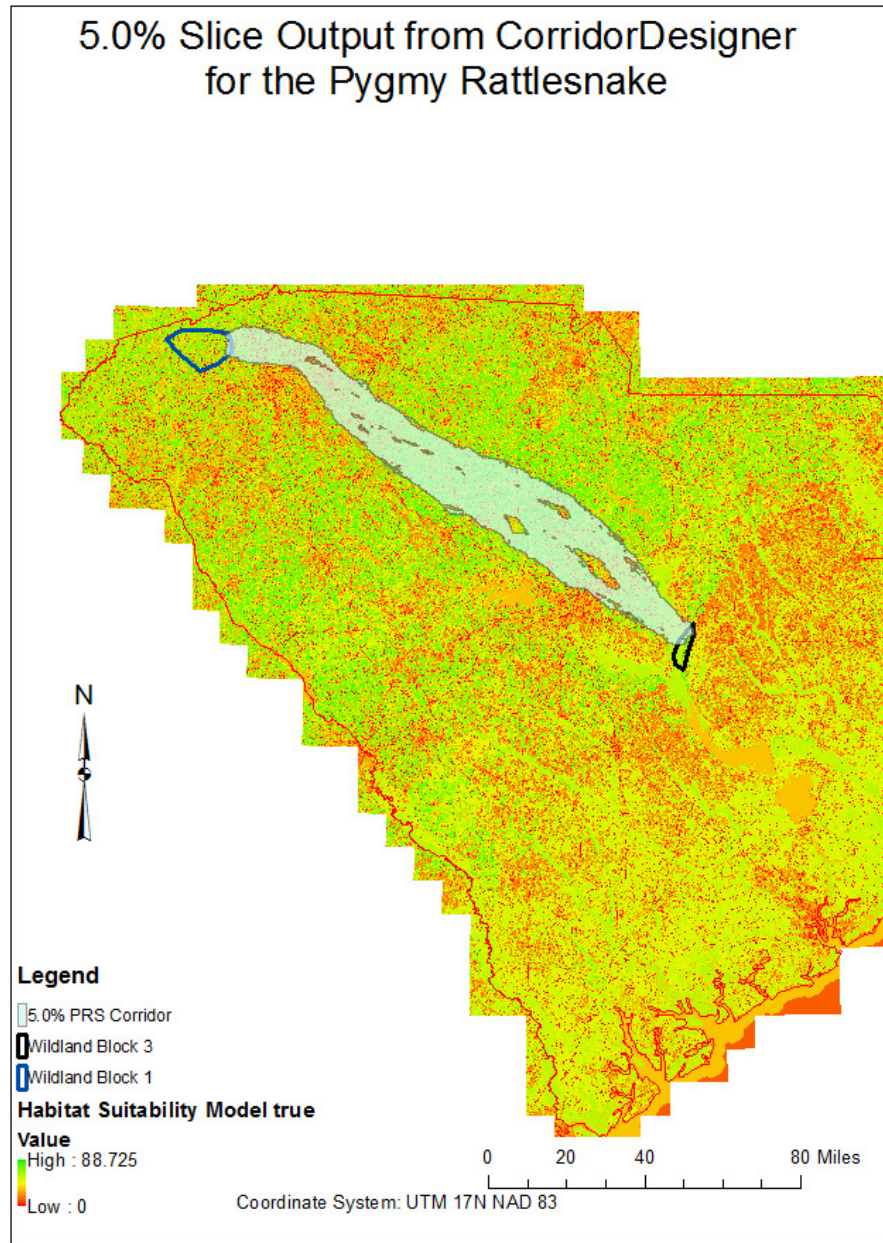


Figure 21.

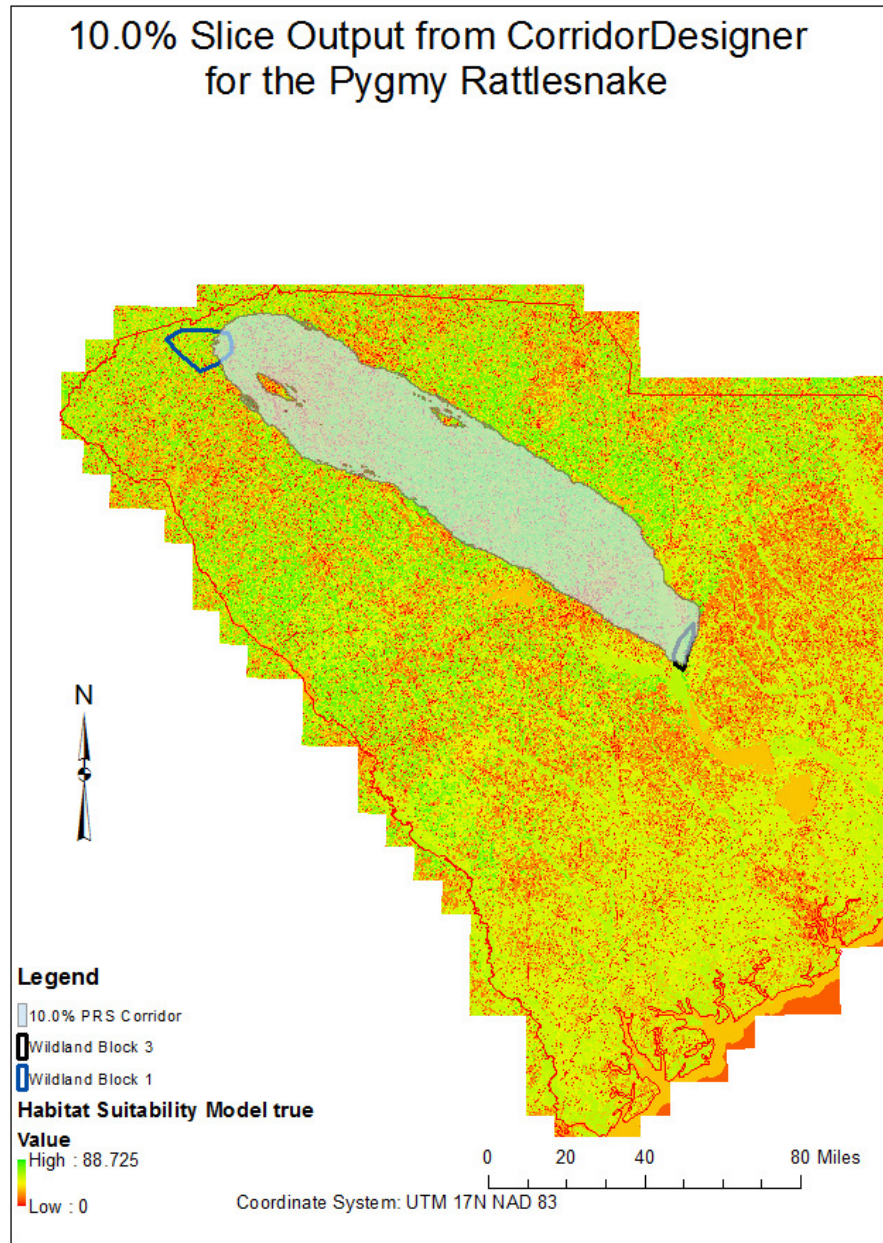


Figure 22.

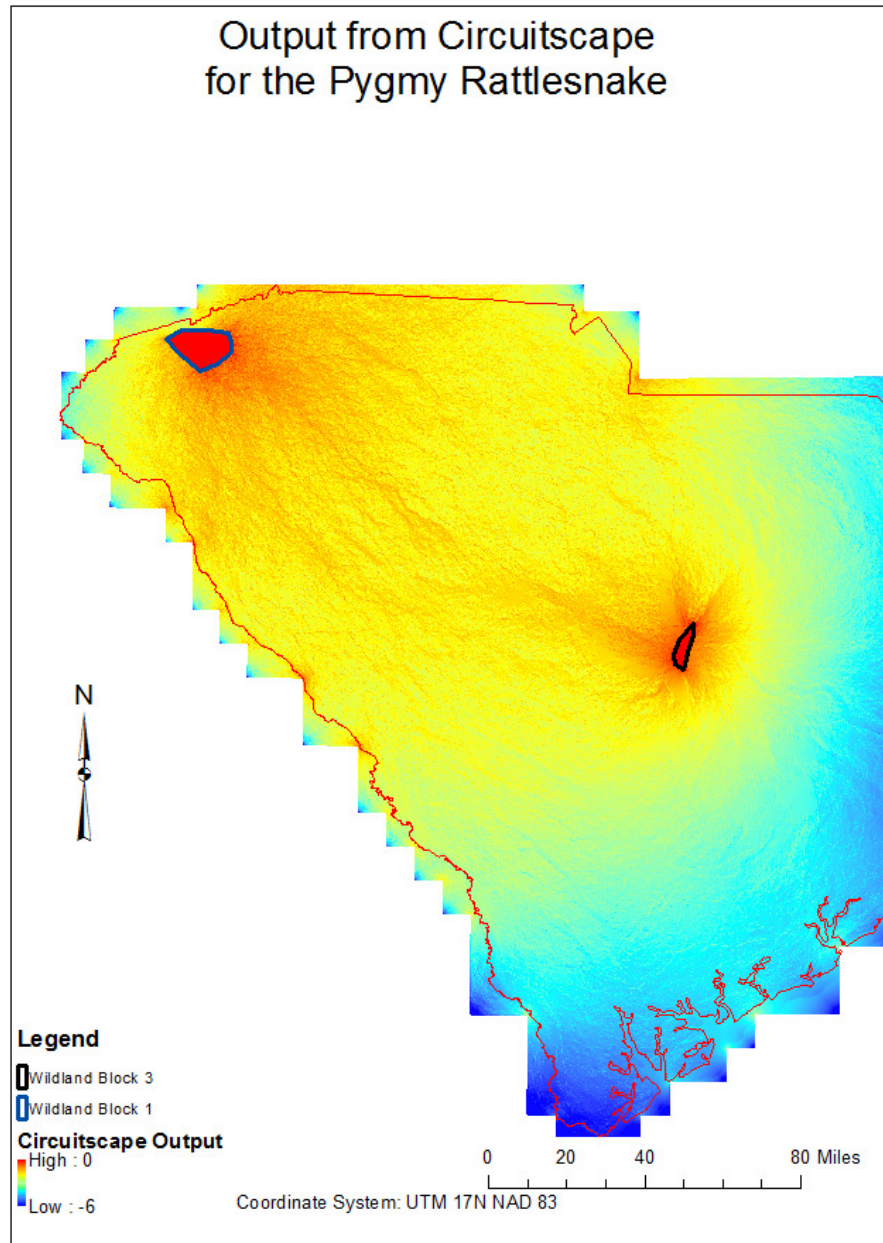


Figure 23.

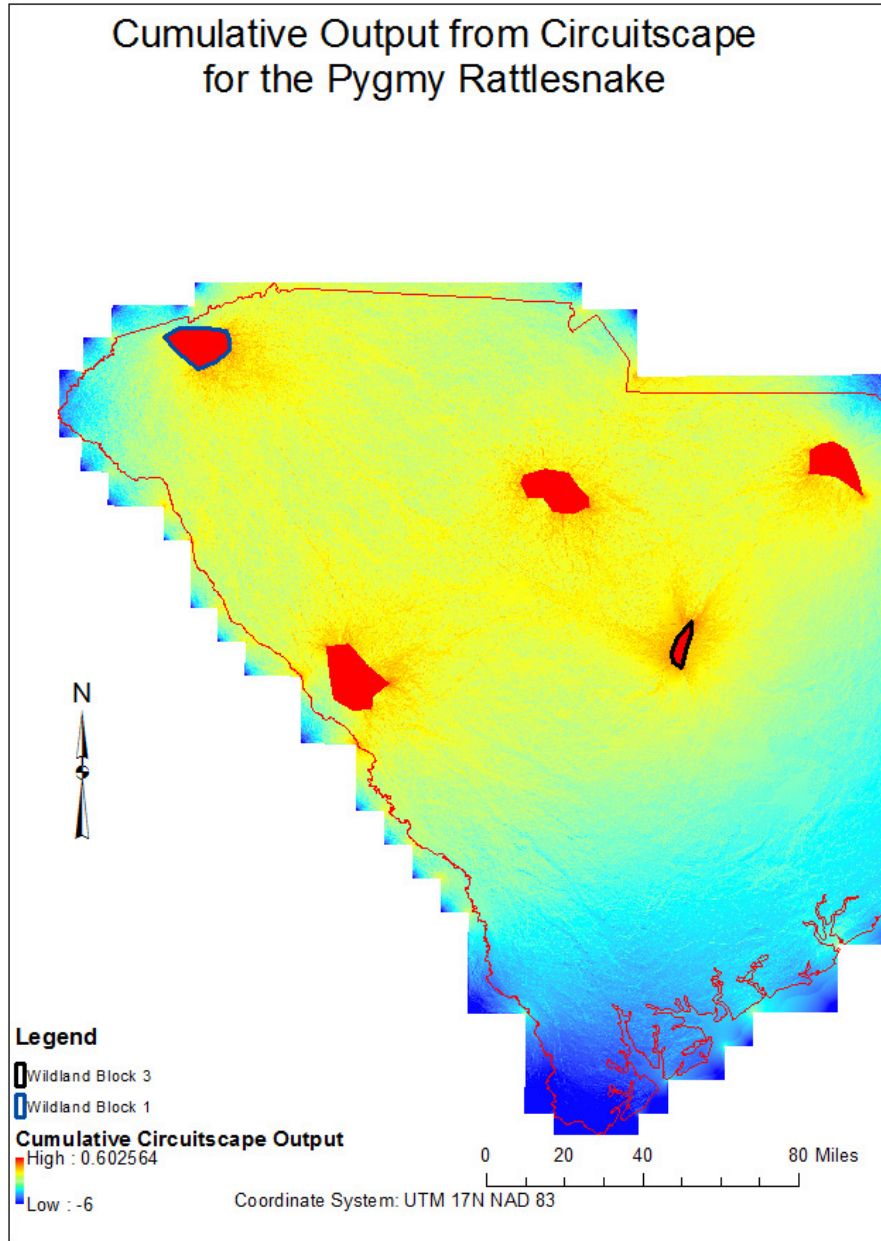


Figure 24.

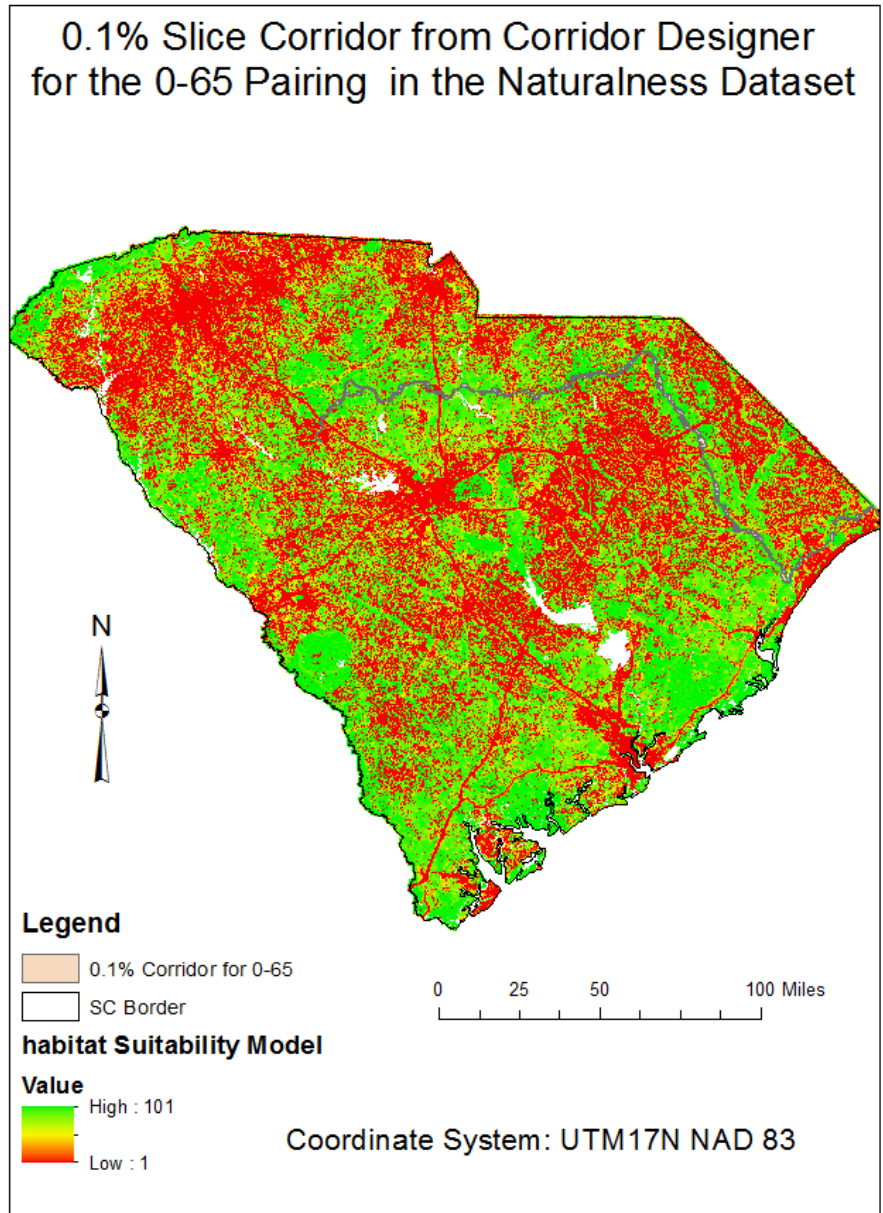


Figure 25.

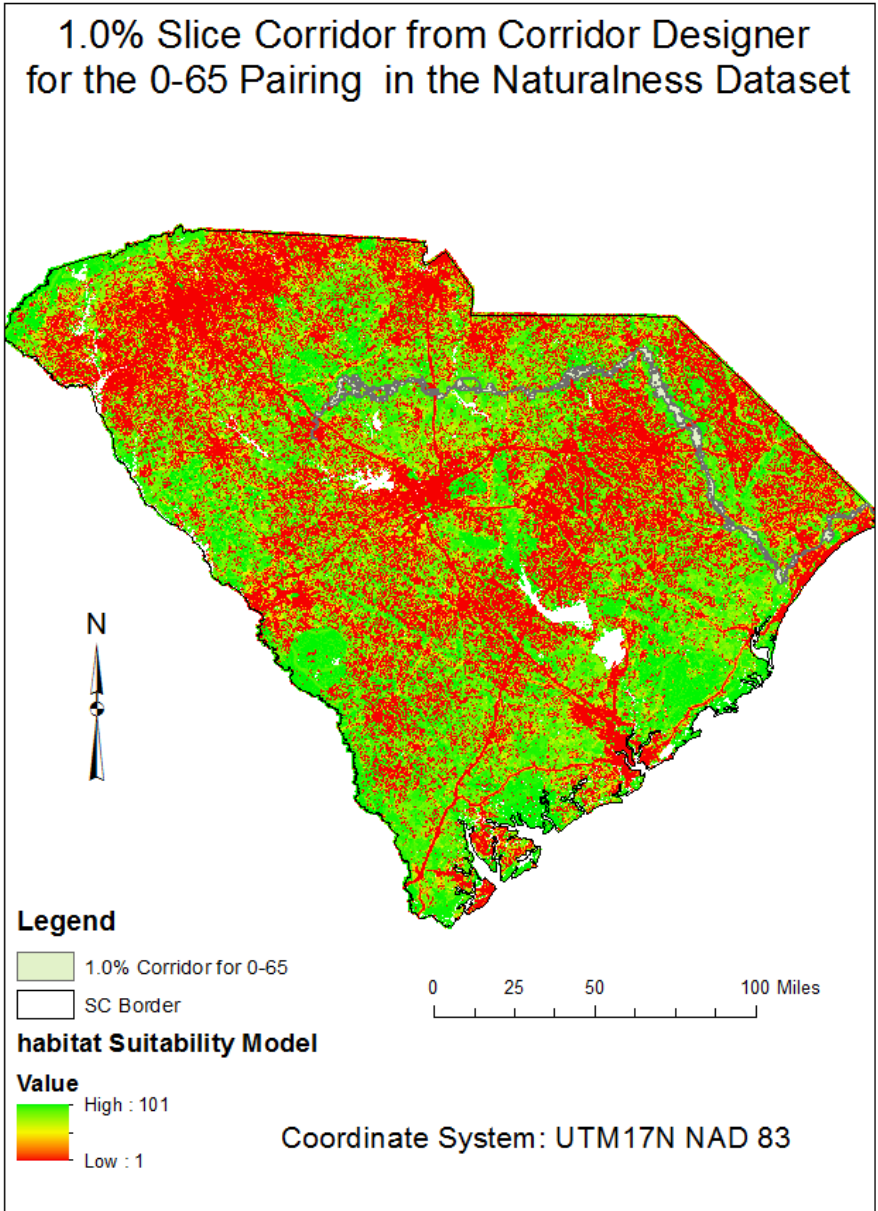


Figure 26.

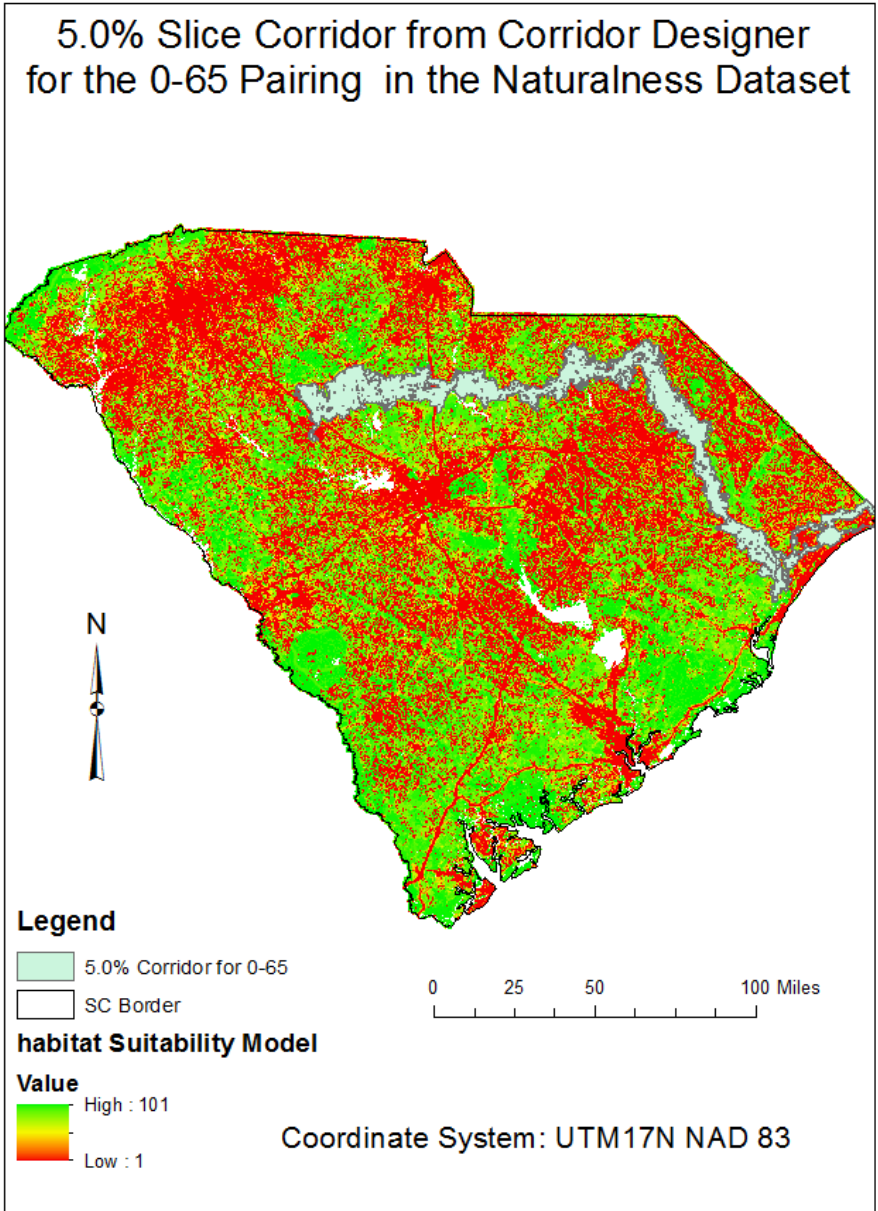


Figure 27.

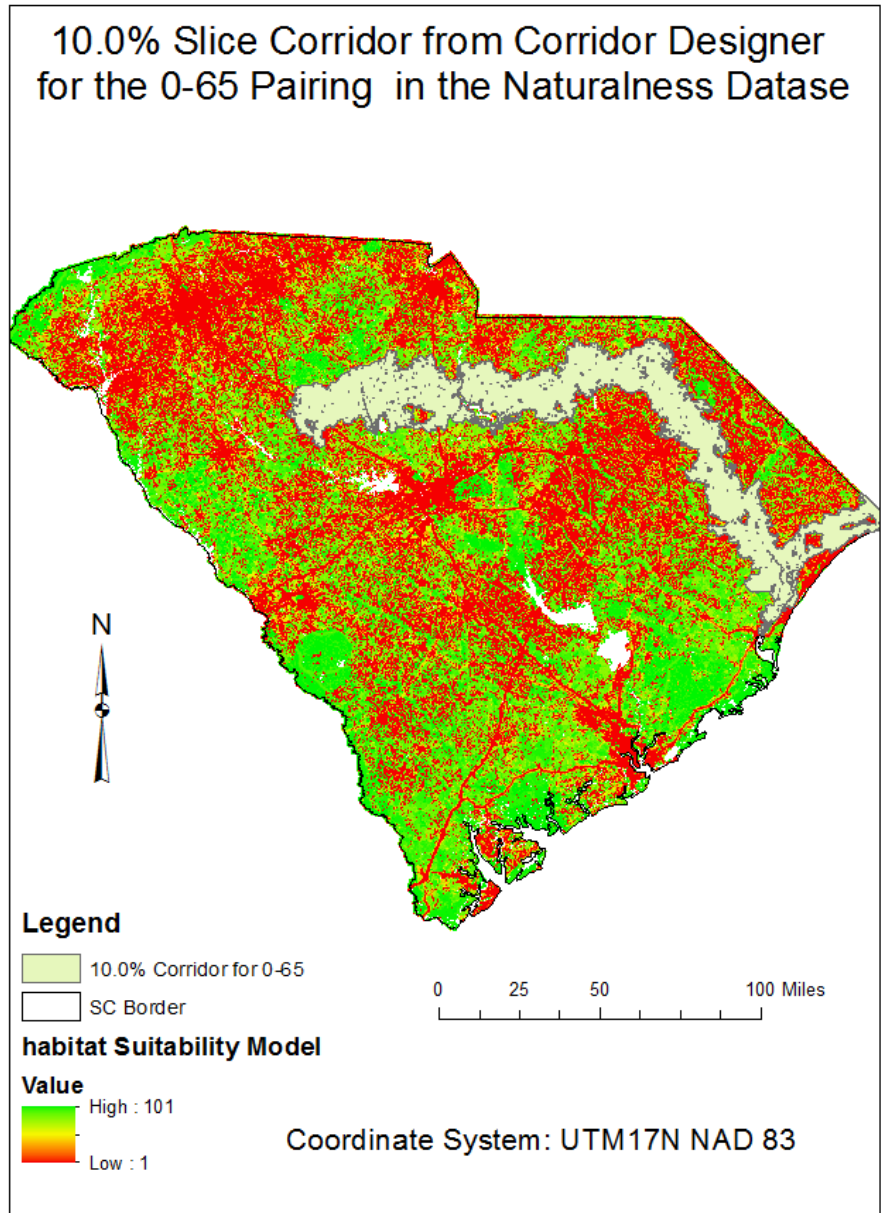


Figure 28.

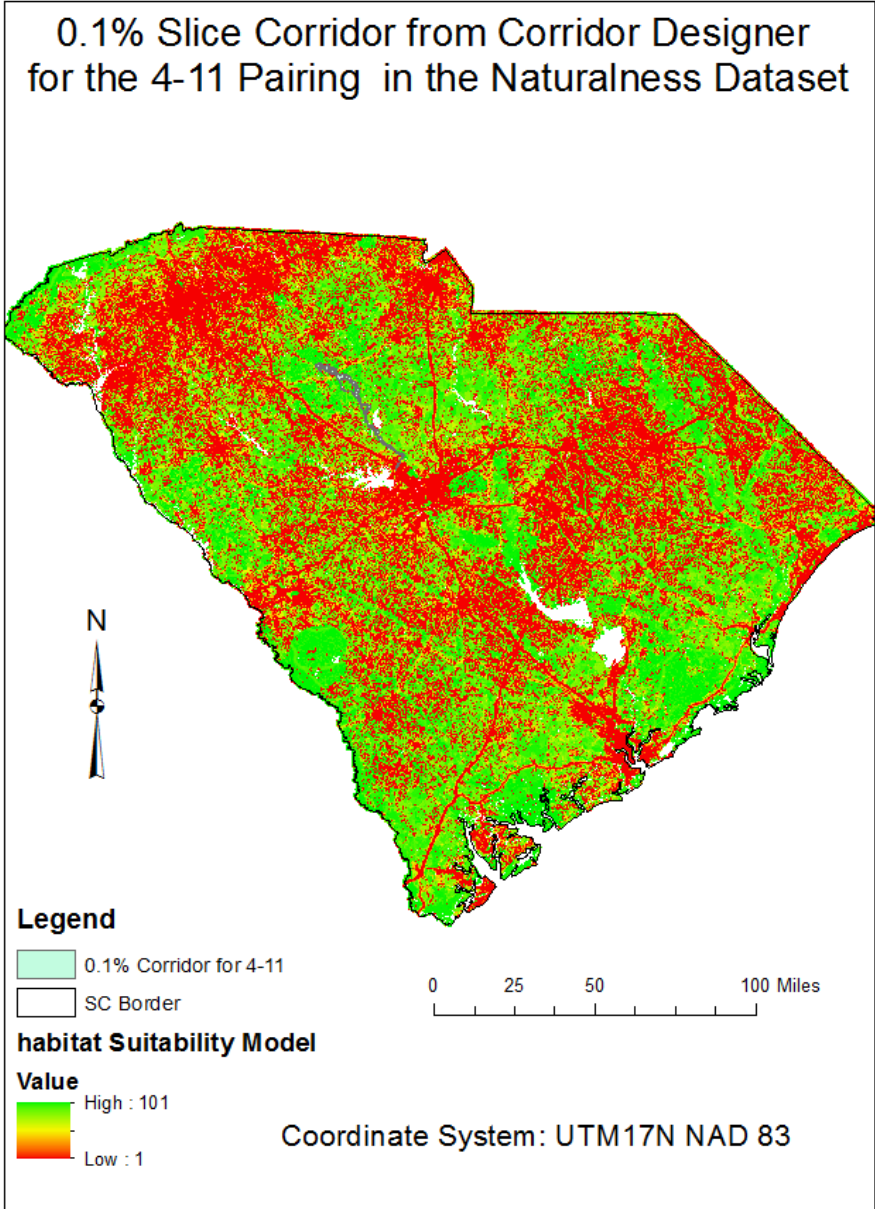


Figure 29.

