Habitat and population modeling as tools for the conservation of the gopher tortoise (*Gopherus polyphemus*)

by

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Abstract

Spatial heterogeneity is an inherent part of landscapes and often has important consequences for the movements, distribution, or persistence of many wildlife species. Quantifying the composition, configuration, and connectivity of suitable habitat and its consequences for populations can provide valuable information about both the ecology and management of many species. This type of information may be particularly useful for informing the conservation and management of threatened or endangered species. The gopher tortoise (*Gopherus polyphemus*) is a species of high conservation concern due to the decline of populations across its range and its role in the ecosystem. To help inform conservation of this species, I assessed connectivity of suitable habitat across a broad portion of the gopher tortoise's range, quantified habitat connectivity under various management alternatives at selected sites in Alabama, and developed a spatially explicit population projection model to predict the future population consequences of various management strategies. This research provides evidence for a broad-scale pattern of changing habitat connectivity across a large portion of the gopher tortoise's range and highlights the importance of considering management effects on connectivity at finer scales. Results from the population projection demonstrate the importance of considering a spatial component when projecting population size into the future and indicate a need for further research on gopher tortoise survival rates. The models developed in this research demonstrate the utility of these types of spatial analyses for informing conservation and management, and could be adapted to other species of conservation concern.

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Introduction

The distribution of an organism across the landscape is of great interest and concern when dealing with rare or endangered species. At the broadest scales, a species' distribution can be described by the physiogeographic range in which it can be found. A species' range is dictated by many factors, including the physiological limits of the organism, competition with other species, and the distribution of abiotic and biotic features that the organism requires to survive (Gaston 2003, Holt and Keitt 2005, Price and Kirkpatrick 2009, Sexton et al. 2009, Geber 2011). While many species have reasonably well-defined and well-studied physiogeographic range boundaries, the distribution of organisms within that range, and the causes of any distributional patterns, are often less well understood.

Within a species' range, populations and individuals may not be uniformly distributed. In general, the abundance of a species may decrease closer to the edges of its geographical range when compared to the center of its range, likely due to its ecological niche requirements (Brown et al. 1995, Enquist et al. 1995). This pattern could arise from any of the limiting factors that restrict the range; i.e., climate, distribution of prey or predators, competition with other species near the range boundary, or changing patterns of suitable habitat near the range boundaries. Such limiting factors may act to reduce the density or abundance of the species near the edge of its range, as conditions become less favorable for the organism.

For rare or endangered species, such as the gopher tortoise (*Gopherus polyphemus*), patterns of lower abundance in parts of the species' range can lead to management concern. Low abundance in one portion of the range may indicate that the species is facing unique challenges there, or that the species is more likely to face extirpation in that area. Gopher tortoises are endemic to the southeastern United States and are found in portions of six states (Figure 1.1). In 1987, gopher tortoises were listed as Threatened under the Endangered Species Act in the western periphery of their range, west of the Mobile and Tombigbee rivers in Alabama (USFWS 2011). The species was petitioned for listing in the remainder of its range in 2006, but listing was eventually found to be warranted but precluded (USFWS 2011). Populations are now considered to be in decline throughout the range (USFWS and SERPPAS 2013), though low abundances in the western range periphery are still a high concern.

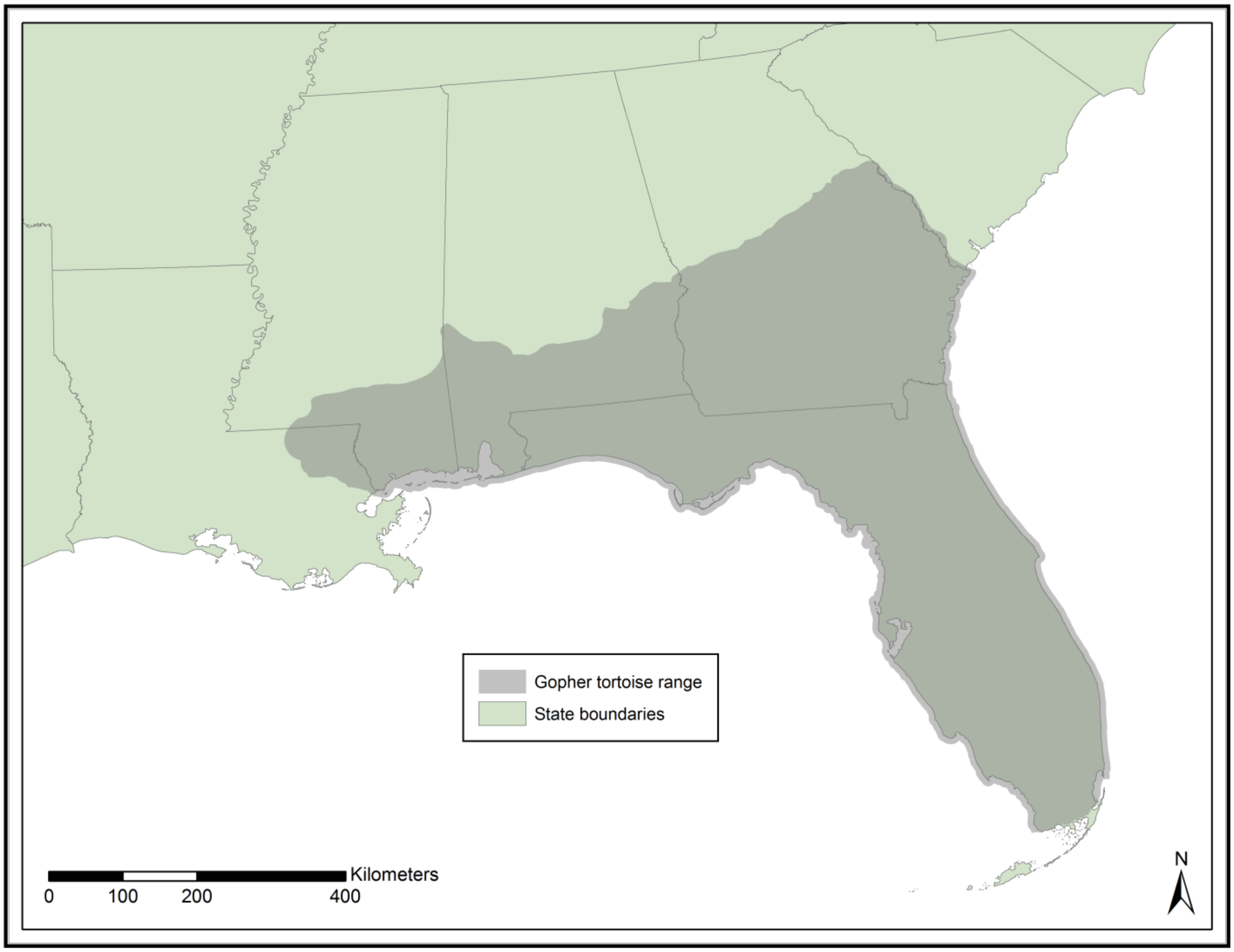


Figure 1.1. Range of the gopher tortoise in the southeastern United States.

Gopher tortoises excavate extensive burrow systems, up to 10 meters in length, in which they spend most of their time (Bonin et al. 2006). These burrows provide shelter, habitat, and protection from fire for many other species including eastern indigo snakes (*Drymarchon couperi*), gopher frogs (*Rana capito*), and northern bobwhite quail (*Colinus virginianus*) (Cox et al. 1987). Because of this burrowing behavior and the multitude of species it supports, gopher tortoises are considered by many to be a keystone species (e.g., Guyer et al. 2012, Perez-Heydrich et al. 2012, Kowal et al. 2014, USFWS and SERPPAS 2013). The tortoise's dependence on its burrow also makes soil type an important habitat factor for the species.

In general, gopher tortoises are believed to require deep, sandy, well-drained soils that are suitable for digging (Auffenberg and Franz 1982). While tortoises may forage on other soil types if those soils support the herbaceous vegetation tortoises require as forage (Hoctor and Beyeler 2010), a tortoise's home range will be limited by the location of its burrow(s). Thus, for an area to be considered suitable gopher tortoise habitat, it must contain adequate area in suitable soils. Various classification schemes have been produced to classify soils according to their suitability for tortoise burrowing. Classification has traditionally been based on soil depth, sand and/or clay content (with sandier soils being more suitable for digging), and documented use of a soil series by tortoises; higher suitability rankings generally indicate that the soil is believed to be able to support a higher density of tortoises (McDearman 2005, Guyer et al. 2011). More recent classification schemes are based solely on soil physical properties such as depth to water table and percent sand content (USFWS and NRCS 2012). Classification of soils according to schemes such as these is an important aspect of delineation of suitable gopher tortoise habitat.

While tortoise population declines are likely due to a number of factors, including habitat loss and human collection of tortoises for food and pets (Smith et al. 2006), the cause of the pattern of reduced populations (and possibly reduced population density) in the western range periphery compared to more central portions of the range is uncertain. This pattern is consistent with the potential for animal abundance to be lower near range peripheries regardless of human influence (Brown et al. 1995, Enquist et al. 1995), which may be due in part to the availability of suitable habitat. It is possible that the deep, sandy soil types that gopher tortoises depend on for survival might become less common and increasingly fragmented near the peripheries of the tortoise's range. If this were the case, there would be less total area of soils suitable for tortoises near the range peripheries, and available areas would be less well connected, potentially affecting population viability.

The purpose of this study was to examine patterns of soils as an important aspect of gopher tortoise habitat across a broad portion of the species' range. I examined soils in the absence of other habitat factors and assessed the connectivity of tortoise habitat as determined by soils and two other habitat factors, hydrology and urbanization, that cannot easily be altered by management activities. Specifically, my objectives were to test the following expectations:

1. Soils appropriate for gopher tortoises will become less common, increasingly fragmented, and more sparsely distributed in the western periphery (federally listed portion) of the tortoise's range compared to areas located closer to the center of the tortoise's range

2. Overall connectivity of habitat for gopher tortoises will vary across the range, but will be lower near the peripheries

3. Connectivity of habitat will be reduced with the addition of urban land cover data

Methods

Study area

Our study area included the entirety of the federally listed portion of the gopher tortoise's range and a large portion of the remainder of the range, including Alabama, part of the Florida panhandle, and western Georgia (Figure 1.2). Peninsular Florida and eastern Georgia were excluded from the study area because changes in soil properties in the centermost portion of the tortoise's range (e.g., higher water tables, high proportional sand content) require special consideration when classifying soil suitability for tortoises and thus complicate comparison across different portions of the species' range.

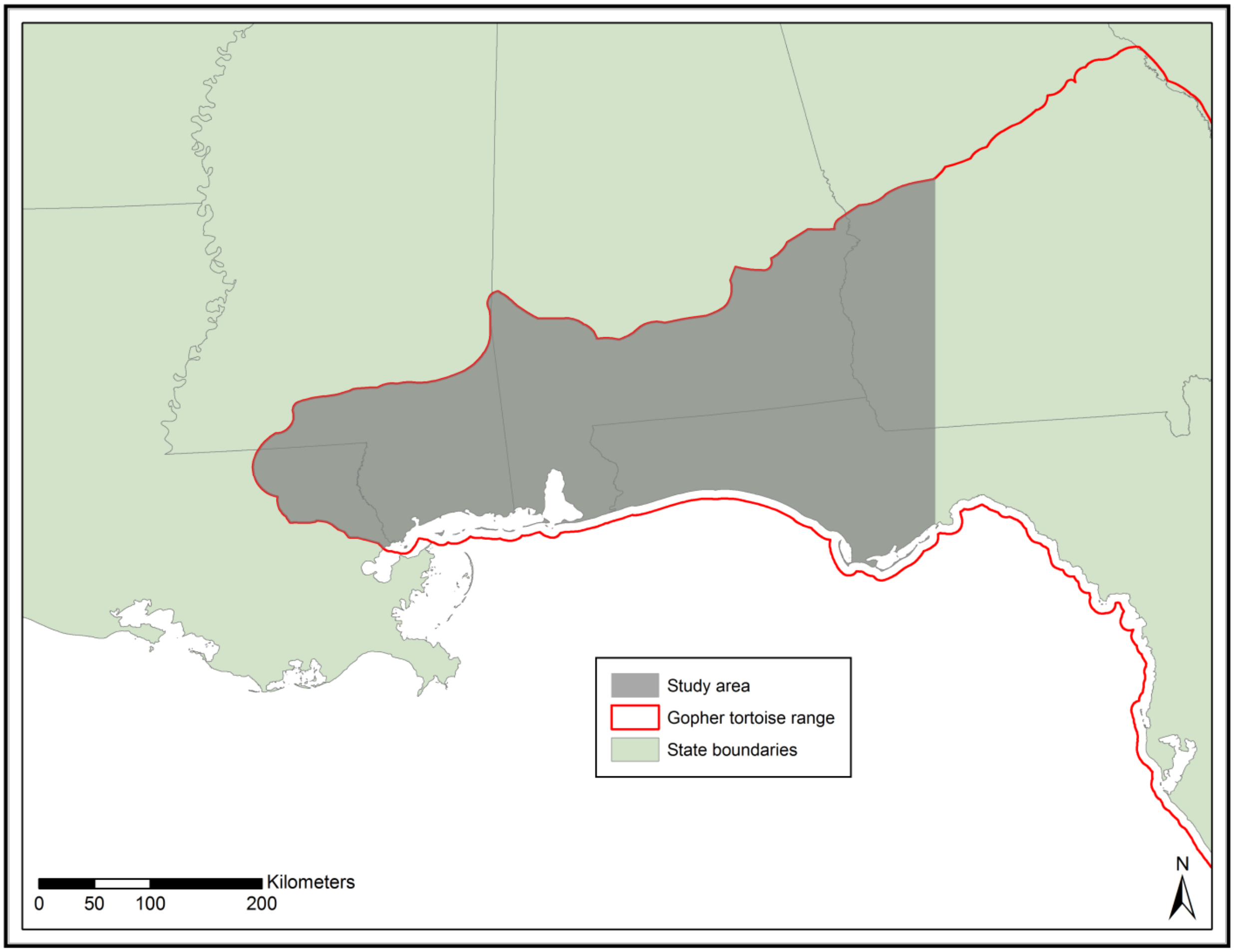


Figure 1.2. Study area for evaluating gopher tortoise habitat connectivity, covering portions of Louisiana, Mississippi, Alabama, Georgia, and Florida.

Soil classification

Soil data were obtained from the United States Department of Agriculture (USDA) Natural Resource Conservation Service (NRCS) Soil Survey Geographic (SSURGO) soils database for all counties within the study area. I classified soil suitability for tortoises based on USFWS and NRCS (2012), which developed a model for classifying soils in the federally listed portion of the range based on previous tortoise soil classifications and input from biologists and soil scientists (USFWS and NRCS 2012). The classification scheme presented in this report is based on soil textural and physical properties and is the most recent gopher tortoise soil suitability classification scheme currently available (USFWS and NRCS 2012).

We used the soil suitability criteria presented in Table 1 of the USFWS and NRCS (2012) report (also presented here in Table 1.1) to classify soils into one of five categories, as defined by the report: Highly Suitable, Moderately Suitable, Less Suitable, Marginal, and Unsuitable. Highly Suitable soils represent deep, sandy, well-drained soils that are preferred by tortoises and support the highest densities of tortoise populations. Moderately Suitable soils are somewhat preferred by tortoises and have few restrictive features, and generally support average to above average population densities. Less Suitable soils contain some features that may limit the establishment or maintenance of burrows on the site, and burrow densities may be below average. Marginal soils contain limiting or restrictive features such that population density will be limited on the site; tortoises are generally expected to choose marginal soils only when other habitat factors (such as extremely dense vegetation) prohibit the use of preferred soil types. Unsuitable soils have properties that prevent the establishment and/or maintenance of tortoise burrows, such as a high water table, frequent flooding, or a high percentage of gravel fragments.

Table 1.1. Gopher tortoise soil suitability ranking criteria. Adapted from USFWS and NRCS (2012).

Suitability Ranking:	Highly Suitable	Moderately Suitable	Less Suitable	Marginal	Unsuitable
Flooding	None	None to Rare	None to Rare	None to Occasional	All Others
Ponding	None	None	None	Non to Rare	All Others
Medium and coarse gravel fragments	< 15%	< 15%	< 15%	≥ 15%	> 35%
Depth to seasonal high water table	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Depth to restrictive layer	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Percent sand	≥ 70%	≥ 50%	≥ 30%	≥ 15%	< 15%
Percent clay	≤ 15%	≤ 18%	≤ 35%	≤ 60%	> 60%
Slope	≤ 15%	≤ 15%	≤ 15%	> 15%	> 35%

I merged the county-level SSURGO spatial data into larger datasets for each state included in the study area for classification using ArcMap v. 10.3 (Environmental Systems Research Institute, Redlands, CA). Soil properties were accessed through the USDA NRCS Soil Data Viewer v. 6.2 tool for ArcMap. Soil properties that were not accessible through the Soil Data Viewer were obtained through the SSURGO soil property tables associated with each dataset.

Soil fragmentation

I conducted a direct comparison between the federally listed and non-listed portions of the study area to assess differences in the extent and fragmentation of soils using descriptive statistics generated by FRAGSTATS v. 4 (McGarigal et al. 2012). The study area was divided into a federally listed region and a non-listed region (Figure 1.3). The federally listed study region included the entire federally listed range of the tortoise. The non-listed study region included the remainder of the tortoise's range in Alabama and the portion of the Florida panhandle south of Alabama. The remainder of our broader study area (portions of western Georgia, some of the Florida panhandle) had to be excluded due to computational memory limitations. The boundary between the federally listed and non-listed portions of the range was approximated by county boundaries: Choctaw, Washington, and Mobile counties in Alabama were considered to be entirely within the federally listed region, and all counties east were considered to be entirely in the non-listed region.

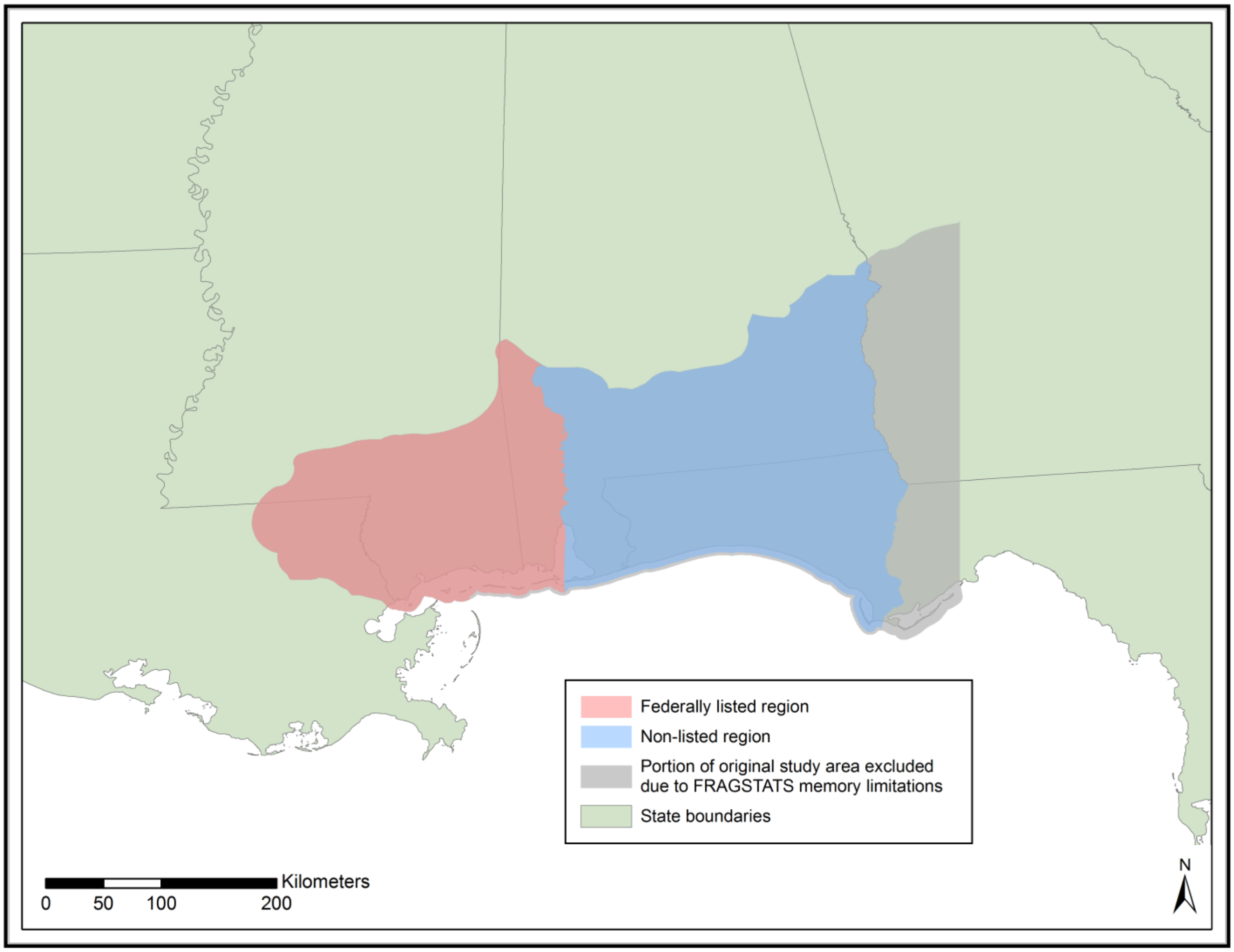


Figure 1.3. Federally listed and non-listed study regions used in the soil spatial pattern analysis.

I included in my analysis Highly Suitable soils on their own, Highly Suitable combined with Moderately Suitable soils, and Highly Suitable combined with Moderately and Less Suitable soils. I also included the above three categories with 100 m buffers around the combined soil polygons, resulting in six different combinations for analysis. A distance of around 100 m between patches of suitable soil is well within the distance that tortoises can disperse (Eubanks et al. 2003, Guyer et al. 2012), and is therefore likely to be inconsequential to population connectivity. Inclusion of the buffer results in actual soil patches that are within 100 m of each other being treated as a single contiguous patch by FRAGSTATS, and results in these buffer areas being counted as suitable habitat.

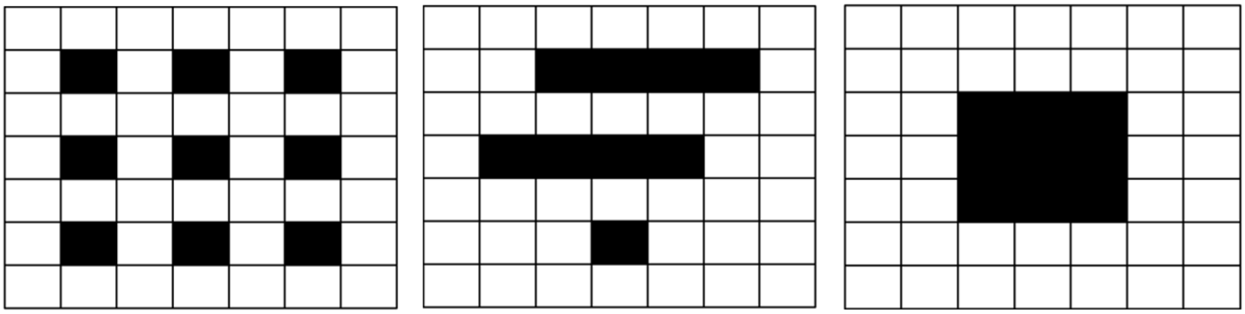
For each of the six soil combination maps, I generated a number of descriptive statistics: total area in suitable soils (including the buffer zone if there was one), total number of patches, patch density, percentage of the landscape in suitable soils, mean patch size, Connectance Index, Aggregation Index, and Clumpiness Index. These metrics provide multiple measures of landscape composition and pattern. A brief introduction to these metrics is presented here; for a more detailed discussion of their calculation, see the FRAGSTATS documentation (McGarigal et al. 2012).

Total area in suitable soils is the total area of the landscape that is in one of the six soil categories examined, calculated based on the number and size of the pixels in the rasters. Total number of patches is the number of individual soil patches within the area of interest. Patch density is the total number of patches divided by the total landscape area (i.e., number of patches per unit land area). Percentage of the landscape in suitable soils is the proportion of the total landscape area that is in one of the six soil categories, expressed as a percentage. Mean patch size is the average (arithmetic mean) size of all patches within the area of interest.