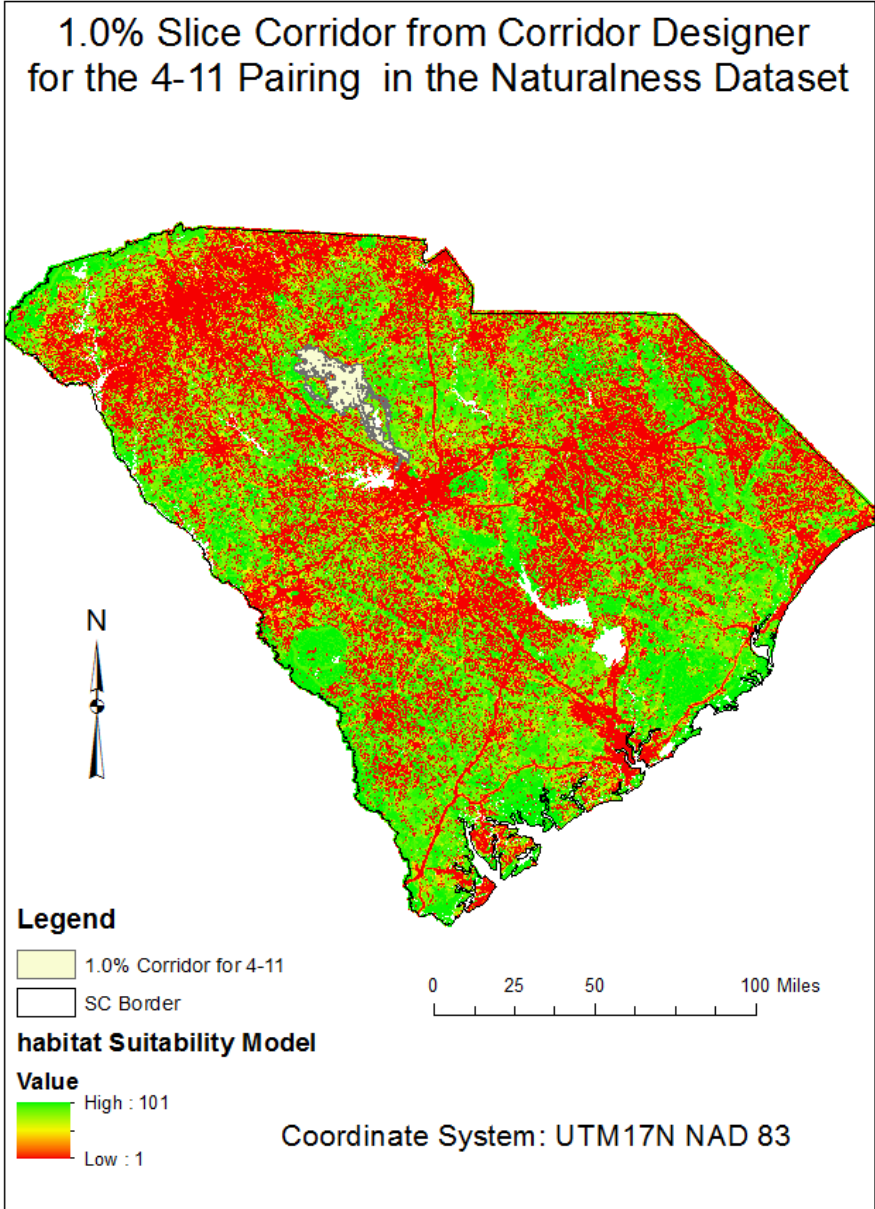


Figure 30.

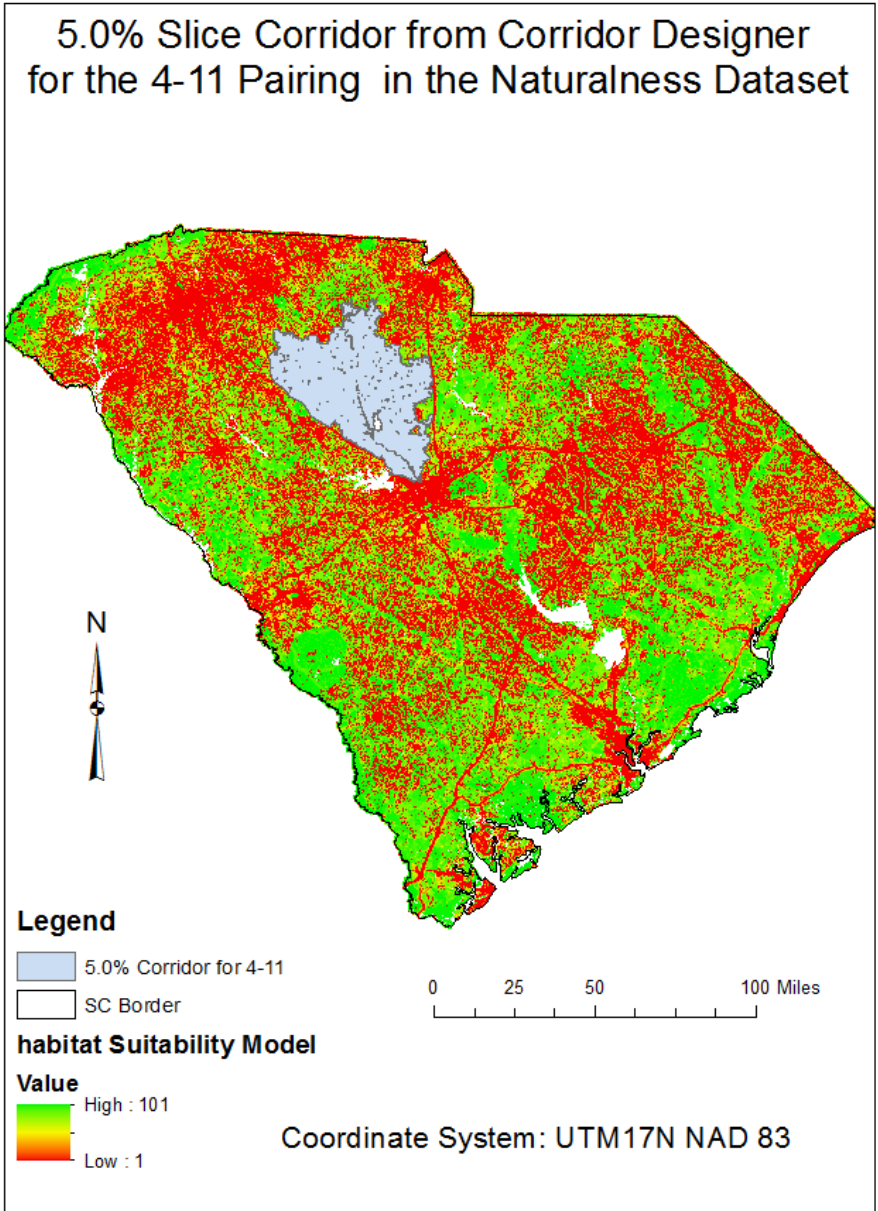


Figure 31.

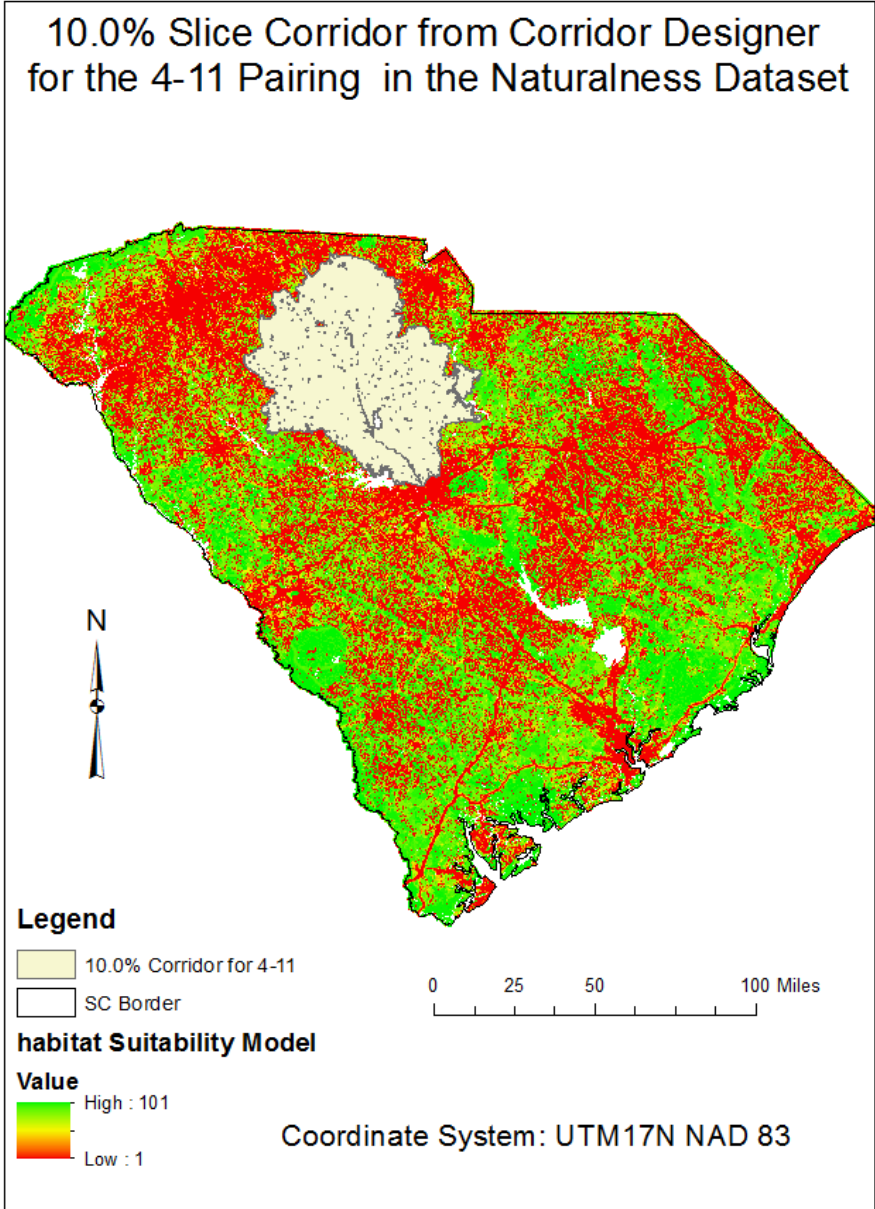


Figure 32.

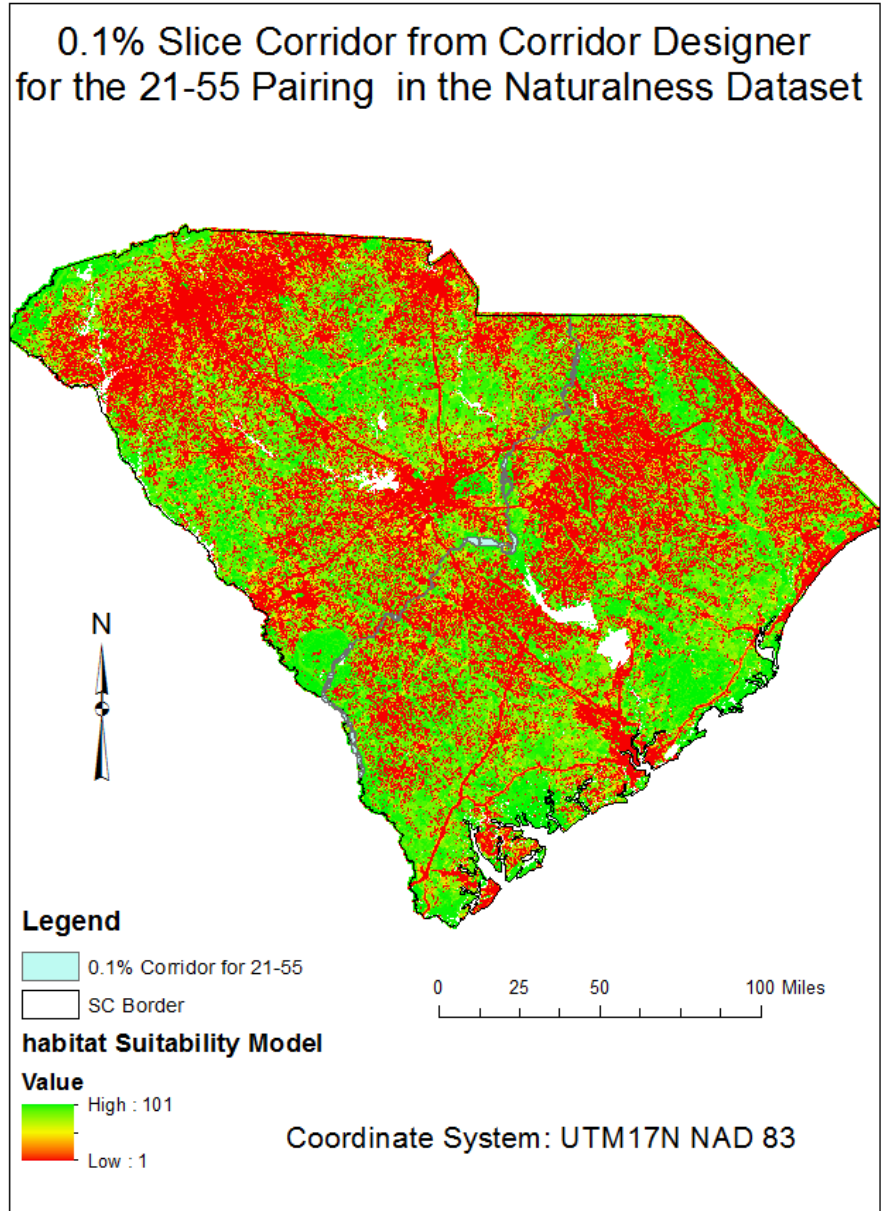


Figure 33.

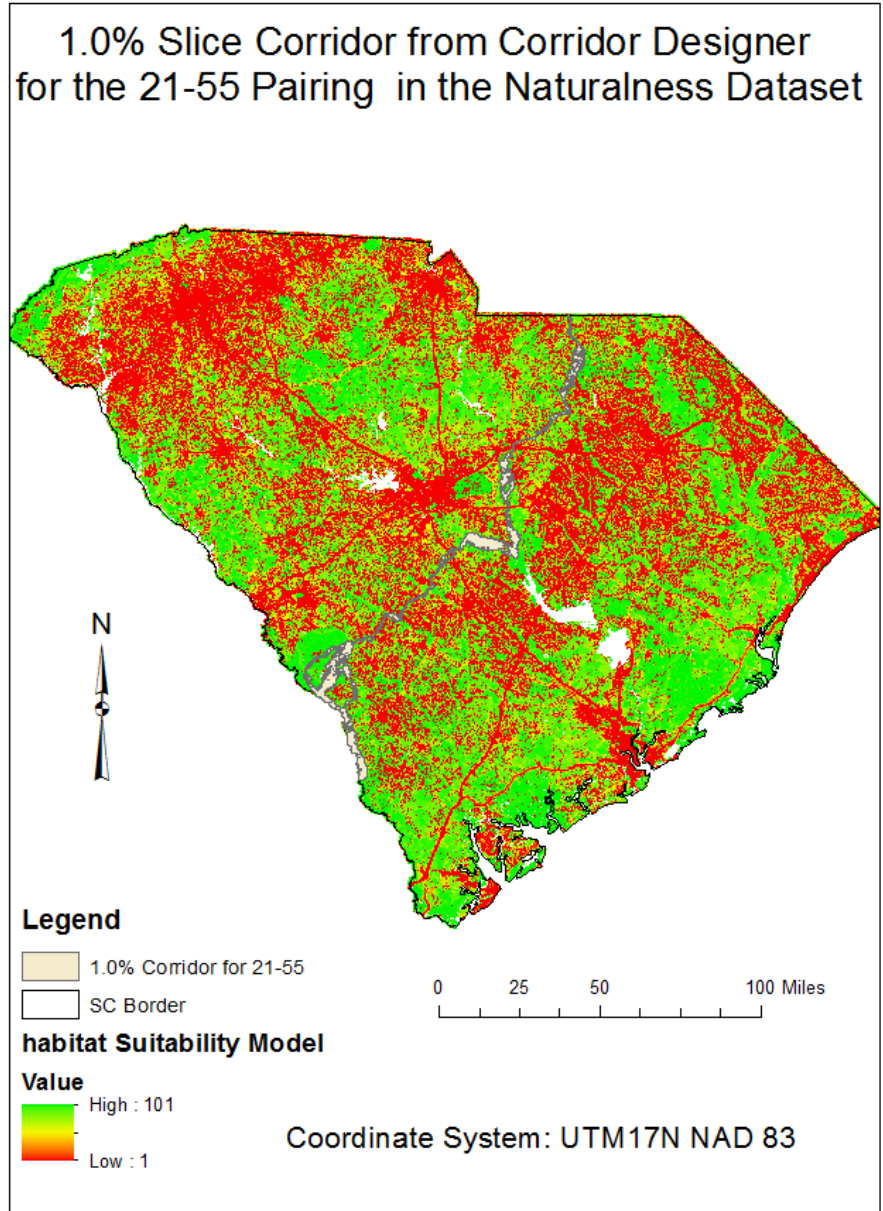


Figure 34.

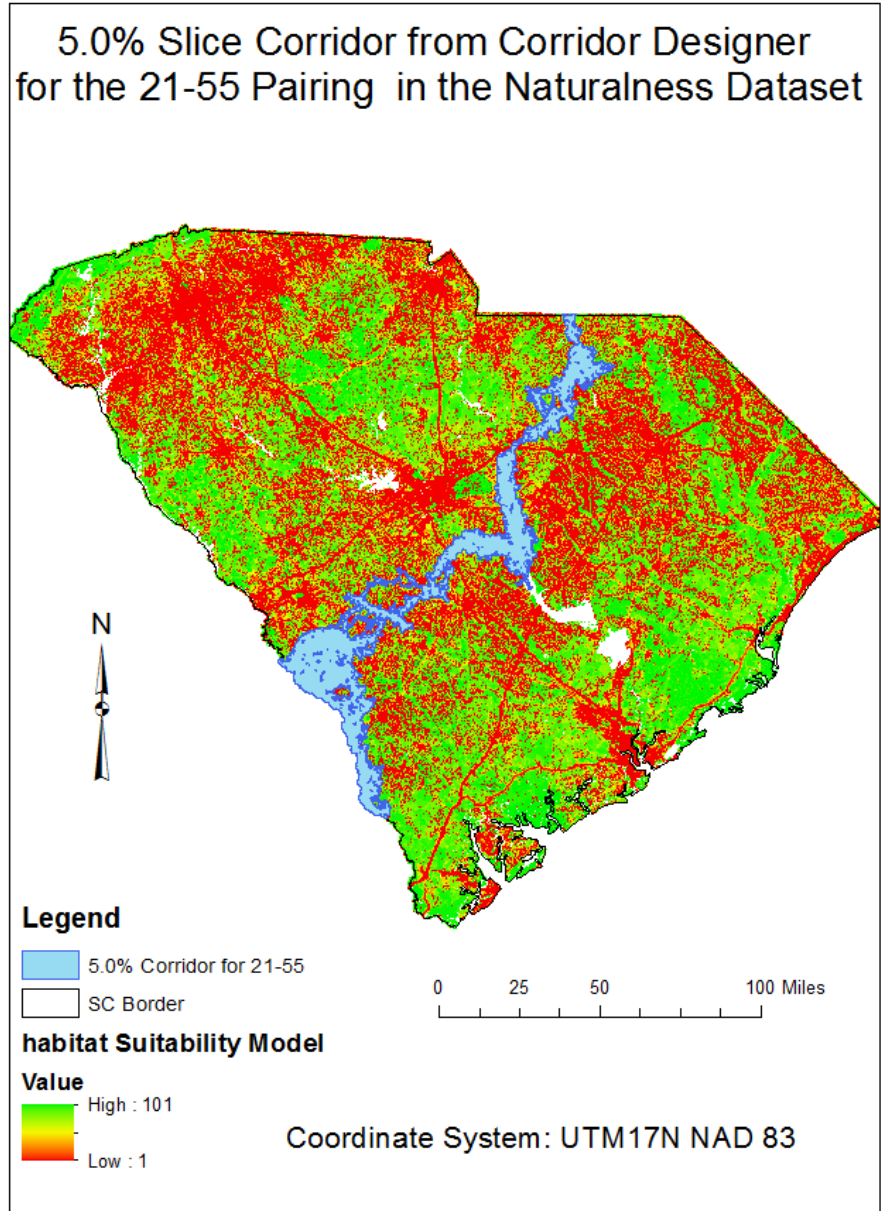


Figure 35.

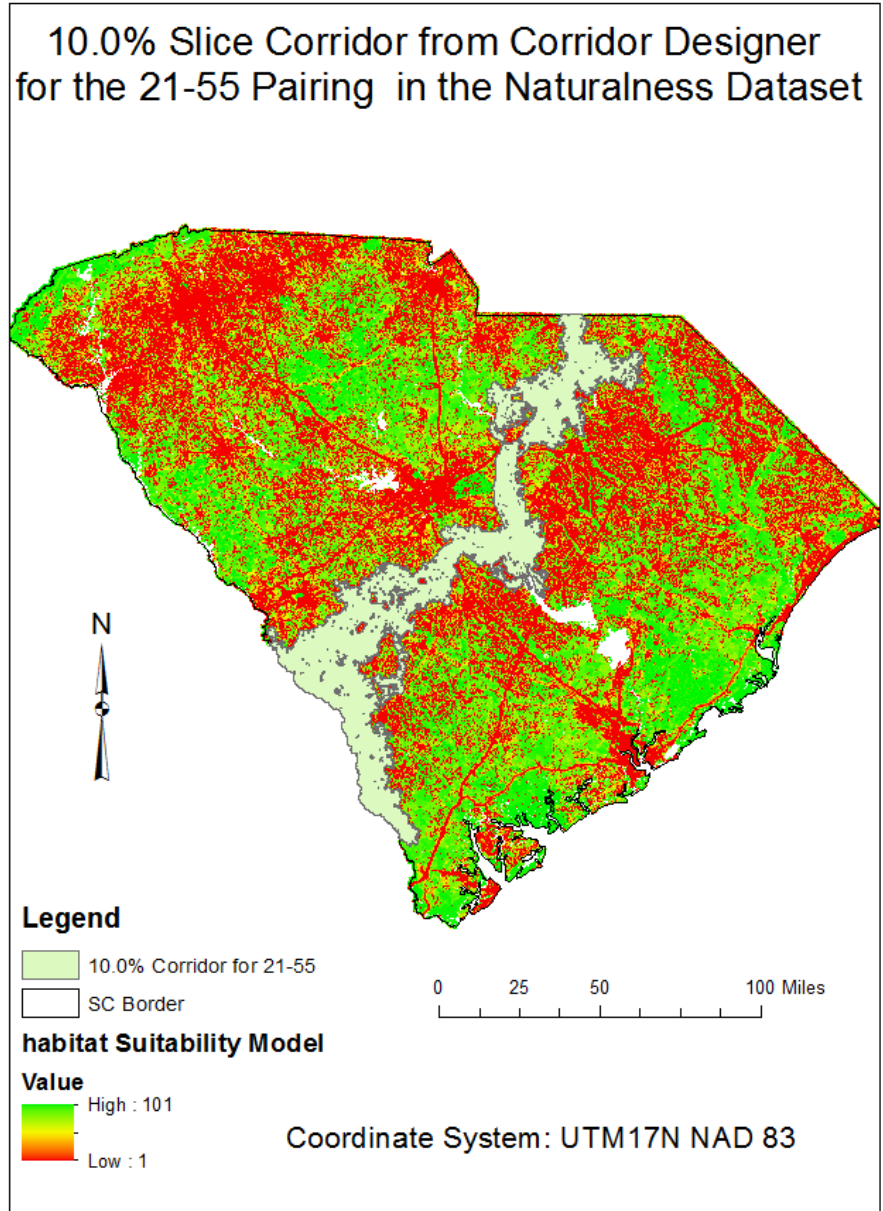


Figure 36.

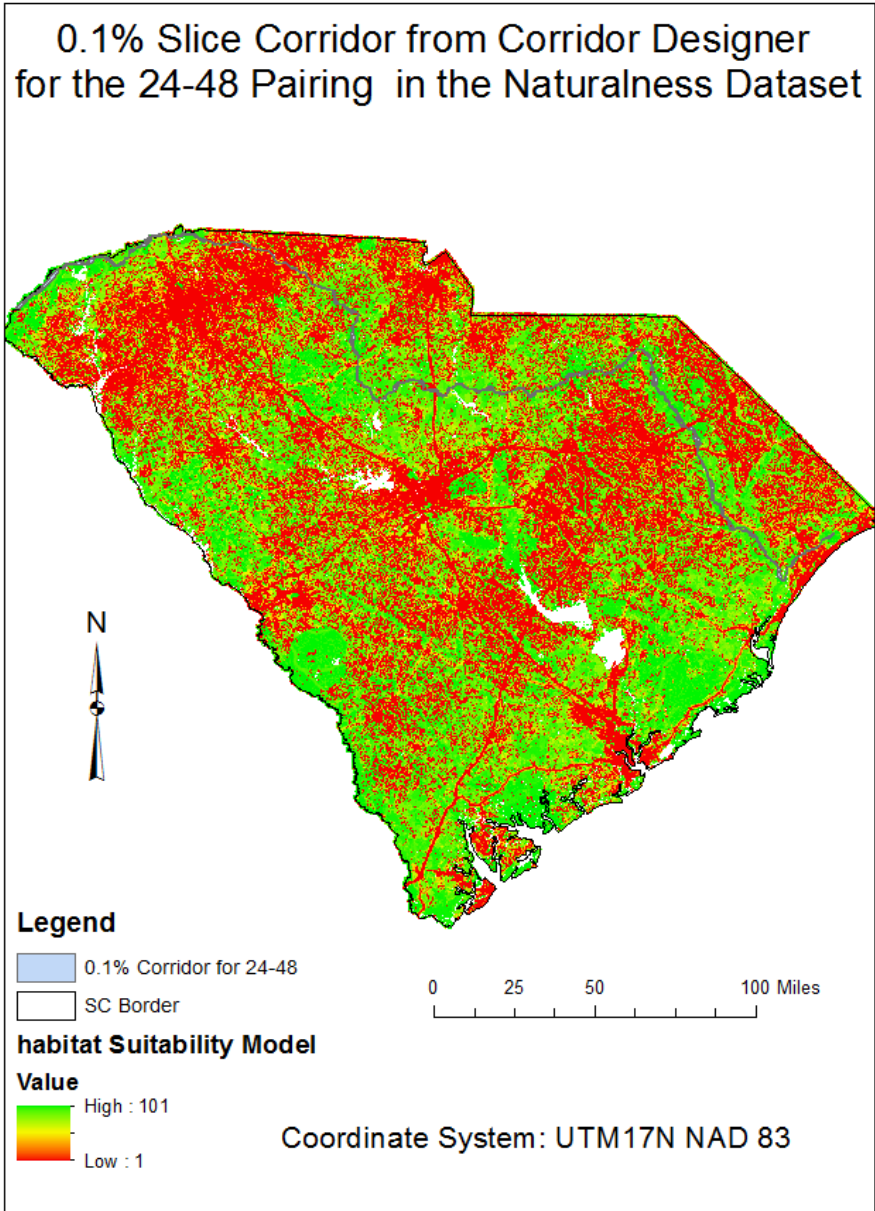


Figure 37.

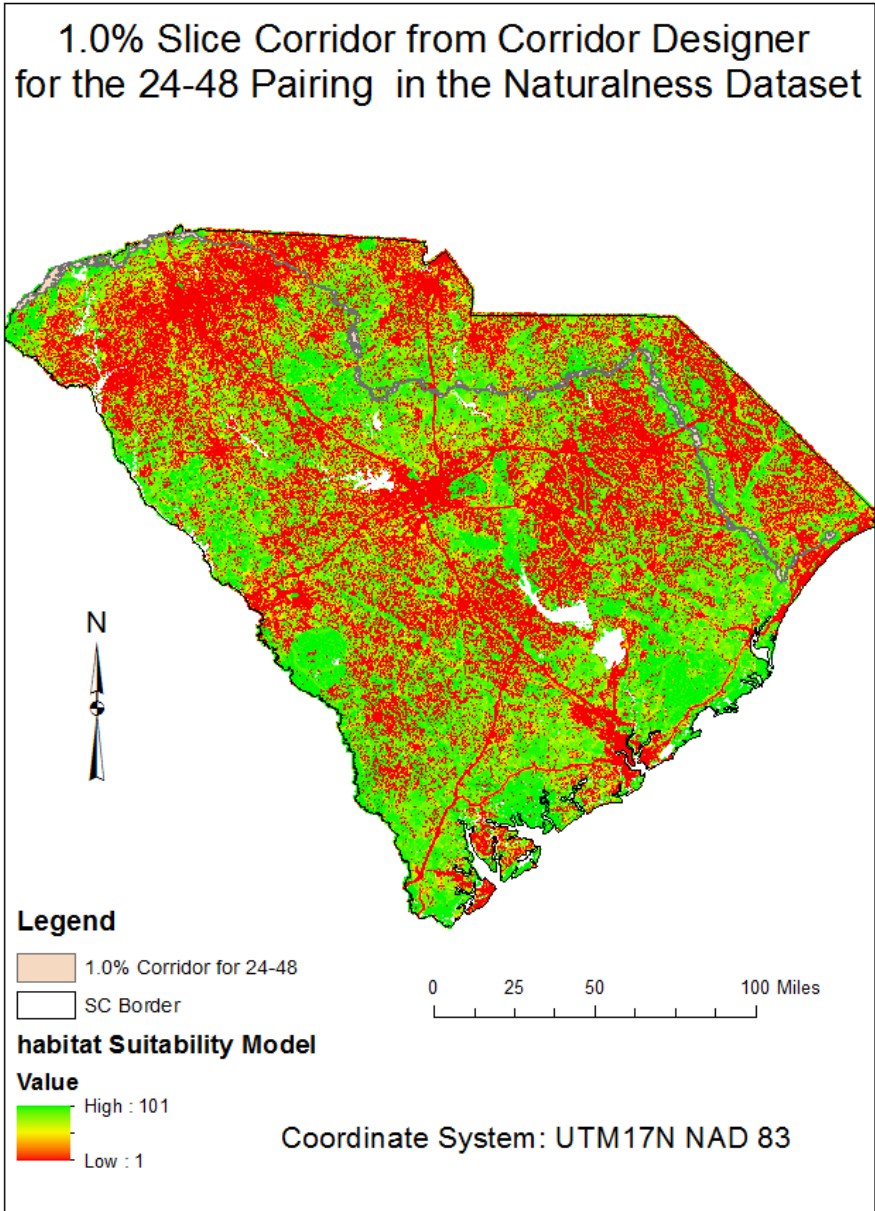


Figure 38.

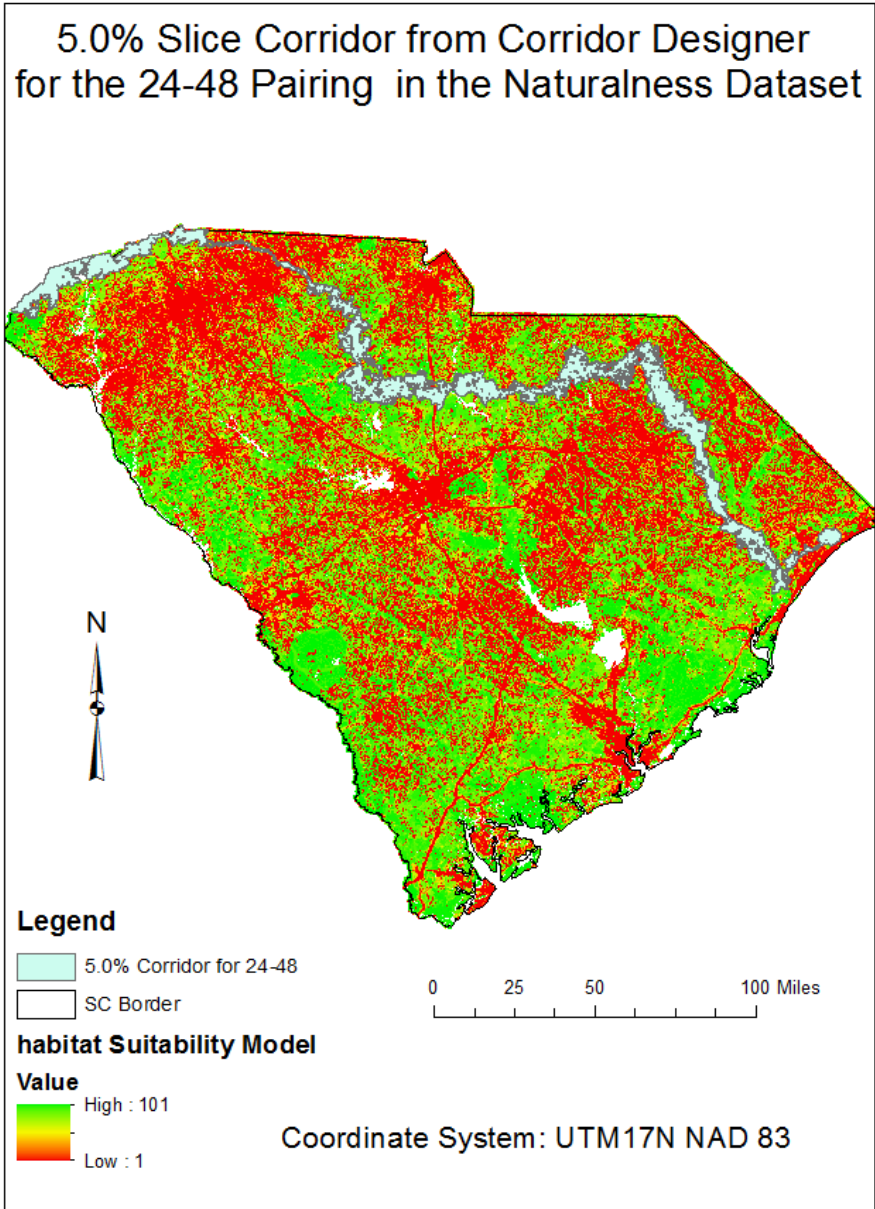


Figure 39.

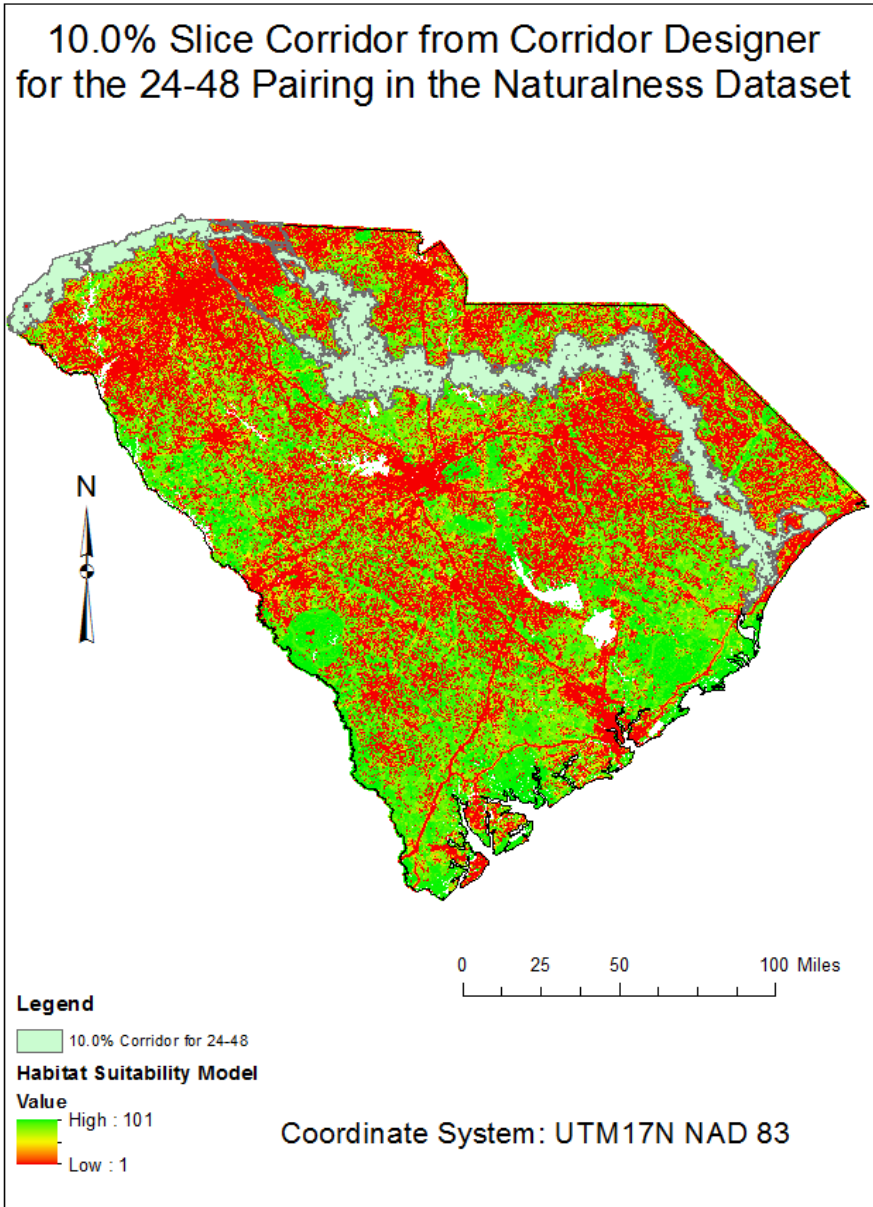


Figure 40.

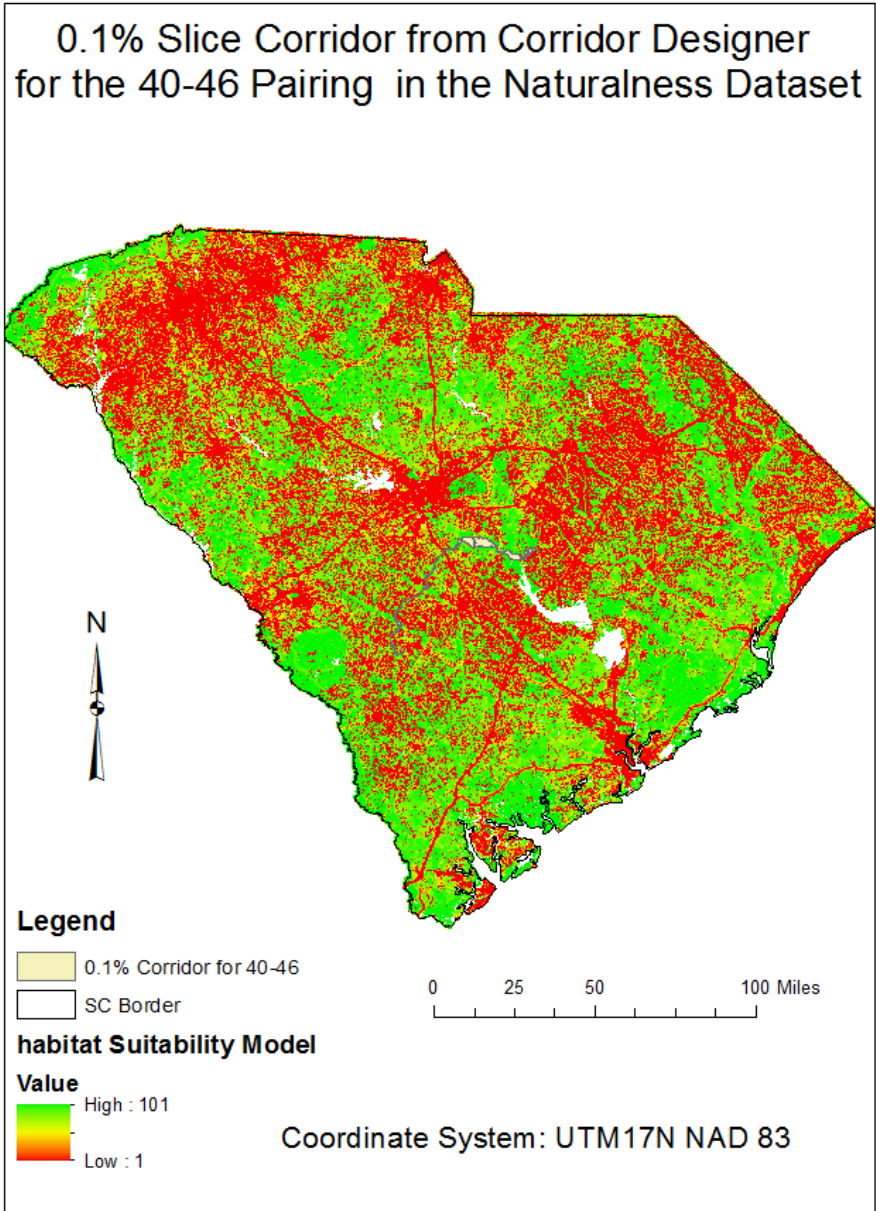


Figure 41.

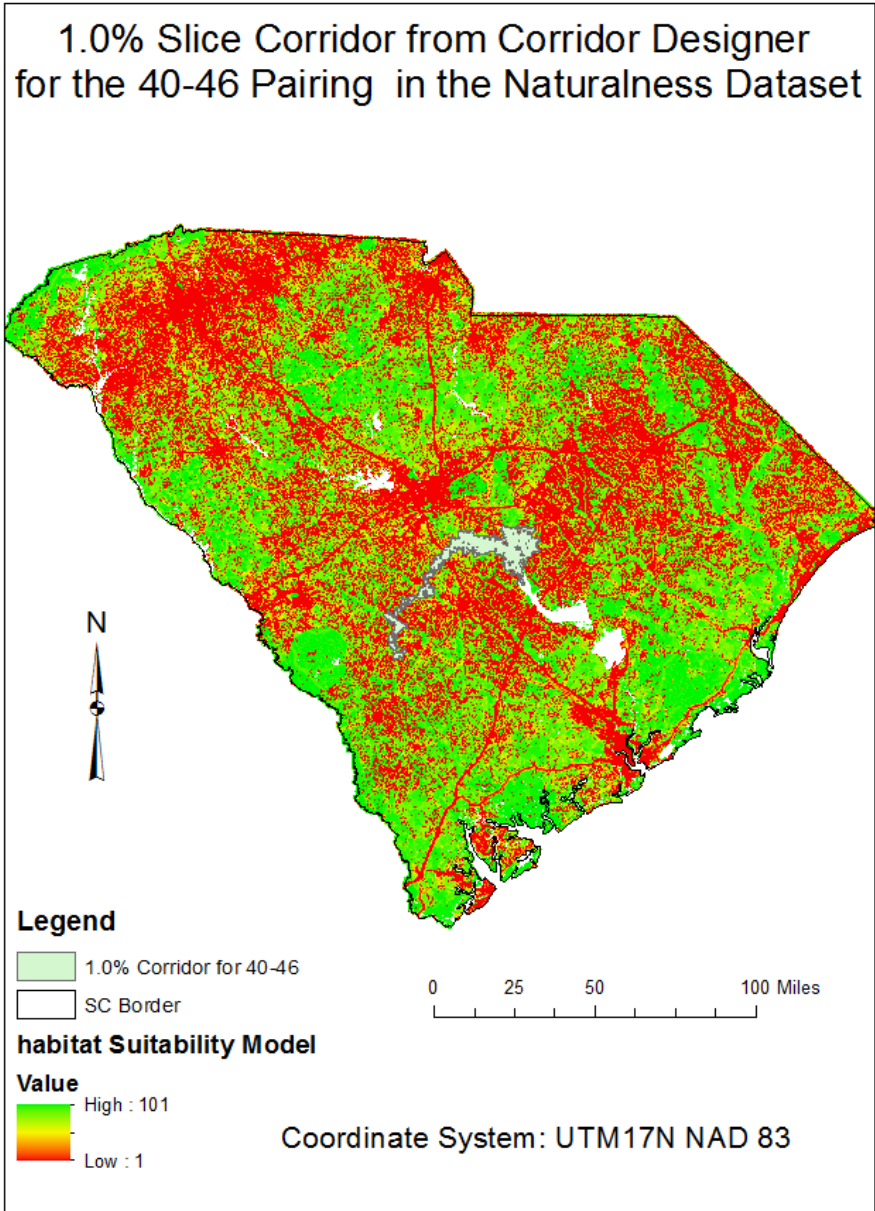


Figure 42.

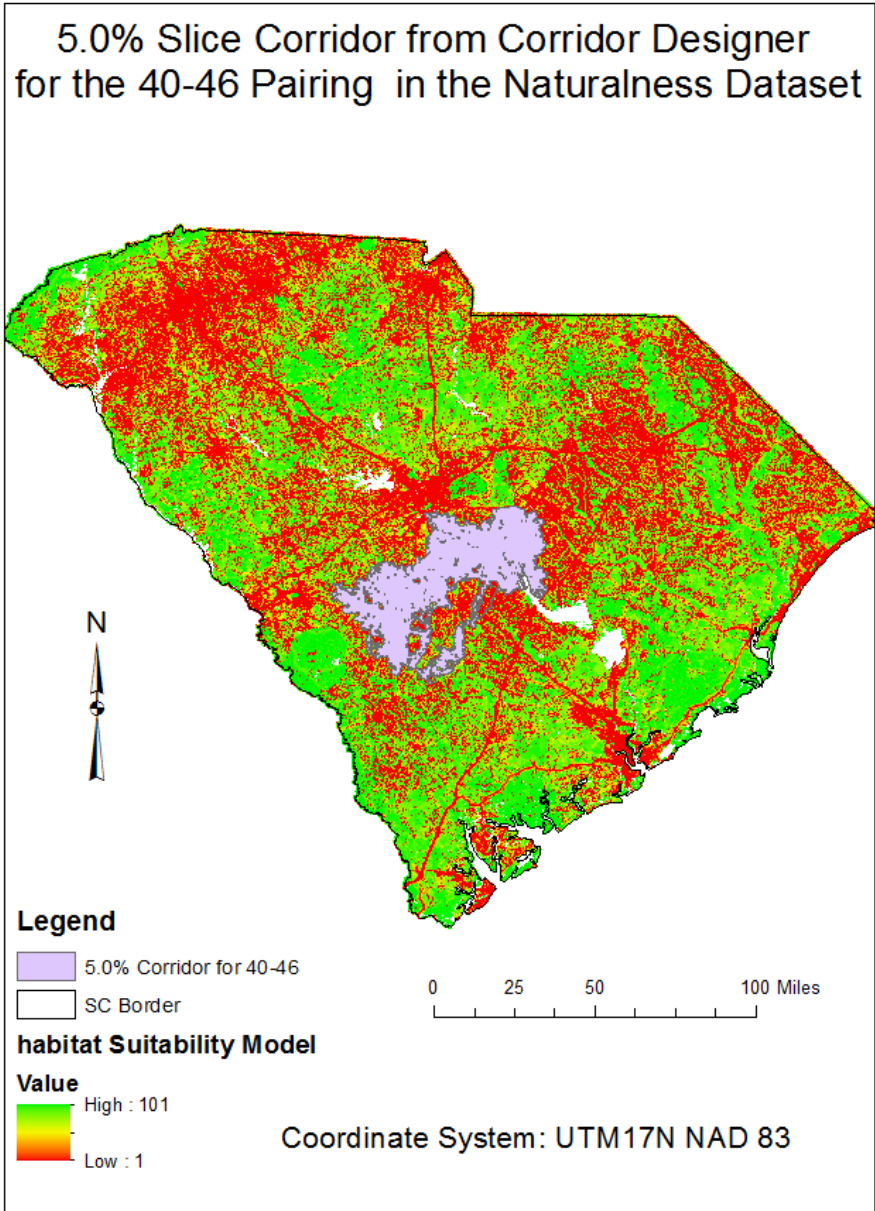


Figure 43.

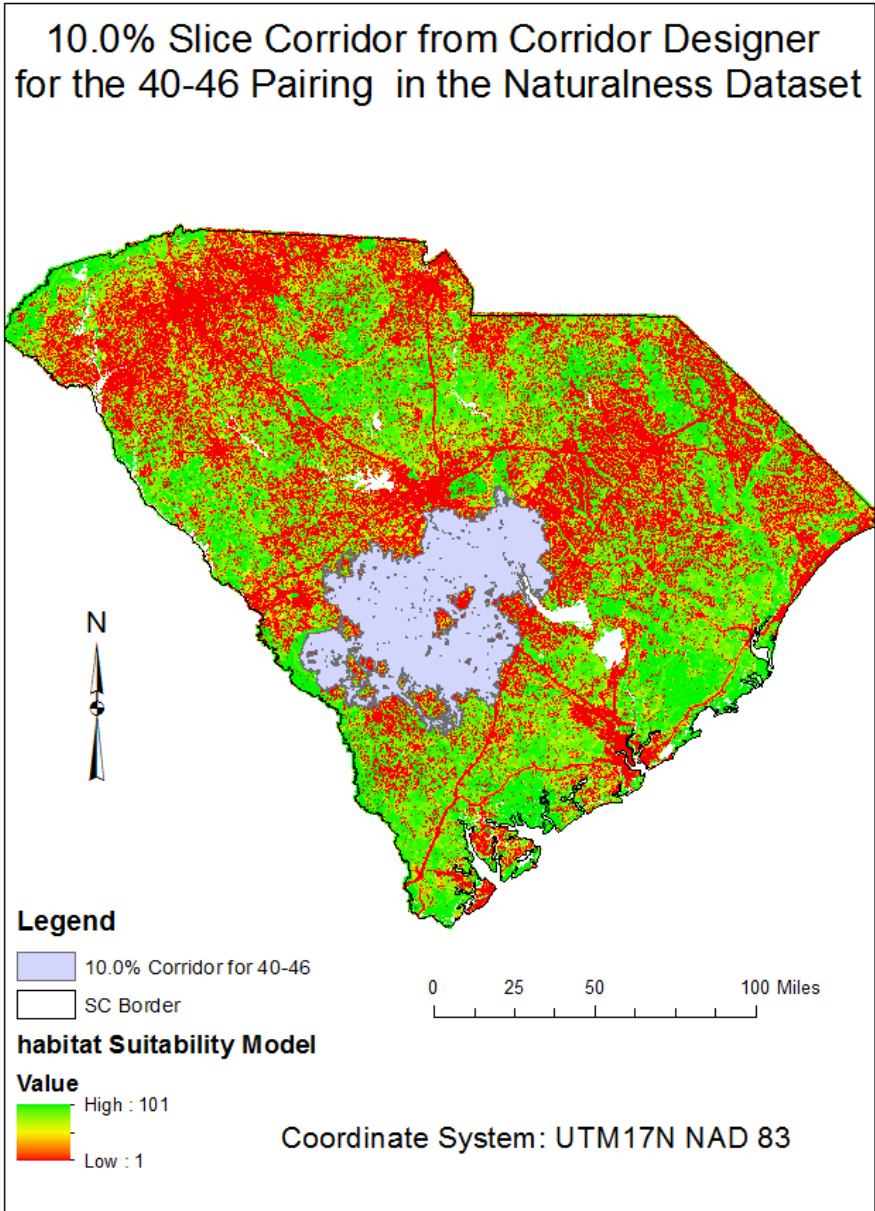


Figure 44.

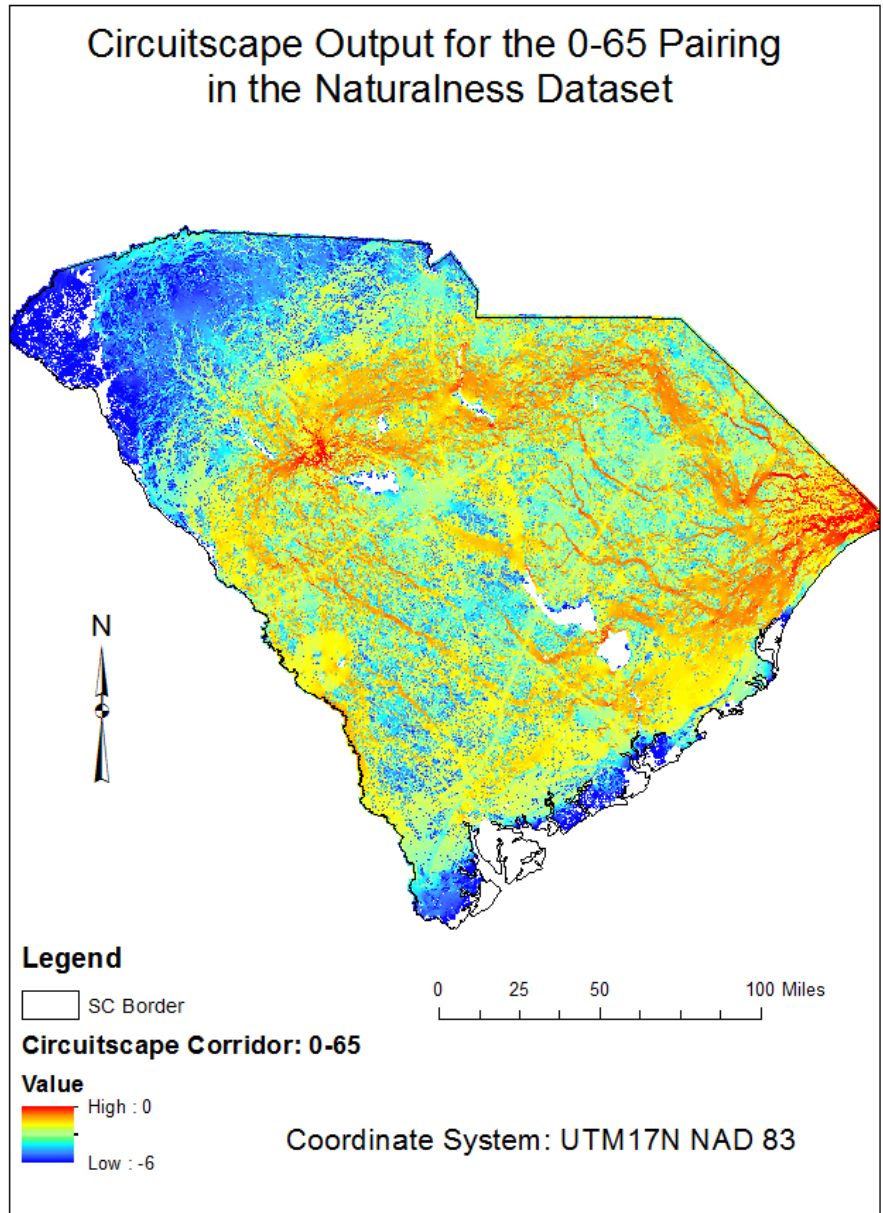


Figure 45.

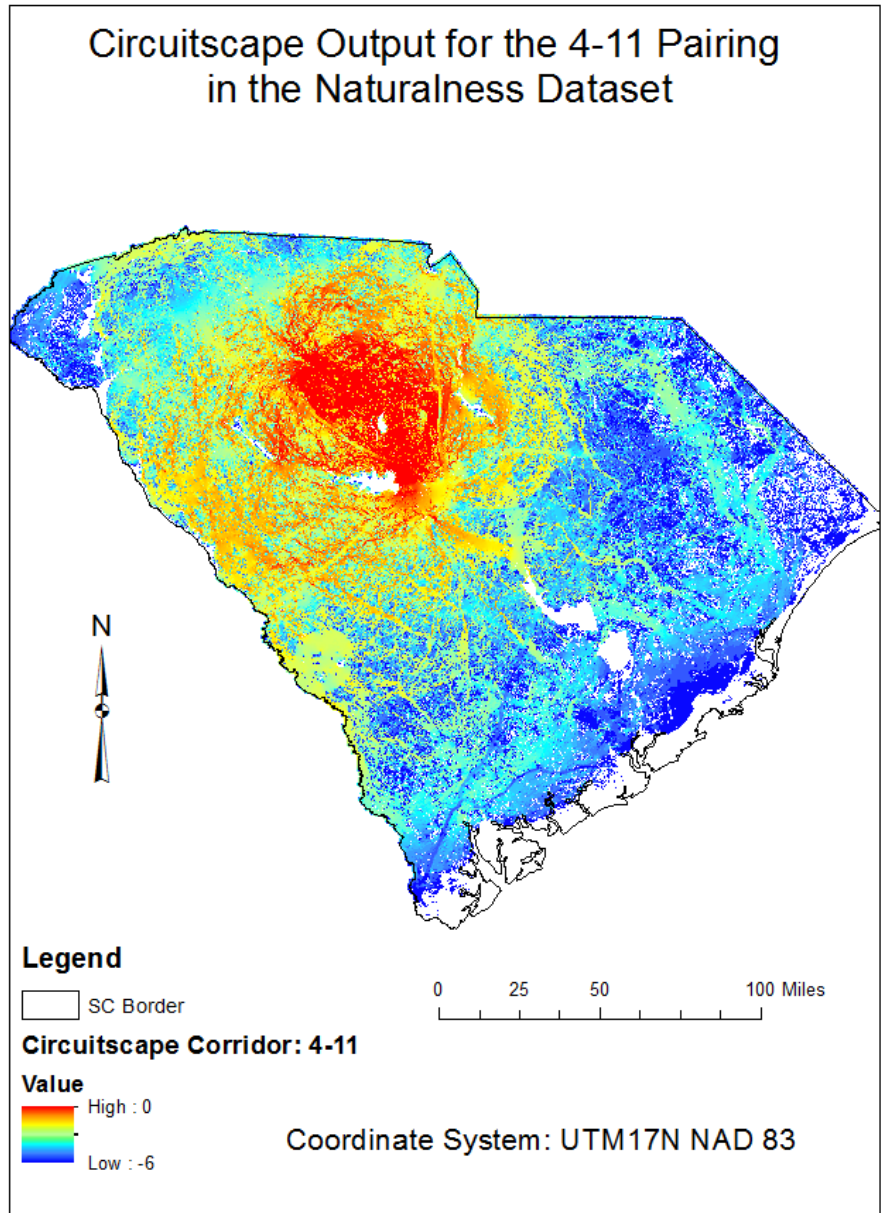


Figure 46.

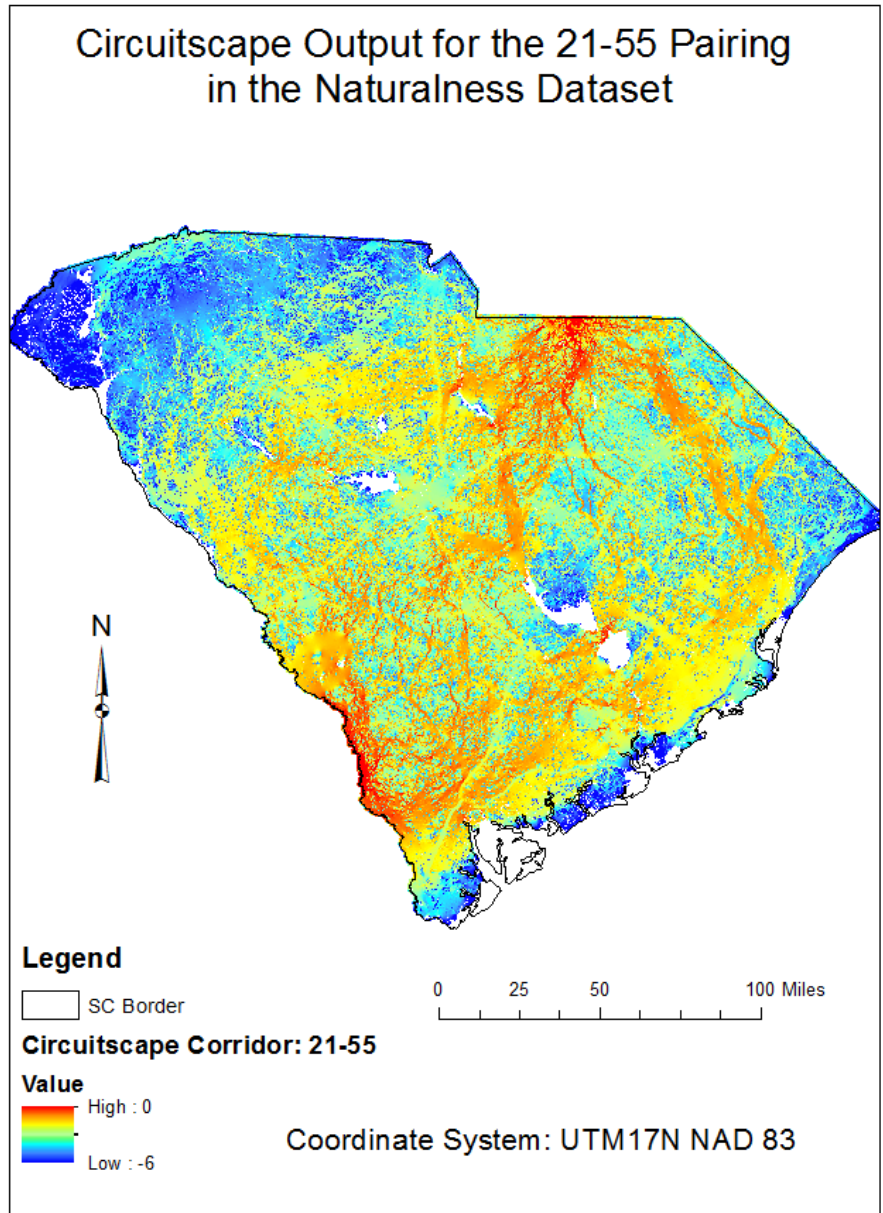


Figure 47.

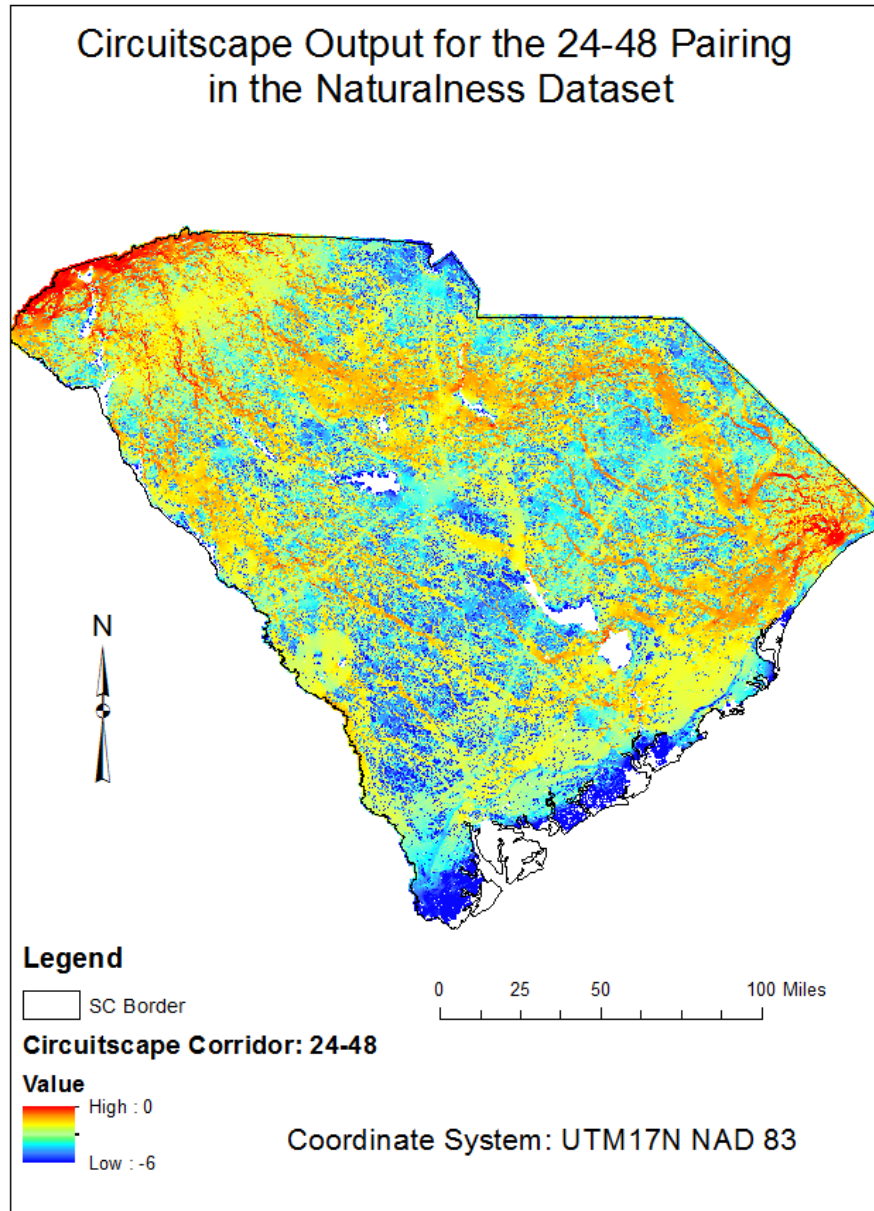


Figure 48.