Connectance Index equals the number of patches that are functionally "connected" out of the total possible number of connected patches, based on a specified Euclidean distance between patches (McGarigal et al. 2012). If every patch in the landscape were connected to every other patch, the Connectance Index would be 100%. I used a threshold distance for connectedness of 100 m. Therefore, all patches that were within 100 m of each other were considered functionally connected. For soil maps that included a 100 m buffer around the actual soil patches, this results in a 200 m actual distance between soil patches as being considered connected; this distance corresponds with the maximum uniform spacing of burrows (i.e., minimum burrow density) at which tortoise populations are thought to remain viable (Guyer et al. 2012, Gopher Tortoise

Council 2013). Thus, the inclusion of both the 100 m buffer zone and the 100 m threshold distance effectively increase the threshold distance for connectivity to 200 m. Because this index is based purely on Euclidean distance, any barriers to movement between patches (e.g., rivers, steep terrain) are not considered.

Aggregation Index is expressed as a percentage, based on the ratio of observed number of like adjacencies (which occur when a raster cell of one habitat type is located next to another cell of the same type) to the total possible number of like adjacencies (He et al. 2000, McGarigal et al. 2012). Aggregation index ranges from 0 when the class is maximally disaggregated (when there are no like adjacencies) to 100 when the class is maximally aggregated (when the maximum number of like adjacencies is achieved), and is independent of landscape composition (Figure 1.4) (He et al. 2000, McGarigal et al. 2012). Because this index is based on the number of like adjacencies of cells, the resulting value is dependent on the resolution (i.e., cell size) of the raster used to calculate it. Aggregation of suitable habitat could have significant impacts on tortoise populations. The more aggregated the habitat, the more likely it is to support larger, more contiguous populations. If habitat is largely disaggregated, populations may be smaller and exist in disconnected fragments.



A. AI = 0 **B.** AI = 50 **C.** AI = 100

Figure 1.4. Three hypothetical landscapes and the corresponding Aggregation Index (AI). Adapted from He et al. (2000).

Clumpiness Index is the proportional deviation of the observed number of like adjacencies from that expected under a spatially random distribution (McGarigal et al. 2012). It ranges from -1 to 1, with a value of 0 indicating a random spatial distribution, values less than 0 indicating less aggregation (greater dispersion) than expected under a random distribution, and values greater than 0 indicating greater aggregation, approaching 1 when the focal class is maximally aggregated (McGarigal et al. 2012). Like Aggregation Index, Clumpiness Index depends on the number of like adjacencies of cells and thus will vary with cell size (resolution). Clumpiness Index is similar to Aggregation Index, but provides a comparison of the level of aggregation to what would be expected if the habitat were distributed randomly, regardless of the proportion of the landscape in the focal class (McGarigal et al. 2012).

I generated all metrics using FRAGSTATS v. 4 (McGarigal et al. 2012) and compared the general patterns of the resulting metrics between the two range portions. Soil maps and buffer zones were generated using ArcMap v. 10.3 and converted to raster format with cell sizes of 30 m x 30 m. Analysis was attempted at smaller cell sizes (e.g., 10 m x 10 m), but failed due to exceeding FRAGSTATS' allocated memory.

Connectivity

Connectivity analysis was based on the soil classification system listed above in combination with 2011 National Land Cover Dataset (NLCD; Homer et al. 2015) data on urban land cover and water/wetland cover. Vegetation cover, type, and structure are important components of gopher tortoise habitat and thus of habitat connectivity, but were excluded from our analysis because vegetation conditions are rapidly changing and accurately quantifying characteristics important to tortoises (e.g., canopy cover, understory cover and composition) over our very broad study area was not feasible. However, soils and hydrology on their own represent potential maximum connectivity if vegetation conditions were not limiting, and may provide some indication to potential historical habitat conditions (i.e., pre-European settlement). Incorporating information on urbanization reveals where human activities may be permanently limiting connectivity. While vegetation conditions may be readily changeable, areas with significant impervious surface development (e.g., paved roads, cities) are rarely returned to a natural state.

Soil data were converted to raster format with a 30 m x 30 m cell size for the entire study area. NLCD categories for development and hydrologic land cover were extracted from the NLCD dataset. These categories included: Open Space (< 20% impervious surface), Low Intensity Development (20-49% impervious surface), Medium Intensity Development (50-79% impervious surface), High Intensity Development (80-100% impervious surface), Wetland (areas where the soil or substrate is periodically saturated or covered with water), and Open Water (< 25% soil or vegetation cover) (Homer et al 2015).

I used Circuitscape (Circuitscape version 4.0.5, http://www.circuitscape.org) to conduct a circuit-theory based analysis of connectivity. This approach takes into account the composition and configuration of the landscape. This type of habitat and connectivity modeling is based on the principles of electrical circuit theory, which represents the flow of electric current through a series of nodes and resistors (McRae et al. 2008). In ecological applications, a landscape can be viewed in terms of resistance to the movement of animals, which is analogous to the flow of electricity through resistors in a circuit (McRae et al. 2008). A landscape can be mapped in a raster format with each grid cell containing a resistance value that represents how difficult it is for an animal to move through that particular cell's habitat type (McRae et al. 2008). Focal patches are defined and set as "sources" of current; the flow of current across the raster grid can then be quantified and mapped, with grid cells with higher current indicating areas where animal movements are likely to be concentrated (McRae et al. 2008). Additionally, the effective resistance across the landscape is calculated, which takes into account all possible pathways between focal areas and the resistances of the grid cells between them (McRae et al. 2008).

It is important to note that our study covers a very broad area over which no individual tortoise could be expected to travel. Therefore, in this study "movement" does not imply individual movement across a landscape but rather movement of populations over time. This can be thought of in terms of "movement" of genes or gene flow across the landscape; landscape resistance to such "movement" derived from circuit-theoretical approaches has been correlated with genetic differentiation between populations in a number of species, including gopher tortoises (Clostio 2010).

I assigned resistance values to raster cells on a scale of 1-10, where a value of 1 indicates the greatest ease of "movement" and a value of 10 indicates the greatest difficulty. Resistance values were based on our current understanding of tortoise's preference for various soil types and ability to move through or occupy various hydrologic or urban conditions. An infinite resistance value (complete barrier) was assigned to ocean (i.e., all areas off the coast) for all runs. I generated four separate sets of resistance rasters, representing a range of possibilities for some habitat variables, presented in Table 1.2.

Table 1.2. Resistance values assigned to land cover types examined in the connectivity analysis.

	Resistance Values			
Habitat Variable	**Set 1**	**Set 2**	**Set 1, with Urbanization**	**Set 2, with Urbanization**
Highly suitable soils	1	1	1	1
Moderately suitable soils	2	2	2	2
Less suitable soils	3	3	3	3
Marginal soils	5	6	5	6
Unsuitable soils	7	9	7	9
Wetland	9	10	9	10
Open water	10	10	10	10
Developed, open space	Not included	Not included	5	5
Developed, low intensity	Not included	Not included	7	7
Developed, medium intensity	Not included	Not included	9	9
Developed, high intensity	Not included	Not included	10	10

Highly Suitable, Moderately Suitable, and Less Suitable soils were assigned resistance values of 1, 2, and 3, respectively. Areas with these soil types are expected to have lower resistance than areas covered by any of the other habitat variables. Resistance is expected to increase with lower soil suitability because tortoises are expected to prefer higher suitability soils and use those when possible. Marginal soils, which tortoises are expected to use only when other habitat conditions exclude them from more suitable soils, were given higher resistance values, either 5 or 6 depending on the run. Unsuitable soils were assigned a resistance value of 7 or 9 depending on the run, to cover a range of possibilities (i.e., from Unsuitable soils being only somewhat worse than marginal soils to being much worse). Wetlands and urbanization represented some of the highest resistance values, as tortoises are unlikely to move through or occupy wet areas or areas dominated by impervious surfaces. Open water was always given a resistance value of 10, as tortoises are least likely to try to move through or occupy this land cover type. The highest (most limiting) resistance value was used when overlap between habitat types occurred (e.g., urban land cover over soils).

I followed the methods of Pelletier et al. (2014) for analyzing the study area: The area was first divided into 1,253 square regions, each 8,100 ha. These regions were then buffered by 6,000 m to create 1,253 square overlapping regions, each 22,500 ha. The purpose of the overlap was to reduce the "seams" (differences in current) between regions when the current map results from individual regions are reassembled into a map representing the entire study area (Pelletier et al. 2014). For each of these overlapping, square regions, 30 m wide focal zones (areas of 0 resistance that are the source of current) were created on each of the four region edges. These focal zones were grouped into North/South and East/West runs. Each region was analyzed twice per resistance grid: once in the North/South direction, and once in the East/West direction. The effective resistance from the North/South and East/West directions for each region was averaged. Cumulative current rasters for each region from the North/South and East/West runs were multiplied together to create omnidirectional current maps for each region, which I then reassembled into current maps for the entire study area. I used the Circuitscape for ArcGIS toolbox in a Python code loop using the ArcPy site package (Environmental Systems Research Institute, Redlands, CA) to iterate through all regions. I generated both current maps and effective resistance values to compare current flow and relative resistance across the study area.

Cumulative current maps for the study area were visually examined for areas of high or low current. The averages of the effective resistances for the North/South and East/West runs were assigned to each region. I fitted a Generalized Additive Model (GAM) to the averaged effective resistances with smoothing functions for the latitude, longitude, and interaction between the latitude and longitude of the region's centroids using R v. 3.2 (R Core Team 2015) and R package mgcv (Wood 2011) to assess the effects of latitude and longitude on landscape resistance and to test the prediction that resistance will be higher (i.e., connectivity lower) near the western range periphery.

As another way of comparing current maps, I generated histograms from the values of cells (current value) from the omnidirectional cumulative current rasters for the federally listed and non-listed portions of the study area for each resistance value set. Visual inspection of current maps is useful for identifying areas with relatively high or low current flow, but it is difficult to quantify the pattern of current flow across the landscape. A pattern of particular interest might be the degree to which the landscape contains "pinch points," areas where there is a high concentration of current (i.e., where there is a high probability or necessity of passing through) (McRae et al. 2008). There are currently no guidelines for identifying such areas, or for what minimum value of current would be needed for an area to qualify as a pinch point (Pelletier et al. 2014). Nonetheless, comparing histograms of current values may yield additional information (Pelletier et al. 2014).

Skewness of the distribution of current values may be a useful measure for comparing the relative tendency of different current maps to contain pinch points. A positive value for skewness indicates a distribution that is right-skewed, with most values being on the lower end of the distribution, while a negative value for skewness indicates a left-skewed distribution. A more positive value for skewness may indicate the presence of pinch points, with most cells having very little to no current flow, and few areas having much higher current, as would be expected if the current is being restricted to smaller areas. I calculated a measure of skewness using the R package moments (Komsta and Novemstky 2015) for the federally listed and non-listed portions of the study area for each resistance set.

In addition to comparing patterns of current flow between the federally listed and non-listed portions of the study area, I quantified the difference in current flow before and after inclusion of data on urbanization to evaluate the potential impacts urbanization has had on broad-scale gopher tortoise habitat connectivity. To compare current flow across the landscape before and after urbanization data were included, I used the Raster Calculator tool in ArcMap to subtract the cumulative current maps with urbanization included from those without urbanization. Resistance set 1 with urbanization was subtracted from set 1 without urbanization, and set 2 with urbanization was subtracted from set 2 without urbanization, resulting in two new maps depicting the difference between similar runs (same resistance values for soil and hydrology) with and without urbanization data included. Positive values in a cell of the new raster indicate that the current value of that cell was higher before urbanization data were included. Negative values indicate the current value was higher after urbanization data were added. Values of zero (or near zero) indicate little or no difference in current values of those cells after urbanization. These maps were visually inspected to identify areas where urbanization may have had the greatest effects on gopher tortoise habitat connectivity.

Results

Soil classification

In general, most of the tortoise's range contained soils classified as Marginal suitability or higher, with the largest expanses of Unsuitable soils occurring near parts of the coast in the Florida panhandle and major river systems (Figure 1.5). The Florida panhandle and western Georgia had large patches of Highly Suitable soils. Mississippi contained largely a mix of Marginal, Less Suitable, and Moderately Suitable soils with relatively small patches of Highly Suitable soils. Louisiana consisted mostly of Marginal and Less Suitable soils, with relatively few, small areas of Moderately Suitable or Highly Suitable soils. Due to differences in soil classification between counties, some county boundaries are visible as differences in the resulting tortoise soil classifications at county lines in the final map (Figure 1.5).

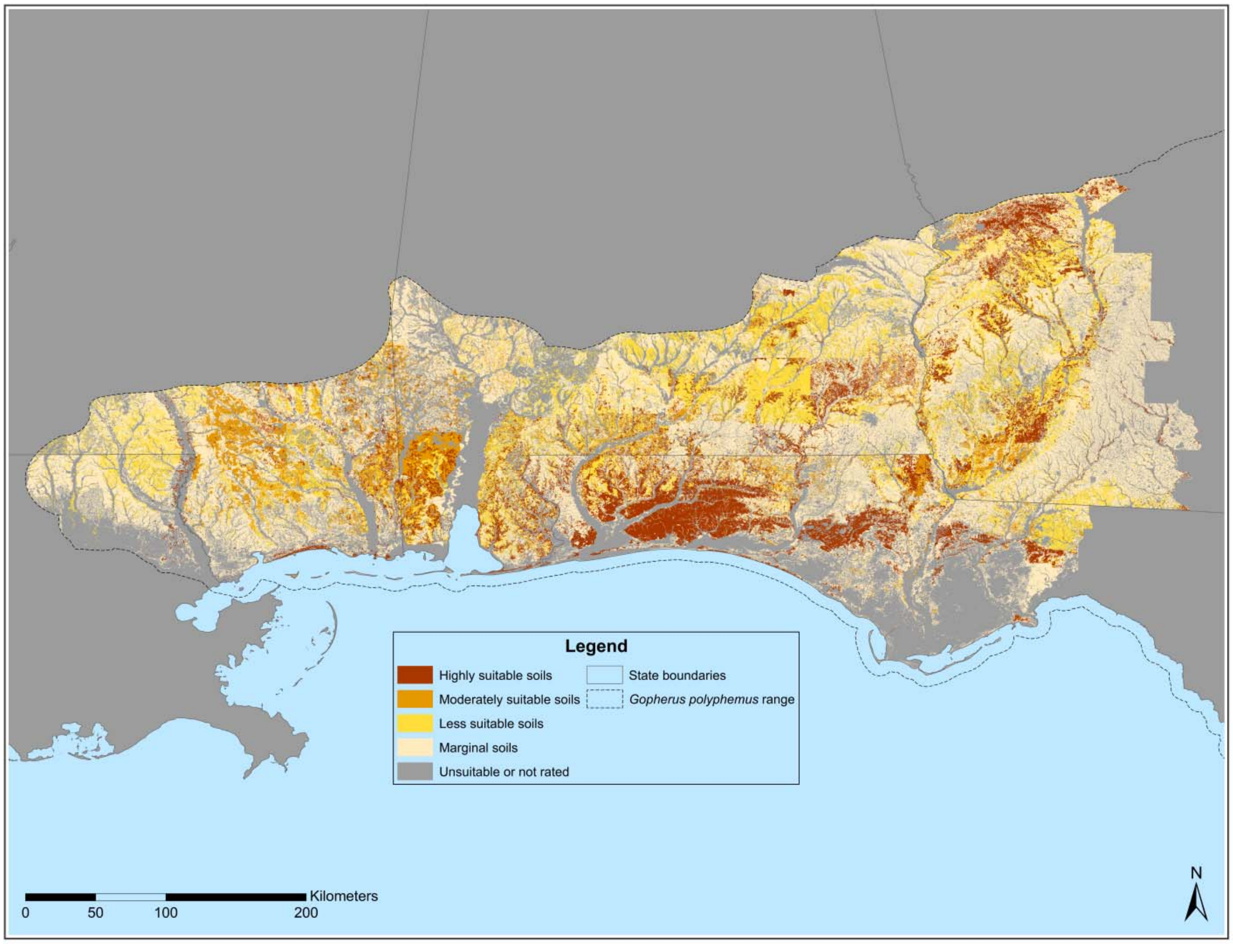


Figure 1.5. Soils classified according to suitability for gopher tortoises within the study area. Soil classification was based on USFWS and NRCS (2012).

Soil fragmentation

All combinations of soils comprised a larger percentage of the landscape in the non-listed portion of the range than in the federally listed portion of the range (Tables 1.3 and 1.4). The non-listed portion of the range also had more suitable patches and a higher density of suitable patches under all soil combinations. The Connectance Index was higher for all soil combinations in the federally listed portion of the tortoise's range. The Aggregation Index was higher in the non-listed portion of the range for Highly Suitable and Highly Suitable plus buffer combinations, but was similar to the federally listed portion of the range for the other soil combinations examined. Clumpiness Index was high for all soil combinations across both regions, indicating that soils exhibit more aggregation than would be expected under a spatially random distribution. Clumpiness Index followed a similar pattern as Aggregation Index, being higher for Highly Suitable and Highly Suitable plus buffer combinations in the non-listed portion of the range, but relatively similar in both range portions for all other soil combinations examined.

Table 1.3. Landscape summary metrics for soil suitability classification combinations without buffers for the federally listed and non-listed portions of the study area.

	Federally Listed Portion of Range			Non-Listed Portion of Range		
Soil classification combination	Highly Suitable	Highly and Moderately Suitable	Highly, Moderately, and Less Suitable	Highly Suitable	Highly and Moderately Suitable	Highly, Moderately, and Less Suitable
Area (ha)	148456	524610	866811	728682	914188	1756393
Number of Patches	6022	8447	12737	18015	23521	24498
Patch Density (patches/ha)	0.064	0.09	0.135	0.158	0.206	0.215
Percentage of the Landscape	1.58	5.57	9.21	6.39	8.01	15.4
Average Patch Size (ha)	24.65	62.11	68.05	40.45	38.87	71.7
Connectance Index	0.008	0.007	0.006	0.004	0.003	0.003
Aggregation Index	88.74	92.77	92.60	92.22	91.7	92.95
Clumpiness Index	0.89	0.92	0.92	0.92	0.91	0.92

Table 1.4. Landscape summary metrics for soil suitability classification combinations with 100 m buffer zones for the federally listed and non-listed portions of the study area.

	Federally listed portion of range			Non-listed portion of range		
Soil classification combinations, with 100 m buffer	Highly Suitable	Highly and Moderately Suitable	Highly, Moderately, and Less Suitable	Highly Suitable	Highly and Moderately Suitable	Highly, Moderately, and Less Suitable
Area (ha)	197026	872114	1408152	1236192	1616051	2790223
Number of Patches	2950	3124	3430	5268	6308	5431
Patch Density (patches/ha)	0.031	0.033	0.036	0.046	0.055	0.048
Percentage of the Landscape	2.09	9.27	14.96	10.84	14.17	24.46
Average Patch Size (ha)	66.79	279.17	410.54	234.66	256.19	513.76
Connectance Index	0.012	0.010	0.011	0.009	0.007	0.010
Aggregation Index	85.05	97.23	97.64	95.23	96.94	97.69
Clumpiness Index	0.85	0.97	0.97	0.95	0.96	0.97

Connectivity

Two of the regions from resistance value set 2 without urbanization (higher resistance assigned to less suitable soils compared to set 1) and one region from set 2 with urbanization failed to run in Circuitscape (either the ArcGIS toolbox version or the standalone version) in the

North-South direction for unknown reasons. These regions are excluded from further analyses using set 2 with and without urbanization.

For all sets, the average effective resistance of regions varied with latitude, longitude, and the interaction between latitude and longitude. Effective resistance increased from east to west in more northern portions of the study area (consistent with my expectation), but in the southern portion of the study area resistance was higher at more eastern longitudes. This general pattern held for all resistance value sets. The sets that included urbanization had higher average effective resistance than the sets without urbanization (averaged across the study area).

Current maps were generated for the entire study area for all runs (examples in Figure 1.6 and 1.7). The broad-scale general patterns of current flow appeared similar between the two resistance value sets (set 1 and set 2; Figures 1.6 and 1.7). Inclusion of urban land cover resulted in altered patterns of current flow within the study area for both runs for which it was included (Figure 1.8). Urbanization resulted in a shift in current across the study area, with current decreasing in many areas and more current being forced through remaining areas where it was lower previously (Figures 1.9 and 1.10). The set 1 with/without urbanization map differences showed a differing pattern from the set 2 differences, with set 1 showing larger expanses of areas where current was higher without urbanization (Figures 1.9 and 1.10). This is likely due to the lower resistance value assigned to unsuitable soil in set 1, where unsuitable soils have a lower resistance than the two highest intensity urbanization classes, thus resulting in a decrease in current flow when areas of unsuitable soils are converted to one of those urbanization classes. In set 2, unsuitable soils have a higher resistance than all but the highest intensity urbanization. While inclusion of urbanization altered the amount of current in each cell throughout the study area, most differences were relatively small. The greatest differences between the current maps with urbanization and those without occurred in and around areas of major urban development, particularly near the coast in the Florida panhandle and around Mobile Bay (Figures 1.11 and 1.12). Areas where relatively large amounts of current were decreased by the addition of urban land cover also showed surrounding area where current increased after urbanization, showing where the flow of current has been diverted by urbanization (Figures 1.13 and 1.14).

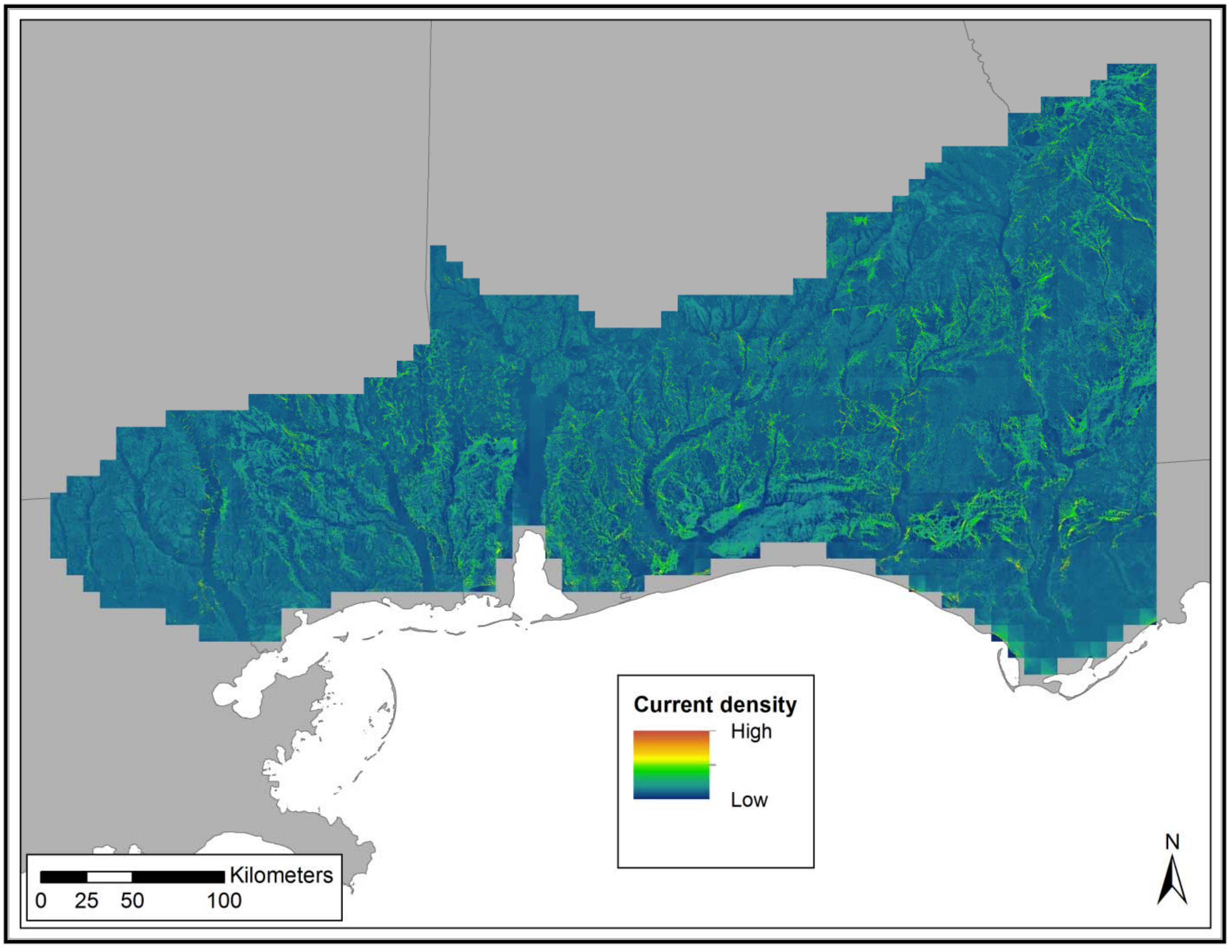


Figure 1.6. Omnidirectional current density map from resistance value set 1, without urbanization. Areas that are more yellow/red indicate greater concentration of current.