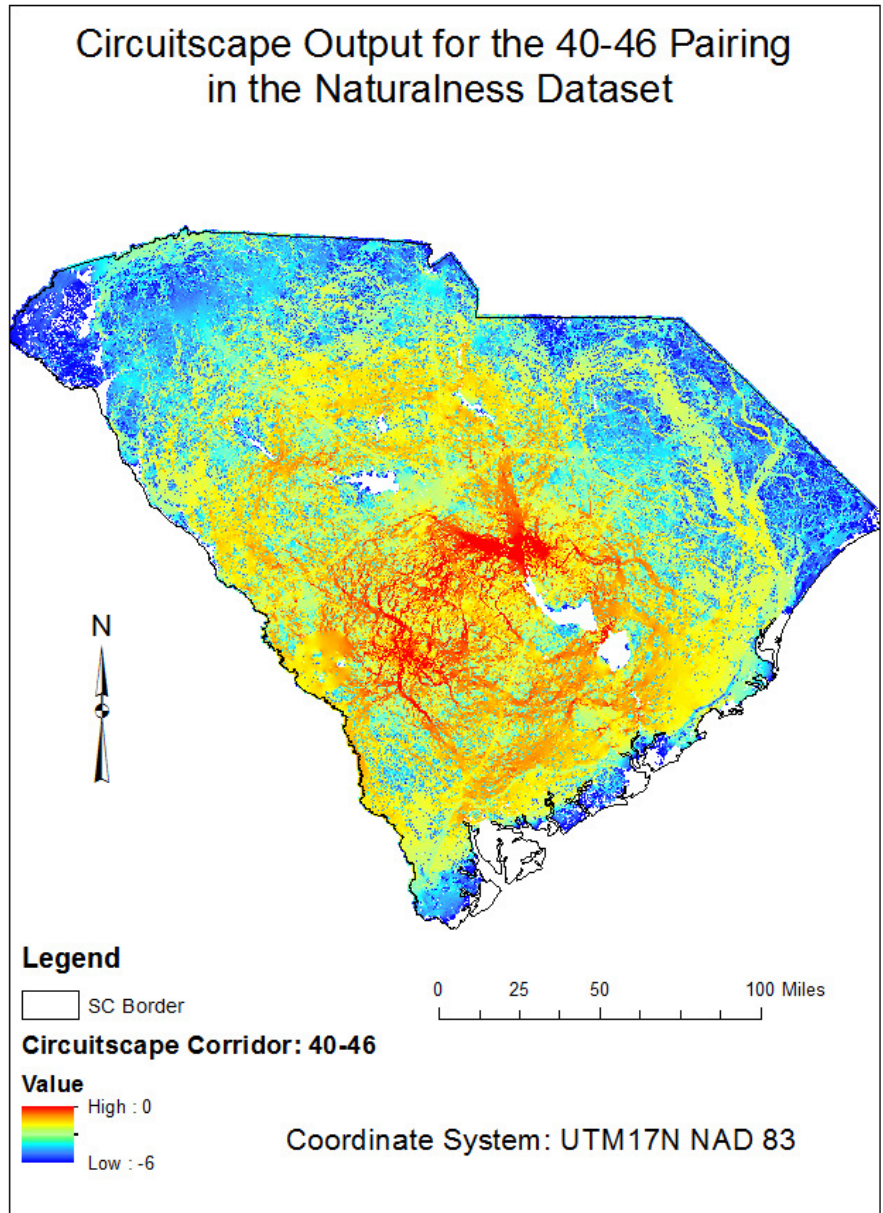


Figure 49.

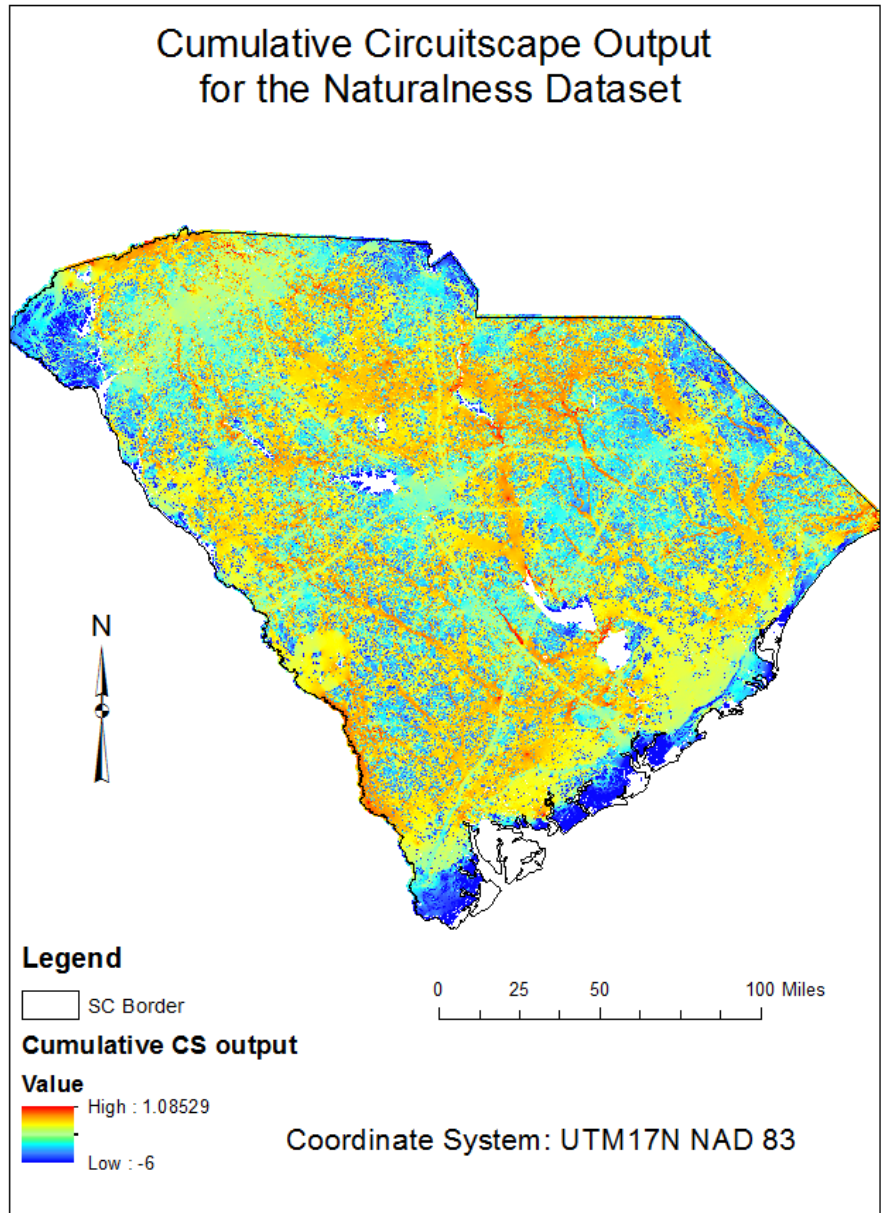


Figure 50.

Appendix 2: Maps Used for Visual Comparisons

The figures in Appendix 2 are maps and images with the CorridorDesigner corridor placed on top of the Circuitscape individual current map. There is one 0.1, 1.0, 5.0, and 10.0% slice corridor from CD. There is one set of maps for each focal species and five for the naturalness dataset.

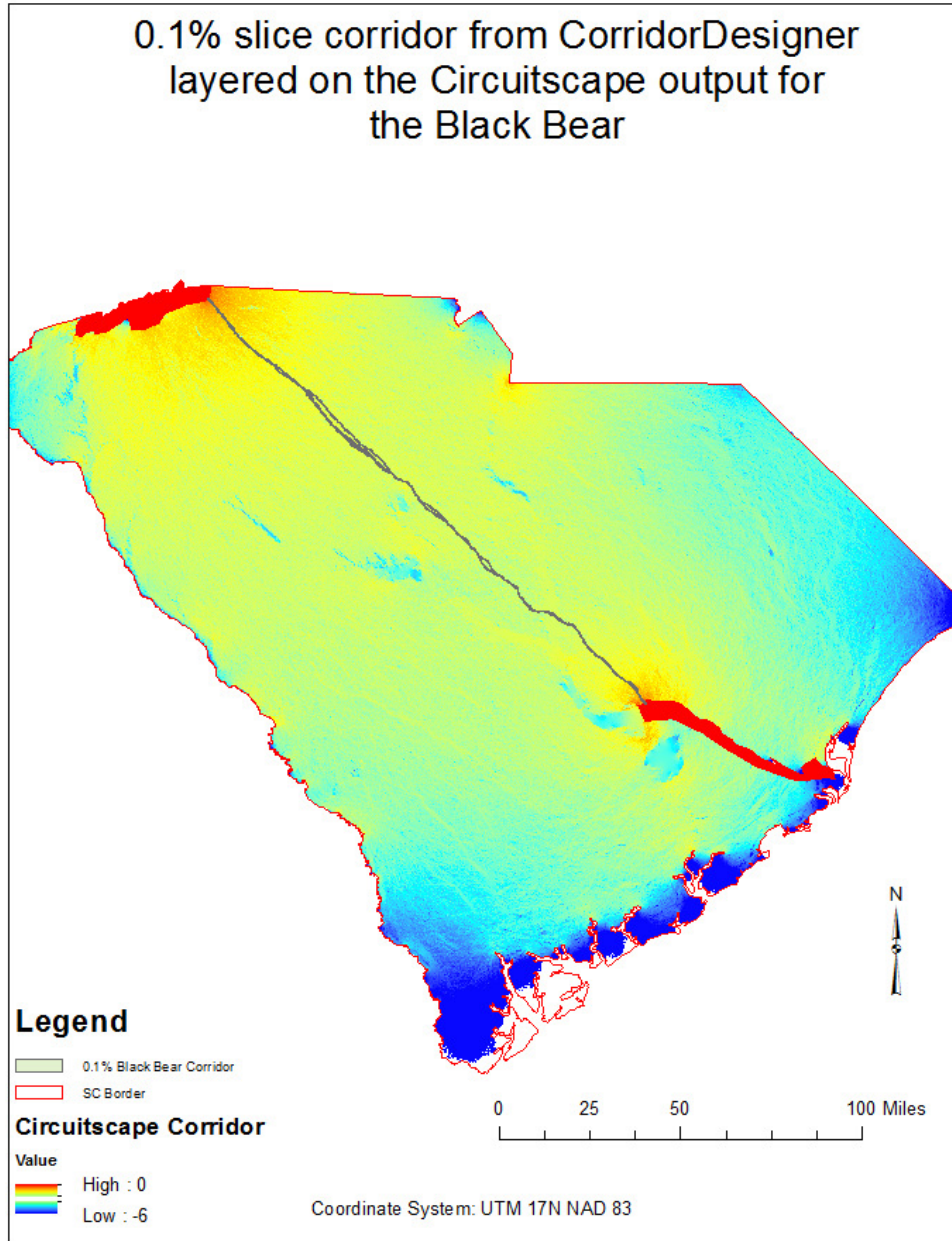


Figure 1.

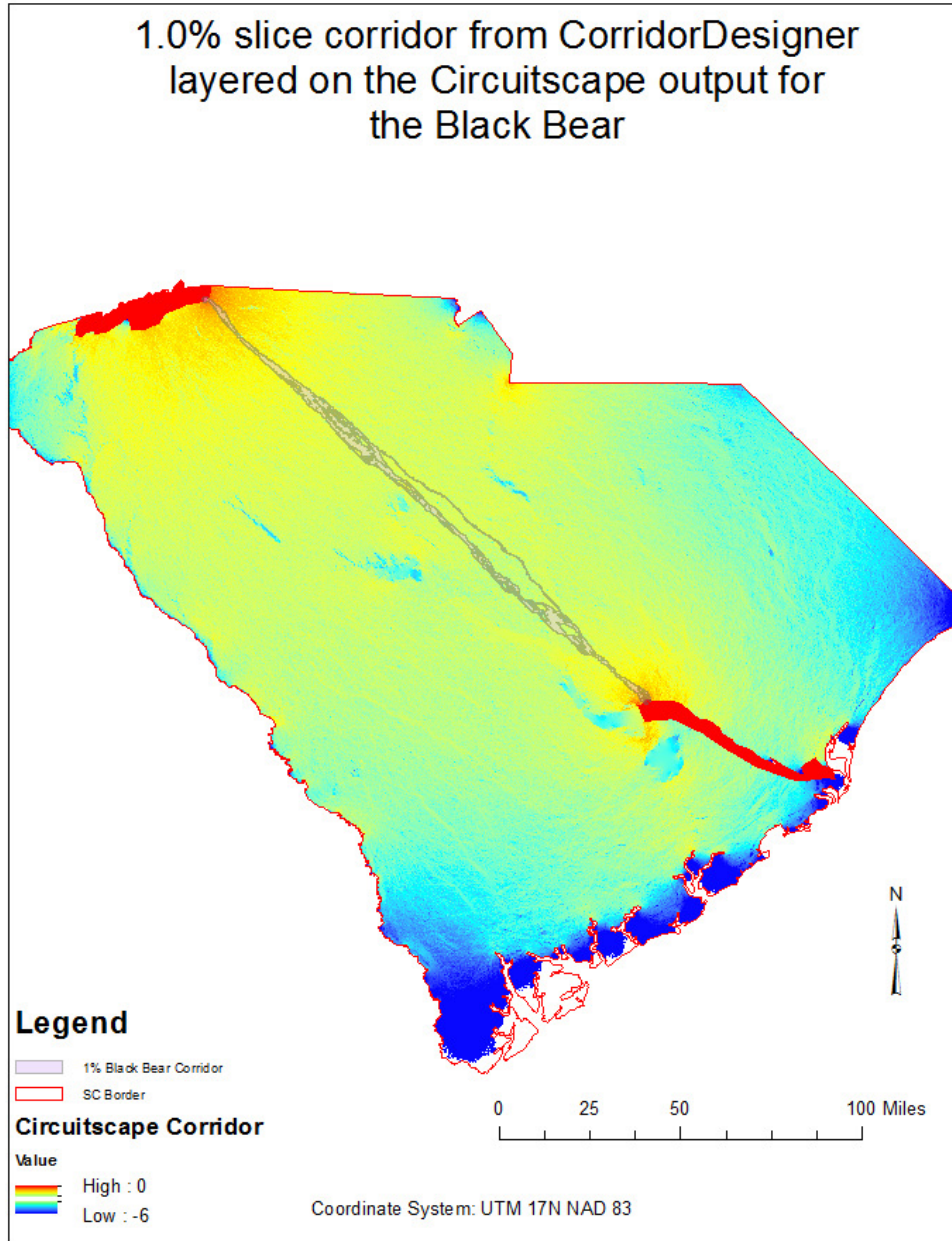


Figure 2.

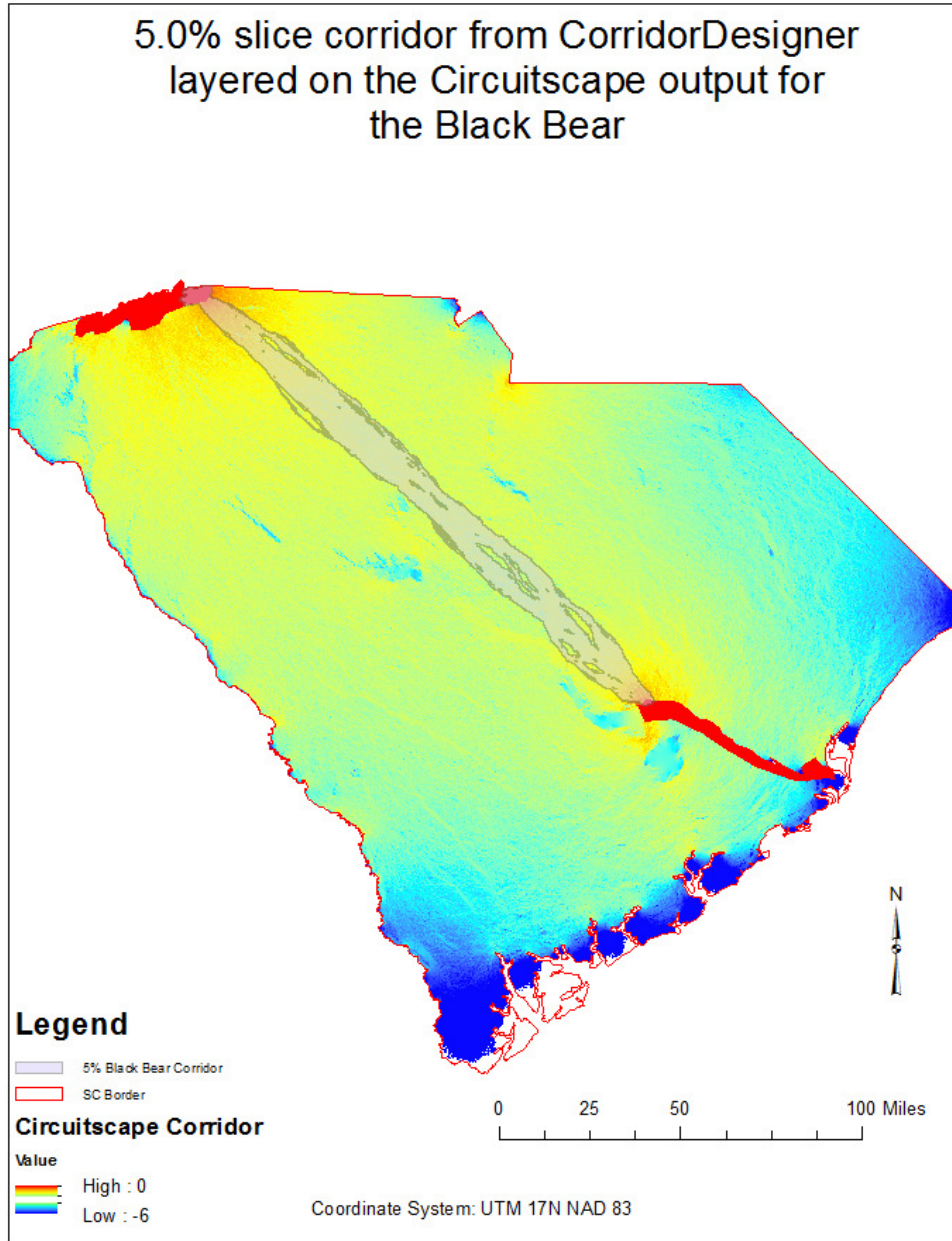


Figure 3.

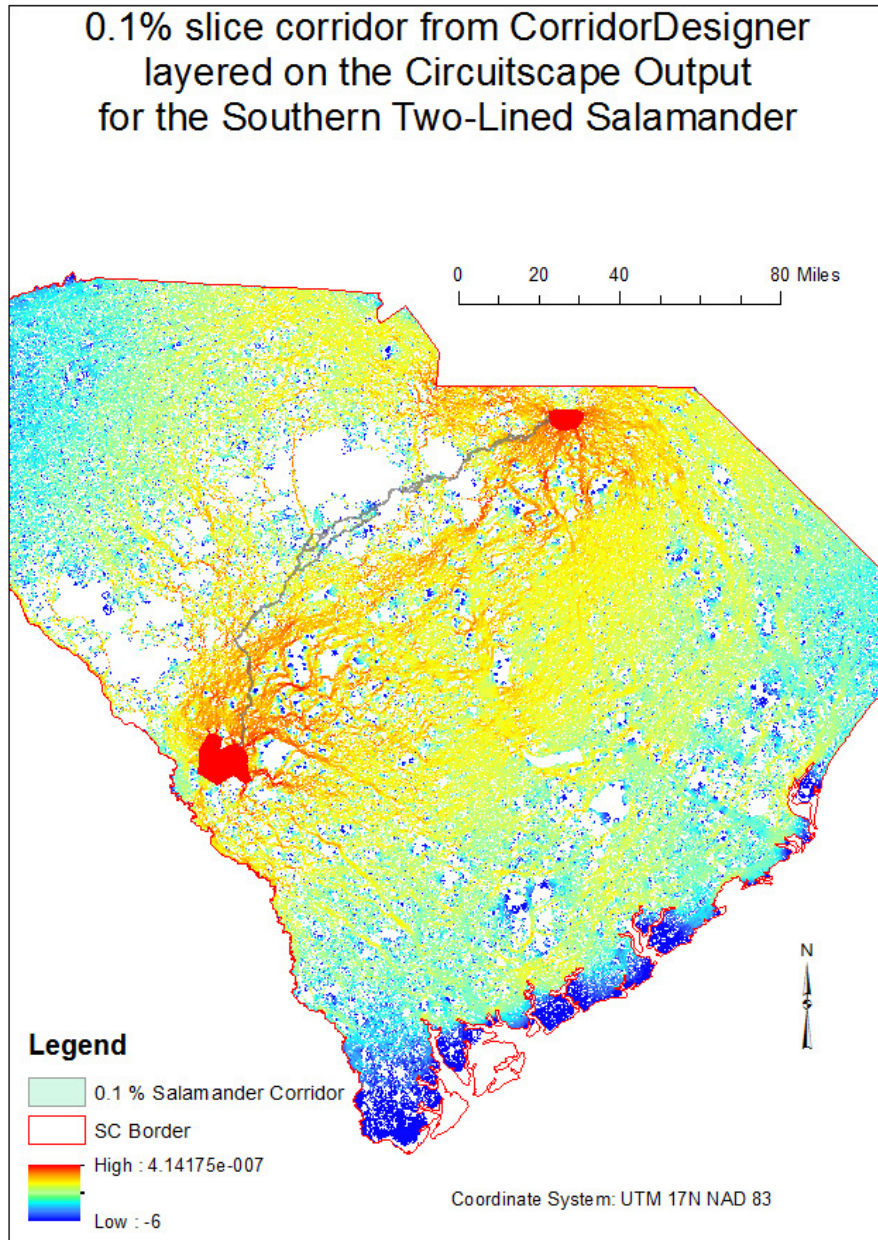


Figure 4.

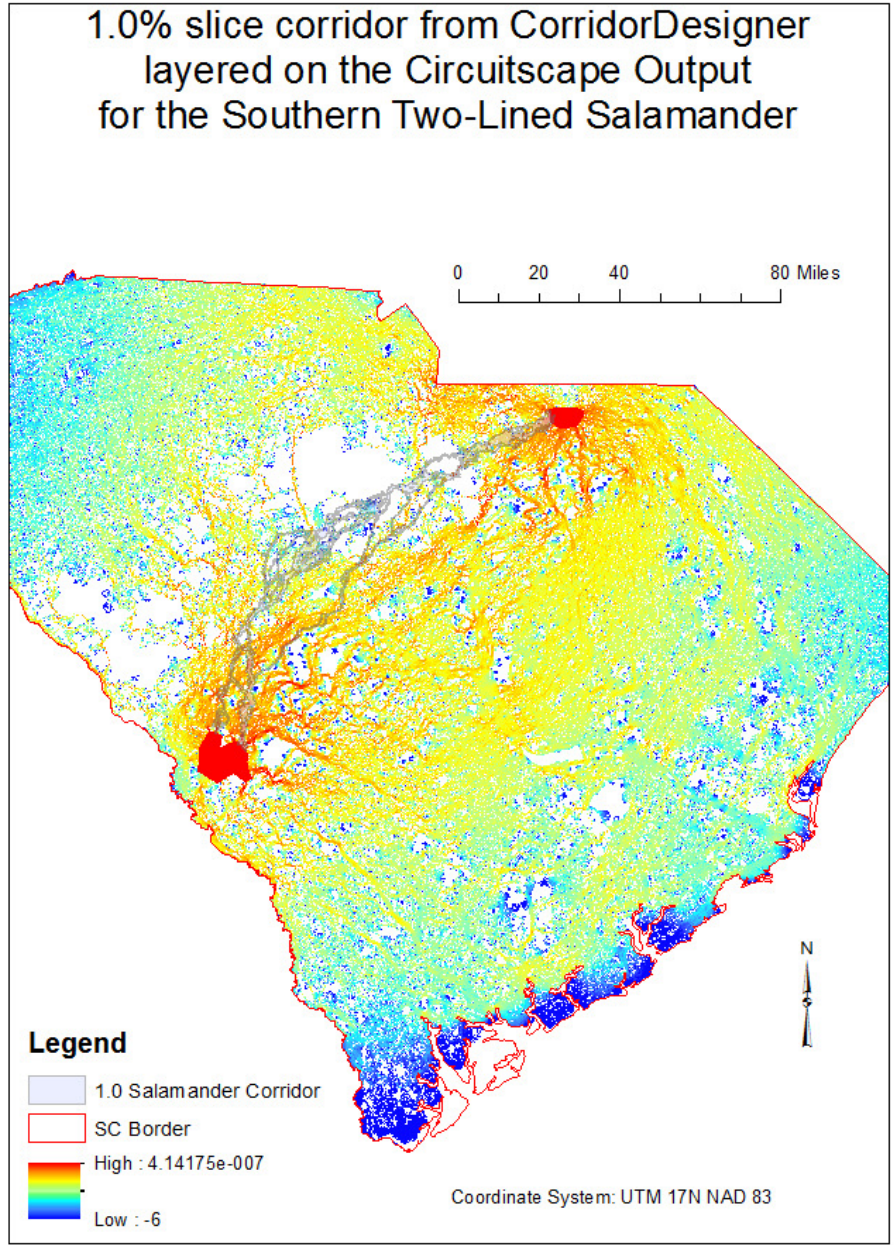


Figure 5.

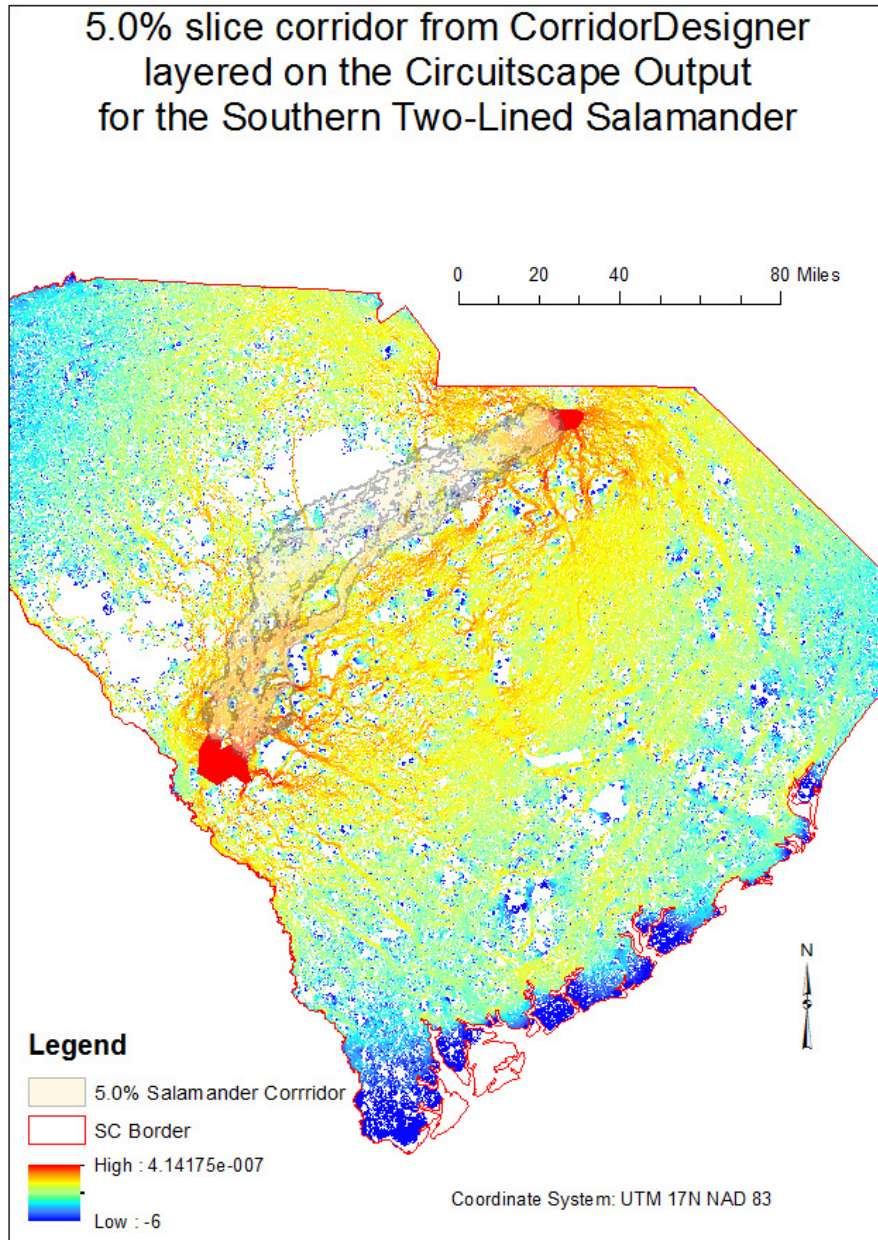


Figure 6.

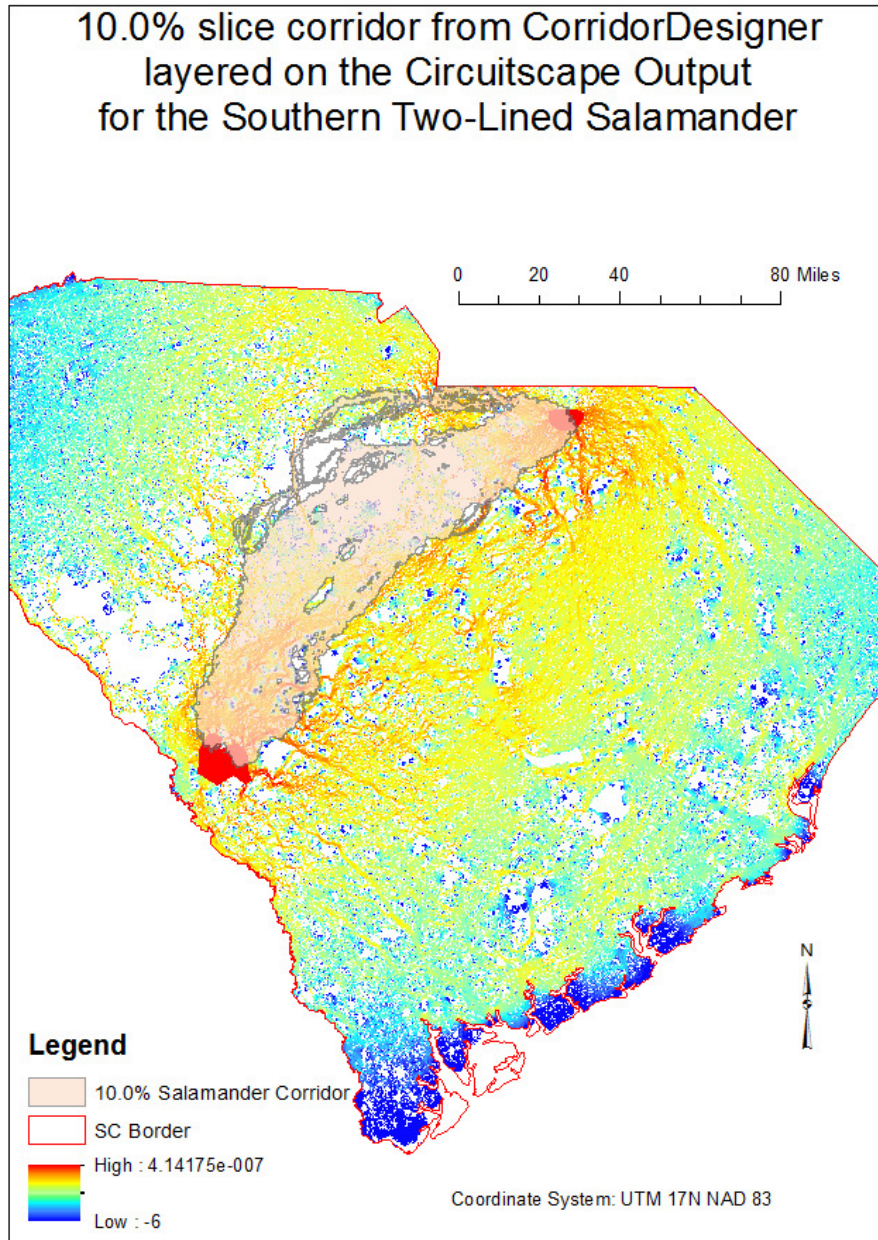


Figure 7.

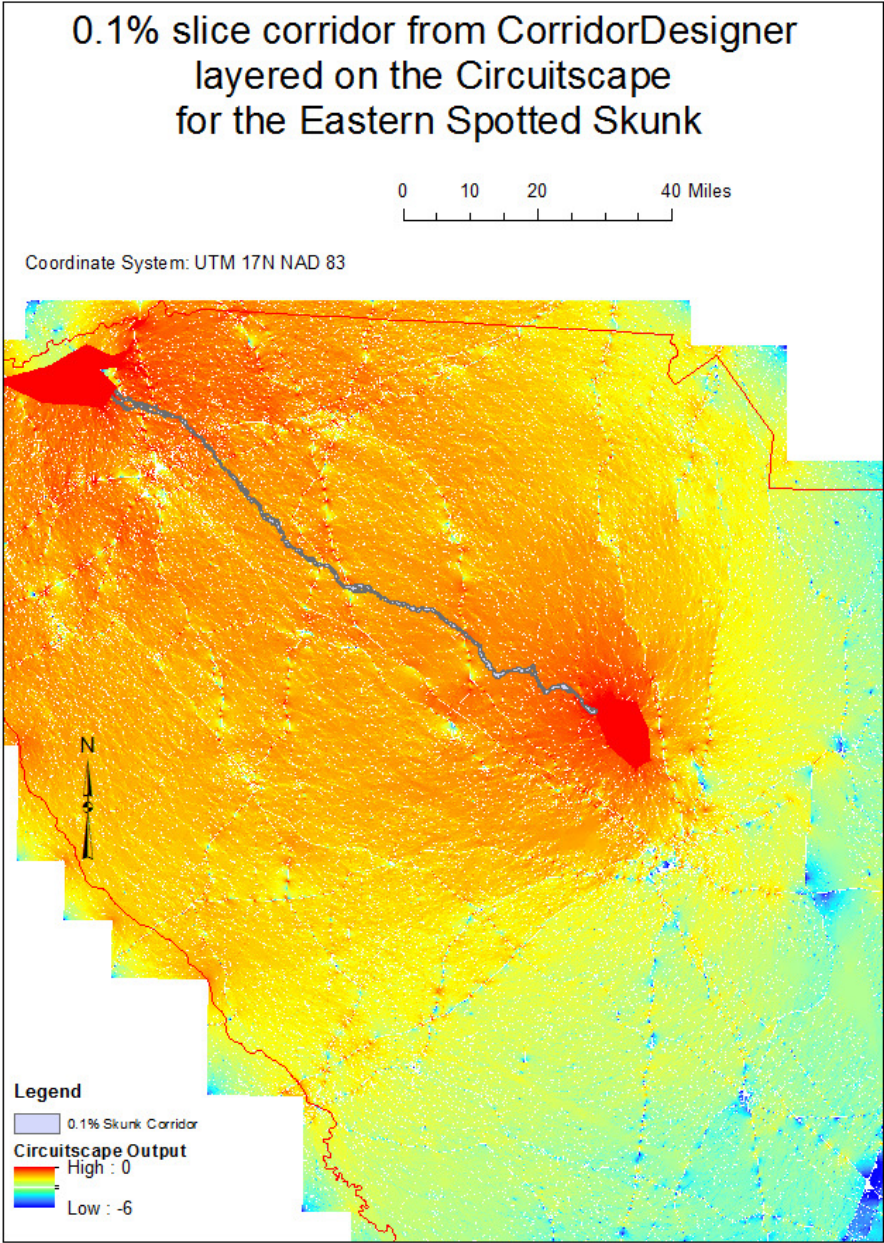


Figure 8.

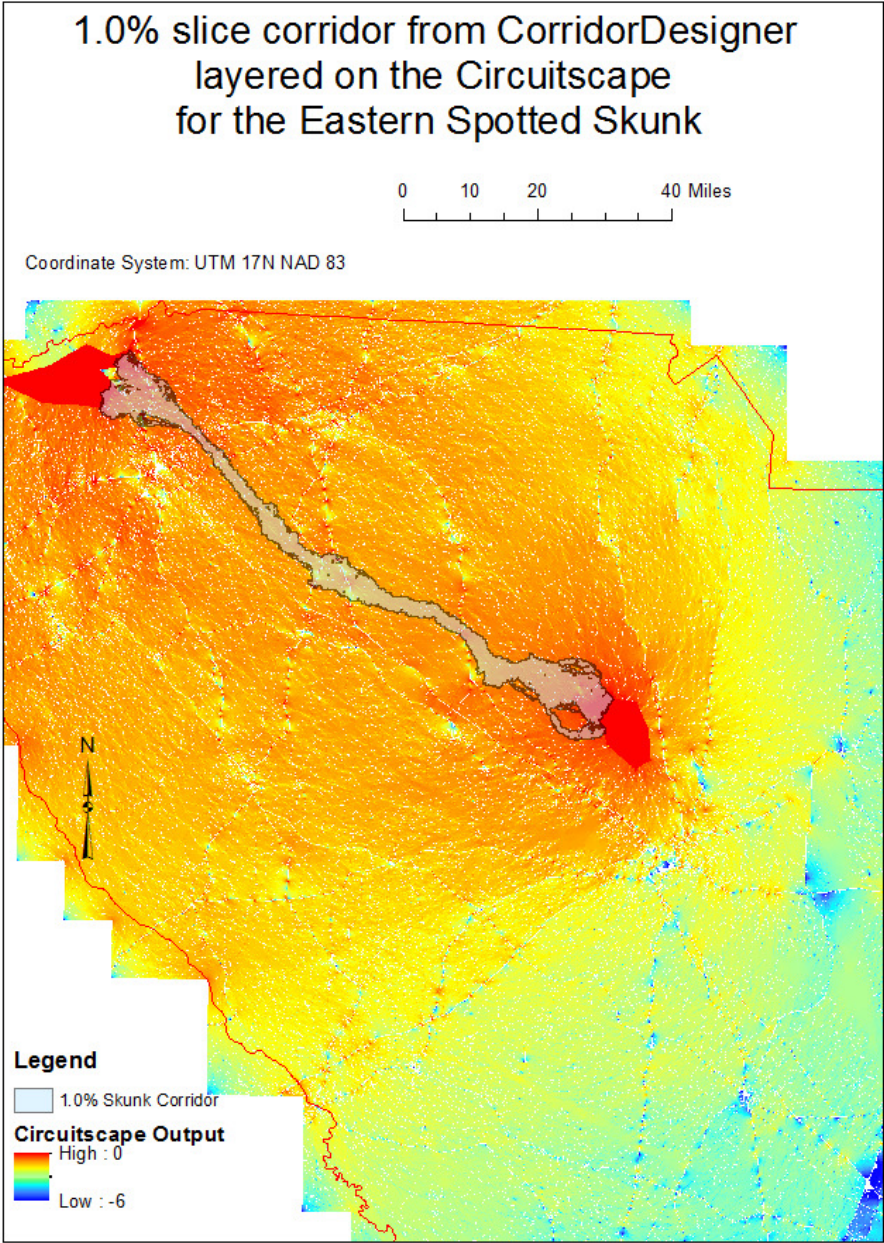


Figure 9.

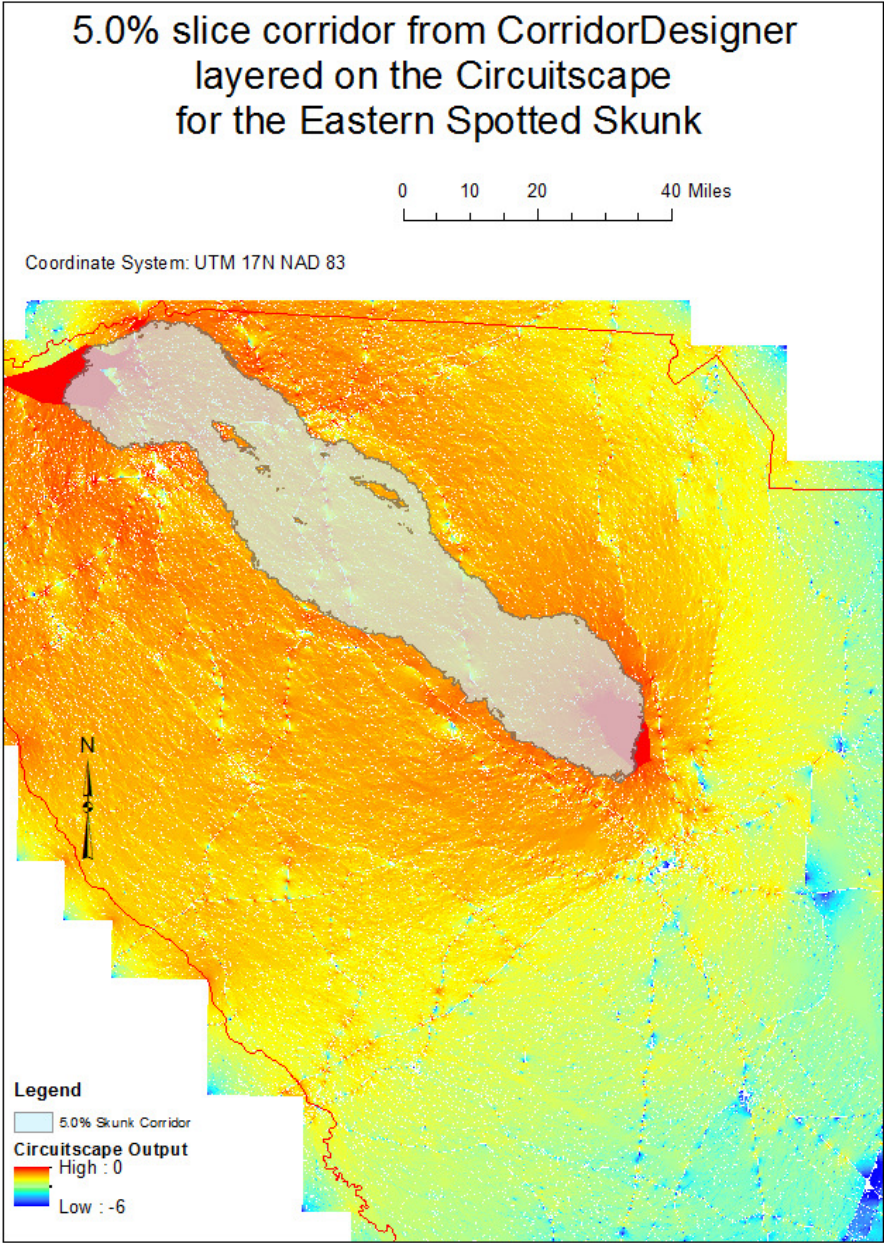


Figure 10.

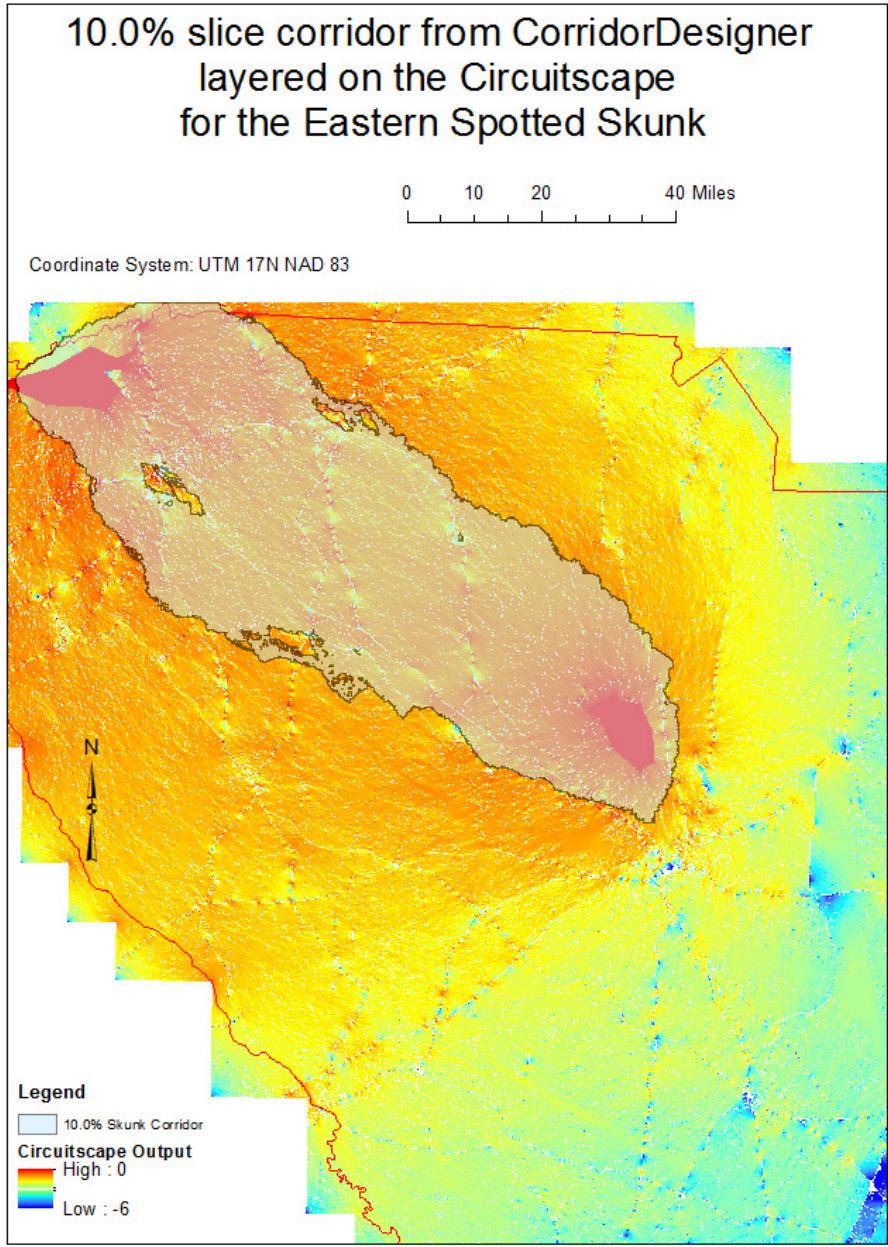


Figure 11.

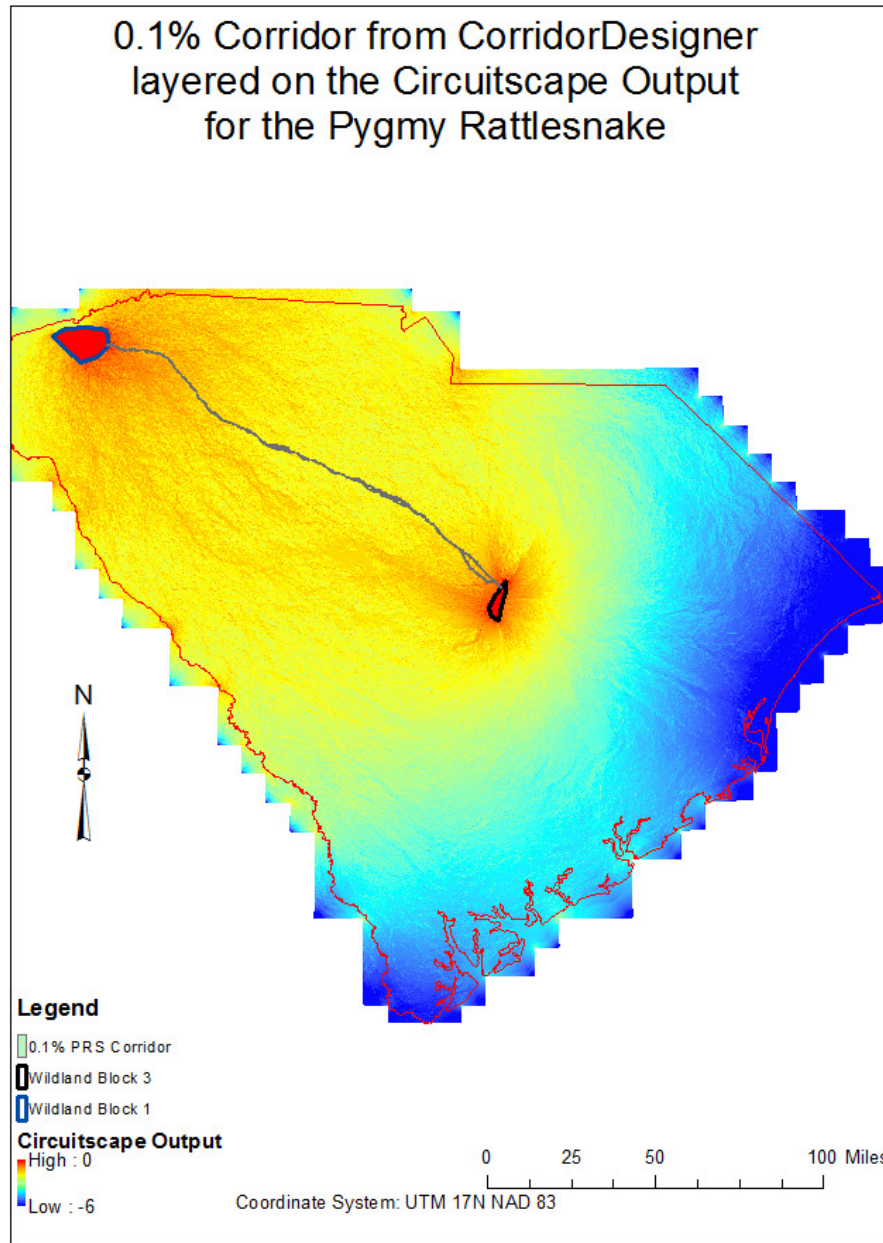


Figure 12.

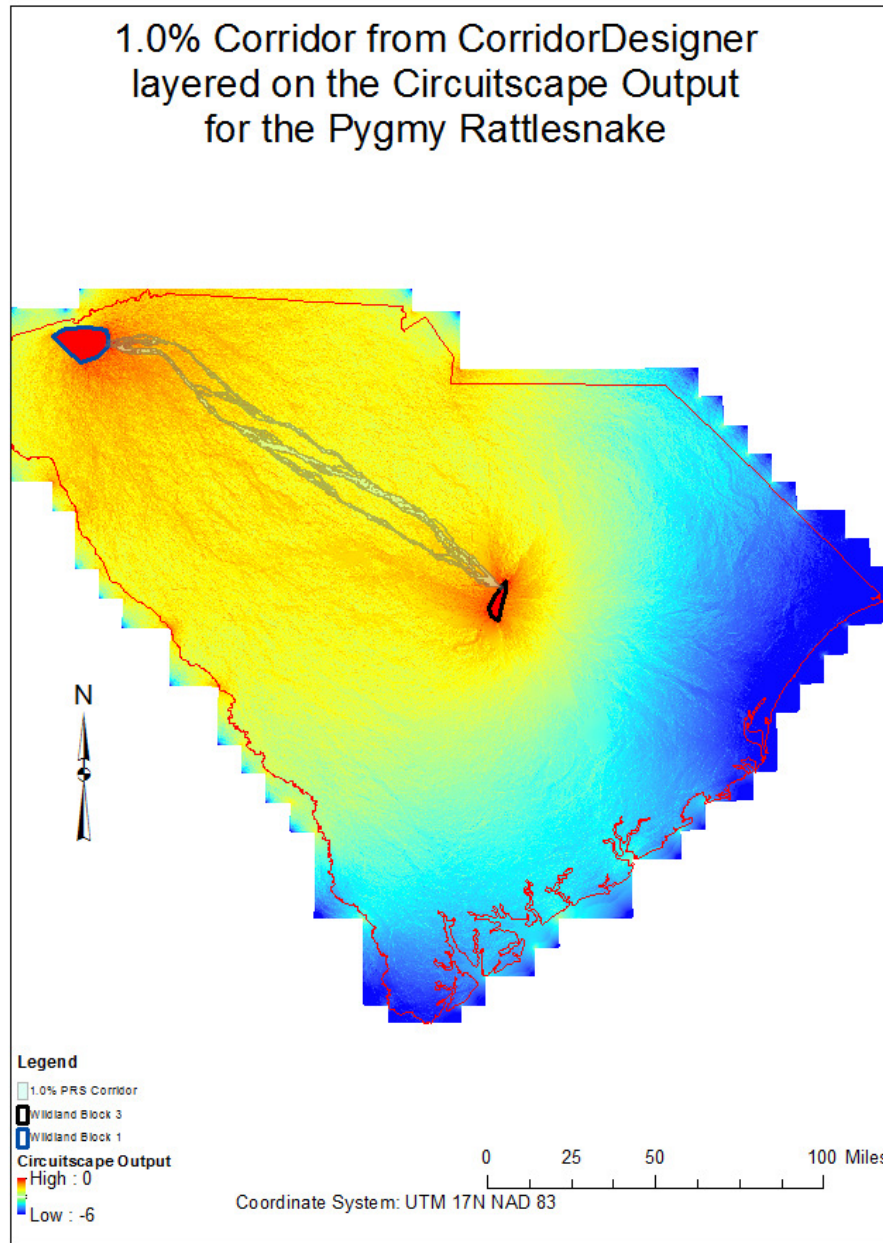


Figure 13.

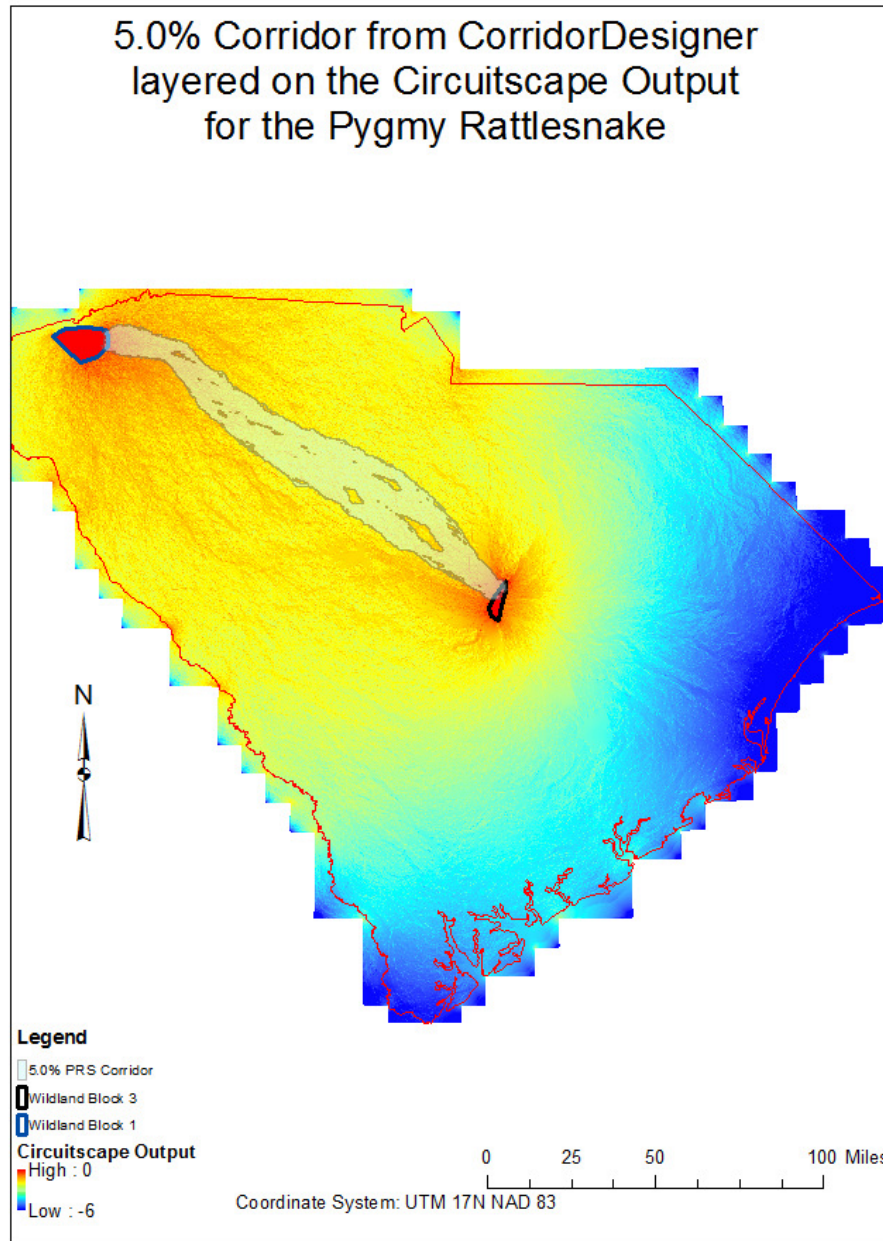


Figure 14.

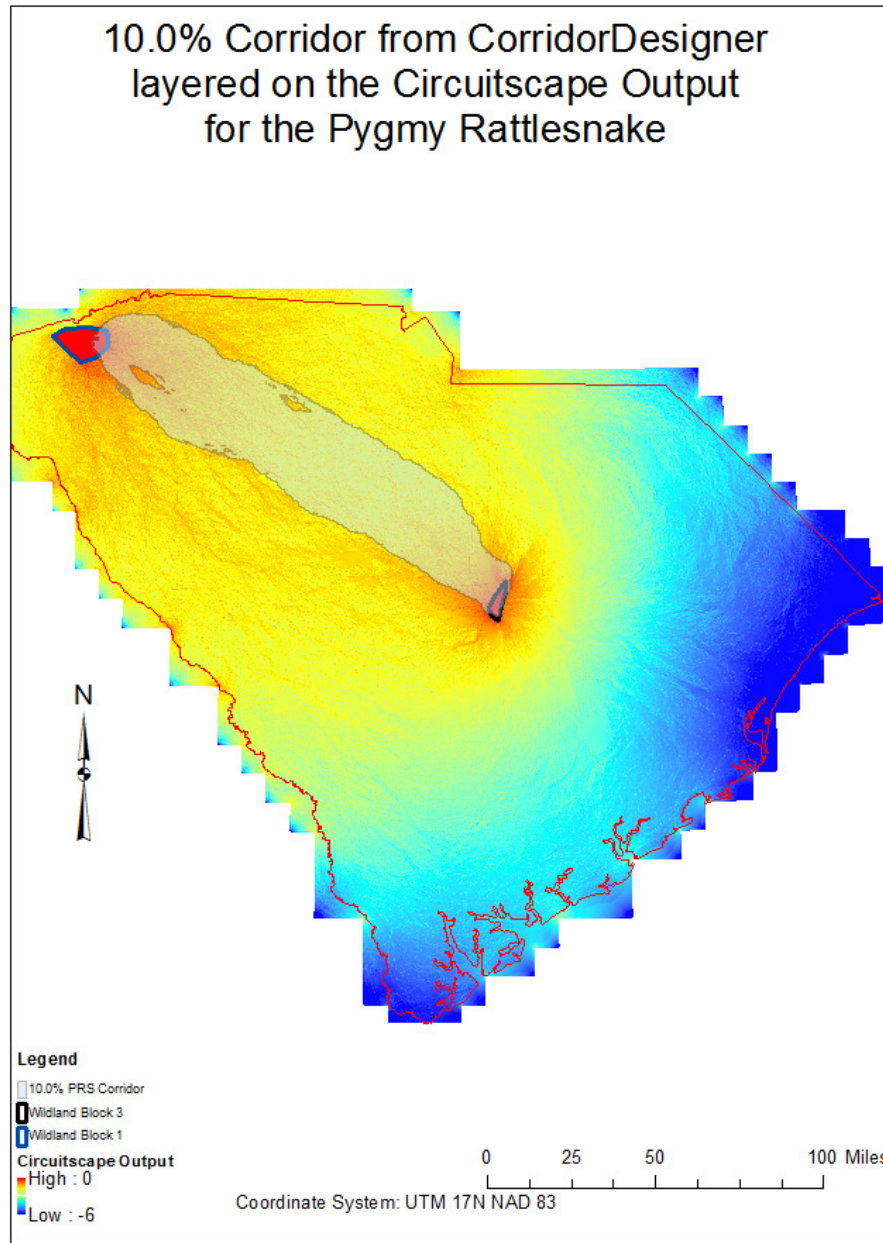


Figure 15.

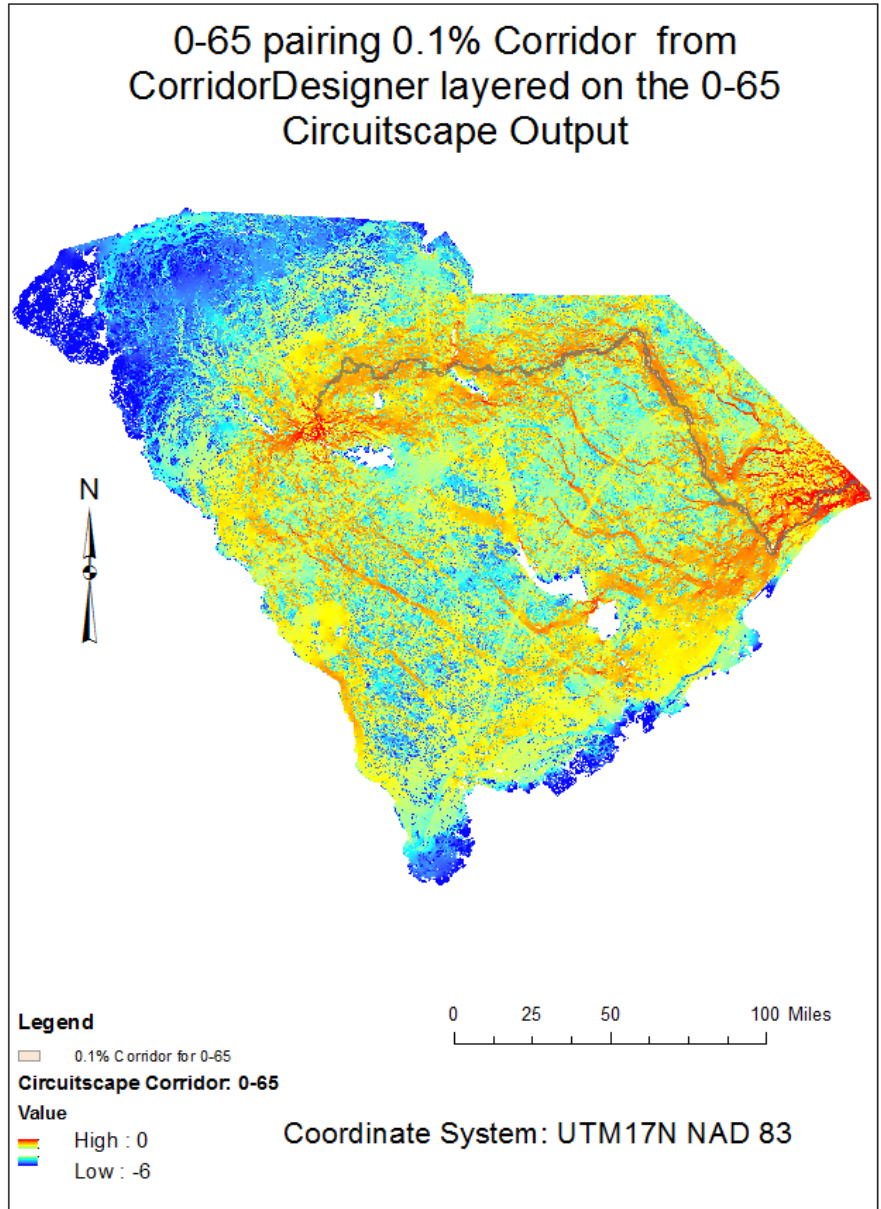


Figure 16.