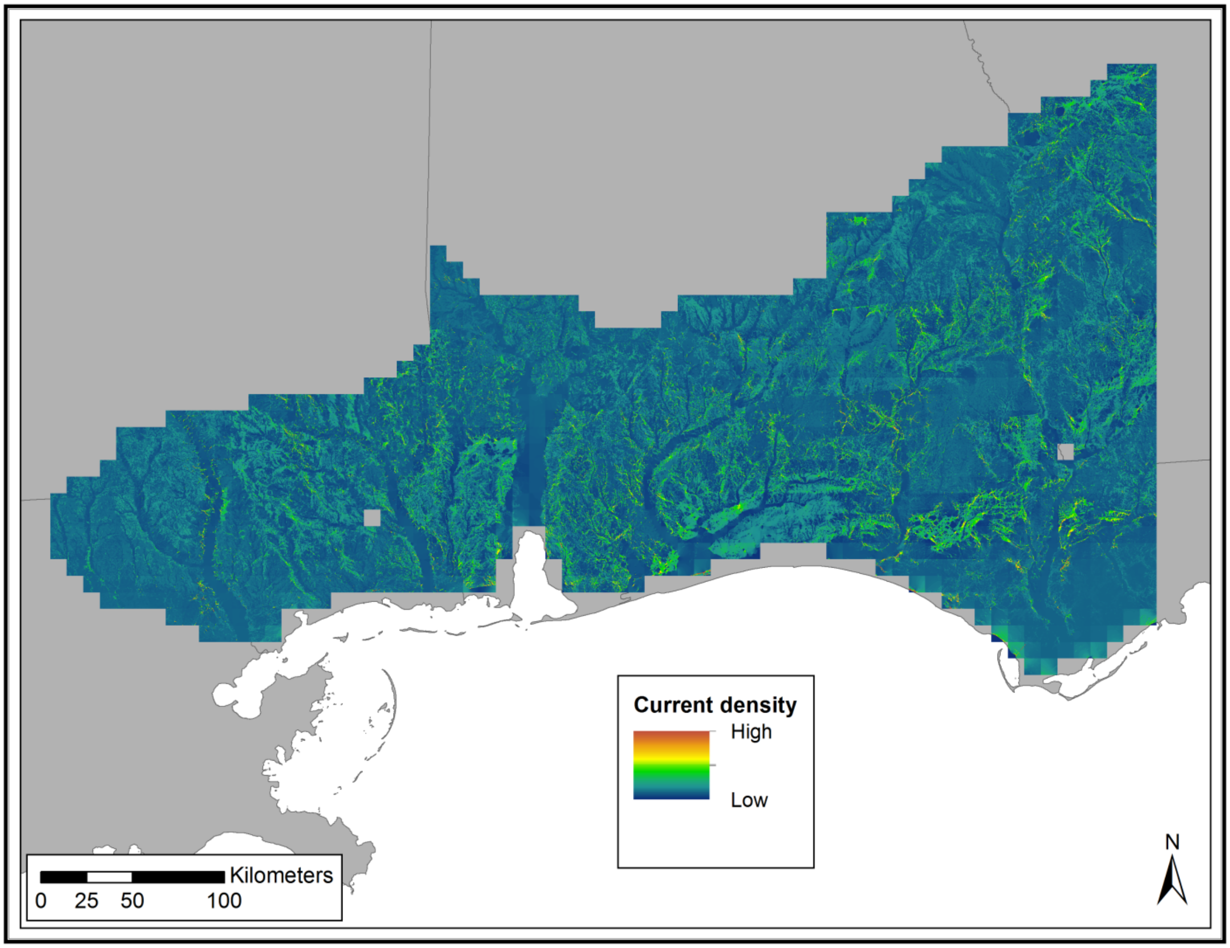


Figure 1.7. Omnidirectional current density map from resistance value set 2, without urbanization. Areas that are more yellow/red indicate greater concentration of current. The empty squares within the study area are the locations of the regions that failed to run in Circuitscape.

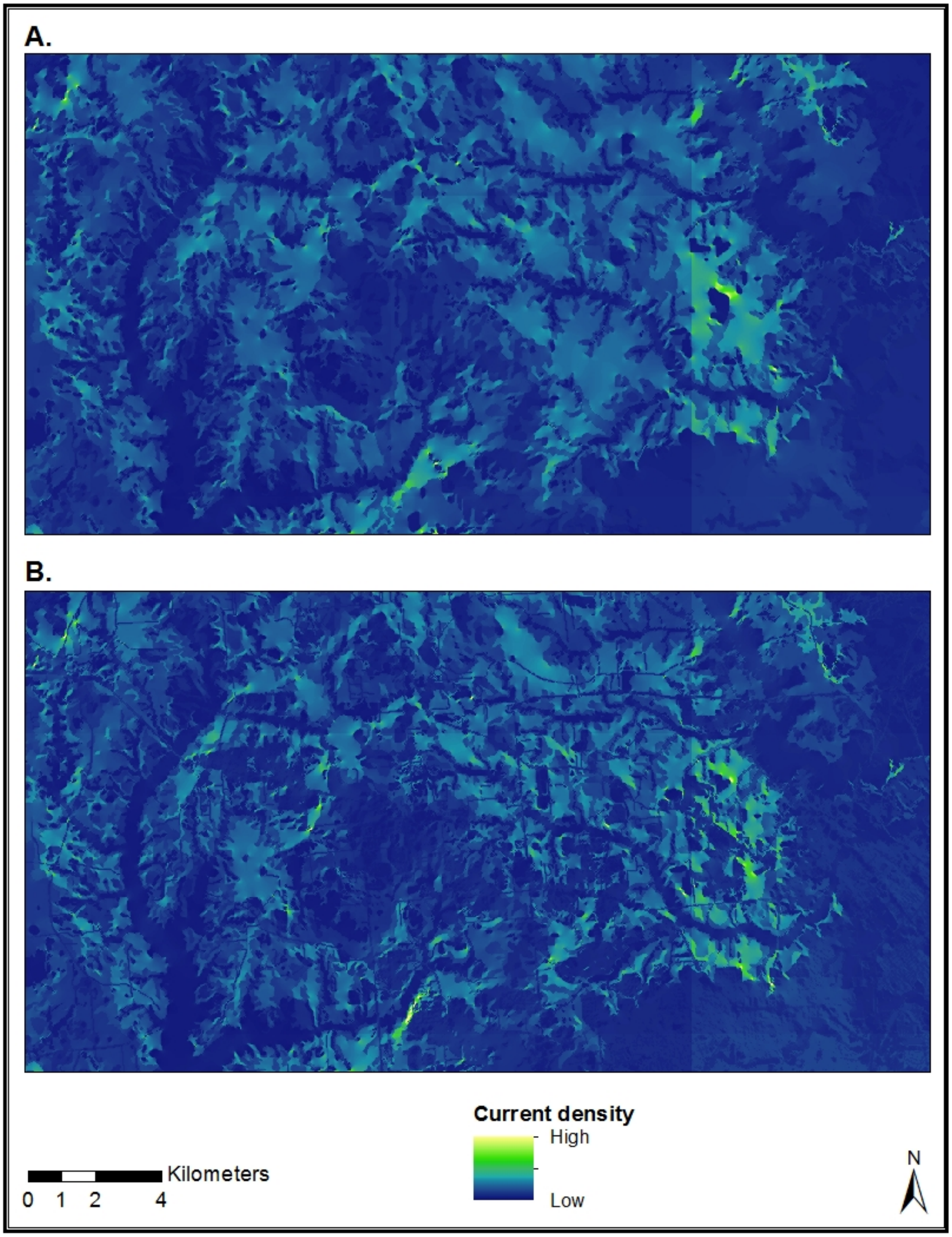


Figure 1.8. Omnidirectional current density mosaic maps for an area on the northwestern side of Mobile, Alabama demonstrating altered current flow with inclusion of urbanization data. A: results from resistance value set 1 without urbanization. B: results from Run 1 with urbanization.

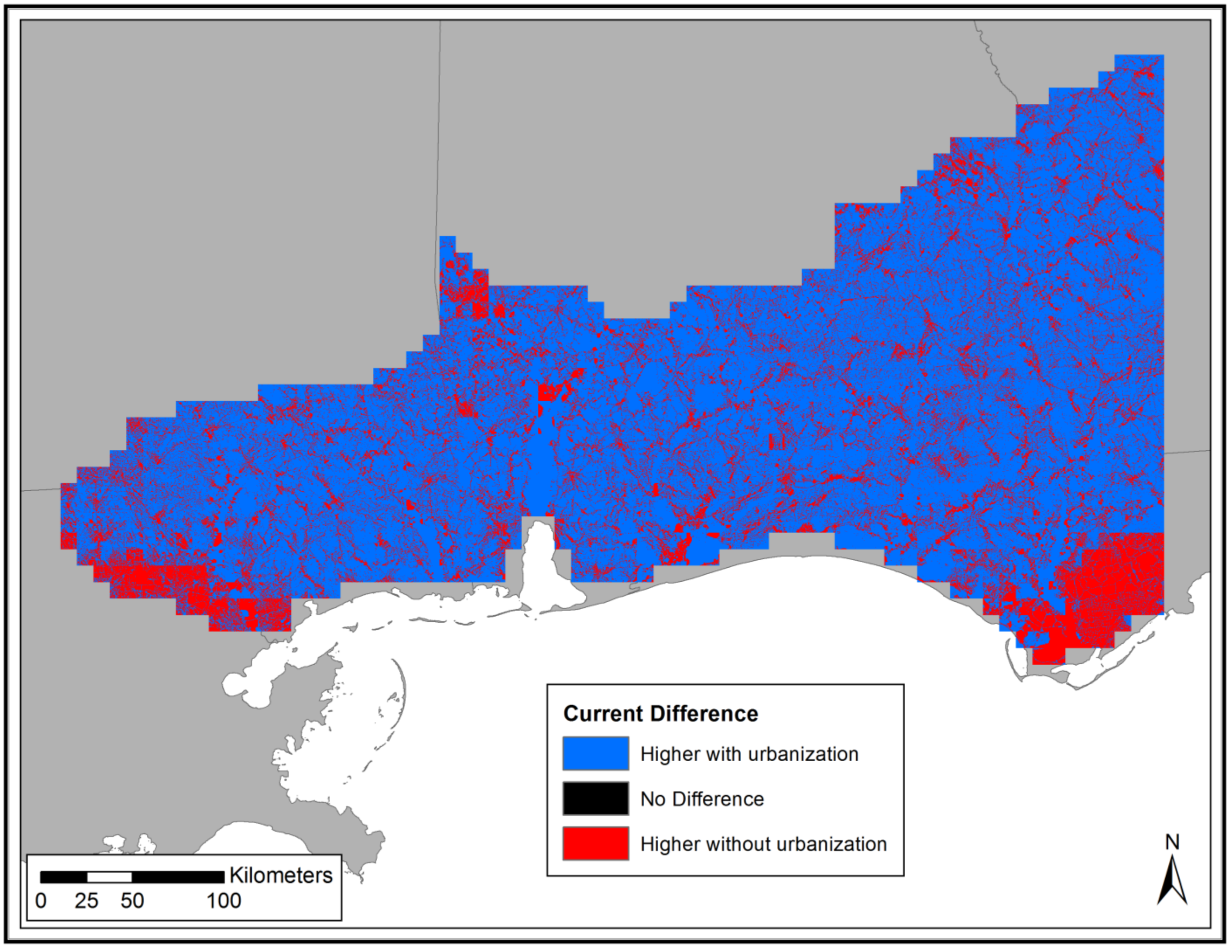


Figure 1.9. Direction of difference in current density between the with urbanization and without urbanization omnidirectional current maps from set 1.

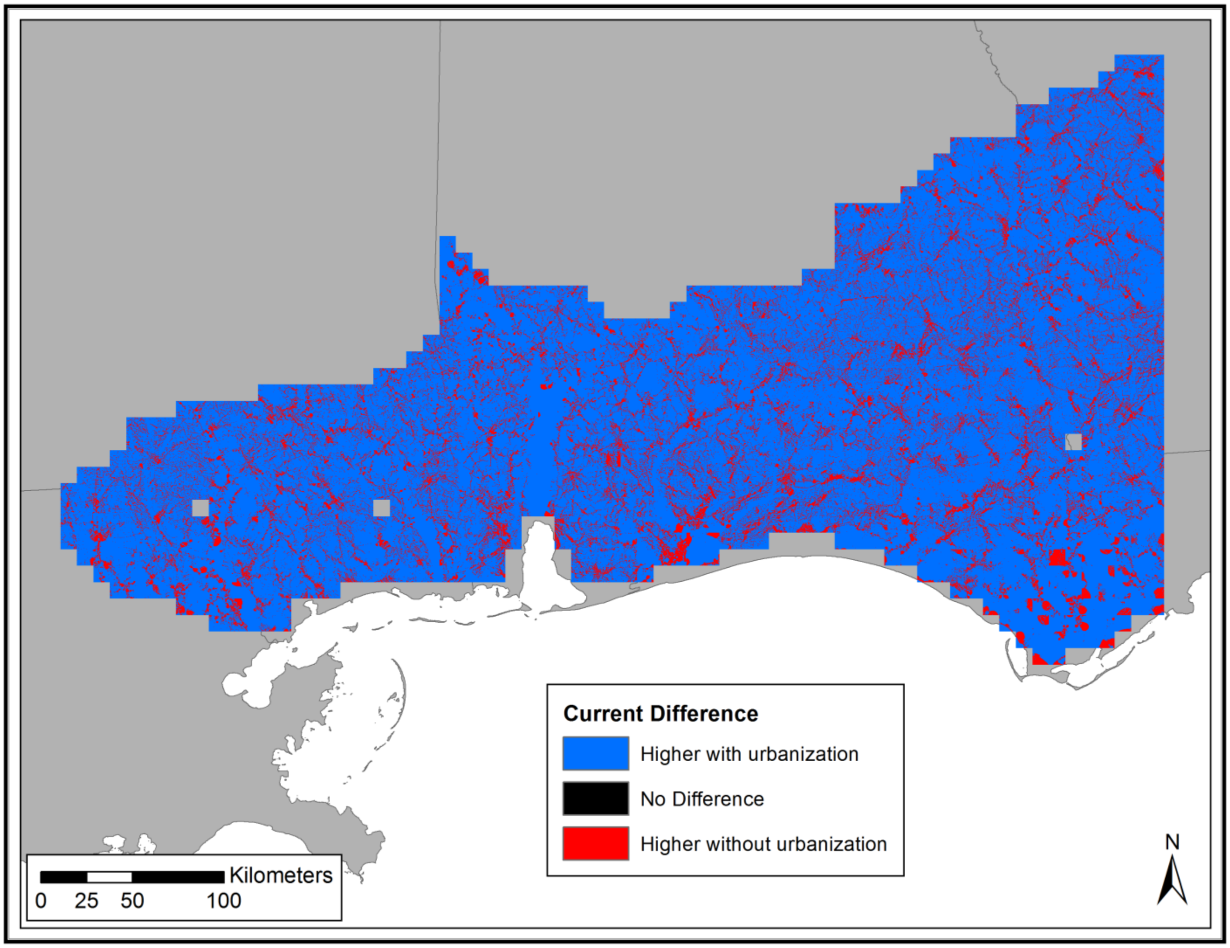


Figure 1.10. Direction of difference in current density between the with urbanization and without urbanization omnidirectional current maps from set 2.

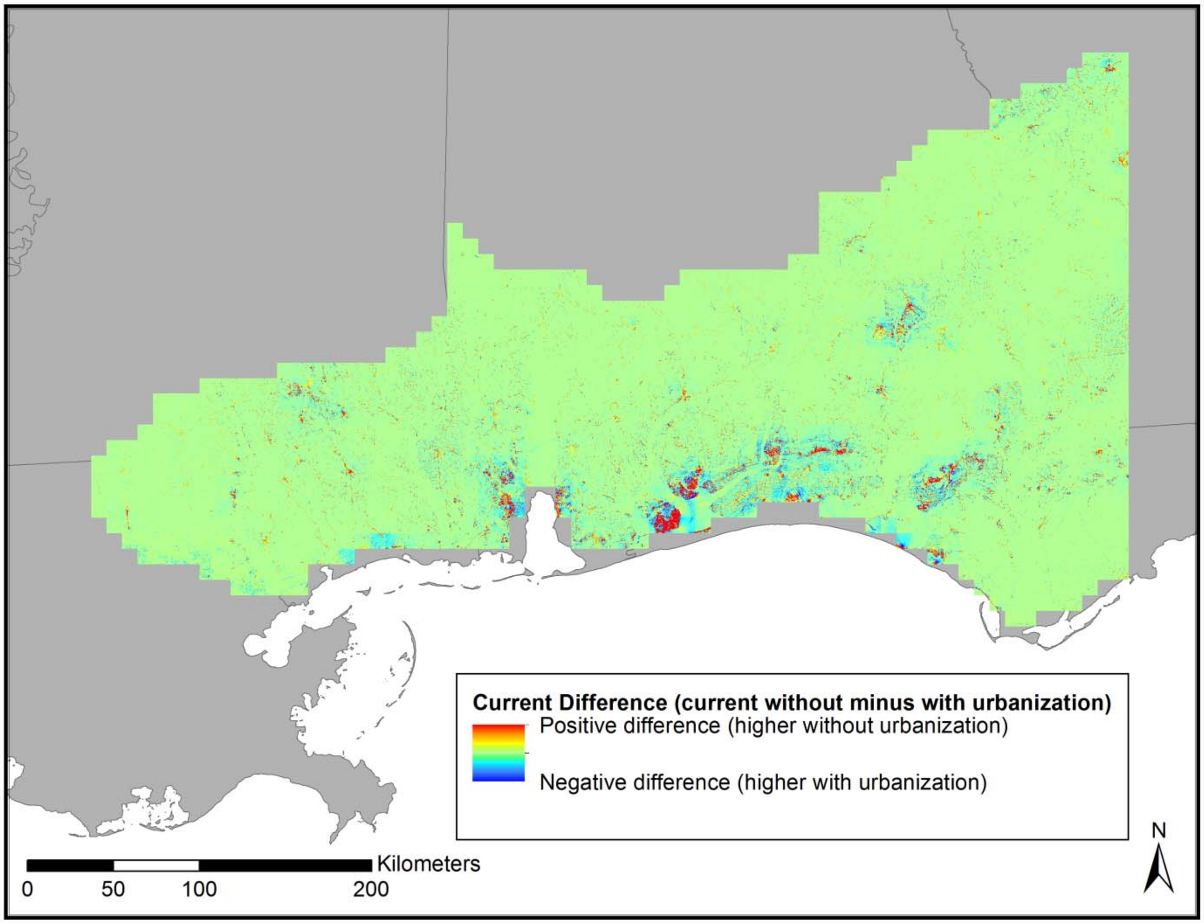


Figure 1.11. Difference in current flow between resistance value set 1 without urbanization and set 1 with urbanization resulting from the subtraction of the set 1 with urbanization omnidirectional current raster from the set 1 without urbanization omnidirectional current raster. The red and dark blue colors on the ends of the color scale represent differences ≥ 2.5 standard deviations away from the mean, indicating the areas of greatest difference between the before and after urbanization maps.

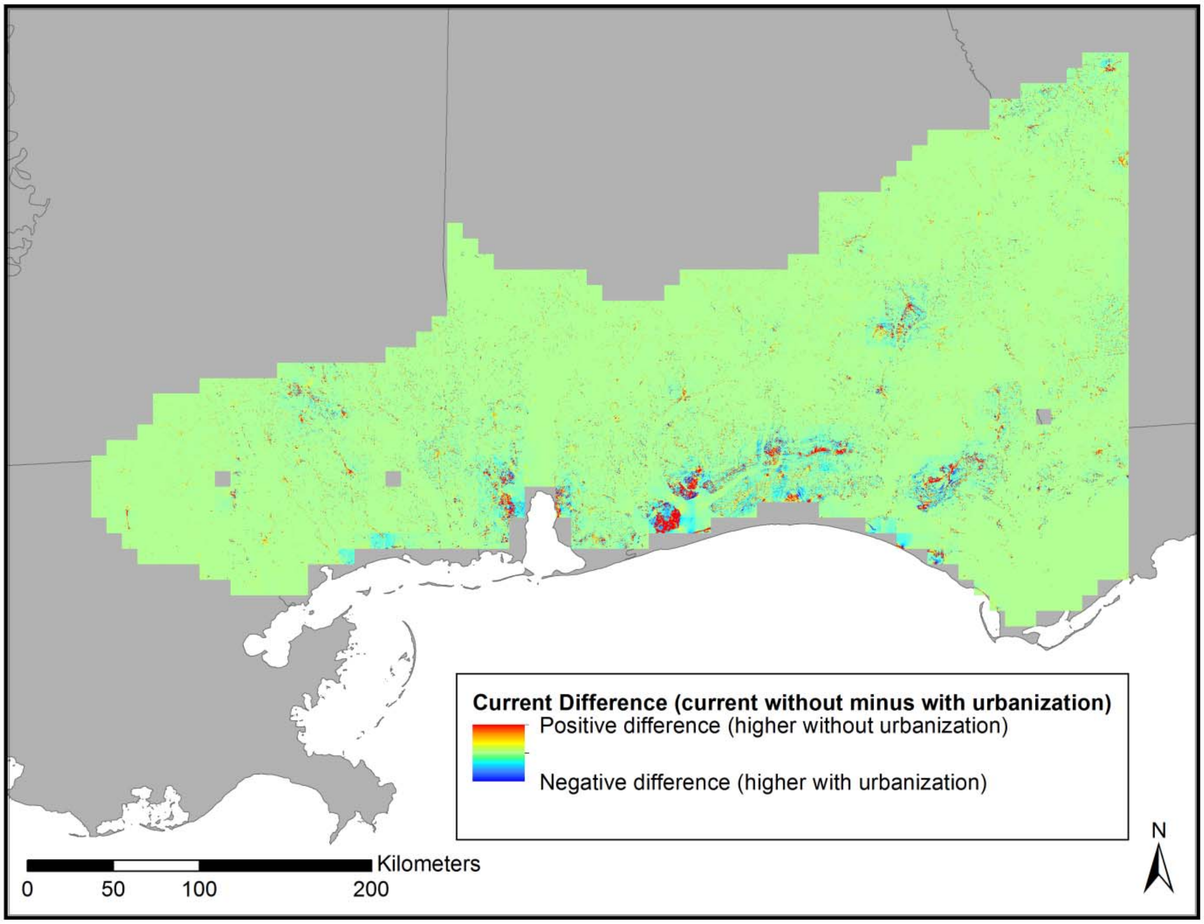


Figure 1.12. Difference in current flow between Run 2 without urbanization and Run 2 with urbanization resulting from the subtraction of the Run 2 with urbanization omnidirectional current raster from the Run 2 without urbanization omnidirectional current raster. The red and dark blue colors on the ends of the color scale represent differences ≥ 2.5 standard deviations away from the mean, indicating the areas of greatest difference between the before and after urbanization maps.