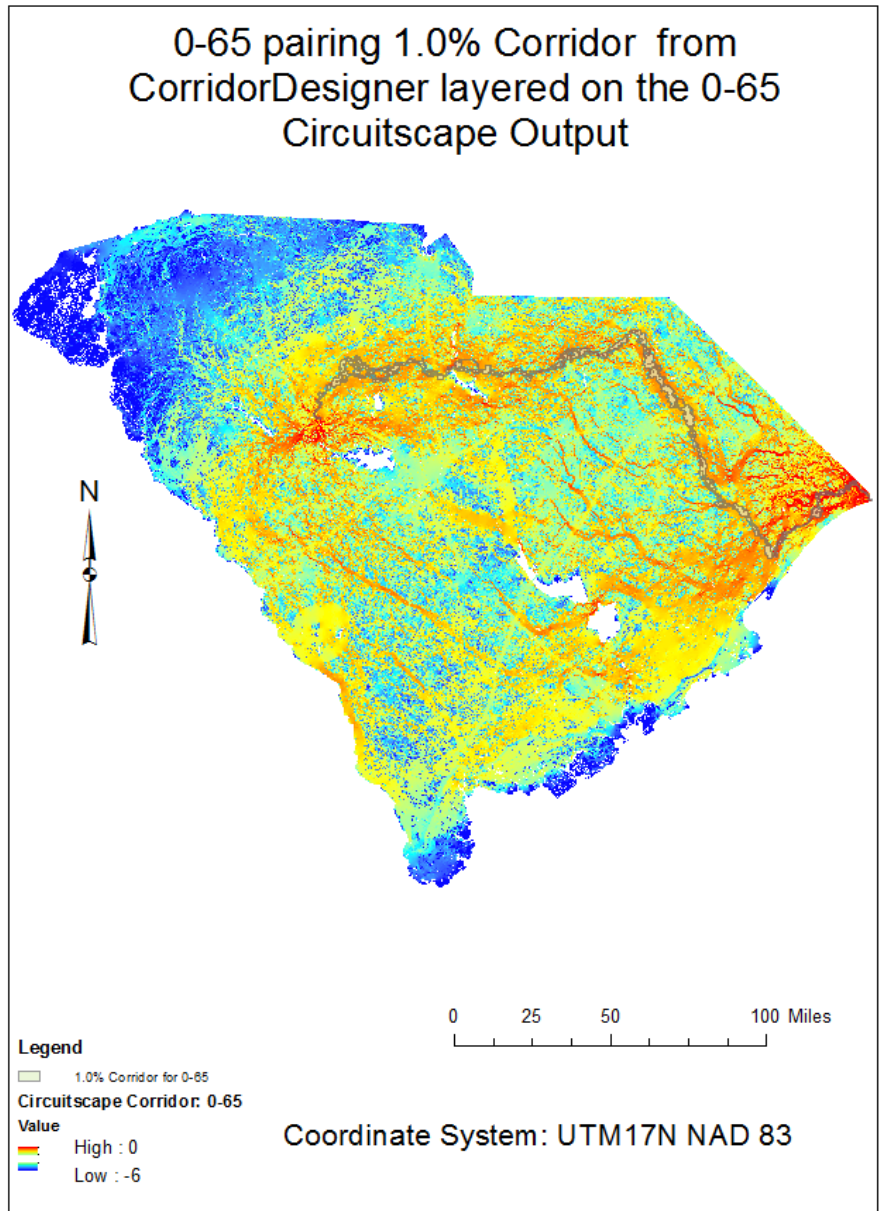


Figure 17.

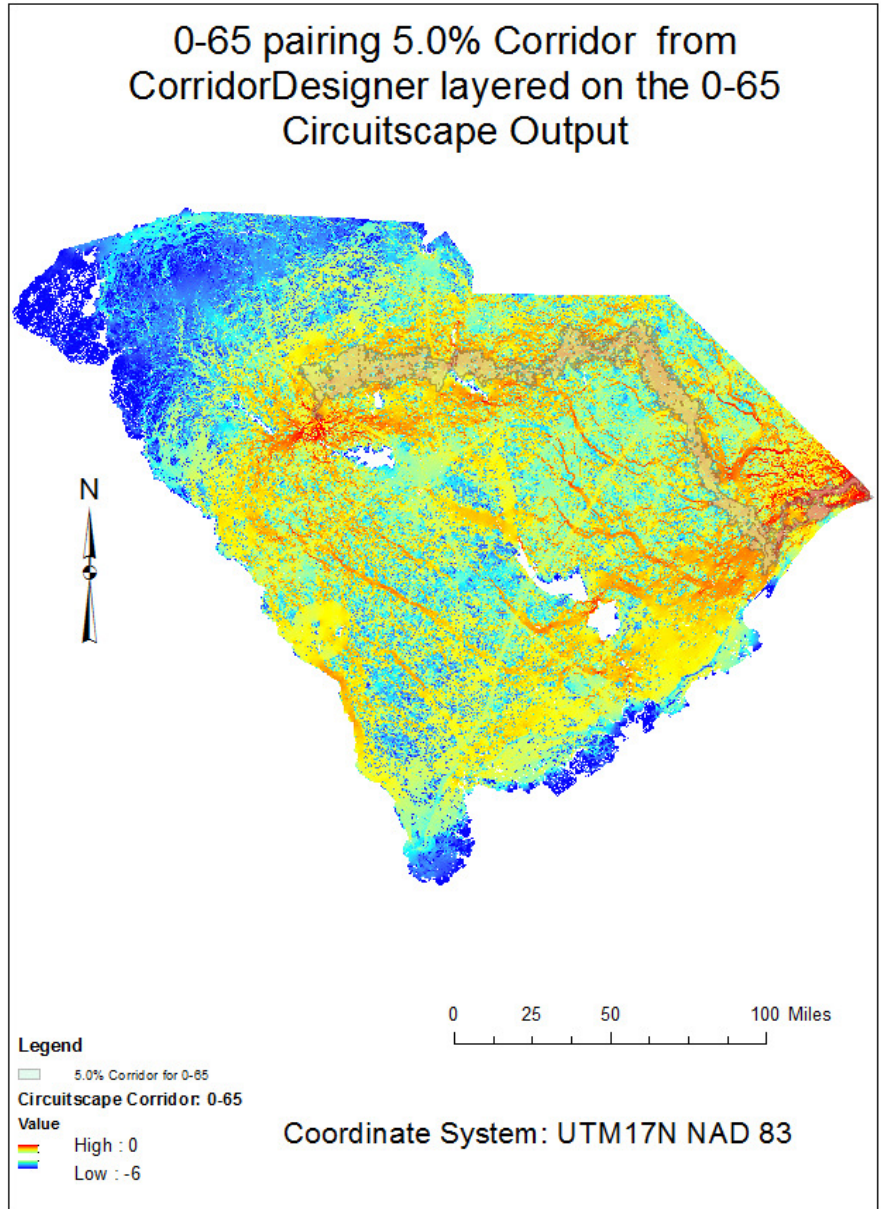


Figure 18.

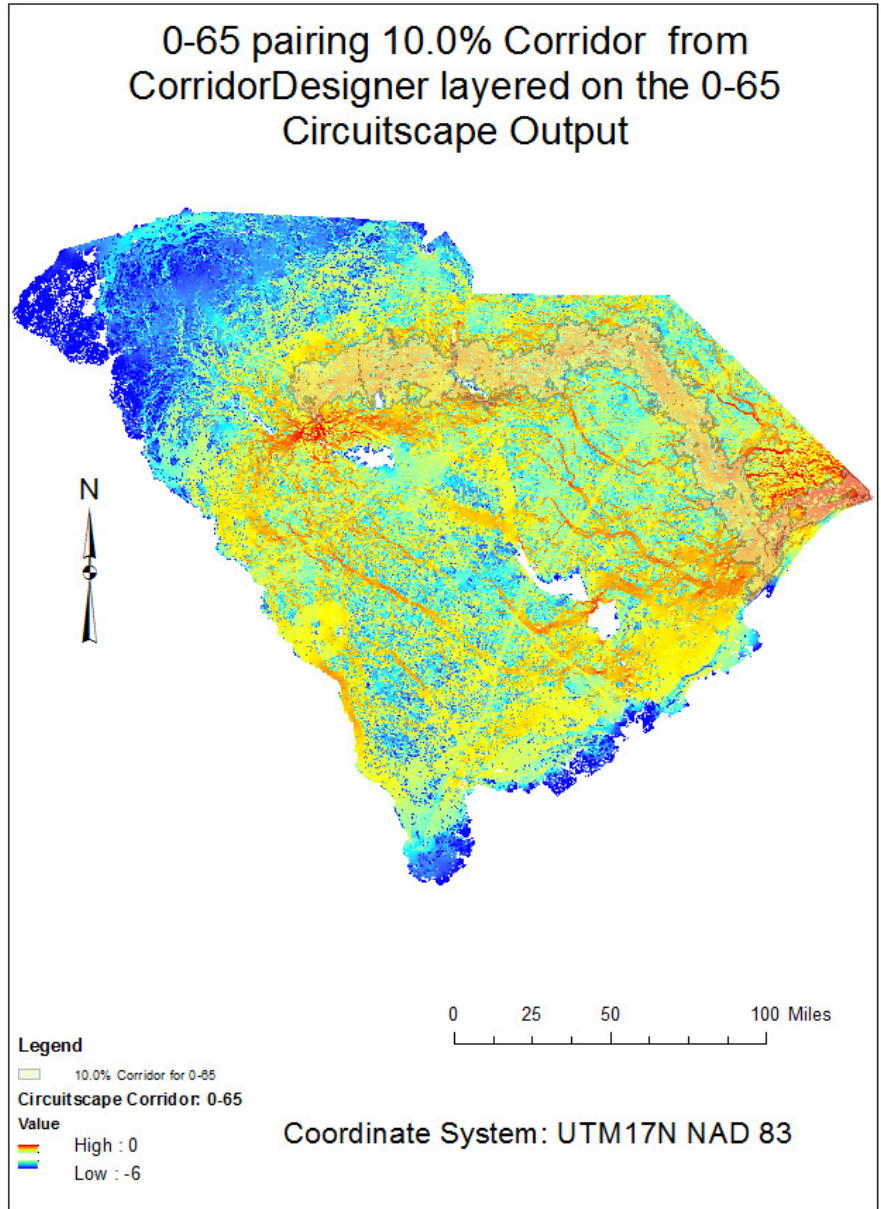


Figure 19.

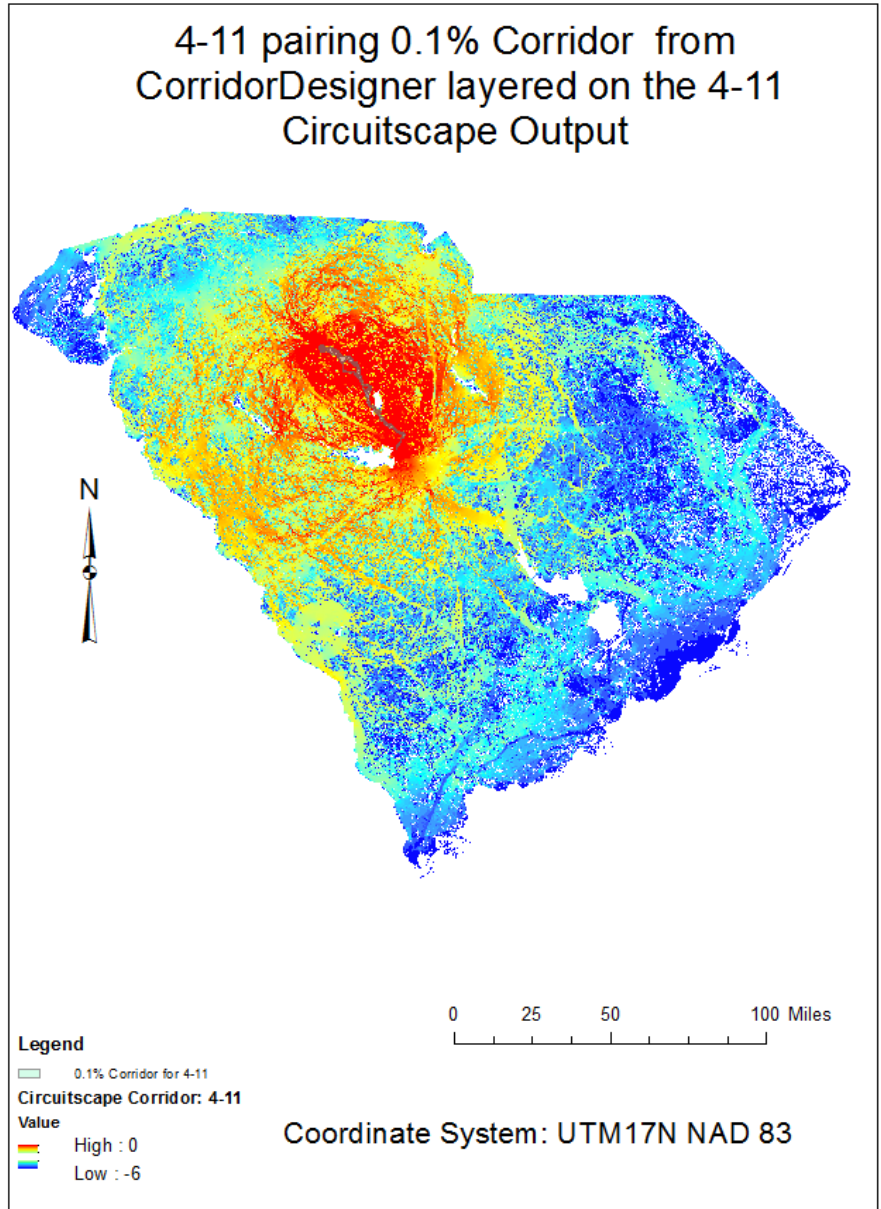


Figure 20.

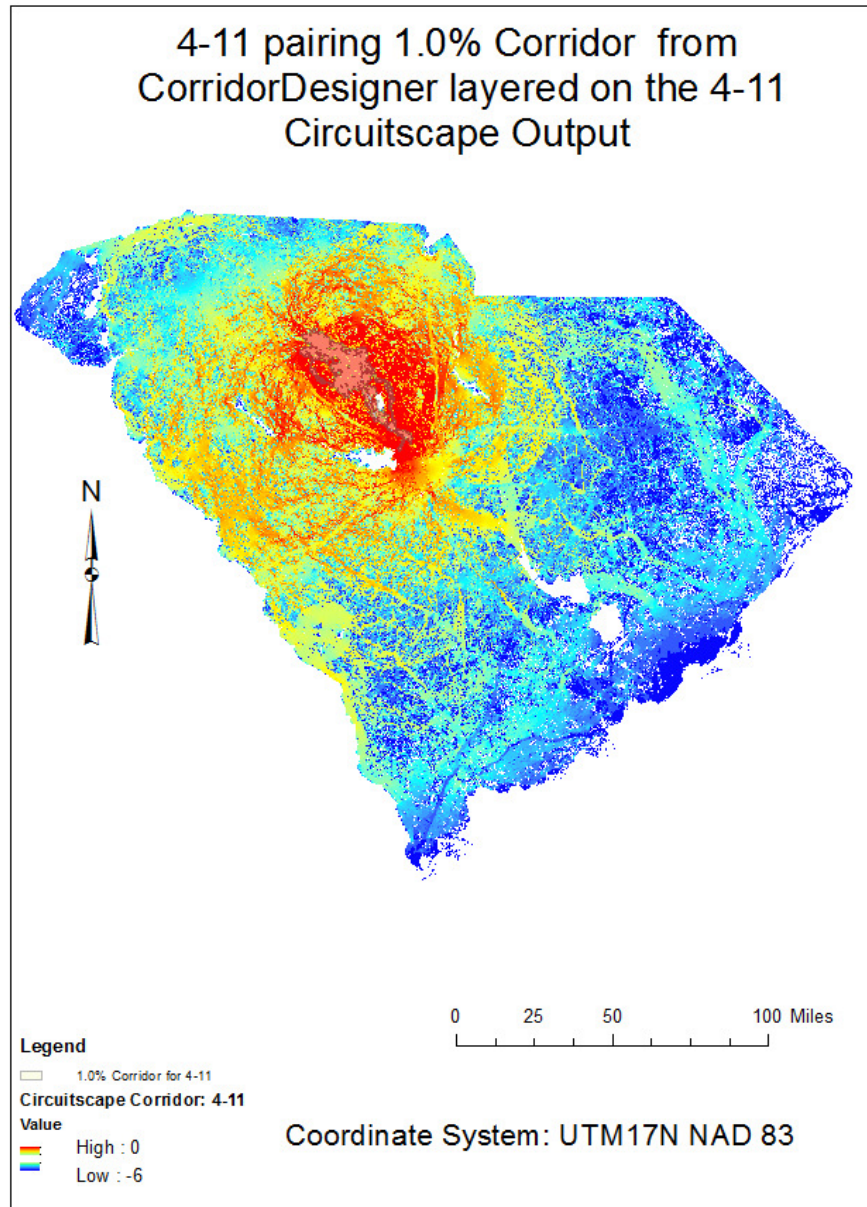


Figure 21.

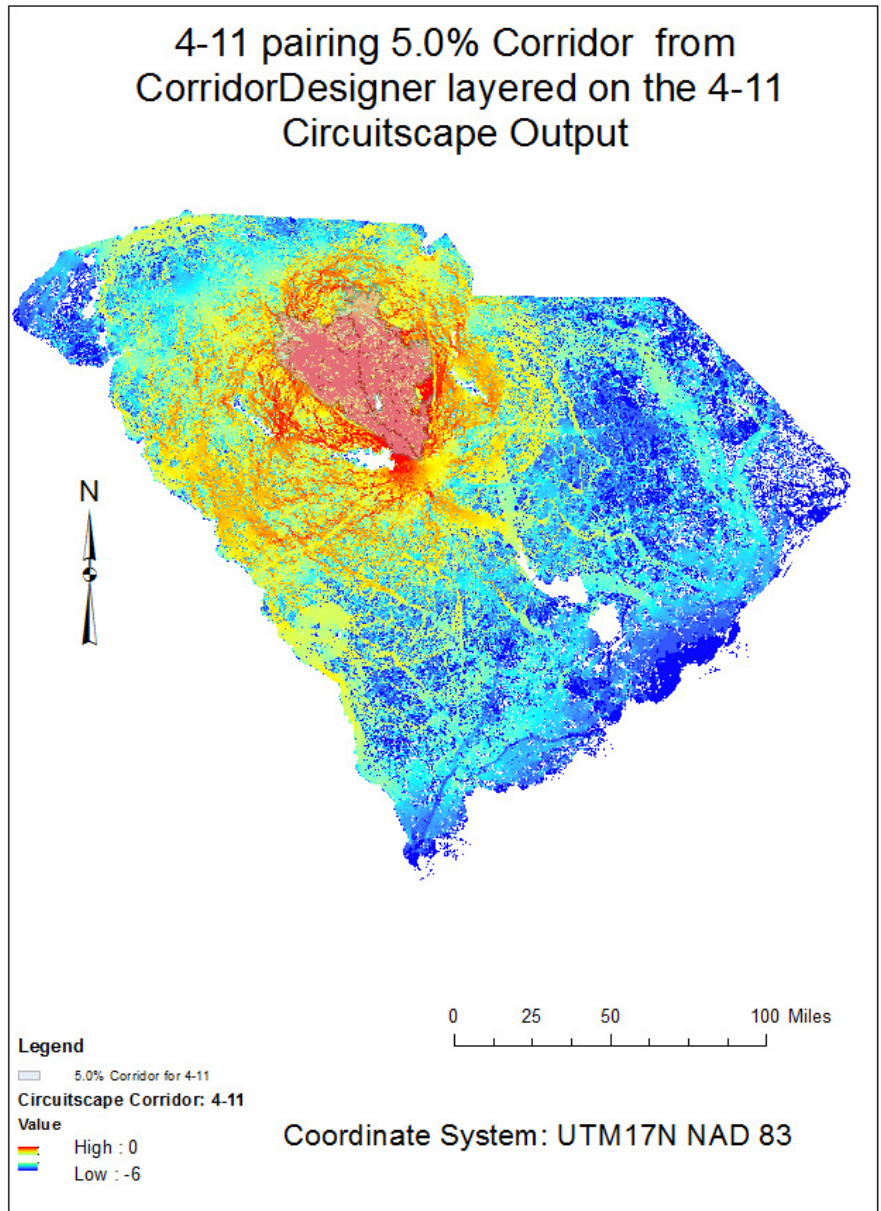


Figure 22.

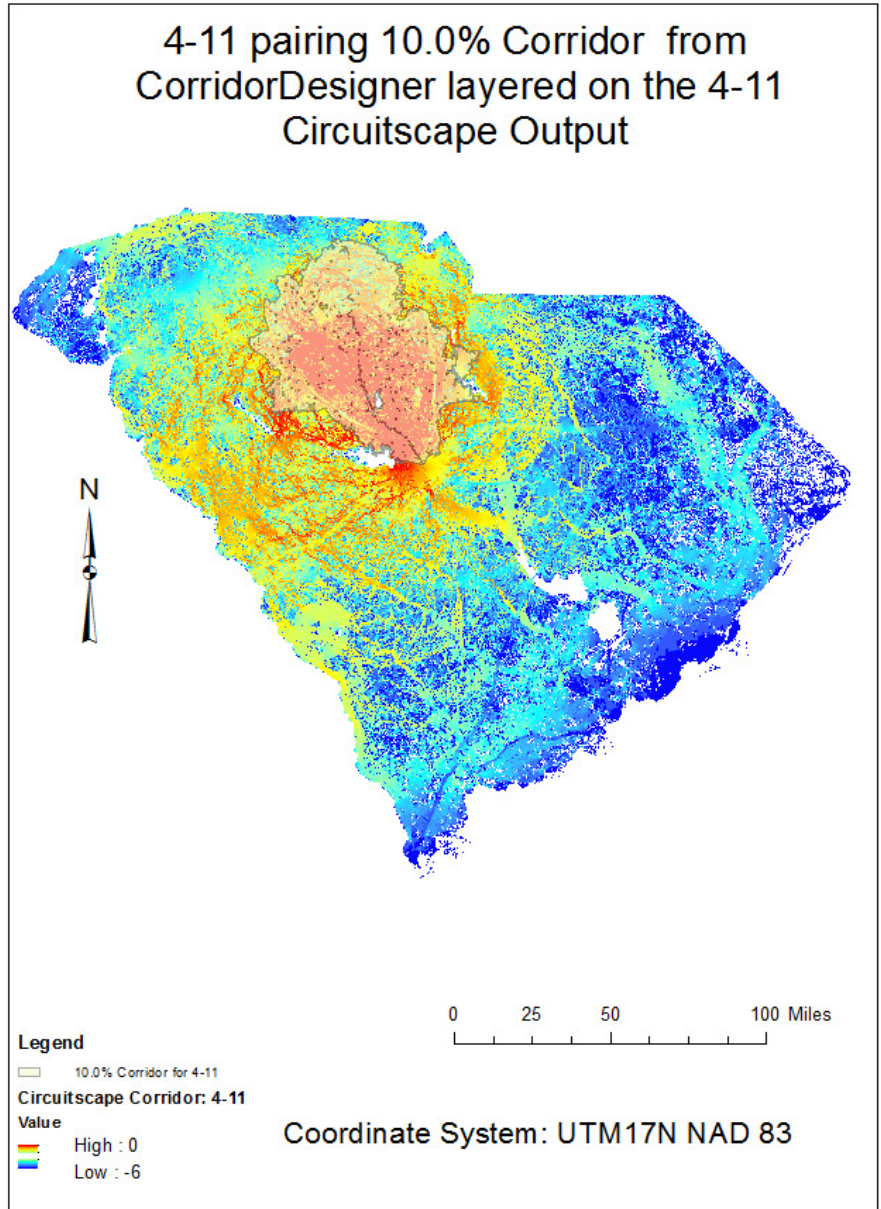


Figure 23.

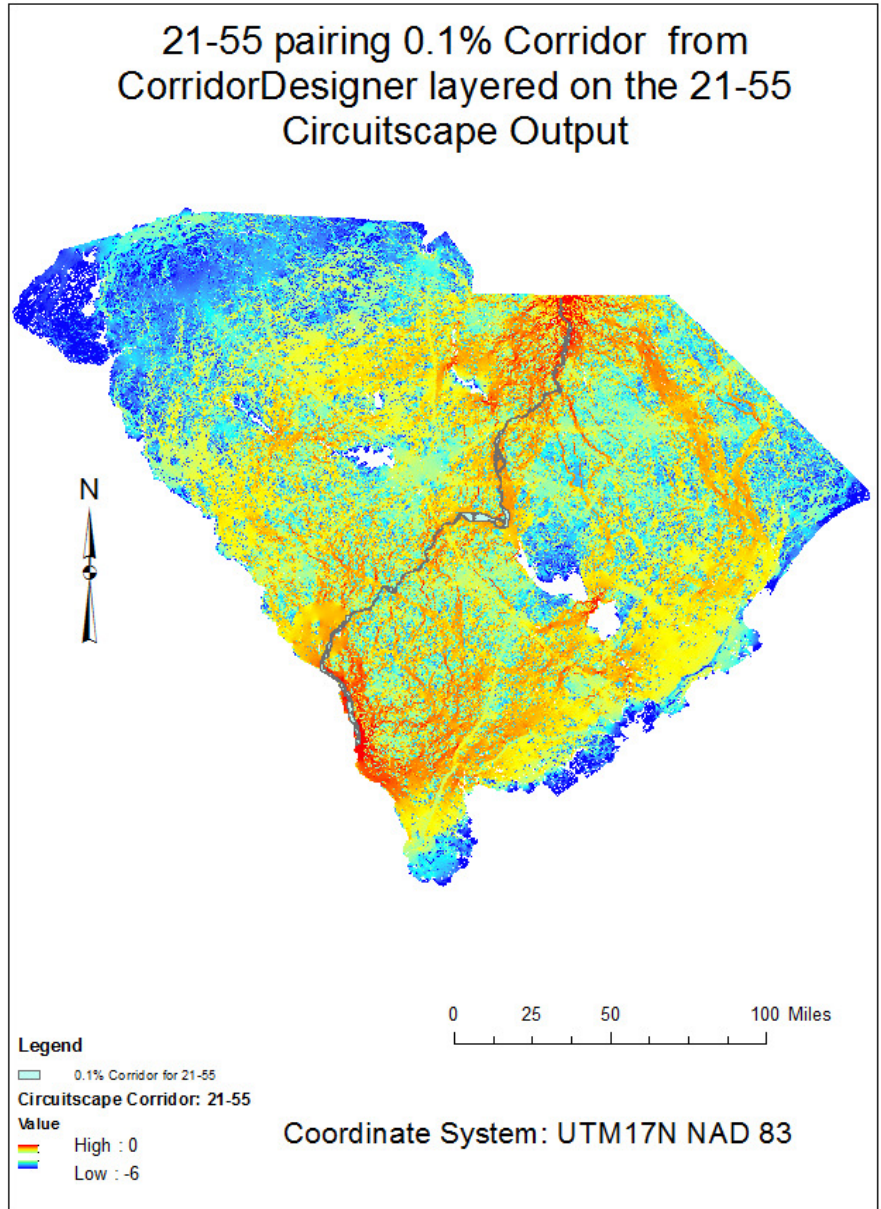


Figure 24.

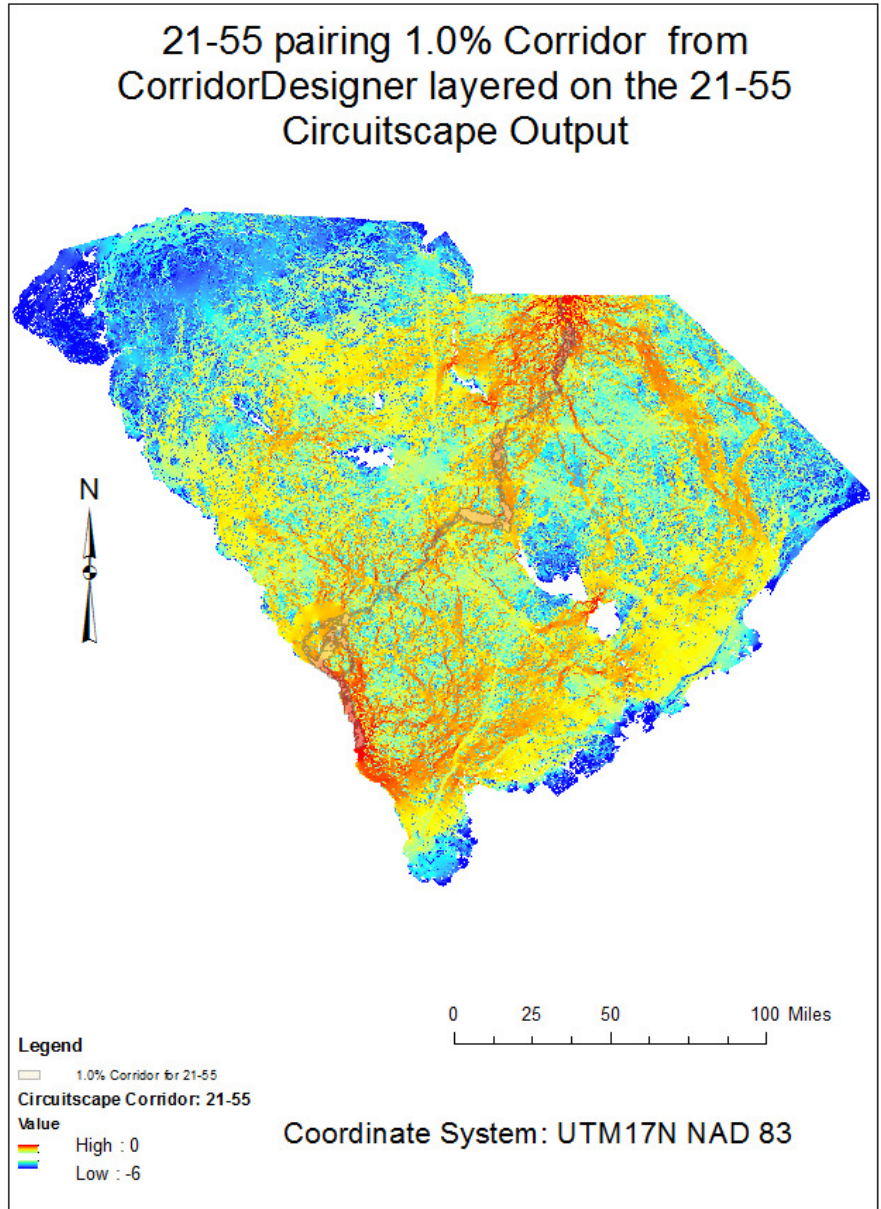


Figure 25.