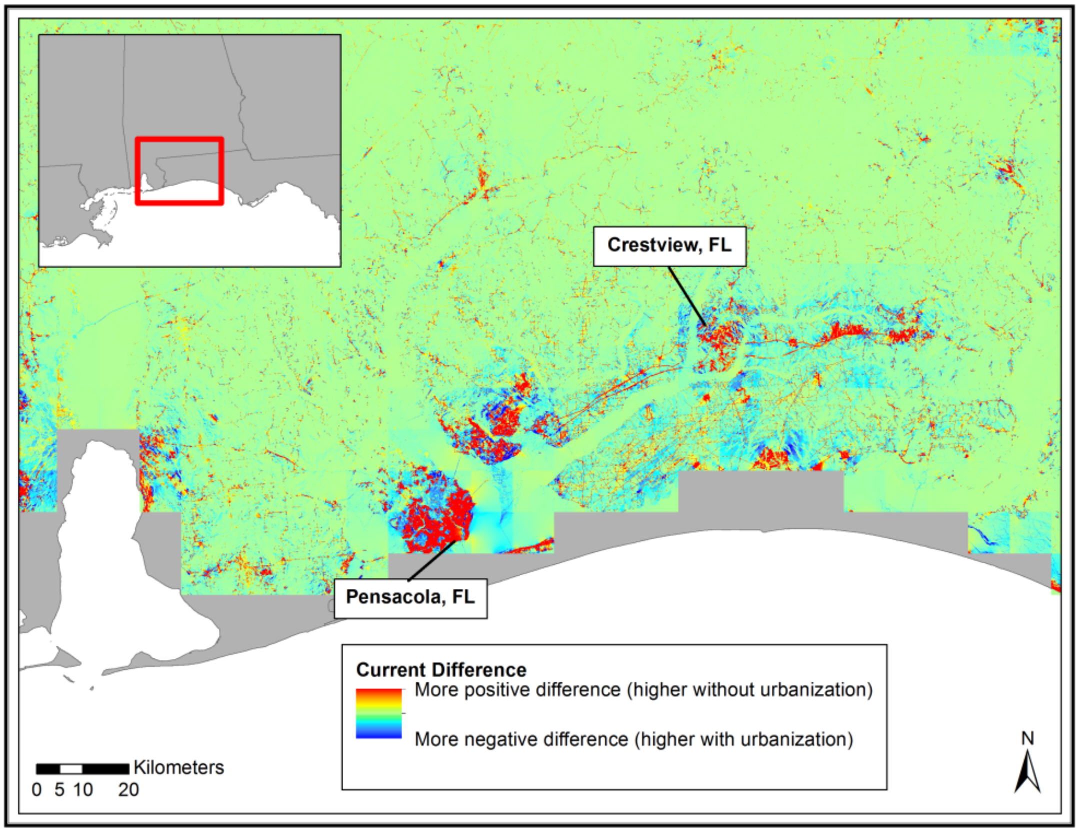


Figure 1.13. Difference in current flow between Run 1 without urbanization and Run 1 with urbanization for the coastal Alabama and Florida panhandle area. The red and dark blue colors on the ends of the color scale represent differences ≥ 2.5 standard deviations away from the mean, indicating the areas of greatest difference between the before and after urbanization maps.

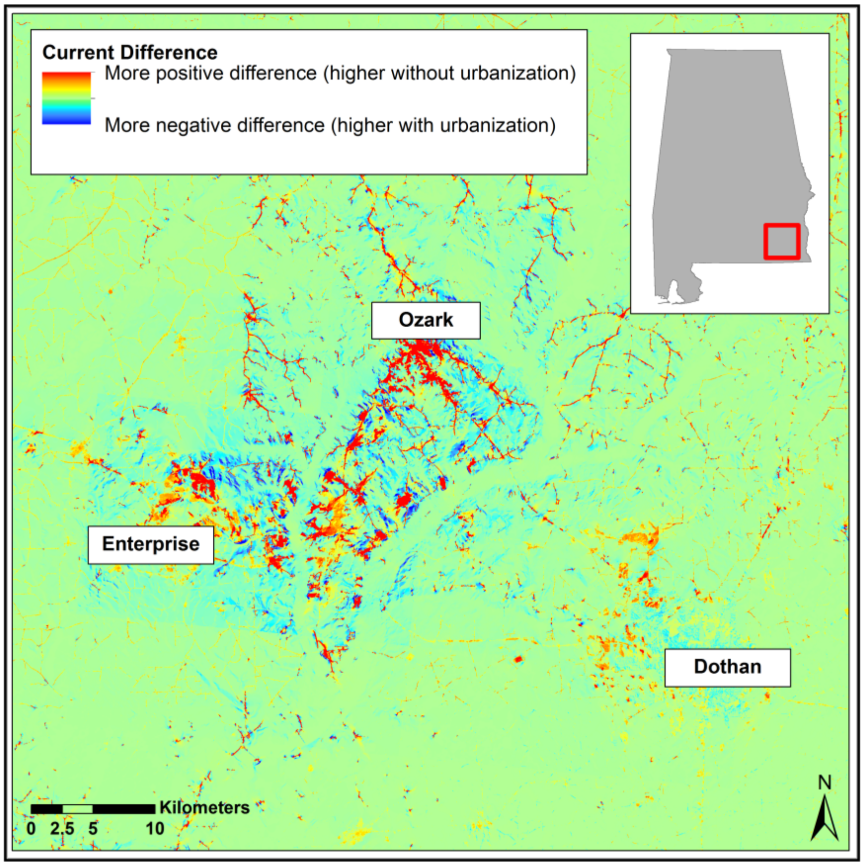
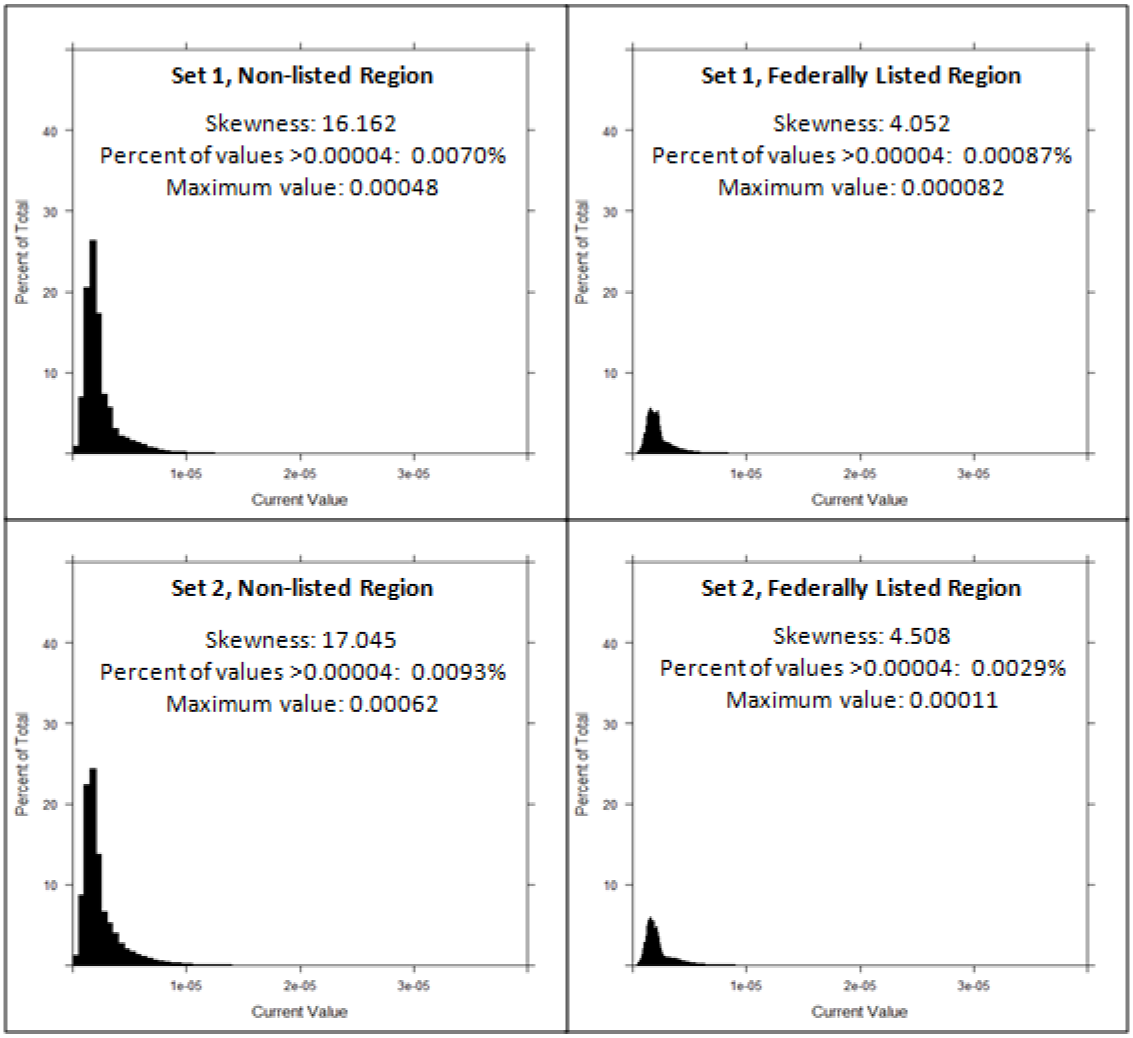


Figure 1.14. Difference in current flow between Run 1 without urbanization and Run 1 with urbanization near Enterprise and Dothan, Alabama. The red and dark blue colors on the ends of the color scale represent differences ≥ 2.5 standard deviations away from the mean, indicating the areas of greatest difference between the before and after urbanization maps.

For all resistance value sets and in both the federally listed and non-listed portions of the gopher tortoise's range, the distribution of current values had a positive (i.e., a right) skew (Table 1.5, Figures 1.15 and 1.16). Thus, most cells in all maps had current values on the lower end of the distribution, with fewer values towards the upper extremes. The non-listed portion of the study area had greater (more positive) skewness than the federally listed portion under all resistance sets, with or without urbanization (Table 1.5). For both set 1 and set 2, there was a greater difference in skewness between the federally listed and non-listed portions of the study area when urbanization was not included (Table 1.5). Set 2, with and without urbanization, had greater skewness than set 1 with and without urbanization (Table 1.5), likely due to the greater differences in resistance values assigned to the different soil suitability categories in this set.

Table 1.5. Measures of skewness for histograms computed from the current values extracted from each cell in the omnidirectional current density maps. Skewness values were calculated separately for the federally listed and non-listed portions of the gopher tortoise's range for each set of resistance values.

	Set 1, without urbanization		**Set 1, with urbanization**		**Set 2, without urbanization**		**Set 2, with urbanization**	
	Federally Listed	Non-Listed	Federally Listed	Non-Listed	Federally Listed	Non-Listed	Federally Listed	Non-Listed
Skewness	4.052	16.162	3.707	3.916	4.508	17.045	4.055	4.452



Set 1, Non-listed Region

Skewness: 16.162

Percent of values >0.00004: 0.0070%

Maximum value: 0.00048

Set 1, Federally Listed Region

Skewness: 4.052

Percent of values >0.00004: 0.00087%

Maximum value: 0.000082

Set 2, Non-listed Region

Skewness: 17.045

Percent of values >0.00004: 0.0093%

Maximum value: 0.00062

Set 2, Federally Listed Region

Skewness: 4.508

Percent of values >0.00004: 0.0029%

Maximum value: 0.00011

Figure 1.15. Histograms of current values from the omnidirectional current density maps in the federally listed and non-listed portions of the study area for the resistance value sets not including urbanization data.

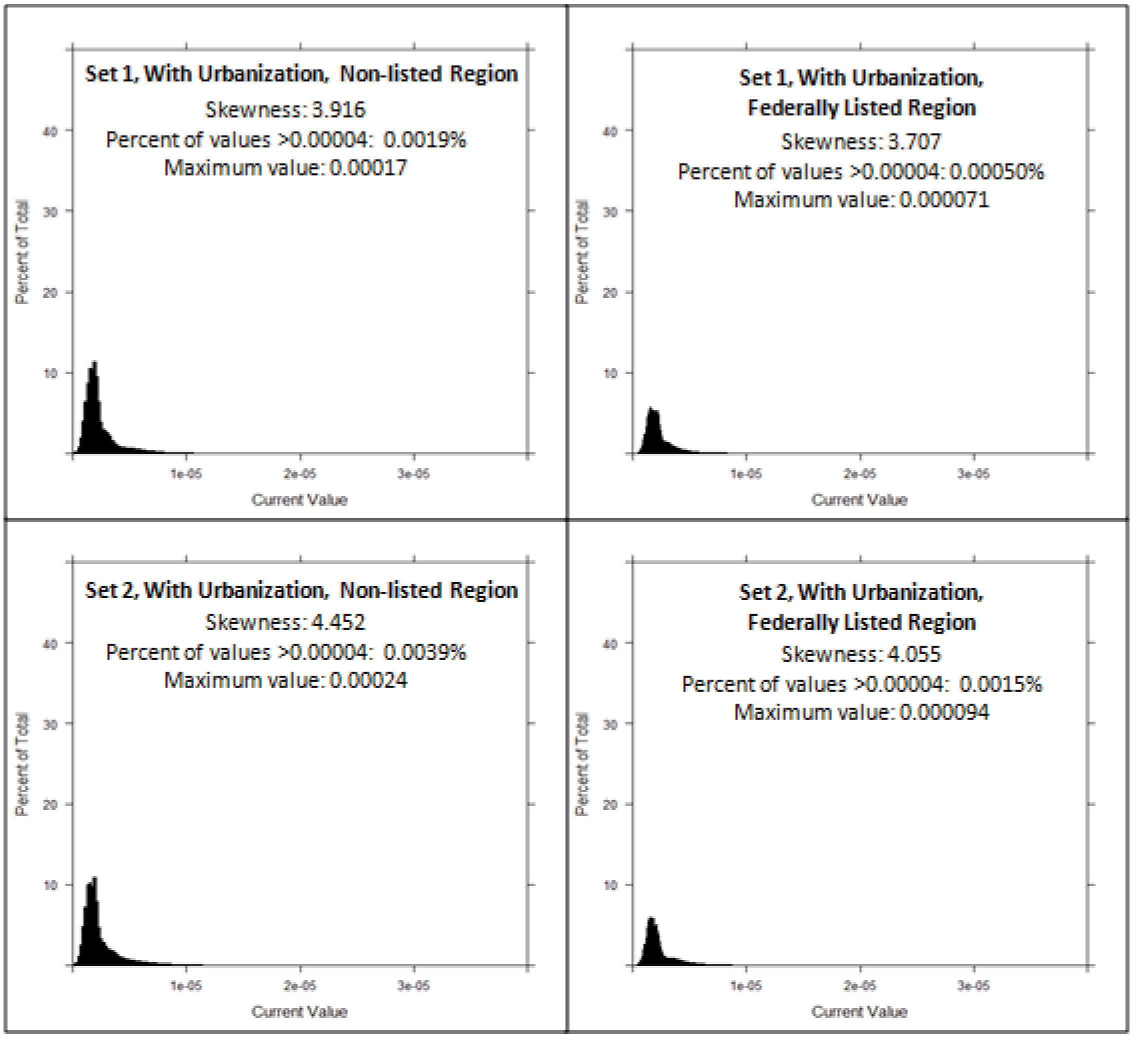


Figure 1.16. Histograms of current values from the omnidirectional current density maps in the federally listed and non-listed portions of the study area for the resistance value sets with urbanization data included.

While this study was primarily designed to assess broad-scale patterns of connectivity across a large portion of the gopher tortoise's range, examining the omnidirectional current maps at finer scales can reveal areas which may have local importance for connectivity. These results do not include the incorporation of vegetation structure, so must be interpreted with caution at the local scale, as they only represent potential connectivity. An example is shown in Figure 1.17, for the Conecuh National Forest in south-central Alabama, a site known to support one of the largest populations of gopher tortoises in the state. Much of the current flow on the western side of the property appears more spread out, while in the central portion of the property current is restricted to smaller areas which may be considered pinch points (Figure 1.17). One area which may be a pinch point (shown in an inset in Figure 1.17) was greatly affected by urbanization; this location is an area of Highly Suitable soils and a highway (Alabama State Route 137).

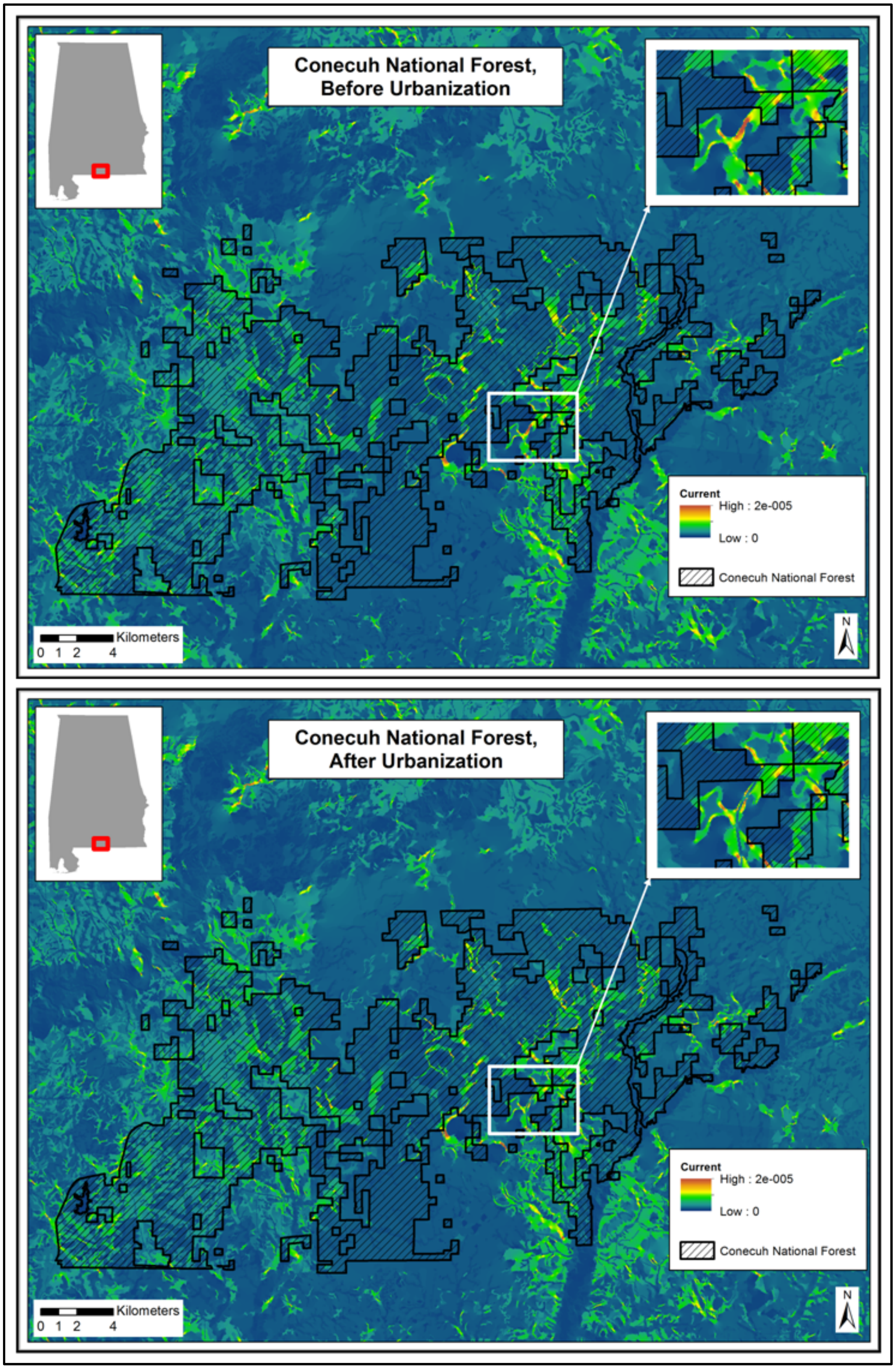


Figure 1.17. Omnidirectional current density maps from resistance set 1 for the Conecuh National Forest and surrounding area in south-central Alabama. The area highlighted with a white frame is a potential pinch point that has been impacted by urbanization.

Discussion

Soil classification

Differences in soil classifications between counties resulted in stark contrasts in tortoise soil suitability across some county boundaries. This was the result of the differences between counties in soil classification in the original SSURGO datasets. It is possible that these discrepancies affected the results. For example, Mobile County in southwestern Alabama has many soils mapped as associations (groupings of multiple soil series), which results in larger, less detailed map units within the county. This in turn leads to large, contiguous patches of soils classified in a single suitability category (e.g., Moderately Suitable). This will affect the average patch size of suitable soils in that region, and possibly alter observed patterns of connectivity.

Unfortunately, the SSURGO soils database was the best soil data available at the time of this study. Broader, state-wide soil datasets (such as STATSGO) do not provide the level of detail needed for classification and mapping in this study. Additionally, too many counties in the study area had some discrepancy or variation across county boundaries to simply exclude those counties from the analysis. Nevertheless, differences in suitability rankings across boundaries tended to be between similar rankings (e.g., soils ranked Marginal on one side of county line and Less Suitable on the other) rather than major differences that would greatly affect results (e.g., Highly Suitable on one side of the county line and Unsuitable on the other), though some small areas did exhibit large differences. The disparities in suitability classifications across county boundaries are not expected to have had a major effect on the results.

Soil fragmentation

The non-listed portion of the gopher tortoise's range contained a greater area in suitable soils (under all soil combinations examined), and had a greater percentage of the landscape in suitable soil. Thus, the non-listed portion of the study area had more suitable soils per unit of land area than the federally listed portion of the range, indicating a potential capacity to support more tortoises per unit land area. However, vegetation conditions, which also play a role in determining suitability of tortoise habitat, were not considered in this study. Additionally, urbanization may impact much of the area in suitable soils on both sides of the tortoise's range and was not considered in this portion of the study. The actual capacity to support tortoises on either side of the range divide is currently unknown, but more suitable soils per unit area (particularly those ranked as Highly Suitable) suggests a greater potential capacity to support tortoises on the non-listed side, given suitability of other habitat factors.

Average size of suitable soil patches was less than 100 ha for all soil combinations on both sides of the range when the 100 m buffers were not included. When buffers were included, a "patch" included any grouping of soil patches that were within 100 m of each other. With the area of the buffers included, average patch sizes for soil with buffer combinations were greater than 200 ha for all combinations on both sides of the range except for the Highly Suitable soils only plus buffer in the federally listed portion of the range. Current guidelines recommend a minimum reserve size of 100 ha for gopher tortoises, if suitability of habitat for tortoises on the site is exceptionally high, to maintain the current estimate for a minimum viable population of 250 tortoises at minimum density of 0.4 tortoises/ha (Guyer et al. 2012, Gopher Tortoise Council 2013). Average patch sizes of less than 100 ha indicate that many patches of suitable soil, without considering connections to other patches, are unlikely to support viable populations of tortoises. With buffers included, average patch size generally increases well past the 100 ha threshold, though the area of the buffer zones themselves was included in these estimates and thus they must be interpreted with caution. Gopher tortoises may be able to forage in buffer zones, provided adequate herbaceous vegetation is available, but are unlikely to use these zones for significant numbers of burrows.

Connectance Index was higher in the federally listed portion of the range than in the non-listed portion of the range for all soil combinations examined. This is likely due to the fact that the federally listed side of the range covers a smaller geographical area than the non-listed side. Thus, a higher proportion of patches within the federally listed portion of the range will be within the minimum connectedness threshold distance than in the non-listed portion of the range, which contains many patches spread over greater distances. In this sense, the federally listed side of the range is better connected in terms of the proportion of patches it contains being within threshold distances of its other patches. However, this metric is affected by the spacing of patches; with more patches spread over a broader area, such as in the non-listed portion of the range, Connectance Index will be lower simply because there are more patches at greater distances from each other.

Both Aggregation Index and Clumpiness Index were higher in the non-listed portion of the range for Highly Suitable soils only and for Highly Suitable soils plus the buffer. Index values for the other soil combinations examined were very similar on both sides of the range. While the values of both of these indices change with the resolution (cell size) of the landscape raster, I do not expect the relative comparisons between the federally listed and non-listed regions to differ significantly within a range of reasonable cell sizes. Additionally, due to the relatively small home range of the gopher tortoise (generally less than 2 ha; Diemer 1992, Eubanks et al. 2003), the 30 m x 30 m cell size used in this study is biologically relevant for this species.

Both Aggregation Index and Clumpiness Index are measures of landscape aggregation, or the tendency of the focal landscape class type to be clumped together into a single patch. Thus, higher values on the non-listed side of the range indicate that the Highly Suitable soils on this side tend to be more clumped together, or aggregated, relative to Highly Suitable soils on the federally listed side. Aggregation of suitable soils is an important concept to consider when assessing tortoise habitat connectivity and population viability in general. Larger expanses of suitable soils located in larger clumps or patches are more likely to support larger contiguous tortoise populations. More dispersion of soils could result in the area in suitable soils possibly being in smaller patches spread further apart. However, only the Highly Suitable soils showed a discernible pattern between the two sides of the range. While Highly Suitable soils are generally expected to support higher densities of tortoises than the other soil categories (USFWS and NRCS 2012), the other categories ranked as “suitable” are also capable of supporting tortoise populations and the actual capacity of an area to support tortoises will depend heavily on other habitat factors (such as vegetation structure). Thus, the effects of greater aggregation of Highly Suitable soils in the non-listed portion of the range depends partly on habitat factors not included in this study.