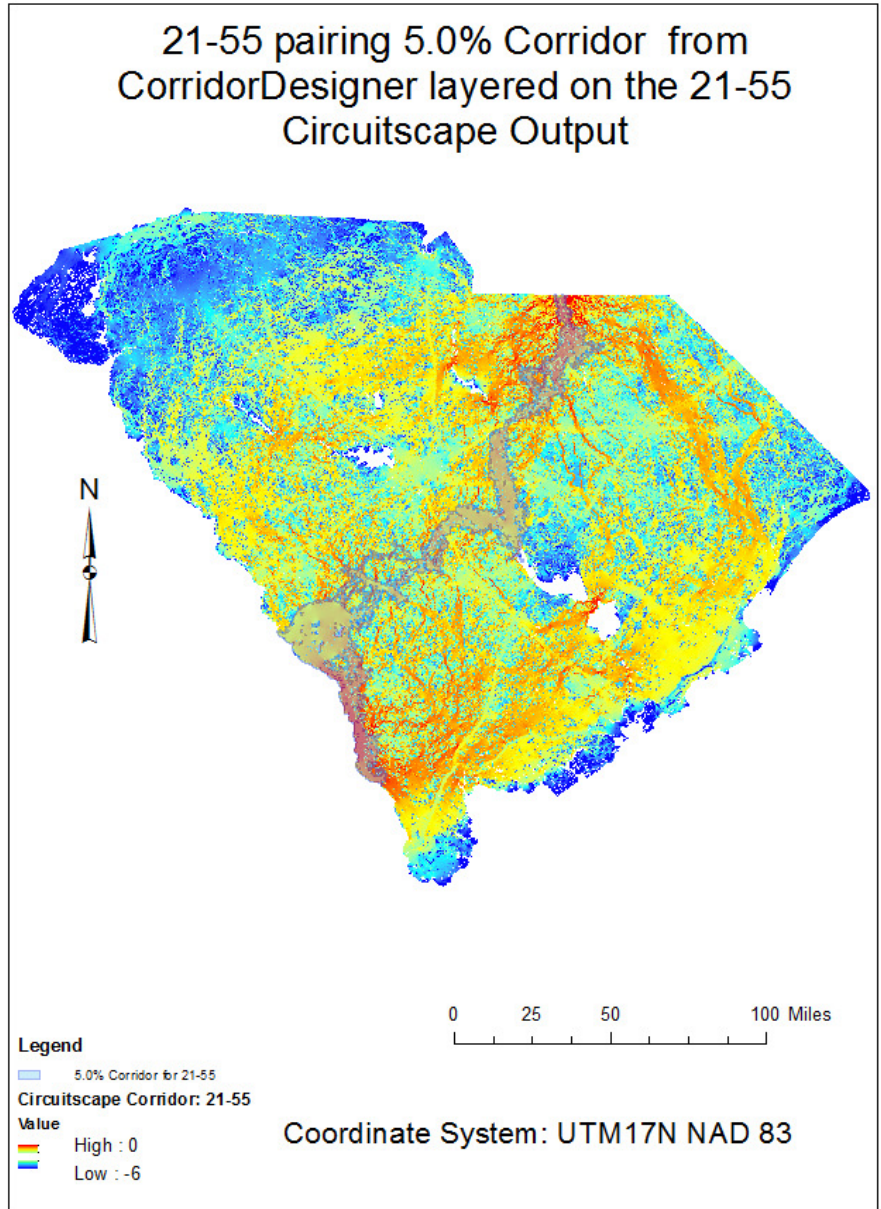


Figure 26.

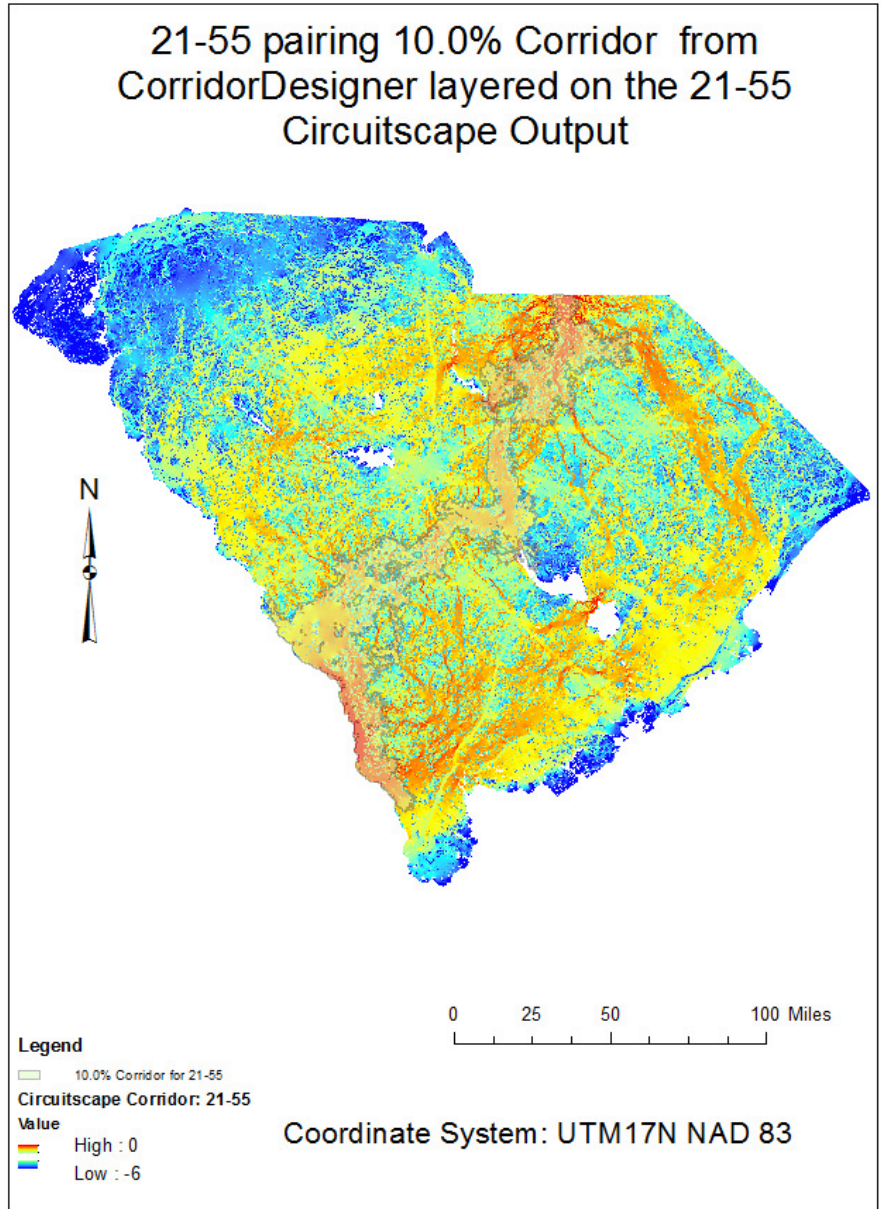


Figure 27.

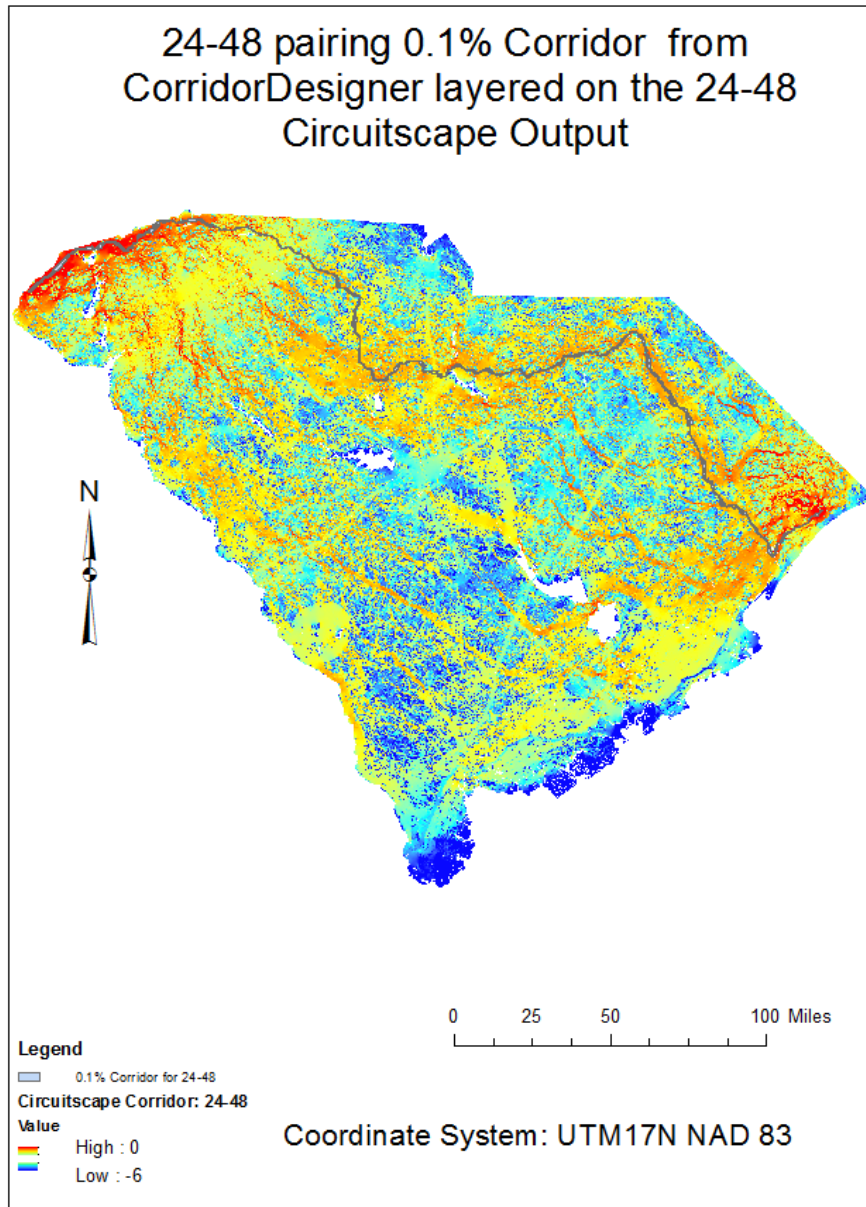


Figure 28.

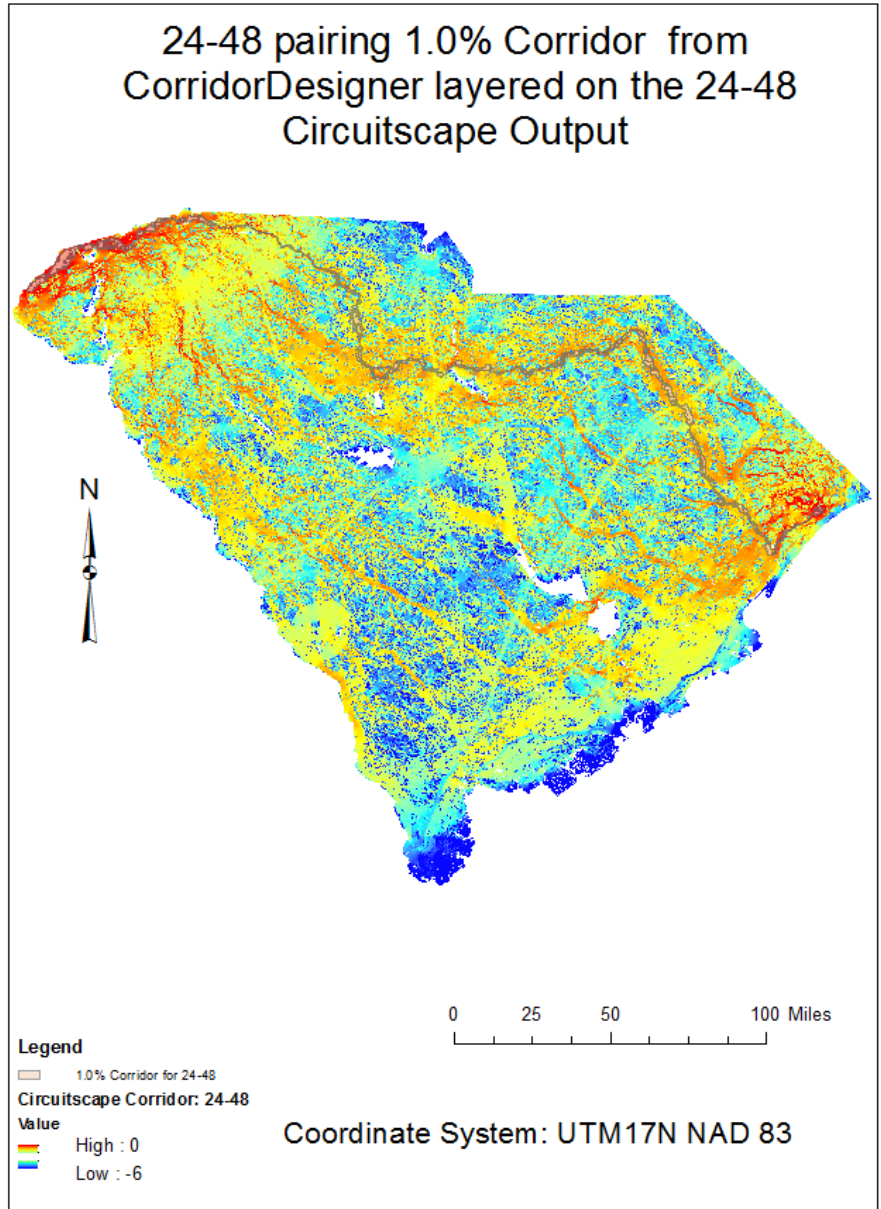


Figure 29.

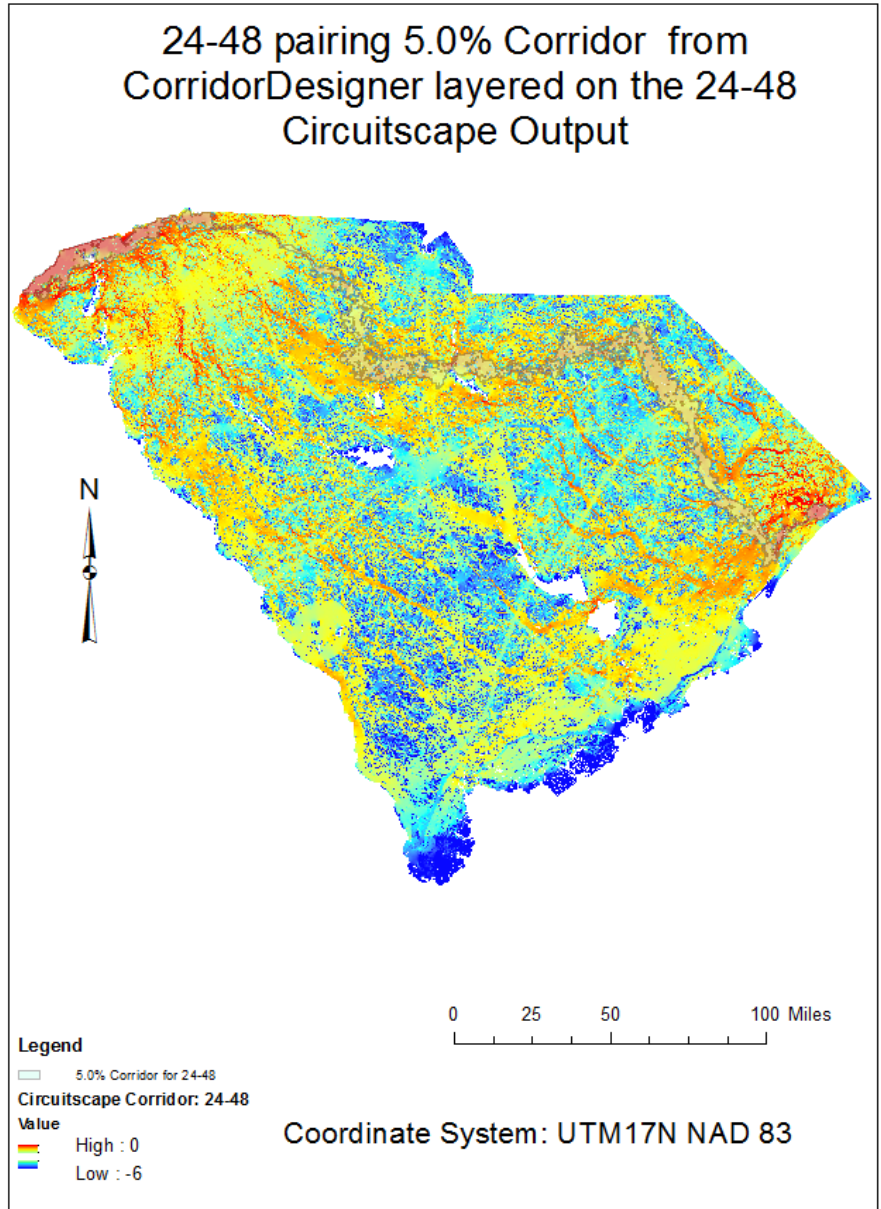


Figure 30.

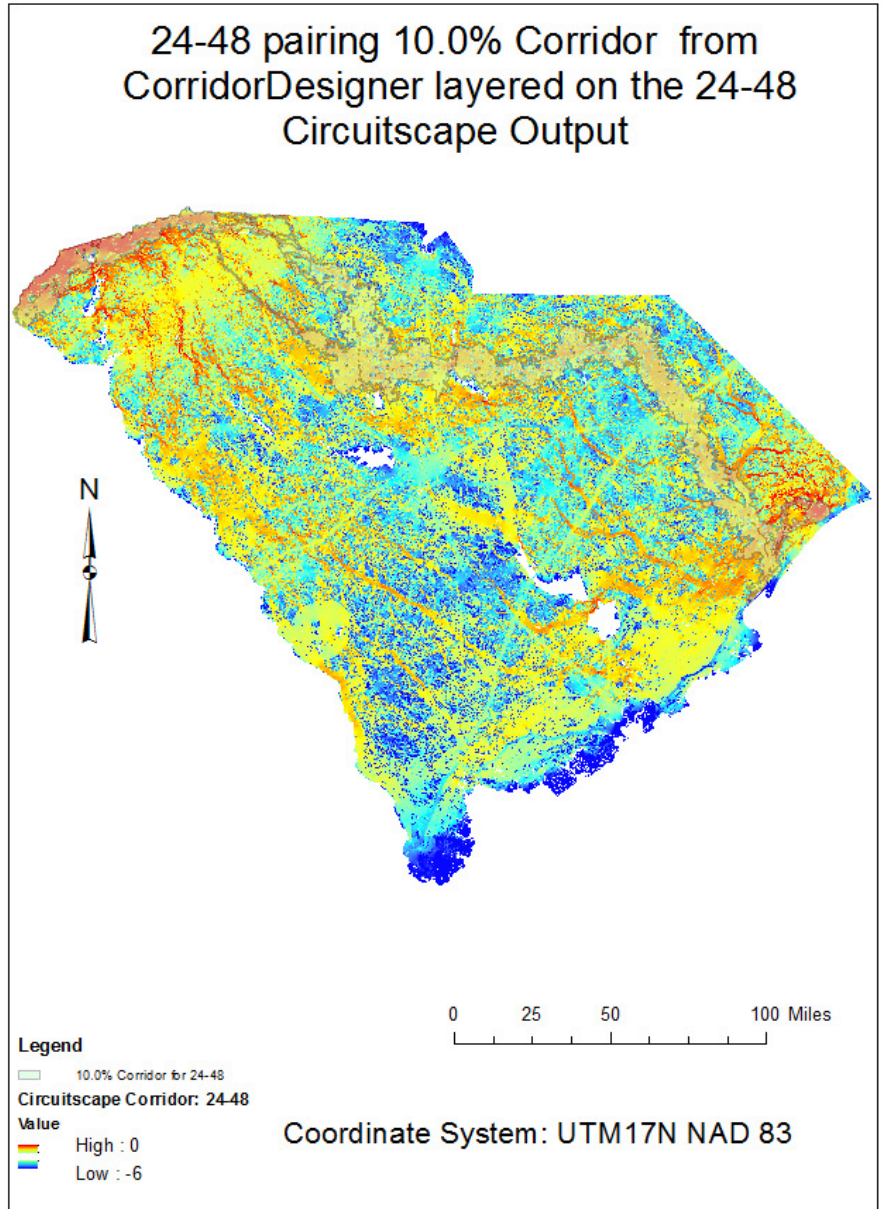


Figure 31.

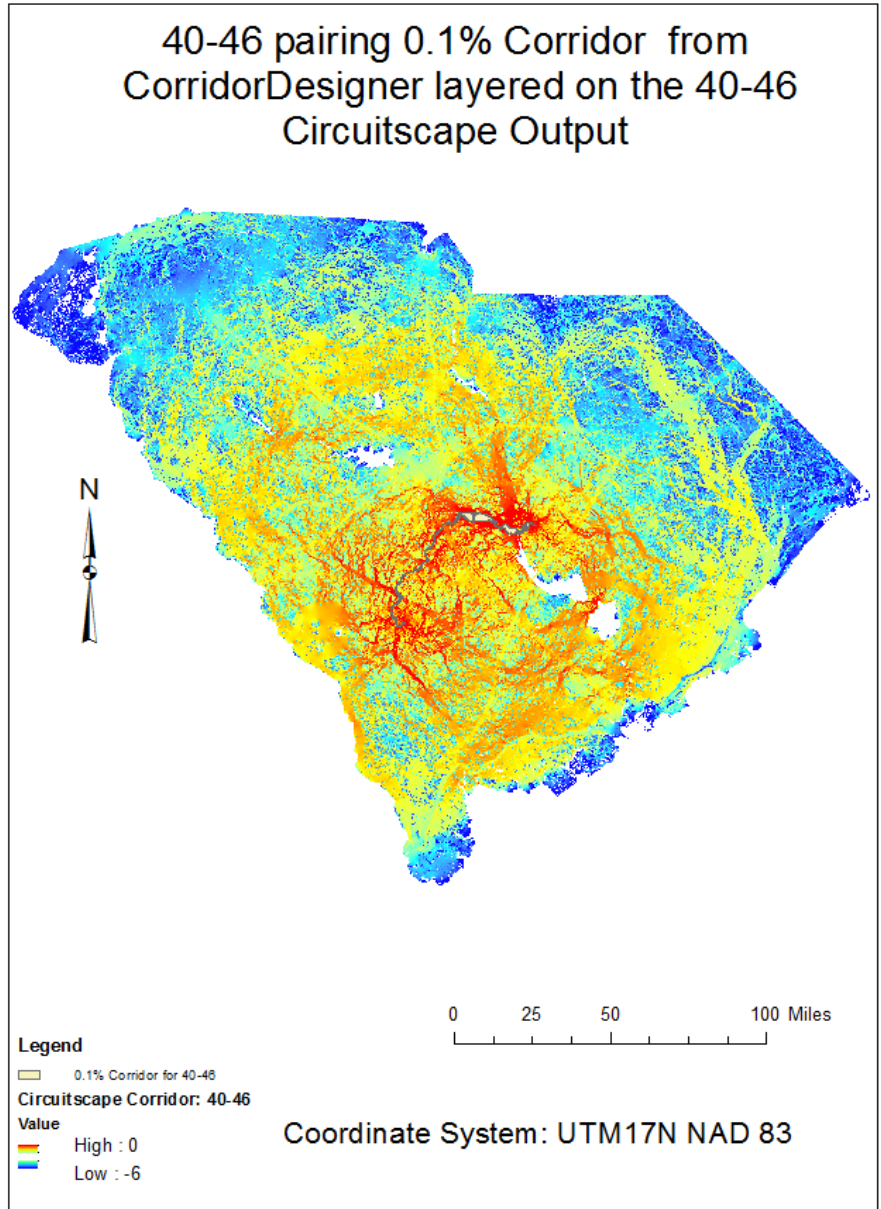


Figure 32.

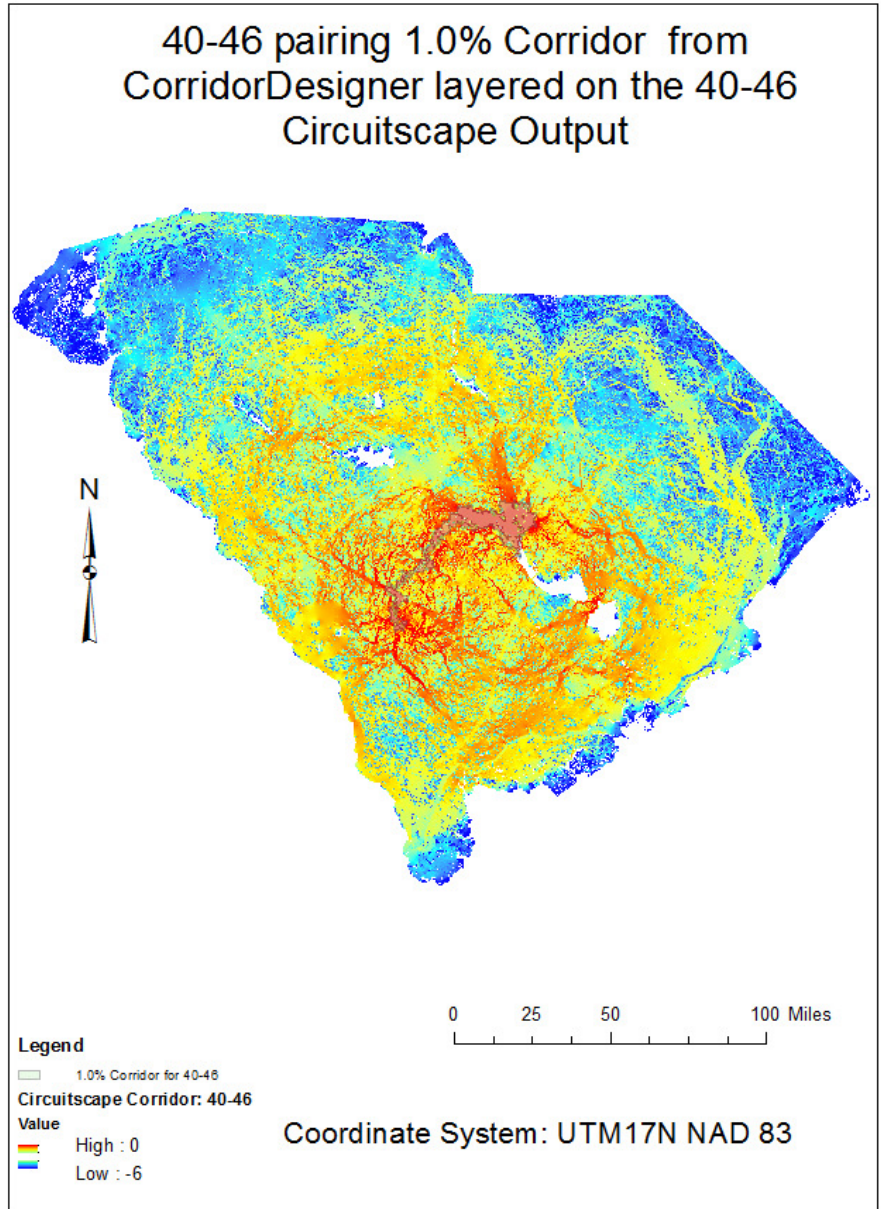


Figure 33.

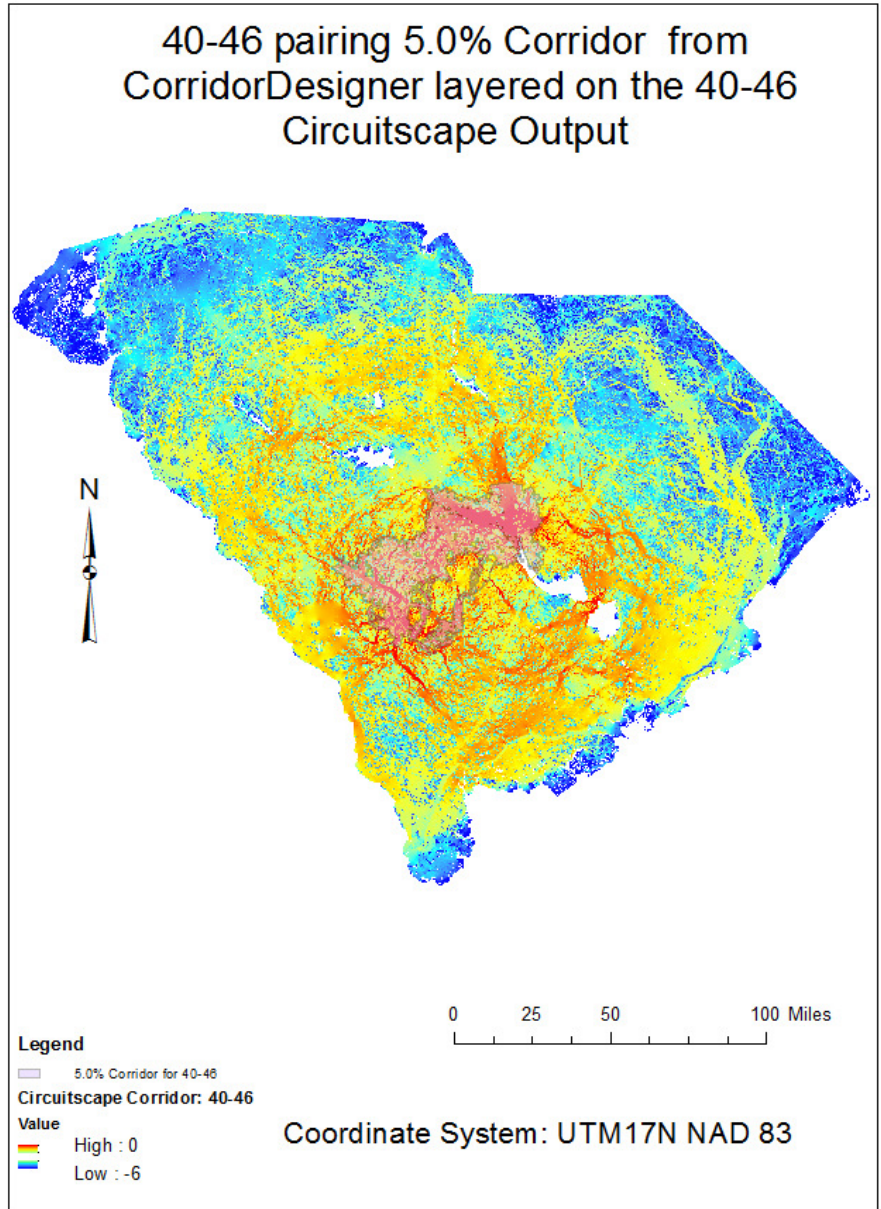


Figure 34.