Connectivity

Effective resistances across regions were higher towards the western periphery of the gopher tortoise's range as predicted, but only at higher (more northern) latitudes. Towards lower (more southern) latitudes, resistance was higher towards the eastern side of the study area. This pattern was found for all runs, including those which included urban land cover, suggesting that this broad-scale pattern is insensitive to the specific resistance values assigned to soils and not affected by urbanization. The pattern observed at more southern latitudes (higher effective resistance in the east) was likely due to major river systems and wetlands near the coast in the Florida panhandle.

Effective resistance may be thought of as the inverse of connectivity; thus, I found that connectivity was lower towards the western range periphery at more northern latitudes within the study area, and lower towards the eastern periphery of the study area at more southern latitudes. Therefore, gopher tortoise habitat connectivity, when considering only suitable soils, hydrology, and urban land cover, tends to be lower towards the federally listed portion of the range (except in more southern latitudes), which is consistent with our expectations. This pattern, if it holds true given actual present day habitat conditions including vegetation structure, has significant consequences for tortoise populations. Connectivity of habitat may affect the viability of populations; it has been linked to population persistence for some species (e.g., Fagan et al. 2002, Anzures-Dadda and Manson 2007). Given the limited dispersal capabilities of gopher tortoises, reduced habitat connectivity could have significant consequences for tortoise populations.

Inclusion of urban land cover altered the pattern of current flow across the study area in both runs in which it was included. Current flow (or density) through a particular node (i.e., cell) in the landscape corresponds to the probability of "movement" through that particular area (McRae et al. 2008). Thus, areas with high current flow (current density) are areas where movements may be concentrated, and indicate potentially important corridors (connectivity would be significantly impacted if these areas were altered) (McRae et al. 2008). Note, however, that because the study area covers a much broader area than individual tortoises could be expected to traverse, "movements" should be interpreted as long-term movements of populations or gene flow over time.

The alteration of current flow across the study area due to urbanization is not surprising, but nonetheless may have important consequences for gopher tortoise habitat connectivity and ultimately fragmentation of habitat and populations. Most of the study area saw small differences in current before and after inclusion of urbanization ($< 1e^{-6}$ units of current). However, it is difficult to determine what change in current would be necessary to have a significant impact on a population for a number of reasons. The amount of current in any given cell will, in part, be determined by the size of the study area; with a larger area or more raster cells in the area, the current from the source(s) (i.e., focal areas) will be dispersed across the greater area. Additionally, the current maps in this study were omnidirectional and created by multiplying the north-south and east-west current values, which results in even smaller current values in the omnidirectional map due to the multiplication of current values less than 1. Nonetheless, it is clear that urbanization has had widespread effects on connectivity.

The areas with the greatest differences in current before and after urbanization generally occurred in the coastal regions of the study area, particularly in the Florida panhandle (Figures 1.11 and 1.12). The Florida panhandle contains relatively large expanses of Highly Suitable soils (Figure 1.4); it also represents an area with significant urban development. In these areas, current is decreased in many areas and increased in others after the inclusion of urbanization data, where current is forced through areas where it was lower before urbanization. If areas of Highly Suitable soils represent areas that historically supported open vegetation (such as open canopy longleaf pine) and thus suitable tortoise habitat, than urbanization may have had a significant impact on what historically could have been a large area of highly suitable tortoise habitat. While management activities are unlikely to significantly reverse urbanization, these areas where connectivity has been most altered from its historical potential may warrant attention, particularly where remnant tortoise populations remain and may be affected by the reduction of connectivity with other populations.

Whether or not urbanization was included, the skewness of the distribution of current values from the cells of the omnidirectional current maps was higher in the non-listed vs. the federally listed portion of the tortoise's range within the study area. This indicates that the non-listed portion of the study area had more cells with higher current values and/or had higher maximum current values (i.e., the distribution had either more weight in the tail or a longer tail towards the upper end of the x-axis). While there are currently no established guidelines for identifying pinch points (Pelletier et al. 2014), higher values for skewness may indicate greater prevalence of pinch points, with greater prevalence of current values near the upper extremes. Thus, the non-listed portion of the study area may have more area in pinch points, or areas where current has a relatively high probability or necessity of passing through. Note, however, that areas of relatively high current can occur on the more highly suited soils where there is a greater concentration of current not out of necessity, but due to the lower resistance of those areas favoring current flow. That is, an area of high current does not necessarily indicate barriers to connectivity in this instance. Likewise, inclusion of urbanization reduced skewness in all instances, which is likely due to current being forced out of areas where it was previously higher due to the higher resistance of urban land cover types forcing current to disperse through other areas. Skewness, or possible pinch points visually identified on a current map, must be considered in combination with effective resistance; an area can appear not to have pinch points because there is no relatively low-resistance path, and current is forced through broad areas of similarly high resistance. Great care must be taken when interpreting current maps and "pinch points" from this and similar studies. There remains a need for a systematic method for identifying and interpreting pinch points, but skewness values may be useful for the relative comparison of distributions of current maps.

Examination of the omnidirectional current maps at finer scales may reveal interesting information about potential connectivity at some sites. Areas that appear as pinch points, such as those near the central portion of Conecuh National Forest in Alabama, may be (or may historically have been) important areas for maintaining or enhancing connectivity across the landscape. These areas could potentially be targets for management if the goal of management at a site is to preserve or enhance connectivity of gopher tortoise habitat across the landscape. However, this study did not include vegetation structure, which is often the target of management actions and would be highly relevant at finer scales. Additional analyses incorporating present day vegetation data and potentially planned management changes to vegetation structure would provide additional information to managers. Nonetheless, areas that are important to connectivity based on soils, hydrology, and urbanization alone may be areas where management for vegetation suitable for gopher tortoises may have the greatest benefit.

Potential implications

The pattern of reduced connectivity towards the western periphery of the tortoise's range (at least at more northern latitudes within the study area) suggests that populations in the federally listed portion of the range may face additional challenges compared to those in the non-listed region. Greater effective resistance of the landscape suggests that there may be reduced gene flow between populations over time when compared to landscapes with lower effective resistance. Future genetic studies on gopher tortoise populations located across broad portions of the tortoise's range could compare the genetic differentiation among populations throughout the study area to assess if modeled patterns of habitat connectivity correlate with genetic differentiation.

In addition to the general patterns of habitat connectivity observed, inclusion of data on urban land cover indicates that urbanization has had widespread impacts on connectivity for gopher tortoises and potentially other species with low dispersal capability that are dependent on deep, sandy, well-drained soils. The impacts of urbanization may go beyond simply reducing the amount of available habitat by reducing connectivity between remaining habitat patches. The patterns of altered current flow observed in Figures 1.8 and 1.9 show a network of areas with reduced current flow surrounding relatively isolated areas or pockets of increased current flow due to current being forced into more limited pathways. This network of barriers may act to reduce gene flow between populations residing in the interstitial areas of higher current flow. Future genetic studies may be able to provide further information on the potential isolating effects of urbanization; however, because gopher tortoises are a very long-lived species, the population genetic consequences of relatively recent urbanization may not yet be detectable. In addition to potential broad-scale genetic consequences, urbanization may have forced tortoises off what historically could have been some of the largest expanses of highly suitable habitat, such as in the Florida panhandle where some of the largest differences in current flow with and without urbanization data were observed.

Conclusions

Patterns of habitat connectivity across a species' range may impact the distribution of populations across the landscape. While many factors have likely contributed to the decline of gopher tortoises across their range, my results indicate that tortoise populations may be limited in the federally listed portion of the range (the western range periphery) regardless of anthropogenic influence due to the underlying distribution of soil types. The federally listed portion of the range had a lower percentage of area in suitable soils than the non-listed portion of the range I examined, and the non-listed portion had a greater pattern of aggregation of the most highly suited soils. The federally listed portion of the range also had higher effective resistance, i.e., lower connectivity than areas closer to the center of the range at more northern latitudes. Lower connectivity in the federally listed portion of the range indicates that gopher tortoise management in that region faces additional challenges that must be considered to ensure tortoise population persistence. Additionally, urbanization has altered connectivity in many areas across the range and has likely had consequences on remaining population distribution and genetic flow.

Soils are only one habitat variable important to gopher tortoises. Other factors, such as canopy cover, understory density, and herbaceous ground cover have a large influence on the suitability of a site for gopher tortoises. Vegetation conditions are difficult to assess accurately over broad landscapes such as our study area; however, inclusion of such information would provide a more accurate assessment of habitat conditions and habitat connectivity. The reduction in current flow caused by inclusion of urban land cover data indicates that urbanization likely has a significant and broad impact on habitat connectivity. Including projected or planned urban land cover in future studies could provide an estimation of how connectivity could be expected to change in the future. For all habitat variables, future studies should assign a variety of resistance values to those variables to further explore the sensitivity of results to assigned resistances.

This study provides evidence for a potential pattern of habitat connectivity across a species' range. Future studies could explore if similar patterns exist for other species, especially for those that rely on a habitat variable that is relatively unaffected by human activities or represents a historical landscape and can be reasonably assessed over broad areas. Such patterns could have consequences for management or conservation decisions, as portions of a species' range, like the gopher tortoise's, may have a reduced capacity to support populations when compared to other portions of the range. This study provides a starting point for future exploration of this pattern in gopher tortoises and other species.

Literature Cited

Anzures-Dadda, A., and R. H. Manson. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69–76.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (Gopherus polyphemus). Pages 95–126 *in* R. B. Bury, editor. North American tortoises: Conservation and ecology (Wildlife Research Report 12). U.S. Fish and Wildlife Service, Washington, D.C., USA.

Bonin, F., B. Devaux, and A. Dupre. 2006. Turtles of the world. P. C. H. Pritchard, editor. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Clostio, R. W. 2010. Use of environmental variables to infer gene flow and population structure in the gopher tortoise (Gopherus polyphemus) and predict the seroprevalence of an emerging infectious disease. Dissertation, University of New Orleans, New Orleans, USA.

Cox, J., D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (Gopherus polyphemus) populations found on lands slated for large-scale development in Florida. Nongame Wildlife Program Technical Report No. 4. Office of Environmental Services, Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Diemer, J. E. 1992. Home range and movements of the tortoise Gopherus polyphemus in northern Florida. Journal of Herpetology 26:158–165.

Enquist, B. J., M. A. Jordan, and J. H. Brown. 1995. Connections between ecology, biogeography, and paleobiology: Relationship between local abundance and geographic distribution in fossil and recent mollusks. Evolutionary Ecology 9:586–604.

Eubanks, J. O., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (Gopherus polyphemus). Herpetologica 59:311–321.

Fagan, W. F., P. J. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction risk in desert fishes. Ecology 83:3250–3256.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, New York, New York, USA.

Geber, M. A. 2011. Ecological and evolutionary limits to species geographic ranges. The American Naturalist 178:1–5.

Gopher Tortoise Council. 2013. Gopher tortoise minimum viable population and minimum reserve size working group report.

Guyer, C., S. Glenos, S.M. Hermann, and J. Stober. 2011. The status of gopher tortoises (Gopherus polyphemus) in Alabama with special reference to three important public properties. Report by the Alabama Division of Wildlife and Freshwater Fisheries.

Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (Gopherus polyphemus). Herpetological Monographs 26:122–134.

He, H. S., B. E. DeZonia, and D. J. Mladenoff. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. Landscape Ecology 15:591–601.

Hoctor, T., and S. Beyeler. 2010. Regional gopher tortoise potential habitat model report. Final report to U.S. Fish and Wildlife Service, Jacksonville Ecological Services Office, Jacksonville, FL.

Holt, R. D., and T. H. Keitt. 2005. Species' borders: A unifying theme in ecology. Oikos 108:3–6.

Homer, C.G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81(5):345-354

Komsta, L., and F. Novomestky. 2015. moments: Moments, cumulants, skewness, kurtosis and related tests. R package version 0.14.

Kowal, V. A., A. Schmolke, R. Kanagaraj, and D. Bruggeman. 2014. Resource selection probability functions for gopher tortoise: Providing a management tool applicable across the species' range. Environmental management 53:594–605.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v. 4: Spatial pattern analysis program for categorical and continuous maps.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

McDearman, W. 2005. Gopher tortoise (Gopherus polyphemus) soil classification in the federally listed range. File Report. U.S. Fish and Wildlife Service, Ecological Services, Jackson, MS.

Pelletier, D., M. Clark, M. G. Anderson, B. Rayfield, M. A. Wulder, and J. A. Cardille. 2014. Applying circuit theory for corridor expansion and management at regional scales: Tiling, pinch points, and omnidirectional connectivity. PLoS ONE 9:1–11.

Perez-Heydrich, C., K. Jackson, L. D. Wendland, and M. B. Brown. 2012. Gopher tortoise hatchling survival: Field study and meta-analysis. Herpetologica 68:334–344.

Price, T. D., and M. Kirkpatrick. 2009. Evolutionarily stable range limits set by interspecific competition. Proceedings of the Royal Society B 276:1429–1434.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Smith, L. L., T. D. Tuberville, and R. A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise 2003: Final results and recommendations. Chelonian Conservation and Biology 5:326–330.

United States Fish and Wildlife Service [USFWS]. 2011. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List the Gopher Tortoise as Threatened in the Eastern Portion of Its Range. Federal Register 76(144):45130-45162.

United States Fish and Wildlife Service [USFWS] and Natural Resources Conservation Service [NRCS]. 2012. Gopher tortoise (Gopherus polyphemus) soil classifications for the federally listed range using the National Soil Information System database. Report, version 1.

United States Fish and Wildlife Service [USFWS], and Southeast Regional Partnership for Planning and Sustainability [SERPPAS]. 2013. 4th annual report, candidate conservation agreement for the gopher tortoise.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1):3-36

Chapter 2:

Gopher Tortoise Habitat Connectivity Under Various Management Alternatives at Selected Sites in Alabama

Introduction

Making informed conservation decisions often requires the ability to make predictions about how management alternatives may affect the system in question and how they may satisfy management objectives (Runge et al. 2013). Without some idea of how an alternative may impact the system in question (e.g., a wildlife population, its habitat, or both), it is difficult to assess how that alternative will affect management objectives (e.g., increasing wildlife population sizes or maintaining habitat structure). A reasonable, defensible decision therefore requires the ability to forecast plausible outcomes for each management alternative (Starfield 1997).

Decisions regarding the management of wildlife are often concerned with population abundance, habitat structure, availability of animals for recreational use, and economic and cultural objectives (Runge et al. 2013). Multiple, well-established methods are available to predict how available management alternatives affect these types of objectives, such as population viability analyses (Boyce 1992), landscape habitat suitability indices, and Bayesian belief networks (Beck and Suring 2009). However, some potential consequences of management actions are rarely predicted when evaluating management alternatives, but may nonetheless be important to achieving the desired outcome, depending on the objectives.

Connectivity of suitable habitat is an important consideration for many species of management concern (Fischer and Lindenmayer 2007), given that connectivity can affect population persistence (e.g., Fagan et al. 2002, Anzures-Dadda and Manson 2007) which is often an objective involved in wildlife management decision making. Although a number of wildlife-habitat models have been developed that are valuable for predicting consequences of management alternatives (Morrison et al. 2006), it is difficult to compare alternatives directly in terms of their effects on habitat connectivity without a means to directly quantify connectivity. There are numerous metrics and indices that attempt to quantify habitat connectivity, patch isolation, and landscape pattern, such as probabilities of adjacency (Turner et al. 2001), proximity index (Gustafson and Parker 1992), and connectance index (McGarigal et al. 2012). However, many of these metrics view the landscape in a binary habitat/non-habitat fashion, and do not take into account the composition and configuration of the matrix (non-habitat). For some species, the composition and configuration of the matrix has important consequences for the effective isolation of habitat patches, as different land cover types can have different resistance to animal movement (Ricketts 2001). Ideally, any measure of habitat connectivity used to compare management alternatives should take into account not only the amount of suitable habitat available, but the relative resistance to movement of the landscape as well.

Habitat models based on the principles of circuit theory, as described by McRae et al. (2008), can be used to quantify habitat connectivity while incorporating the resistance of various land cover types to animal movement. This type of habitat and connectivity modeling is based on the principles of electrical circuit theory, which represents the flow of electric current through a series of nodes and resistors (McRae et al. 2008). In ecological applications, a landscape can be viewed in terms of resistance to the movement of animals, which is analogous to the flow of electricity through resistors in a circuit (McRae et al. 2008). A landscape can be mapped in a raster format with each grid cell containing a resistance value that represents how difficult it is for an animal to move through that particular cell's habitat type (McRae et al. 2008). Focal patches are defined and set as "sources" of current; the flow of current across the raster grid can then be quantified and mapped, with grid cells with higher current indicating areas where animal movements are likely to be concentrated (McRae et al. 2008). Additionally, the effective resistance across the landscape is calculated, which takes into account all possible pathways between focal areas and the resistances of the grid cells between them (McRae et al. 2008). In a decision-making context, effective resistances of the area of interest can be compared under competing management alternatives. Additionally, current flow can be compared under various alternatives to see how potential pathways may be altered by management.

The importance of considering habitat connectivity depends on the level of habitat specialization and dispersal capabilities of the species of interest, relative to the spatial scale and landscape conditions in the area under consideration. Evaluating habitat connectivity may be especially important for species such as the gopher tortoise (*Gopherus polyphemus*). Gopher tortoises are medium-sized tortoises endemic to the southeastern United States (Bonin et al. 2006). The species was listed as Threatened under the Endangered Species Act in the western portion of their range (west of the Mobile and Tombigbee rivers in Alabama) in 1987 (USFWS 2011). The species was also petitioned for listing in 2006, but was found to be warranted but precluded (USFWS 2011). Gopher tortoise populations are believed to be in decline throughout their range (USFWS and SERPPAS 2013), and are a species of conservation concern in all states in which they occur. Population declines are likely due to a variety of factors, including human harvest of the animals for food and pets, invasive species, disease, habitat loss, and habitat fragmentation (Smith et al. 2006). Conservation of gopher tortoises will require a holistic approach to address multiple threats. However, management decisions often must be made regarding the creation, restoration, and maintenance of suitable habitat for the species. Maintaining connectivity of suitable habitat will be important to ensuring future population persistence.

Like other members of the genus *Gopherus*, the gopher tortoise is a burrowing species, creating burrows that may be up to 10 meters in length (Bonin et al. 2006). These burrows provide shelter, habitat, and protection from fire for many other species including eastern indigo snakes (*Drymarchon couperi*), gopher frogs (*Rana capito*), and northern bobwhite quail (*Colinus virginianus*) (Cox et al. 1987). The need to create burrows generally limits gopher tortoise activity to deep, sandy, well-drained soils that are suitable for digging (Auffenberg and Franz 1982). Tortoises also require an open forest canopy to allow adequate sunlight for the growth of preferred herbaceous forage and for basking, a thermoregulatory behavior (Auffenberg and Franz 1982). Gopher tortoises are consistently associated with upland, open-canopy habitats and sandy soils (Boglioli et al. 2000, Jones and Dorr 2004, Baskaran et al. 2006, Kowal et al. 2014). Gopher tortoises have also been found to avoid areas with dense vegetation and dense canopy cover (McCoy et al. 2013). Such information on habitat associations can be used to assign relative resistance values to various land cover and habitat types in a circuit-theory based analysis of habitat connectivity. Indeed, a circuit theory-based approach has already been used to correlate landscape attributes, such as soil type, canopy cover, and land cover type to genetic distance between tortoise populations (Clostio 2010). The use of a circuit-theory based approach to quantify habitat connectivity has great potential to be applied in a decision-making context.

In this study, I evaluated the connectivity of gopher tortoise habitat on public properties in Alabama under alternative management scenarios. The objectives of this study were: 1. To demonstrate the feasibility of using a circuit theory-based analysis of habitat connectivity to compare the effects of habitat management alternatives on the future connectivity of habitat, and 2. to compare the effects of a set of management alternatives on habitat connectivity for gopher tortoises at two public properties in Alabama. Results from this study can be used to inform the conservation and management of tortoises in Alabama. Additionally, the method has potential to be applied to other properties and other species for which habitat connectivity is a concern.

Methods

Study Areas

Two sites were chosen for habitat connectivity analyses: the landscape composed of the Barbour Wildlife Management Area and Wehle Forever Wild Tract ("Barbour/Wehle") in Barbour and Bullock counties in southeastern Alabama, and the Perdido River Wildlife Management Area ("Perdido WMA") in Baldwin county in southwestern Alabama (Figure 2.1). Both properties are state-owned and potentially important sites for gopher tortoise conservation in Alabama. Both sites were also included in a recent analysis done in a structured decision making framework to evaluate the consequences and relative value of various forest management alternatives to wildlife and management objectives (Silvano 2013). While this analysis was a complete decision analysis that provided valuable, needed information to managers, it did not address landscape configuration in comparing alternatives. Future management concerns regarding the connectivity of habitat for target species could be addressed through an additional analysis of habitat connectivity under the available alternatives.

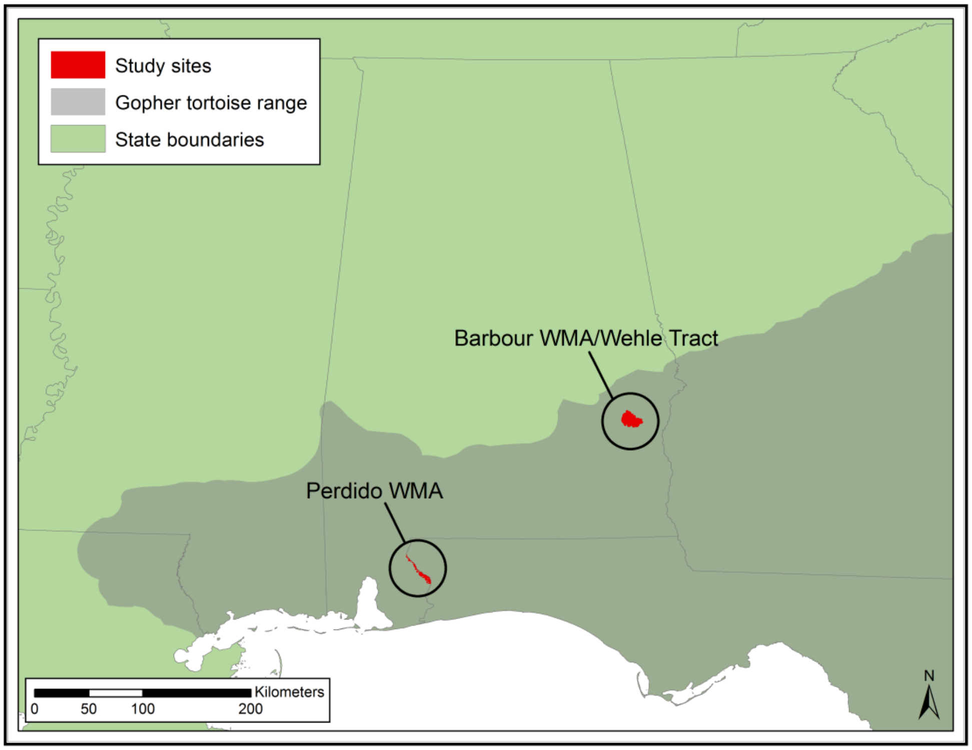


Figure 2.1. Barbour Wildlife Management Area/Wehle Forever Wild Tract and Perdido River Wildlife Management area in Alabama.

The Barbour Wildlife Management Area and Wehle Forever Wild Tract (Figure 2.2) are two adjacent properties located in the upper coastal plain region of Alabama, close to the northern edge of the gopher tortoise's range within the state. The Barbour WMA covers approximately 11,659 ha and the Wehle Forever Wild Tract covers approximately 630 ha. Barbour WMA contains a diverse array of habitat types, including longleaf (*Pinus palustris*) and loblolly (*Pinus taeda*) pine stands of various ages and densities, mixed hardwood stands, food plots, and clearings. The Wehle Forever Wild Tract consists largely of open canopy longleaf pine.

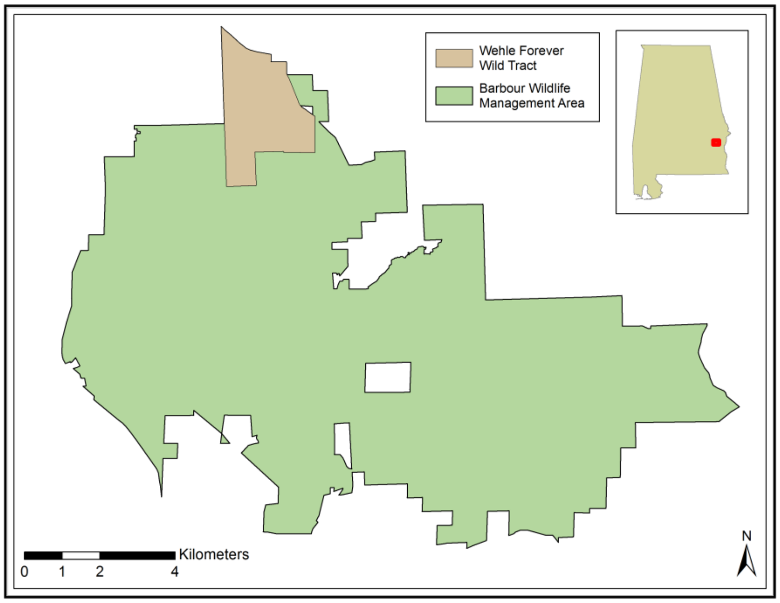


Figure 2.2. Barbour Wildlife Management Area and Wehle Forever Wild Tract in Alabama.

Gopher tortoises were reintroduced to the Barbour/Wehle area through a reintroduction effort on the Wehle Tract in which 55 tortoises from southeast Alabama and West Georgia were released from 2006-2009 (E. Soehren, Alabama Department of Conservation and Natural Resources State Lands Division, personal communication). As of the summer of 2013, 13 of the 55 tortoises originally released remained on the Wehle Tract. Other surviving individuals may have moved onto the adjacent Barbour WMA, where a few tortoises are currently known to occur (E. Soehren, personal communication). While the present day gopher tortoise population in the Barbour/Wehle area is small relative to other properties in Alabama on which tortoises occur, it provides an opportunity to conserve tortoises near the northern extent of their range in the state and is a viable option for future tortoise releases.

Perdido WMA is a 7,327 ha property located in the southern coastal plain region in Alabama, adjacent to the border with Florida (Figure 2.3). The property runs along the Perdido River and includes dense timber pine stands, recent clearcuts, intermittent bogs, and some areas of longleaf pine restoration. Much of the property contains deep, sandy soils that are suitable for gopher tortoises. The site supports gopher tortoises, mostly in the central to southern portions of the property. Much of the property was, until recently, dominated by dense timber pine stands unsuitable for gopher tortoises. As a result, many of the tortoises found on Perdido WMA are clustered in the remaining open areas, including utility line right-of-ways. The property is currently undergoing significant changes in habitat structure, including clearcut logging of much of the area that was in dense pine stands.

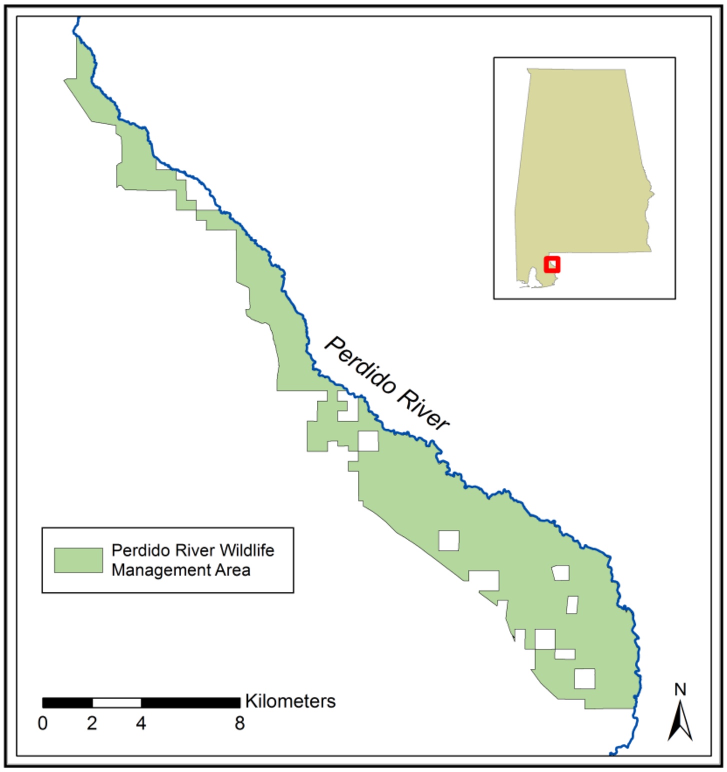


Figure 2.3. Perdido River Wildlife Management area in Alabama.

Soil classification

Because gopher tortoises require deep, sandy, well-drained soils for creation of their burrows, soil type is an important habitat attribute that should be considered in any habitat analysis for this species. I categorized soils based on their suitability for gopher tortoises for use in the connectivity analysis. Soil data were obtained from the United States Department of Agriculture (USDA) Natural Resource Conservation Service (NRCS) Soil Survey Geographic (SSURGO) soils database for all counties within the study area. I classified soil suitability for tortoises based on USFWS and NRCS (2012), which developed a model for classifying soils in the federally listed portion of the tortoise's range based on previous tortoise soil classifications and input from biologists and soil scientists (USFWS and NRCS 2012). The classification scheme presented in this report is based on soil textural and physical properties and is the most recent gopher tortoise soil suitability classification scheme currently available (USFWS and NRCS 2012).

I used the soil suitability criteria presented in Table 1 of the USFWS and NRCS (2012) report (also presented here in Table 2.1) to classify soils into one of five categories, as defined by the report: Highly Suitable, Moderately Suitable, Less Suitable, Marginal, and Unsuitable. Highly Suitable soils represent deep, sandy, well-drained soils that are preferred by tortoises and support the highest densities of tortoise populations. Moderately Suitable soils are somewhat preferred by tortoises and have few restrictive features, and generally support average to above average population densities. Less Suitable soils contain some features that may limit the establishment or maintenance of burrows on the site, and burrow densities may be below average. Marginal soils contain limiting or restrictive features such that population density will be limited on the site; tortoises are generally expected to choose marginal soils only when other habitat factors (such as extremely dense vegetation) prohibit the use of preferred soil types. Unsuitable soils have properties that prevent the establishment and/or maintenance of tortoise burrows, such as a high water table, frequent flooding, or a high percentage of gravel fragments.

Table 2.1. Gopher tortoise soil suitability ranking criteria. Adapted from USFWS and NRCS (2012).

Suitability Ranking:	Highly Suitable	Moderately Suitable	Less Suitable	Marginal	Unsuitable
Flooding	None	None to Rare	None to Rare	None to Occasional	All Others
Ponding	None	None	None	None to Rare	All Others
Medium and coarse gravel fragments	< 15%	< 15%	< 15%	≥ 15%	> 35%
Depth to seasonal high water table	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Depth to restrictive layer	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Percent sand	≥ 70%	≥ 50%	≥ 30%	≥ 15%	< 15%
Percent clay	≤ 15%	≤ 18%	≤ 35%	≤ 60%	> 60%
Slope	≤ 15%	≤ 15%	≤ 15%	> 15%	> 35%

I merged the county-level SSURGO spatial data into larger datasets for the study areas for classification using ArcMap v. 10.3 (Environmental Systems Research Institute, Redlands, CA). Soil properties were accessed through the USDA NRCS Soil Data Viewer v. 6.2 tool for ArcMap. Soil properties that were not accessible through the Soil Data Viewer were obtained through the SSURGO soil property tables associated with each dataset. Soils were selected from the larger dataset based on the criteria presented in Table 2.1 and assigned to one of the five suitability categories.

Management alternatives

In addition to soils, vegetation structure is an important component of gopher tortoise habitat. Alteration of vegetation is likely the most common management strategy that affects this species. This study evaluated the effects on connectivity of 11 habitat management alternatives identified by Silvano (2013) (Table 2.2). These alternatives were identified with land managers and foresters from the Alabama Department of Conservation and Natural Resources (ADCNR) during four two-day workshops (Silvano 2013). A common goal identified was the conversion of even-aged forest stands to an uneven-aged structure to promote a greater diversity of wildlife species; thus, under each alternative, all forested management units were converted to uneven-aged forest (Silvano 2013). Additionally, each alternative included the presence of a Streamside Management Zone (SMZ) at least 35 ft from stream banks with >50% tree cover (Silvano 2013).

Table 2.2. Management alternatives compared in the connectivity analysis. Adapted from Silvano (2013).

Alternative	Description (text from Silvano 2013)
1	All forest types managed for uneven-age distribution. Mixed pine hardwood succeeds to upland hardwood. Openings retained in either agricultural crops or native warm-season grasses.
2	Same as alternative 1, but openings are reforested to adjacent forest type.
3	Hardwood and forested wetlands managed for uneven-age distribution. Mixed pine-hardwood stands are thinned and managed to uneven-aged hardwood. Pine forests on north-facing slopes are converted to uneven-aged hardwoods. Openings retained in either agricultural crops or native warm-season grasses.
4	Same as alternative 3, but openings are reforested to adjacent forest type.
5	All forest types managed for uneven-age distribution. Pine and upland hardwoods in floodplains are managed for flood plain forest types. Openings retained in either agricultural crops or native warm-season grasses.
6	Same as alternative 5, but openings are reforested to adjacent forest type.
7	All forest types managed for uneven-age distribution. Pine forests on north-facing slopes are converted to uneven-aged hardwoods. Pine and upland hardwoods in floodplains are managed for flood plain forest types. Openings retained in either agricultural crops or native warm season grasses.
8	Same as alternative 7, but openings are reforested to adjacent forest type.
9	All forest types except existing floodplain forests are converted or managed for uneven-aged pine. Openings retained in either agricultural crops or native warm-season grasses.
10	Same as alternative 9, but openings are reforested to adjacent forest type.
11	Prescribed fire is used to manage forest type and structure. Wildlife openings are allowed to succeed to surrounding forest type.

Stand conditions

Silvano (2013) developed a state-space model to project stand conditions at selected public properties in Alabama from a circa 2011 baseline 100 years into the future. This model included transitions representing both natural and management-induced processes (Silvano 2013). The model included 25 possible states for each stand or management unit, and projections resulted in each stand being assigned a probability that it was in each of the 25 states at each time step (Silvano 2013). I evaluated connectivity for the initial state, 25, 50, and 100 years into the future using the most probable state for each stand at each time step. The Barbour WMA/Wehle Tract landscape contained 1,835 stands and management units, and the Perdido WMA contained 703 stands and management units. Because of the probabilistic nature of the model, there is some uncertainty in projected stand conditions, which increases with time. However, the habitat state with the most relevance to tortoises (uneven-aged pine) overall had a high (≥ 75%) probability of being achieved in target stands in 100 years (Silvano 2013). Inholdings (areas within the study sites not owned by the state) were not included in the stand projections and were thus excluded from the connectivity analysis. While tortoises could potentially pass through these areas, they are largely unsuitable habitat and are unlikely to play an important role in connectivity.

Connectivity

Habitat connectivity analyses were based on the soil classification described above and the 25, 50, and 100 years projected stand conditions under each of the 11 management alternatives. I used Circuitscape (Circuitscape version 4.0.5, http://www.circuitscape.org) to conduct the circuit-theory based analysis of connectivity. All data were converted to raster format with a 10 m x 10 m cell size for analysis using ArcMap for use with Circuitscape. I used the Circuitscape for ArcGIS toolbox (Circuitscape version 4.0.5, http://www.circuitscape.org) in a Python code loop using the ArcPy site package (Environmental Systems Research Institute, Redlands, CA) to iterate through alternatives and time points.

A circuit theory based analysis of connectivity requires that each habitat type is assigned a resistance value representing how difficult it is for an animal to move through or occupy that habitat (McRae et al. 2008). In this study, resistance values for the initial resistance rasters were assigned based on the soil rankings (using the classification system described above) and stand state for each time step and alternative examined (Tables 2.3 and 2.4). Three different sets of resistance values were used to explore the effects of alternative resistance parameterization on the results. Resistance value sets 1 and 2 were based on current knowledge about tortoise habitat preferences and expert input. Set 1 was based on my own understanding of the relative resistance of various habitat types, while set 2 was created with expert input. Set 3 represents a minimum information scenario, where many habitat types are assigned the same resistance. For example, in set 3, all pine stands and openings within pine stands were assigned the same value, regardless of stand age or structure. All soil types except those unsuitable for tortoises were also assigned the same resistance value. This represents a scenario where there is minimal information available about the habitat, or, alternatively, little is known about the true resistance of various land cover types. Resistance values from the soil dataset were added to resistance values from the stand dataset to create the final resistance raster for use with Circuitscape.

Table 2.3. Resistance values assigned to each stand state/habitat type for use in the Circuitscape analysis. Values are on a scale of 1-20, with 1 being the lowest resistance and 20 being the highest.

	Resistance Values		
Stand State	Set 1	Set 2	Set 3
Open	1	1	1
Uneven-aged Pine	2	1	1
Ag	3	1	1
Trees >12dbh pine	3	5	1
Two age pine	3	5	1
Disturbed (to Pine)	5	5	1
Poles/Small trees pine	5	10	1
Seedling/Sapling pine	5	5	1
Ag (Hardwood)	7	8	5
Disturbed (to Hardwood)	7	10	5
Hardwood savannah	7	15	5
Mixed Pine/Hardwood	7	10	5
Open (Hardwood)	7	8	5
Hardwood	8	20	5
Poles/Small trees hardwood	8	20	5
Seedling/Sapling hardwood	8	15	5
Trees >12dbh hardwood	8	20	5
Two age hardwood	8	20	5
Uneven-aged Hardwood	8	20	5
Bottomland/Riparian	9	20	10
Developed	9	5	3
Water	20	20	10

Table 2.4. Resistance values assigned to each soil suitability category for use in the Circuitscape analysis.

	Resistance Value	
Soil Ranking	Sets 1 & 2	Set 3
Highly Suitable	1	1
Moderately Suitable	2	1
Less Suitable	3	1
Marginal	5	1
Unsuitable	7	5

Connectivity analysis using Circuitscape requires defined focal patches which serve as the "sources" and destinations of current (McRae et al. 2008). I defined focal patches as relatively large, contiguous patches of soils suitable for gopher tortoises (i.e., soils that received a ranking of Less Suitable or higher based on the soil classification system described above). Two focal patches were chosen for Perdido WMA (Figure 2.3). These represent the largest contiguous patches of Highly Suitable soil in the central and southern portions of the property, with the southern focal patch being approximately 323 ha in size and the northern focal patch approximately 223 ha.

Eight focal soil patches were chosen for Barbour/Wehle (Figure 2.4). Because Barbour/Wehle does not contain soils ranked as Highly Suitable, focal patches were chosen from Moderately Suitable and Less Suitable soils. Focal patches ranged in size from approximately 18.4-213 ha, with the smallest of these (18.4 ha) being a patch of Moderately Suitable soils. Six focal patches consisted of the larger contiguous patches of Less Suitable soils on the property. One focal patch included both Moderately and Less Suitable soils in one contiguous patch. Two of the focal patches in the northern end of the property included the release sites for the gopher tortoise reintroduction on the Wehle Tract. The two focal patches to the south of the Wehle Tract area represent potential "stepping stone" pathways if the tortoise population were to spread out to the larger Barbour/Wehle landscape. The remaining focal patches were spread across the landscape in order to capture a large portion of the landscape in the connectivity analysis.

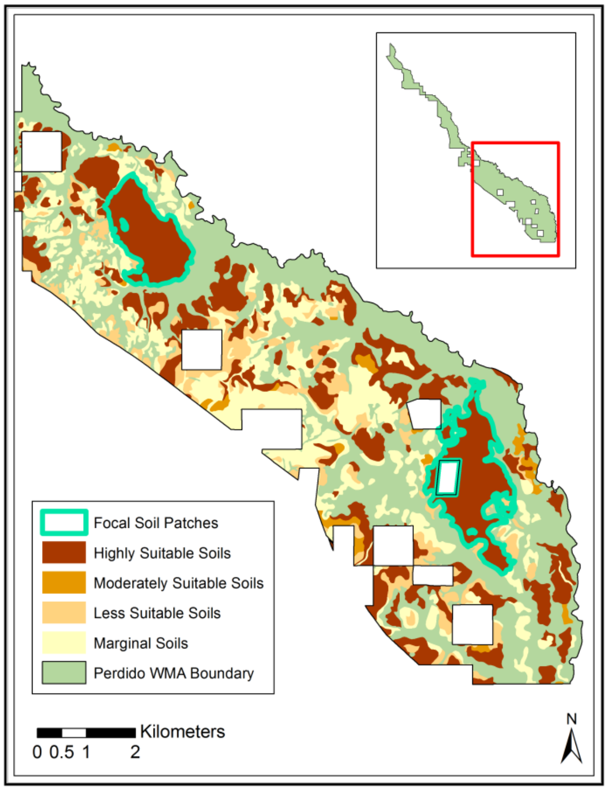


Figure 2.3. Distribution of soil suitability classes and the location of focal soil patches in the southern portion of Perdido Wildlife Management Area.

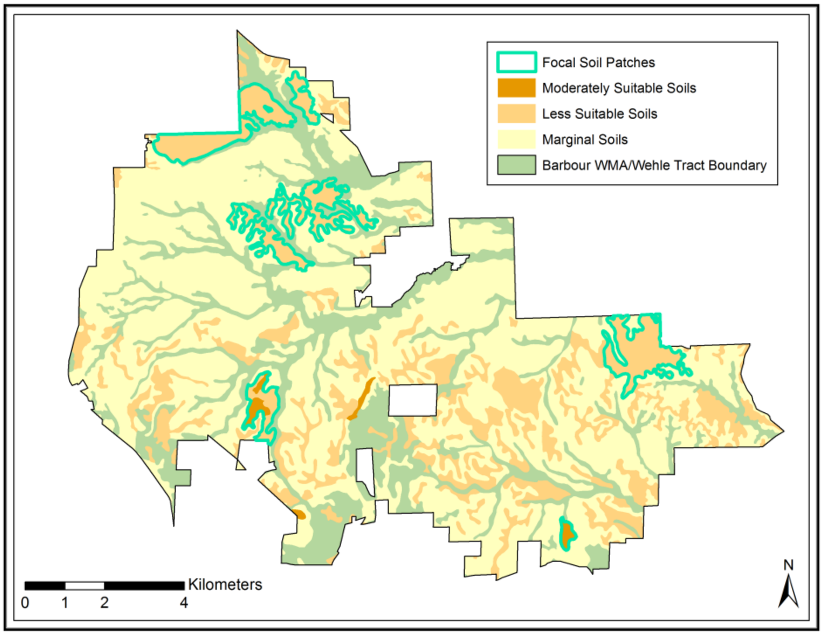


Figure 2.4. Distribution of soil suitability classes and the location of focal soil patches in Barbour Wildlife Management Area and the Wehle Tract.

To summarize results from the connectivity analysis, I examined effective resistance and current flow. Effective resistance values summarize connectivity across the landscape, and can be compared between management alternatives. Effective resistance is based on the composition of the landscape (i.e., the individual resistance assigned to each habitat type) and all possible pathways between each pair of focal patches (McRae et al. 2008). It is the resistance of a single resistor that would conduct the same amount of current as the circuit (i.e., landscape) itself (McRae et al. 2008). Additionally, maps of current flow across the landscape can be used to examine potential likely pathways across the landscape and how those may vary under different management alternatives, i.e., locations where management may be facilitating or restricting connections between focal areas. Cumulative (summed between all focal pairs) current maps were visually examined for areas of high or low current flow. Effective resistance values were averaged between all focal pairs at Barbour WMA, and the means and distributions were compared among management alternatives. Because Perdido WMA had only one pair of focal areas, only one effective resistance value was generated for each management alternative and compared among alternatives.

While current maps can be visually examined to identify areas with relatively high or low current flow, it is difficult to quantify the pattern of the flow of current across the landscape. For example, visual examination of a current map can reveal "pinch points", or areas where animals have a high probability or necessity of passing if moving through the landscape (McRae et al. 2008). However, there are currently no guidelines for what minimum current value threshold constitutes a "pinch point" or how to systematically identify such areas (Pelletier et al. 2014). Still, it may be possible to extract more information by comparing the histograms of current values between maps (Pelletier et al. 2014), as the distribution of the frequency of current values may indicate the degree to which current is restricted to portions of the landscape. I generated histograms of current values (i.e., the values of each cell in the cumulative current raster map) for each resistance value parameterization set, alternative, and site using R v. 3.2 (R Core Team 2015). Skewness and the estimator of Pearson's measure of kurtosis were calculated using the moments package for R (Komsta and Novemstky 2015). A positively skewed distribution indicates a distribution of current values that is skewed to the right, where most values are on the lower end of the spectrum with less frequent higher values. A negatively skewed distribution would indicate a left-skewed distribution of current values, where most values are on the upper end of the spectrum, with less frequent lower values. Higher (more positive) values for kurtosis indicate a greater frequency of values in the tails of a distribution (DeCarlo 1997), which in the case of a distribution of current values, may indicate shift of current to higher values with a corresponding increase in the frequency of lower values, as the flow of current is forced out of some areas and into others, e.g., when a pinch point is created.

Results

Resistance

Average effective resistance (averaged among all focal pairs) after 100 years was lowest for management alternatives 9 and 10 under all three sets of parameterization resistance values for the Barbour/Wehle landscape (Figures 2.5, 2.6, and 2.7). Under alternatives 9 and 10, most of the landscape (except for existing floodplain forest/SMZs) is converted to uneven-aged upland pine, with openings retained under alternative 9 and allowed to revert to forest under alternative 10. As tortoises are expected to prefer mature, uneven-aged pine over many other available land cover types, this result is consistent with expectation. The lower effective resistance under these alternatives indicates greater connectivity between the focal patches. Resistance sets 2 and 3 showed a somewhat greater difference in average effective resistance between alternatives 9 and 10 and the other alternatives than did resistance set 1 (Figures 2.5, 2.6, and 2.7). Resistance set 3 had overall lower effective resistance values than sets 1 and 2 due to the lower resistances assigned to many land cover types, but the pattern of relative effective resistances among alternatives was very similar among all sets (Figure 2.7). Among all alternatives and resistance sets, average effective resistance was similar for all three time points examined (25, 50, and 100 years into future), though increased slightly with time.

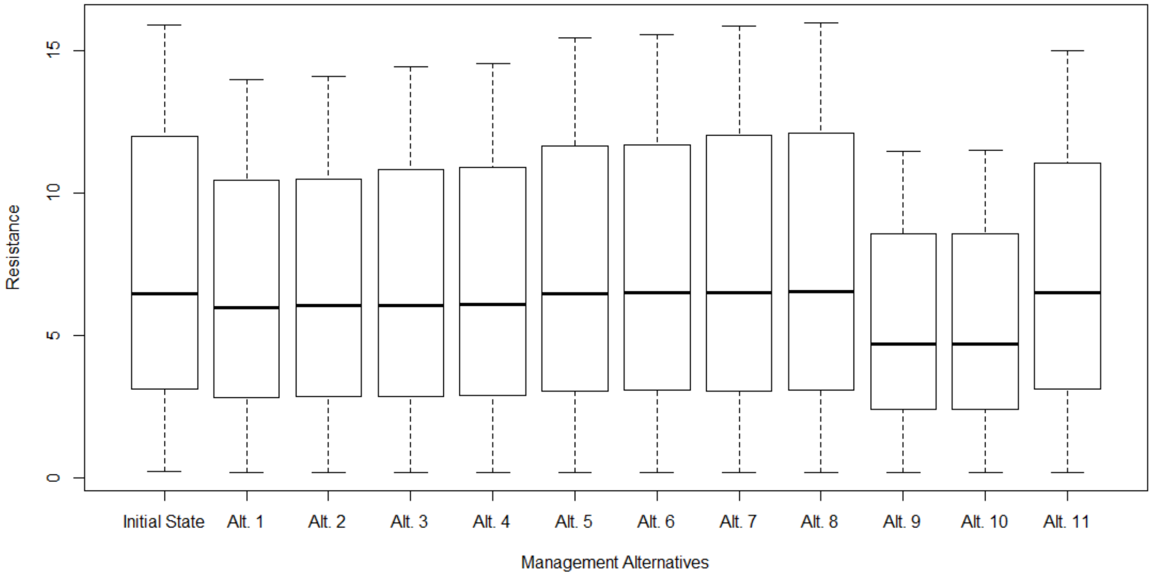


Figure 2.5. Means and distributions for effective resistance between 8 focal patches at Barbour/Wehle under different management alternatives using resistance value parameterization set 1.