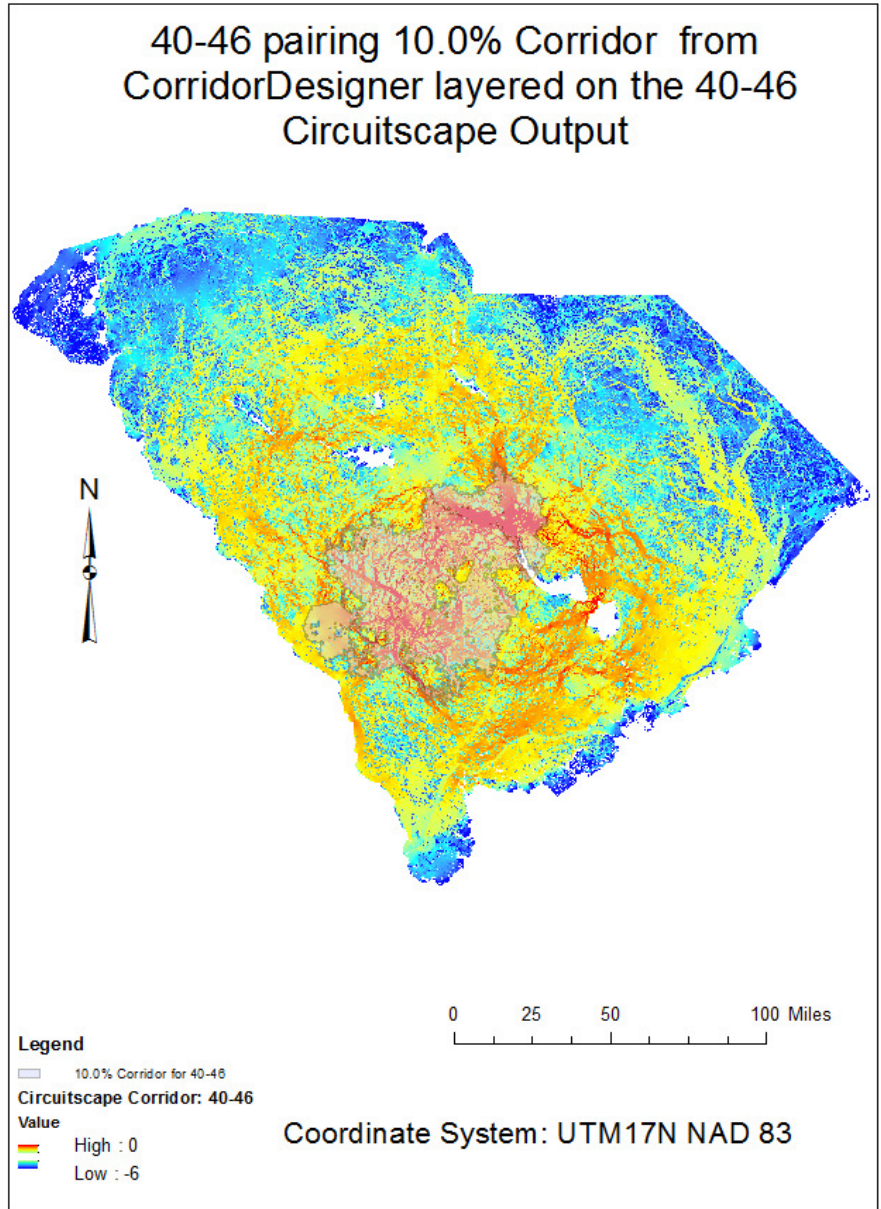


Figure 35.

Appendix 3: Map Results from the Additional Experiments

The figures presented in Appendix 3 are additional maps resulting a change in the paramaters of the map making proceedure (further explained in the Results). Maps are the result of resolution, barrier, point origination, and external wildland block experiments which were carried out for the Black Bear only.

1.0 % Corridor Produced by CD at 30 Meter Resolution
for the Resolution Experiment

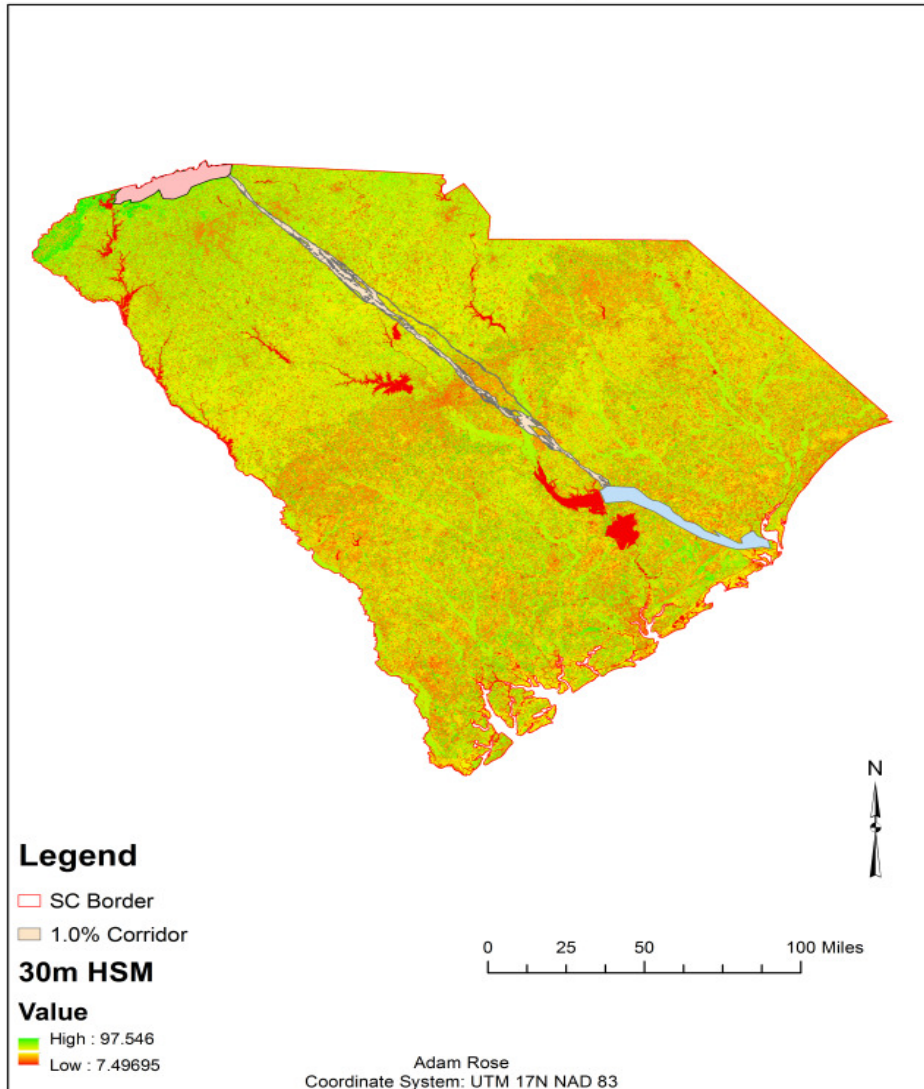


Figure 1.

1 Kilometer Resolution of the Circuitscape Output for the Resolution Experiment

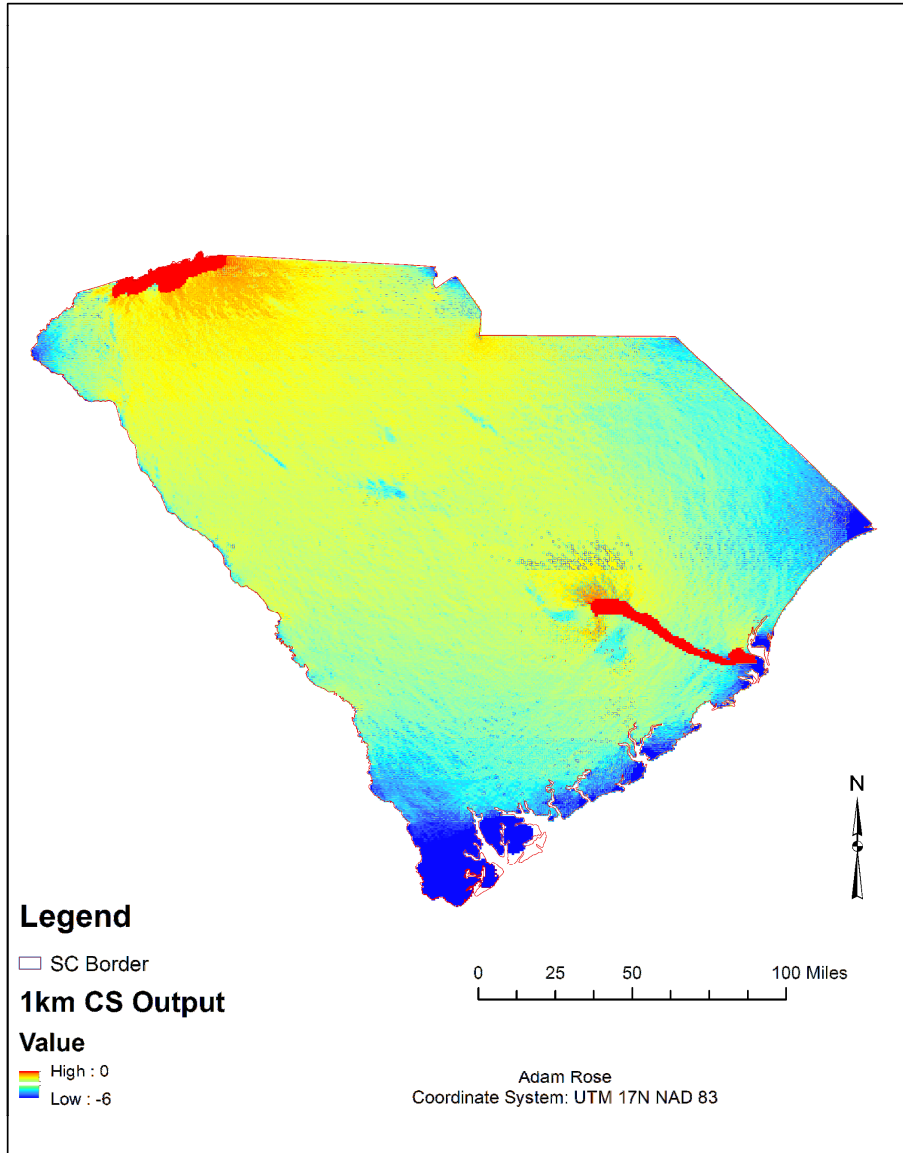


Figure 2.

1.0 % Corridor Produced by CD at 100 Meter Resolution for the Barrier Experiment

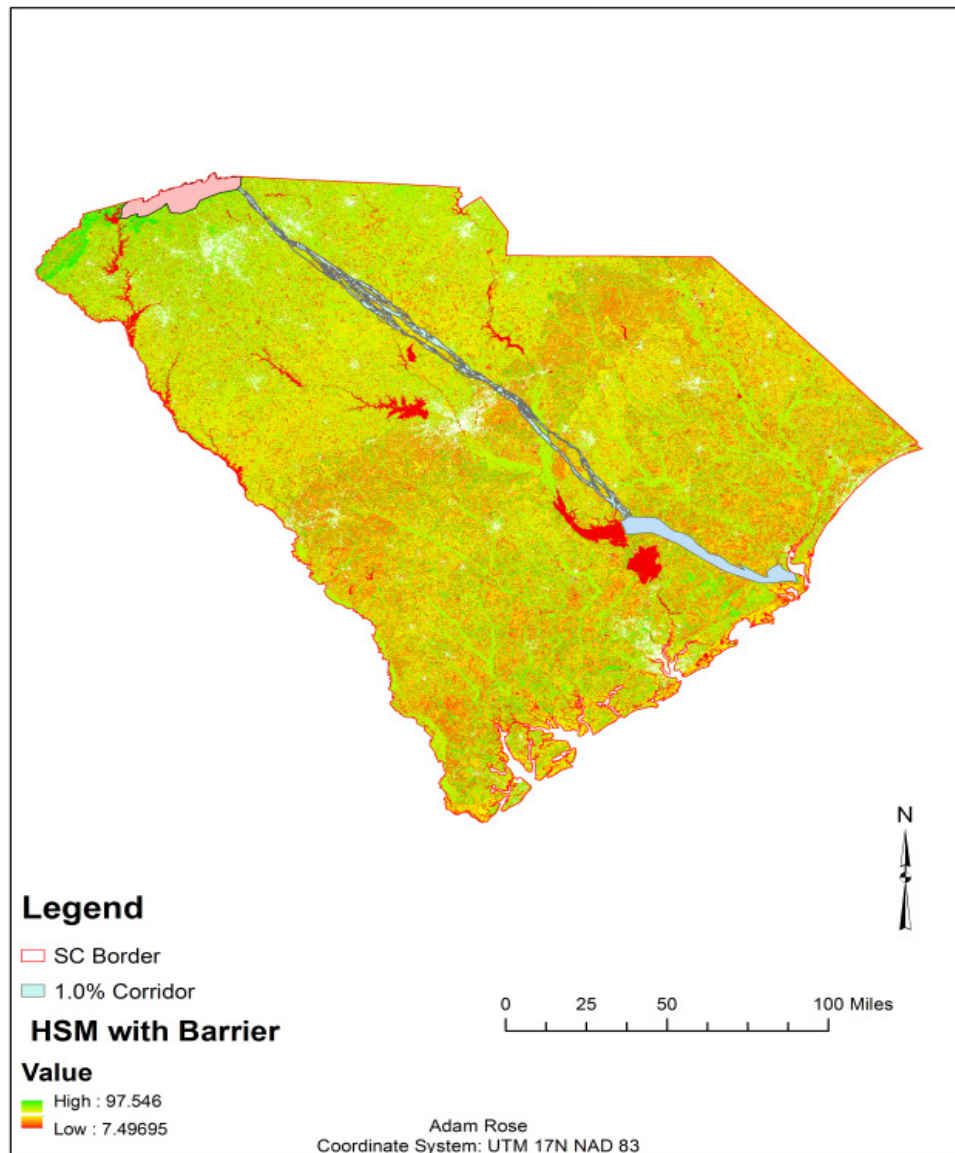


Figure 3.

1.0 % Corridor Produced by CD at 100 Meter Resolution for the Barrier Experiment

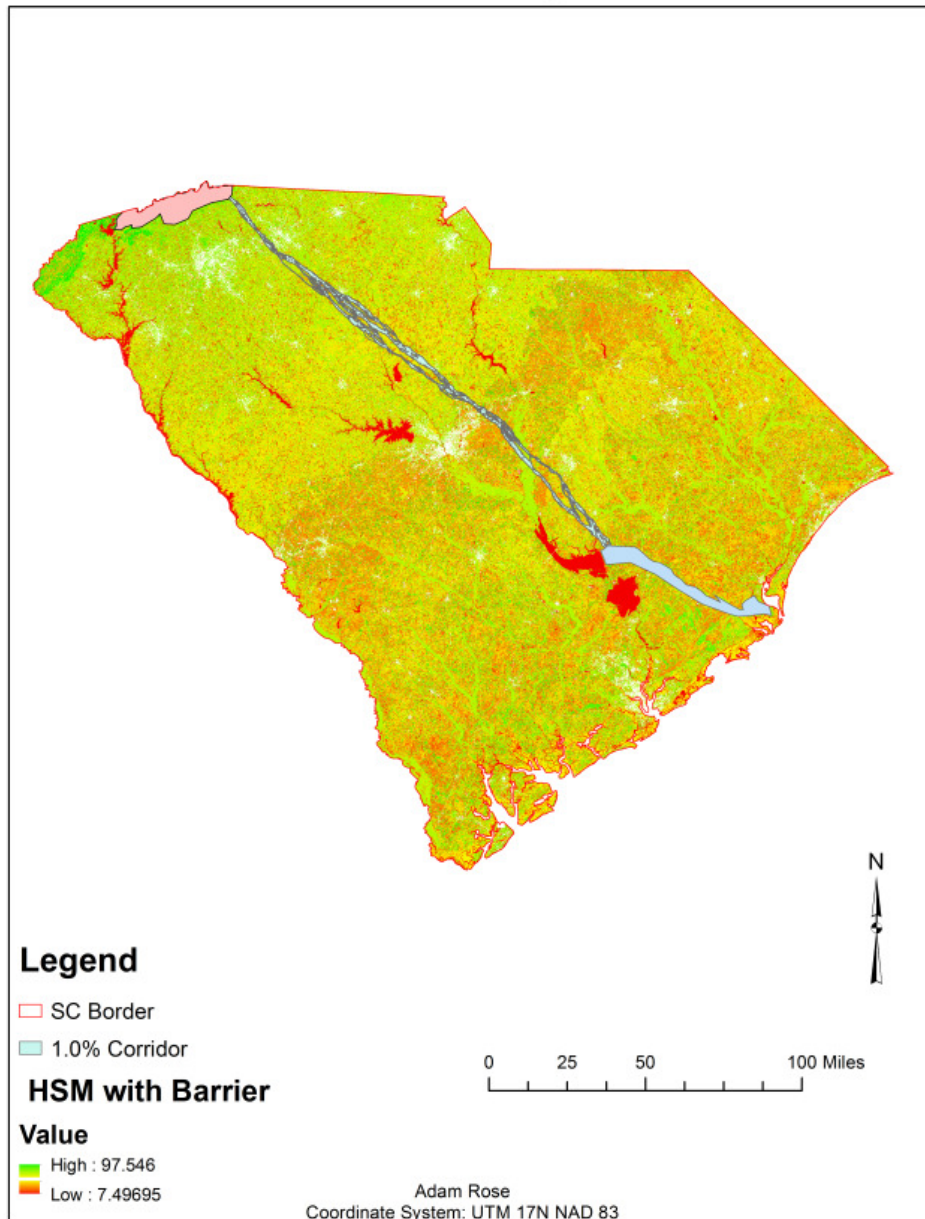


Figure 4.

100 Meter Resolution of the Circuitscape Output
for the Barrier Experiment Experiment

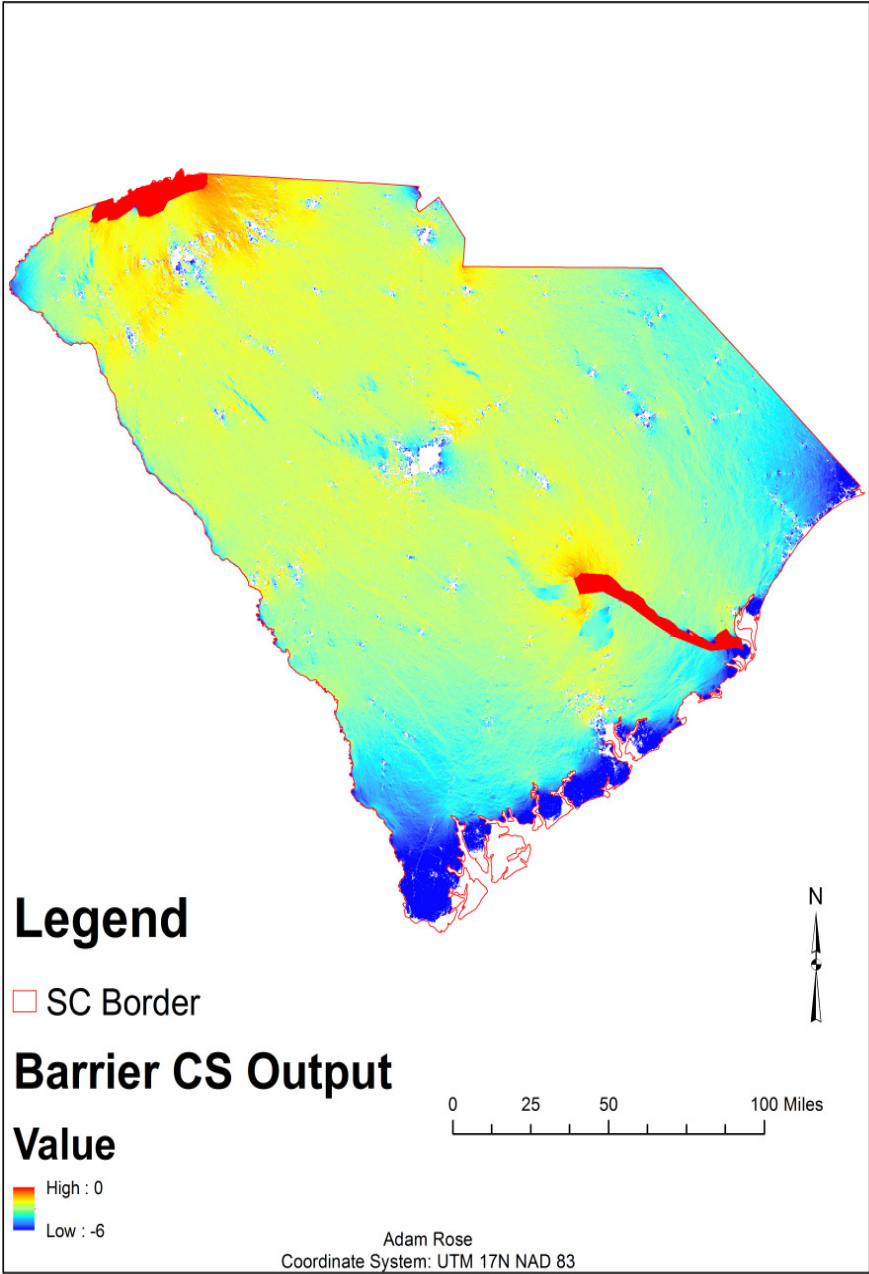


Figure 5.

1.0% Corridor Produced by CD at 100 Meter Resolution for the Point Origination Experiment

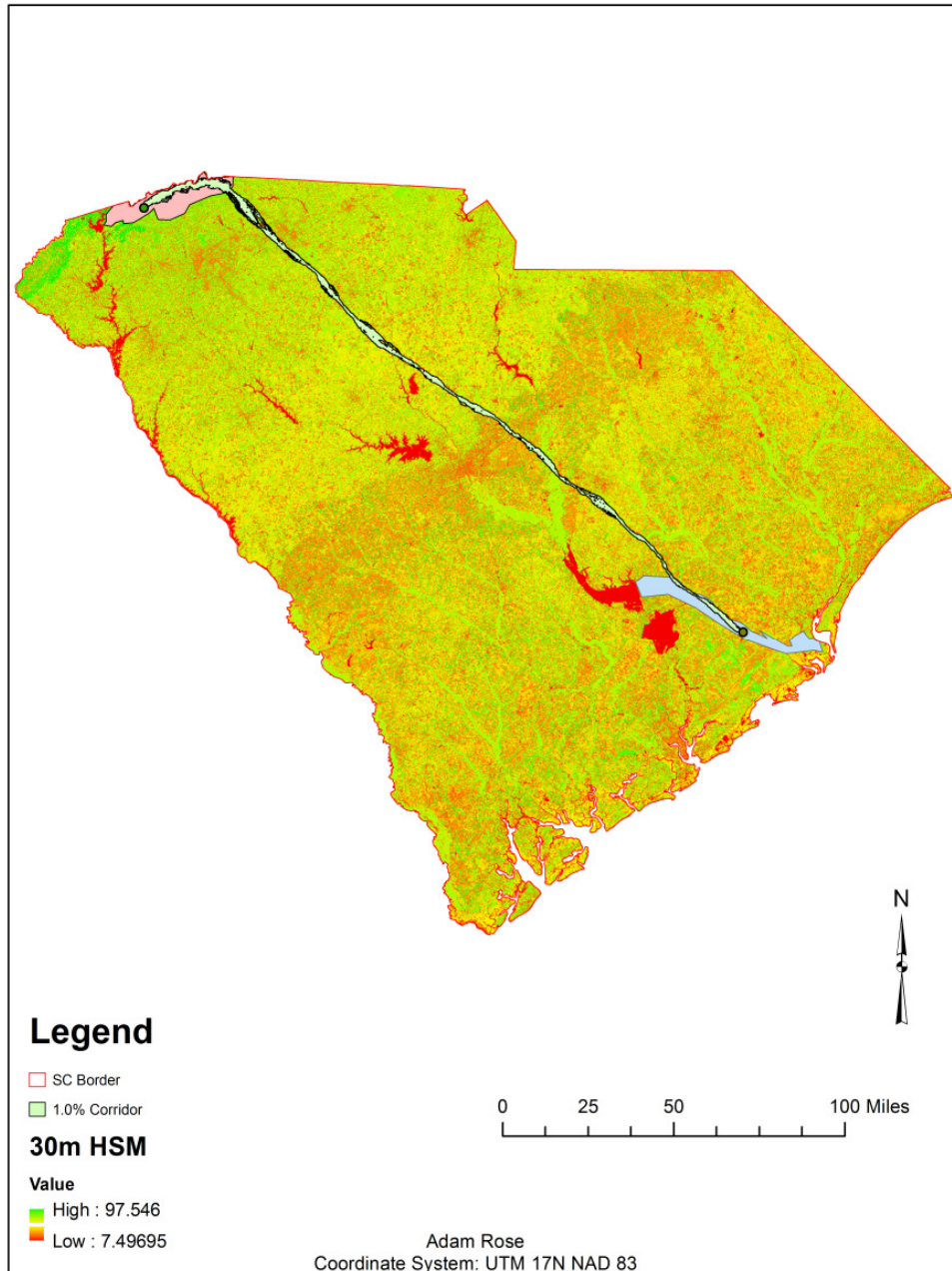


Figure 6.

100 Meter Resolution of the Circuitscape Output for the Point Origination Experiment

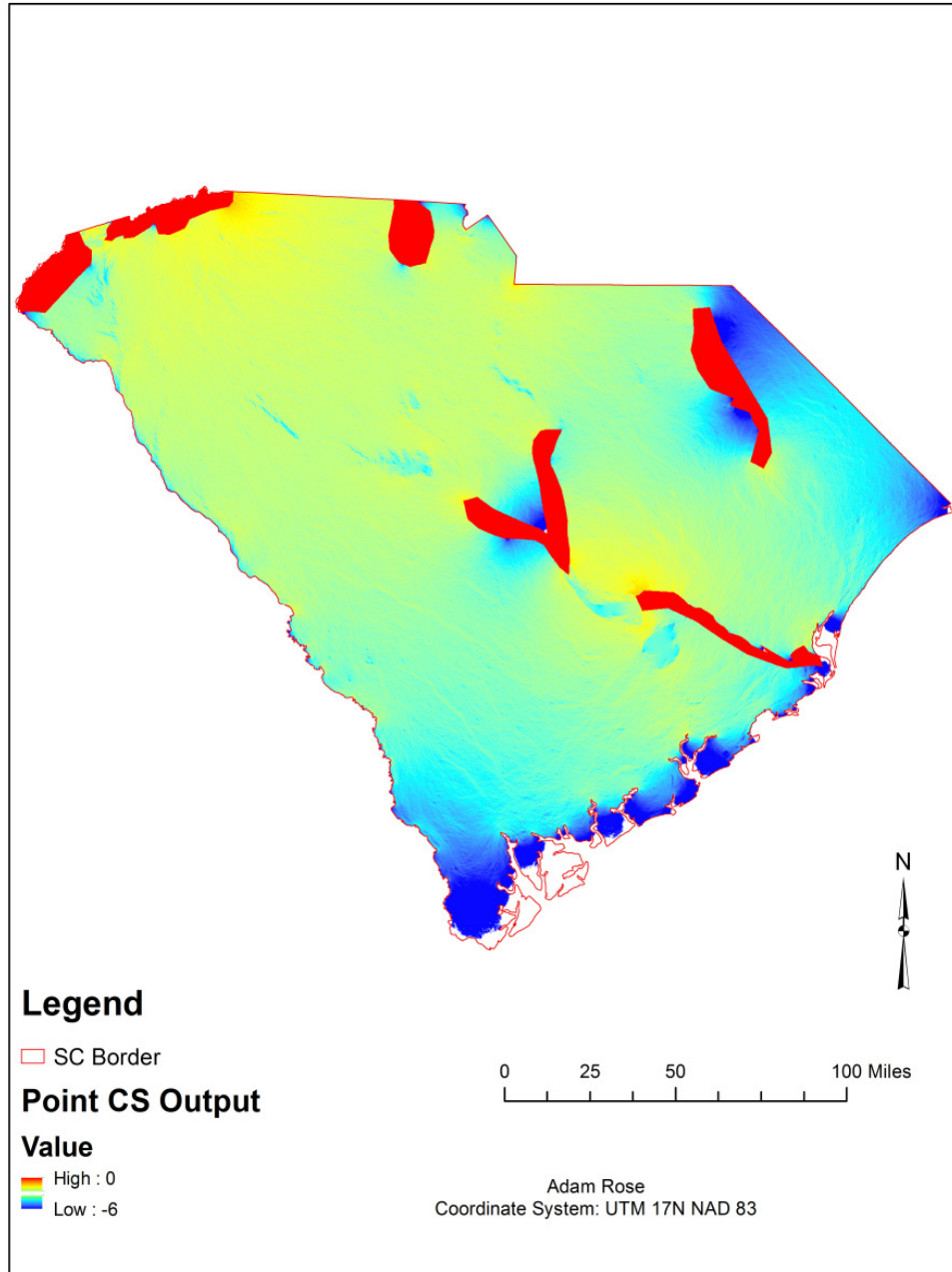


Figure 7.

1.0% Corridor Produced by CD at 100 Meter Resolution
for the Outside Wildland Block Experiment

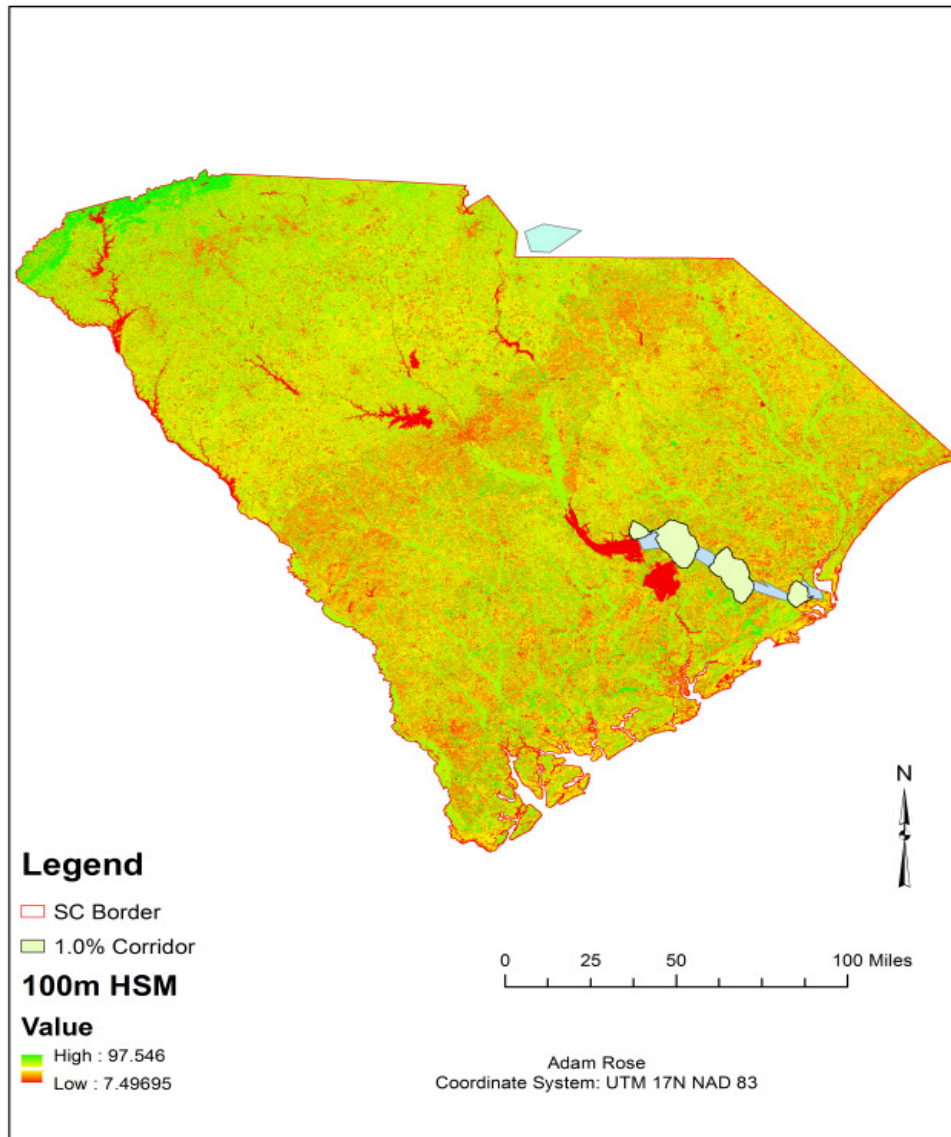


Figure 8.