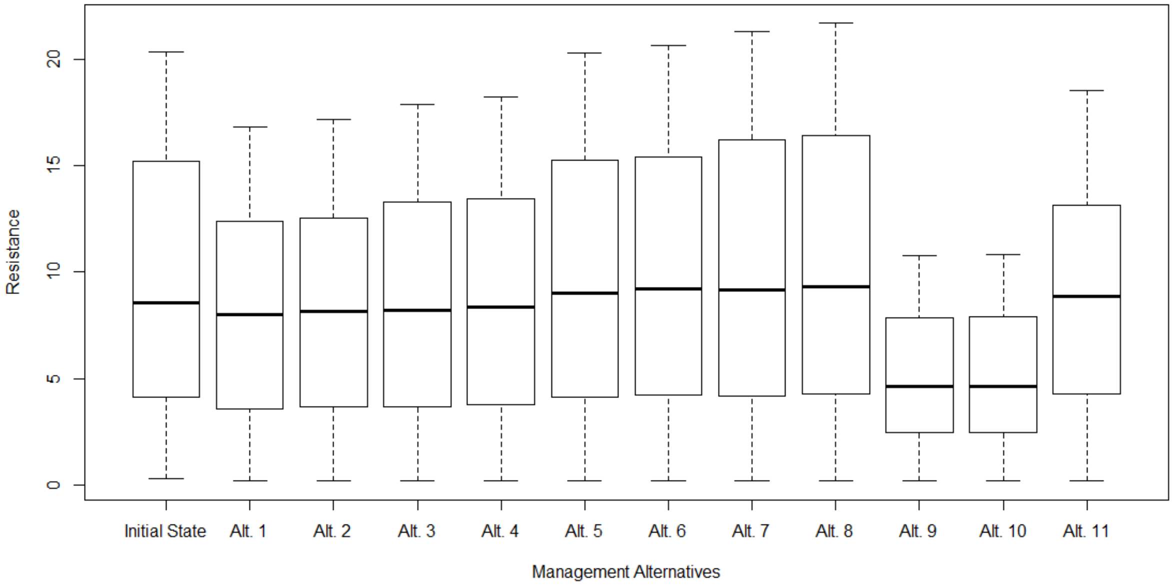


Figure 2.6. Means and distributions for effective resistance between 8 focal patches at Barbour/Wehle under different management alternatives using resistance value parameterization set 2.

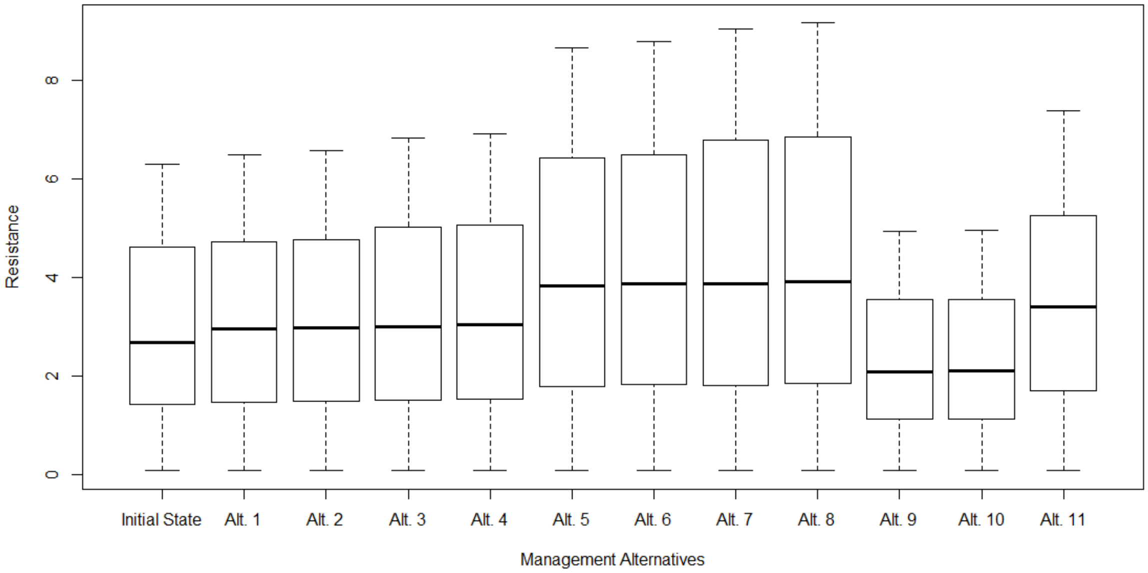


Figure 2.7. Means and distributions for effective resistance between 8 focal patches at Barbour/Wehle under different management alternatives using resistance value parameterization set 3.

Because there was only one pair of focal nodes for Perdido WMA, only one value for effective resistance was generated for each alternative and time step. Similar to the results for Barbour/Wehle, effective resistance between the two focal patches at Perdido WMA after 100 years was lowest under alternatives 9 and 10, where much of the landscape is converted to uneven-aged pine, under all three resistance sets (Figures 2.8, 2.9, and 2.10). Under all resistance sets, after 100 years, alternatives 1 through 8 had very similar effective resistance; this is likely due to 100 years being an insufficient amount of time for the landscape to have a high probability of having achieved its target state (Figures 2.8, 2.9, and 2.10). Results after 100 years for the initial stand conditions at Perdido WMA differed for resistance set 3 compared to sets 1 and 2. Under sets 1 and 2, the initial state had higher effective resistance than conditions under alternatives 1-10 (Figures 2.8 and 2.9). Under set 3, however, effective resistance of the initial state was lower than it was under any of the alternatives except 9 and 10 (Figure 2.10), likely due to the high prevalence of dense timber pine stands in the initial conditions that were ranked equally with all other pine types under this minimum information resistance set. Under resistance sets 1 and 2, effective resistance decreased through time under all alternatives except 11, where it increased from year 25 to year 50, then decreased from year 50 to year 100. Under resistance set 3, effective resistance remained similar among years for all alternatives except alternative 11, where it increased from year 25 to year 50, and remained similar between year 50 and year 100.

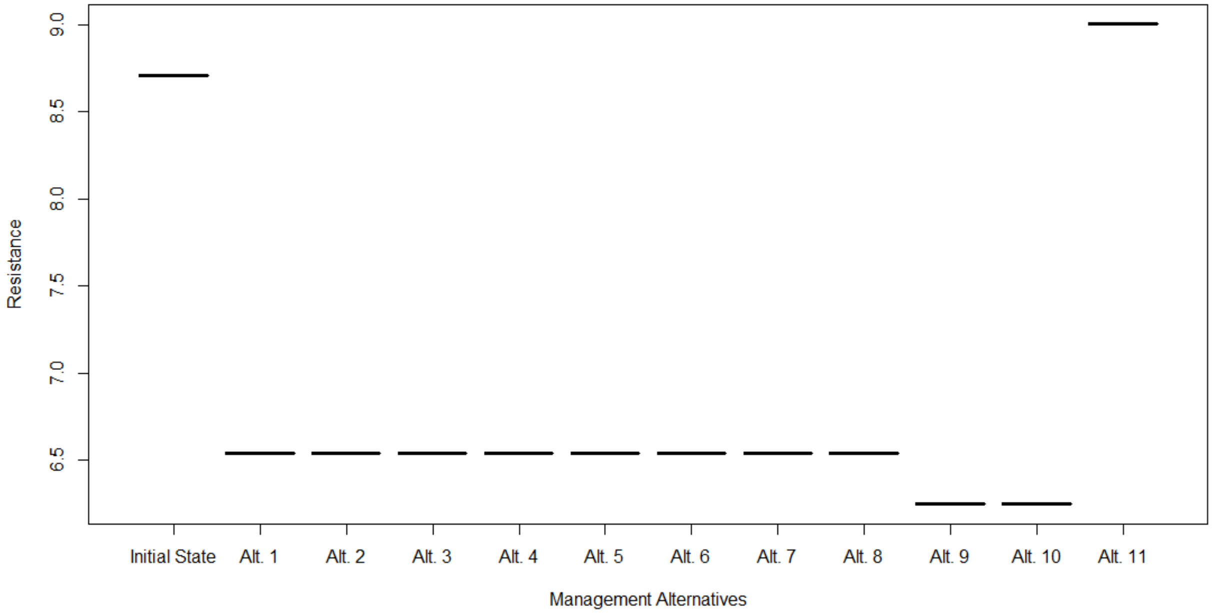


Figure 2.8. Effective resistance between 2 focal patches at Perdido Wildlife Management Area under different management alternatives using resistance value parameterization set 1.

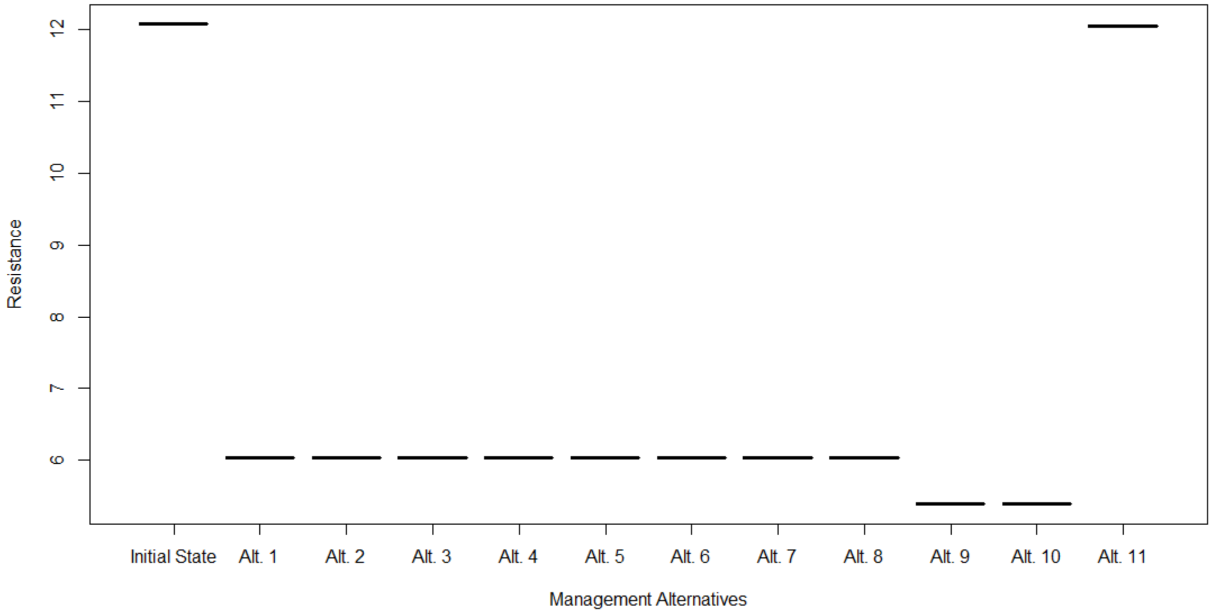


Figure 2.9. Effective resistance between 2 focal patches at Perdido Wildlife Management Area under different management alternatives using resistance value parameterization set 2.

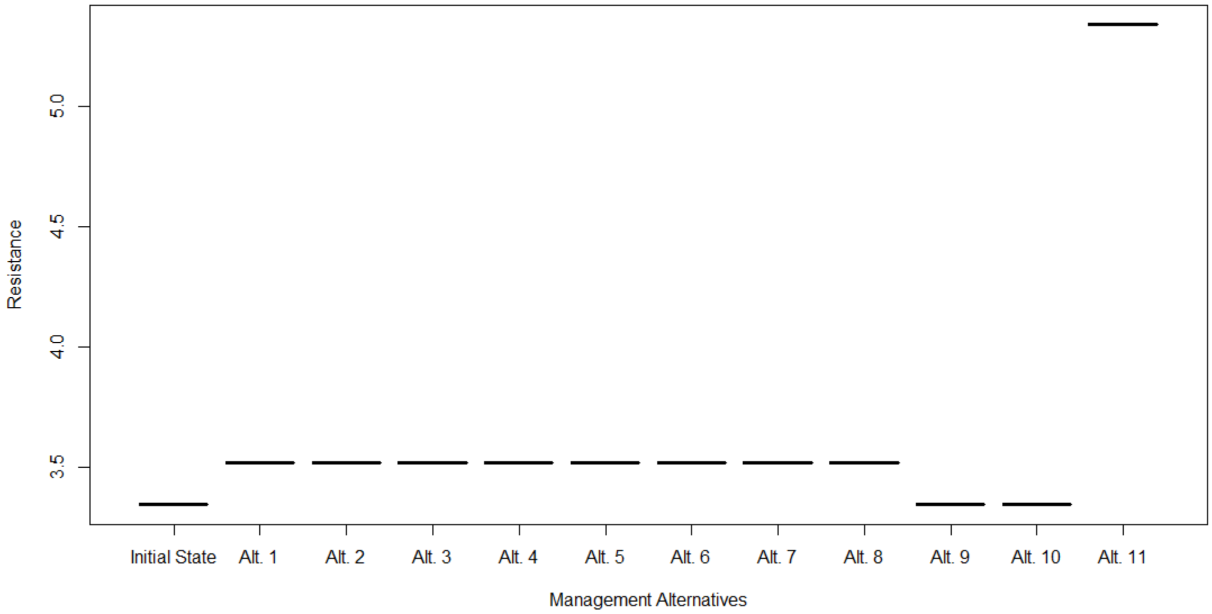


Figure 2.10. Effective resistance between 2 focal patches at Perdido Wildlife Management Area under different management alternatives using resistance value parameterization set 3.

Current Flow

Current maps of both study sites for initial stand conditions and stand conditions after 100 years under all resistance sets are available in Appendix 1. Current maps of both study sites after 25 and 50 years are available from the author upon request. Overall patterns of current flow appeared similar under all resistance value sets; thus, following examples will focus on one resistance set (resistance set 2, which had somewhat stronger patterns visible than the other sets due to greater differences in the resistance values assigned to habitat types in this set). Management alternatives did appear to affect the flow of current across the landscape at both sites, changing the amount of current through a particular area and sometimes altering the general patterns of current flow (examples in Figures 2.11 and 2.12). For both study sites, the general pattern of current flow was similar after 100 years under alternatives 1 through 8

(Appendix 1), likely because the differences between these alternatives are largely in the management of habitat types that are unsuitable for gopher tortoises (Table 2.2). For both study sites, alternatives 9 and 10 appeared to have more dispersed flow of current across a broader area, whereas the other alternatives appeared to have more restricted flow. This is likely due to most of the landscape being converted to uneven-aged pine under alternatives 9 and 10, resulting in more lower-resistance pathways when compared to the other alternatives.

Some areas on both study sites may be potential pinch points. For both study sites, there were a few areas that consistently seemed to have greater concentrations of current flow. At Barbour WMA, four areas (highlighted in Figure 2.12 C) appeared as potential pinch points under all alternatives except 9 and 10, where current in these areas seemed more diffused across a broader area, probably due to the greater number of relatively low resistance uneven-aged pine pathways available. These areas did not shift over time, though the degree to which current was restricted to these areas increased with time. That is, under a given alternative, the areas that had relatively high current remained as having relatively high current through time, though the differences in this areas compared to others became more exaggerated with time (except under alternatives 9 and 10, where current was more diffused across the landscape). At Perdido WMA, one potential pinch point located near the northern edge of the southern focal patch and north of an inholding was visible to some degree under all alternatives except alternative 11, where high amounts of current appeared concentrated in a potential pinch point to the west (Figure 2.11). As with Barbour WMA, the general patterns in flow remained similar for each alternative at the time steps examined.

Both study sites under all resistance value sets, alternatives, and years, had right-skewed histograms, with many cells of the resulting current raster maps containing low or no current (examples in Figures 2.13-2.16). At Perdido WMA, the resulting distributions had a very large proportion of cells with zero or close to zero current (Figures 2.15 and 2.16) due to a large portion of the landscape not occurring between the focal patches. Kurtosis was not consistently related with maps that visually appeared to have more pinch points (e.g., Figure 2.12 C visually appears to have more pinch points, but has lower kurtosis than Figure 2.12 B). Higher values for skewness did appear to be related with maps that visually appeared to have more pinch points (Figures 2.11 and 2.12). Skewness, or perhaps some combination of skewness and kurtosis, may be useful metrics for quantifying the tendency of a current map to have pinch points relative to similar maps. Skewness and kurtosis values for all alternatives, years, and resistance value sets are available in Appendix 2.

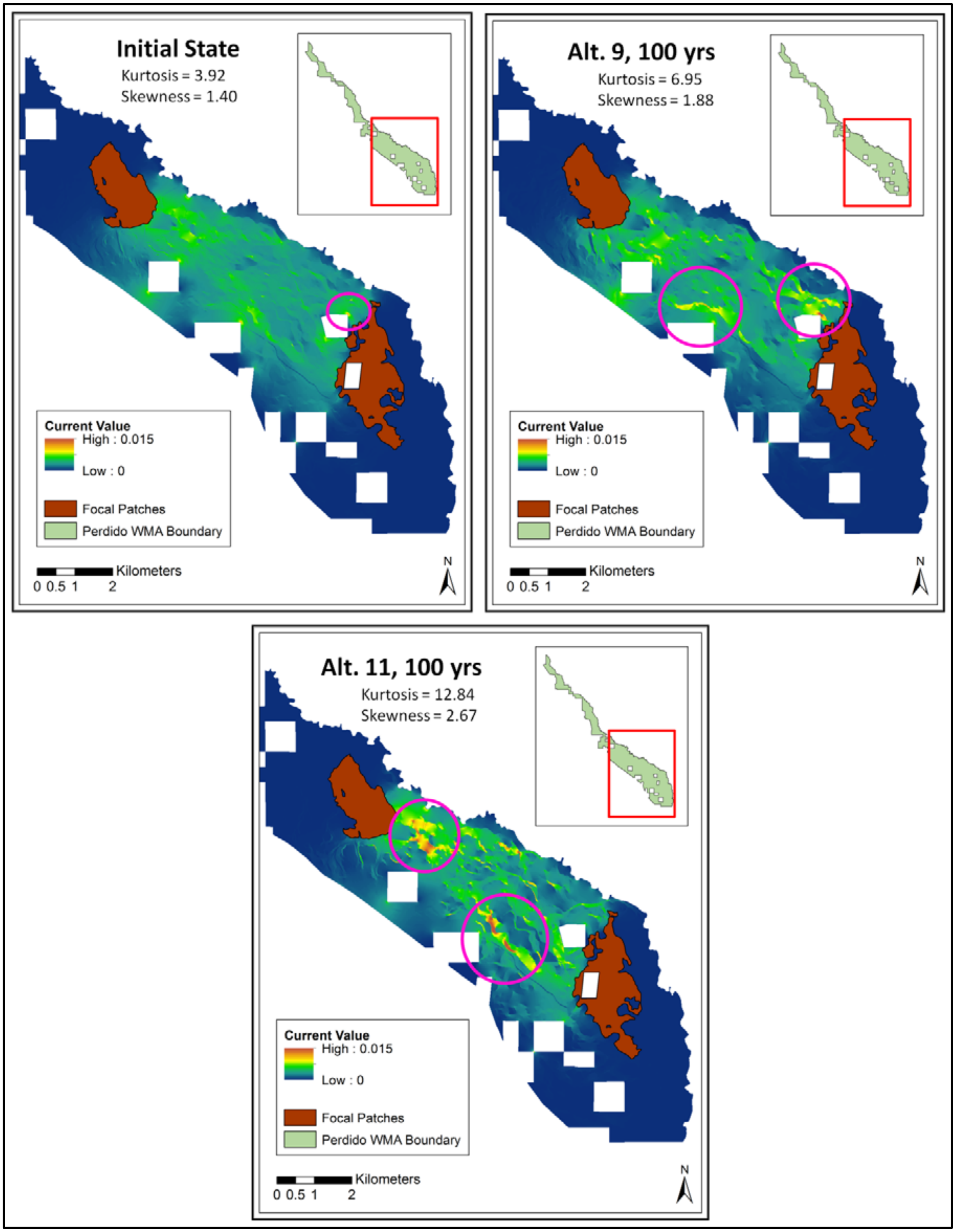


Figure 2.11. Current maps for Perdido WMA under resistance set 2 for the initial state, after 100 years under alternative 9, and after 100 years under alternative 11, with kurtosis and skewness for the histograms of current values from these maps. Pink circles indicate potential pinch points.

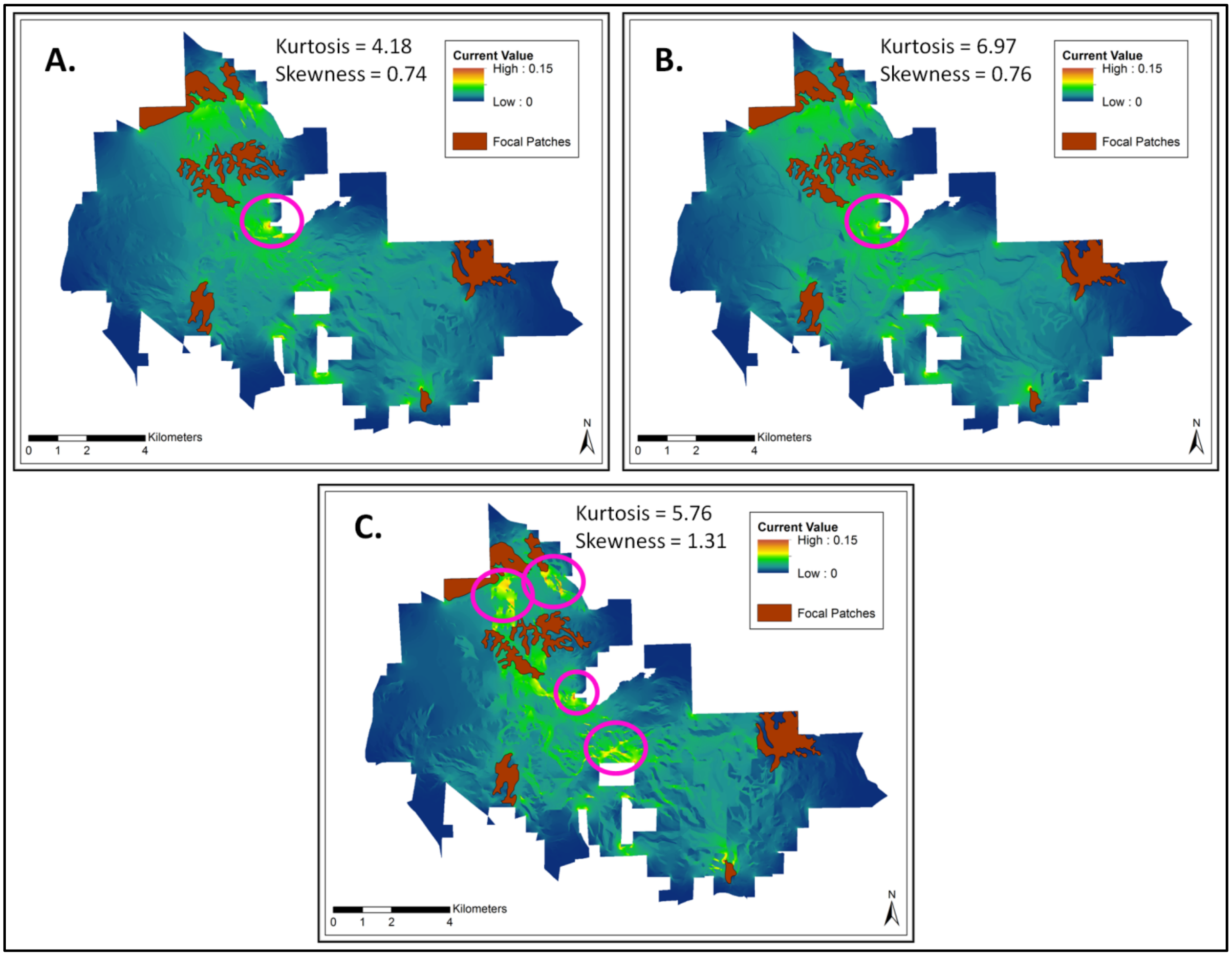


Figure 2.12. Current maps for Barbour/Wehle under resistance set 2 for A: the initial state, B: after 100 years under alternative 9, and C: after 100 years under alternative 11 with kurtosis and skewness for the histograms of current values from these maps. Pink circles indicate potential pinch points.

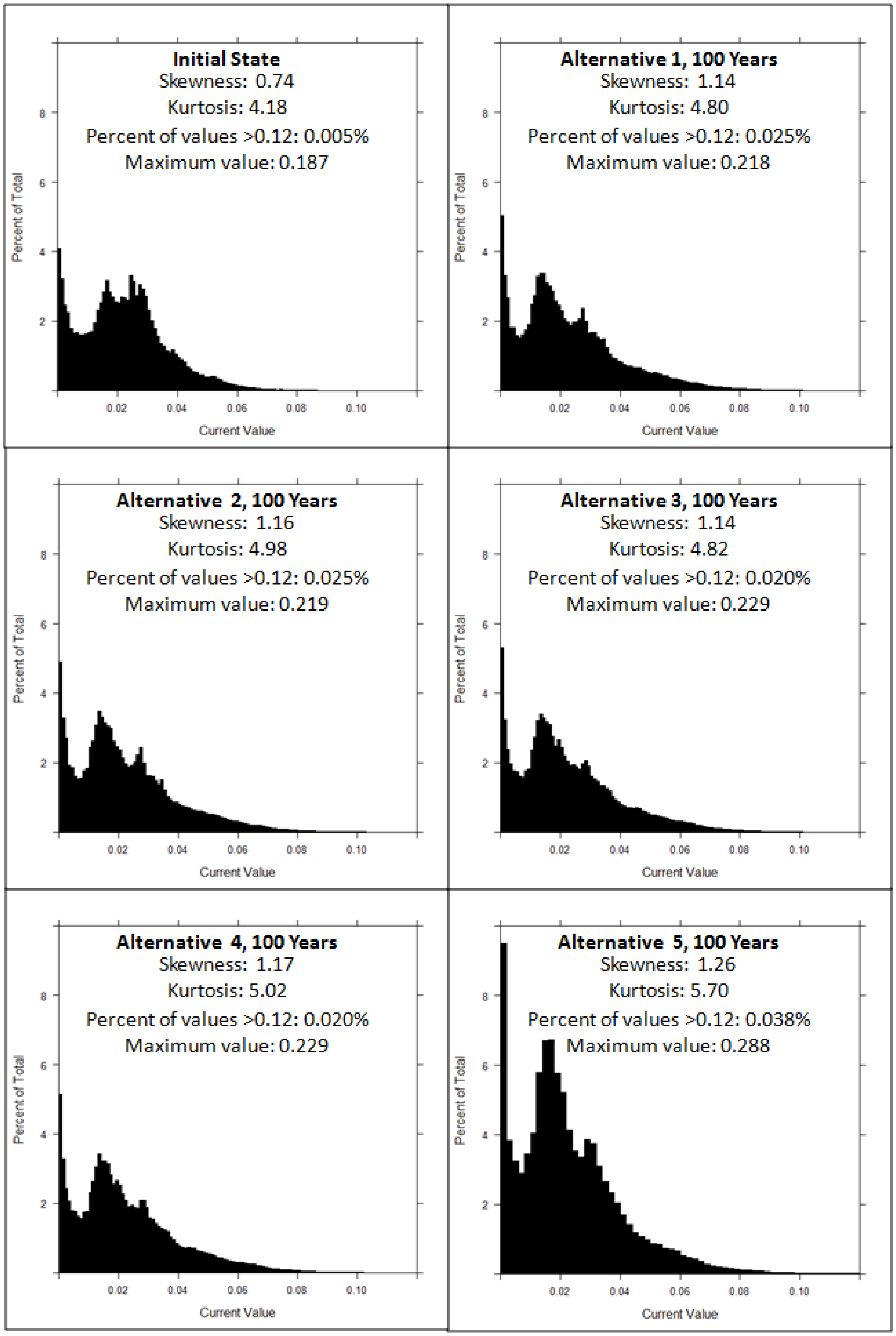


Figure 2.13. Histograms of current values using resistance set 2 for the Barbour Wildlife Management Area and Wehle Forever Wild Tract, under habitat management alternatives 1-5.

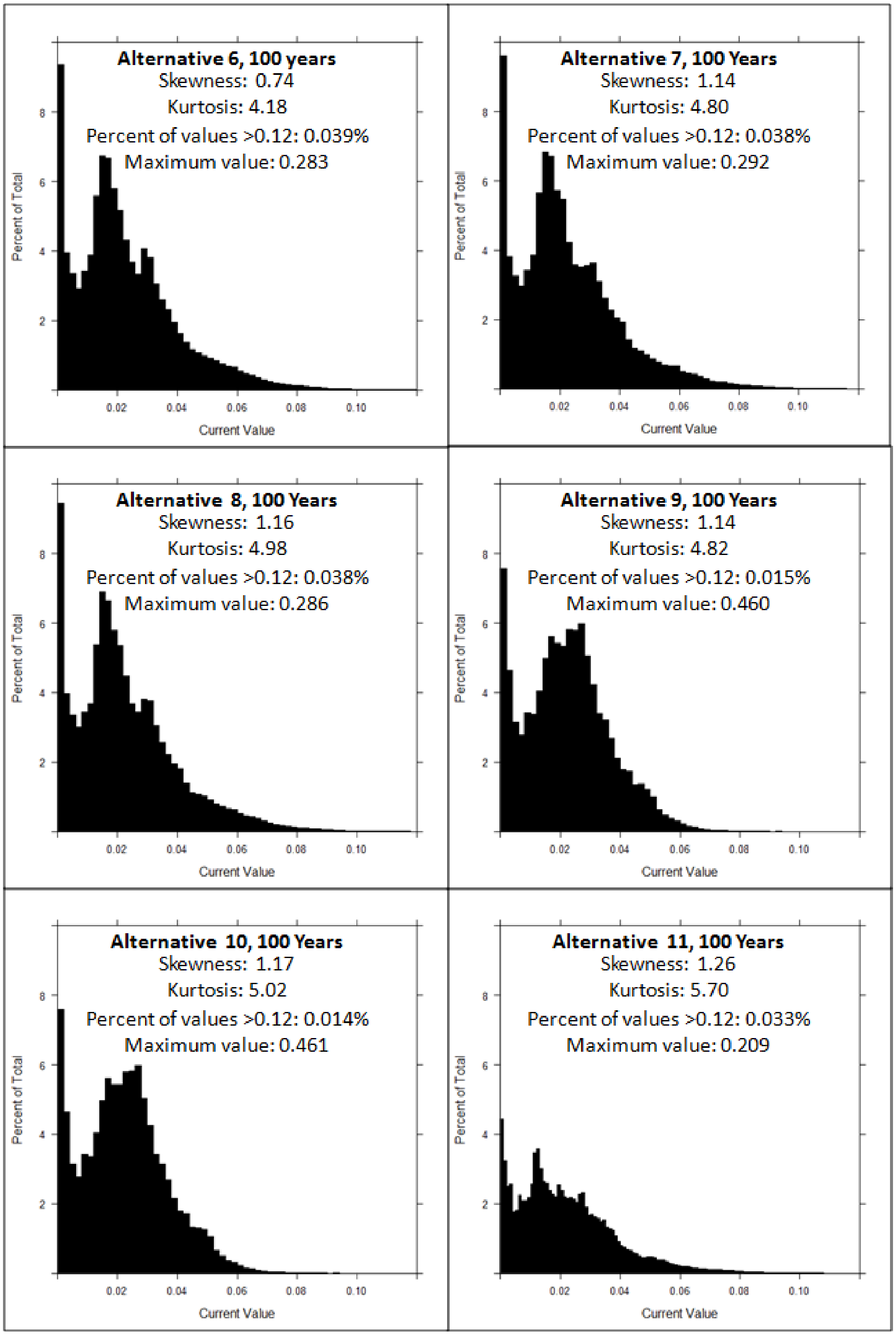


Figure 2.14. Histograms of current values using resistance set 2 for the Barbour Wildlife Management Area and Wehle Forever Wild Tract, under habitat management alternatives 6-11.

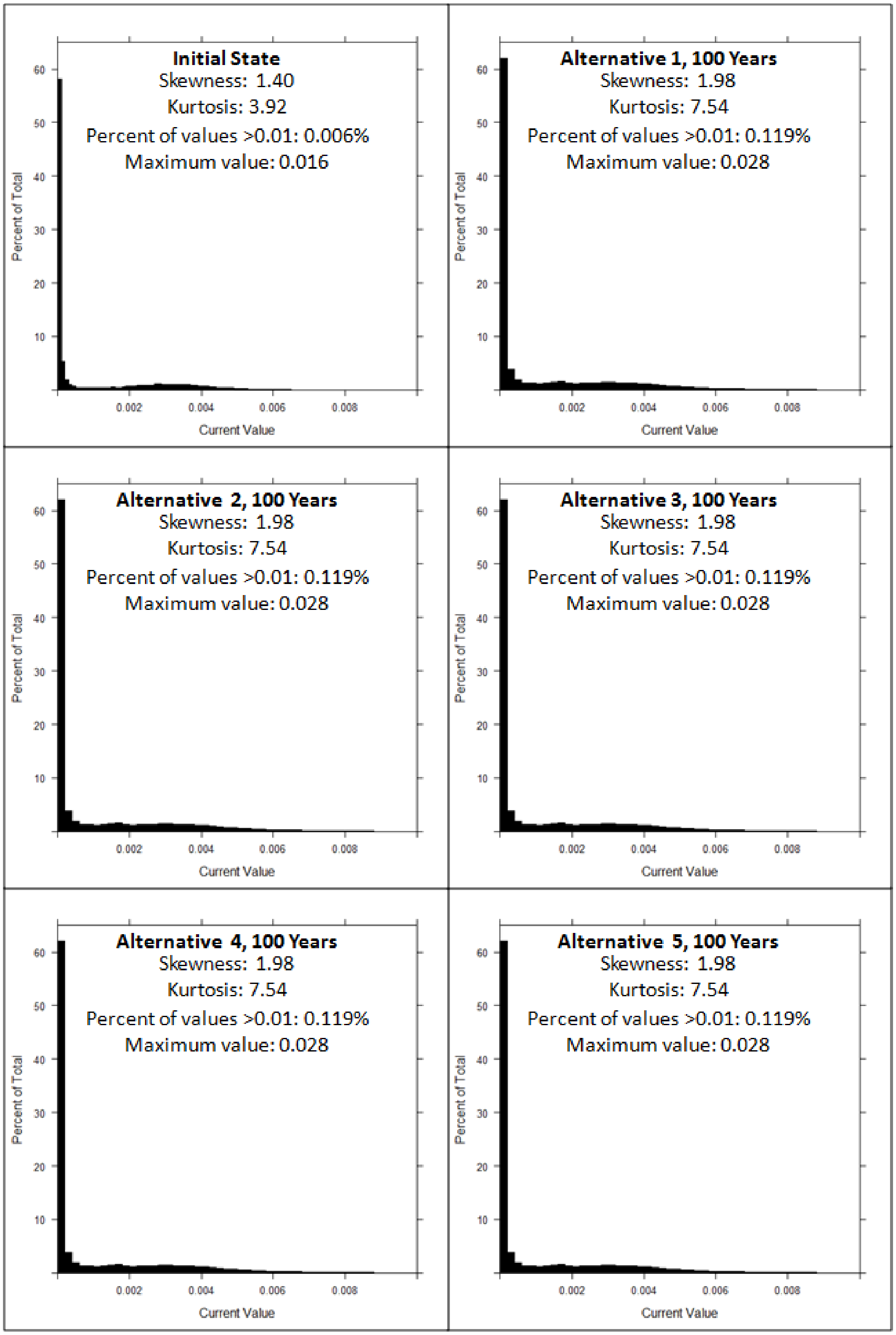


Figure 2.15. Histograms of current values using resistance set 2 for the Perdido Wildlife Management Area, under habitat management alternatives 1-5.

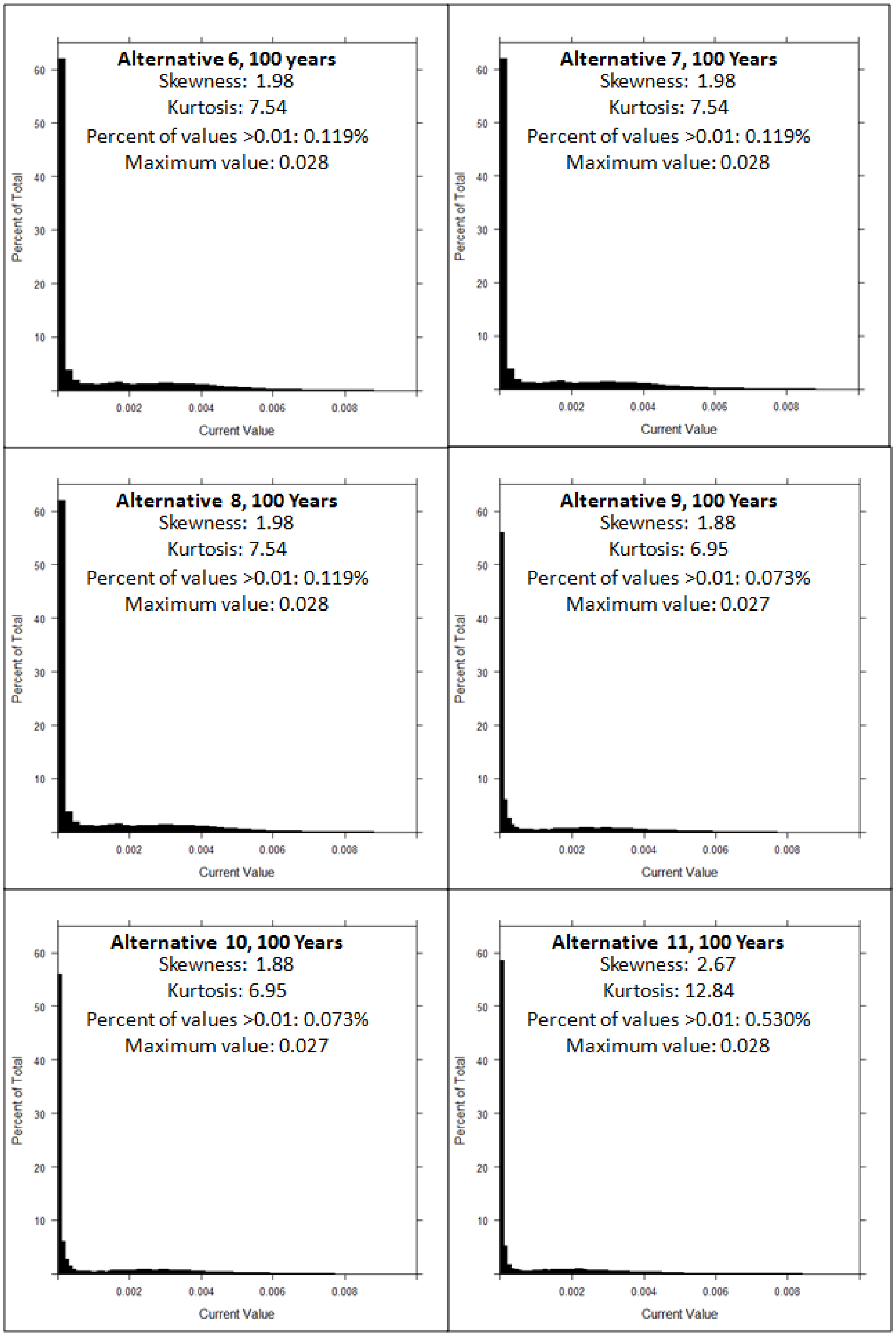


Figure 2.16. Histograms of current values using resistance set 2 for the Perdido Wildlife Management Area, under habitat management alternatives 1-11.

Discussion

If the goal of management at my two study sites was to maximize connectivity of habitat for gopher tortoises (i.e., minimize effective resistance), the results would be similar using any of the three resistance value parameterization sets examined in this study. This is a promising result, as assigning resistance values is a significant challenge to implementing a circuit-theory based analysis of habitat connectivity (McRae et al. 2008). Even though true resistance values are unknown, even minimum information on what habitat types may have higher or lower resistance than others may prove useful if the goal is to compare a set of alternatives for a landscape. More accurate or precise information about the relative resistance of various habitat types and the magnitude of difference in resistance for those habitats would likely yield more accurate results for maps of current flow and true effective resistance, but relative effective resistance may still be compared among alternatives and provides useful information regarding the relative potential impacts of management alternatives. Considering the habitat associations of gopher tortoises are fairly well known and some information is available on the movement preferences of the species, the resistance values of sets 1 and 2 used in this study are likely reasonable. So long as there is enough information to rank habitats in order of lowest to highest resistance, the absolute value assigned may be of little importance if the goal is to compare the relative (not the true or absolute) effective resistance among alternatives.

Current maps, such as those created in this study, may serve as an additional source of information to inform management. Areas of higher current density indicate areas where animals are more likely to move through if traversing the landscape (McRae et al. 2008). In this study, many of the focal patches examined may be too distant from each other for an individual gopher tortoise to move in a single excursion. Gopher tortoises have relatively small home ranges (e.g., Diemer 1992, Eubanks et al. 2003, Guyer et al. 2012), though they may rarely travel relatively large distances, particularly when relocated (e.g., Lohoefener and Lohmeier 1986, Burke 1989, Tuberville et al. 2005, 2008, Ashton and Burke 2007). However, "movement" in a circuit-theory analysis can be thought of as "movement" of populations or the spread of genes over time. Current maps must be interpreted with care, particularly if the resistance value parameterization is uncertain, but can nonetheless provide useful information on potentially important corridors for maintaining connectivity between subpopulations or habitat patches.

Visual inspection of current maps may also reveal "pinch points," areas where there is a high probability of animal movement or where animals must pass through if traversing the landscape (McRae et al. 2008). These areas may represent critical points for maintaining connectivity between two patches, areas where if they are removed or converted to a land cover type with higher resistance there may be significant consequences for connectivity. In addition to examining overall landscape resistance, considering where pinch points are located and how they may be managed would be an important step if the goal was to manage for connectivity. This study identified a few areas on both study sites that may be pinch points. Currently, there are no guidelines for how high current density must be for something to qualify as a pinch point, or how to systematically identify and quantify the phenomenon (Pelletier et al. 2014). Pelletier et al. (2014) suggested comparing the histograms current density values from resulting current maps. My results indicate that histogram skewness may be a useful metric for comparing the tendency of a current map to contain pinch points relative to others. The use of such a metric should be explored further in future studies, perhaps with simulated landscapes, to explore precisely how they change with visual interpretation of pinch points.

If the goal of management at the Barbour WMA and Perdido WMA were to maximize connectivity of habitat for gopher tortoises, alternatives 9 and 10 would best achieve that goal. These alternatives had a combination of lowest overall effective resistance, greater diffusion of current across the broader landscape (i.e., not restricted to pinch points), and less skewed distributions of current compared to the other alternatives. This is not surprising given that these alternatives manage for uneven-aged pine across most of the landscape. It is important, however, not to consider any one of these factors in isolation. For instance, at Perdido WMA, the initial state had a distribution of current with a lower skew than any of the alternatives and visually appeared not to have areas in obvious pinch points, but the effective resistance between the focal patches was much higher than under any of the management alternatives (except 11) under resistance sets 1 and 2. This is likely due to the current being forced through broad areas of equally high resistance. Additionally, presence of pinch points may not be negative depending on the management situation. For instance, a relatively narrow path between two patches containing gopher tortoises may be sufficient to maintain connectivity between those patches, and additional pathways may not be necessary. The results of studies such as this can provide valuable information to managers, but the best course of action will depend on the management context, goals, and tradeoffs between other objectives.

As is the case with any model of wildlife-habitat relationships, this study makes some generalizations. At the scale of the management areas used in this study, it is difficult to quantify very fine-scale features which may have some impact on tortoise movement. For instance, gopher tortoises may use narrow fire breaks between stands or small dirt roads and paths for movements and may establish their burrows in such areas, particularly if the surrounding habitat has dense vegetation or canopy cover. These landscape details were not captured in the stand maps used in this study. Additionally, the land cover classes defined by Silvano (2013) and used in this study do not explicitly capture the amount of canopy cover in forested areas, which is an important factor in determining gopher tortoise habitat quality. However, management for mature, uneven-aged longleaf pine is likely to result in an open-canopy environment suitable for gopher tortoises, and similar assumptions can be made about management for the other land cover classes.

Because the land cover projection model did not include inholdings or any of the property surrounding the study sites, these areas were excluded from the connectivity analysis. While tortoises have access to these areas and could potentially move through them, they are not managed by the state and often consist of poor quality habitat for tortoises, so excluding them from the model reflects the scenario where these areas are unavailable to tortoises. However, it is possible that areas outside the property boundaries contain suitable habitat and that tortoises may move off the property. Because this analysis was limited to property boundaries, inference is limited to connectivity and potential pathways within the properties.

Finally, because the state-space model developed and used by Silvano (2013) to project stand conditions into the future was probabilistic in nature, it was necessary to assign only the land cover state with the highest probability of occurring in a stand to that stand for that time step to carry out the connectivity analysis. Thus, there is some uncertainty in the habitat type for each stand that increases with the length of time since the initial state. Additionally, there is uncertainty in the state transition probabilities used to project stand conditions, particularly in management alternatives that focus on prescribed burning (such as alternative 11). The effects of prescribed burning vary depending on many factors, including the season of burn, fuel moisture, weather conditions, the initial fuel load, and initial site conditions (Streng et al. 1993). Thus, the results of the habitat projections are likely to vary depending on the assumptions made about the prescribed burning that occurs and depending on the conditions at the site, and care must be taken when evaluating the results.

Potential implications

Higher effective resistance between focal patches under some alternatives suggests a greater degree of isolation between those patches when compared to other alternatives. Greater resistance of the landscape to movement over time, or greater isolation, could have important consequences for gene flow between subpopulations and for processes such as recolonization of restored habitat. Although tortoises located within the boundaries of a property are often considered a single population, isolation between habitat patches within a property may limit interaction between groups of tortoises; the degree of such isolation may be affected by different long-term habitat management strategies. Furthermore, pinch points on the landscape may limit long-term movement, particularly for a species with very limited dispersal such as the gopher tortoise. This study provides some evidence for skewness of current values as being a useful method for comparing the relative propensity of a landscape to contain pinch points under various landscape conditions, which should be explored further in future studies.

While the analysis in this study is based on our best current knowledge of gopher tortoise habitat preferences and movement, there are relatively few studies on long-term tortoise movement or dispersal patterns. Future field studies could not only track the distance tortoises move or their start and end points, but could provide more information on the specific habitat types tortoises were willing to move through or avoided. This type of information could drastically improve our understanding of patterns of habitat connectivity and the potential for long-term gene flow between populations.

Despite some inherent limitations, the methods used in this study have great potential to be applied to other sites and other species for which habitat connectivity is a management concern. The results of this study may also be directly applicable to other upland species of conservation concern in the southeast, such as the southeastern pocket gopher (*Geomys pinetis*), which has similar requirements for deep, sandy, well-drained soil and open vegetation. Circuit theory-based analyses have potential to be useful tools for quantifying and comparing habitat connectivity among alternatives, taking into account the complexity and configuration of the landscape in question and the preferences and habitat needs of the species in question. While a quantitative projection of stand conditions is useful for assessing the consequences of management alternatives, in a decision-making context one could simply identify a set of potential target landscapes and compare effective resistances and current maps. Such analyses should be a standard part of habitat projections given the recognized importance of spatial pattern to population and community dynamics.

Literature Cited

Anzures-Dadda, A., and R. H. Manson. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69–76.

Ashton, K. G., and R. L. Burke. 2007. Long-term retention of a relocated population of gopher tortoises. Journal of Wildlife Management 71:783–787.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (Gopherus polyphemus). Pages 95–126 *in* R. B. Bury, editor. North American tortoises: Conservation and ecology (Wildlife Research Report 12). U.S. Fish and Wildlife Service, Washington, D.C., USA.

Baskaran, L. M., V. H. Dale, R. A. Efroymson, and W. Birkhead. 2006. Habitat modeling within a regional context: An example using gopher tortoise. American Midland Naturalist 155:335–351.

Beck, J. L., and L. H. Surling. 2009. Wildlife-habitat relationships models: Description and evaluation of existing frameworks. Pages 251-286 *in* J. J. Millspaugh and F. R. Thompson, editors. Models for Planning Wildlife Conservation in Large Landscapes. Academic Press, Burlington, Massachusetts, USA.

Boglioli, M. D., W. K. Michener, and C. Guyer. 2000. Habitat selection and modification by the gopher tortoise, Gopherus polyphemus, in Georgia longleaf pine forest. Chelonian Conservation and Biology 3:699–705.

Bonin, F., B. Devaux, and A. Dupre. 2006. Turtles of the world. P. C. H. Pritchard, editor. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology, Evolution, and Systmatics 23:481–506.

Burke, R. L. 1989. Florida gopher tortoise relocation: Overview and case study. Biological Conservation 48:295–309.

Clostio, R. W. 2010. Use of environmental variables to infer gene flow and population structure in the gopher tortoise (Gopherus polyphemus) and predict the seroprevalence of an emerging infectious disease. Dissertation, University of New Orleans, New Orleans, USA.

Cox, J., D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (Gopherus polyphemus) populations found on lands slated for large-scale development in Florida. Nongame Wildlife Program Technical Report No. 4. Office of Environmental Services, Florida Game and Freshwater Fish Commission, Tallahassee, FL.

DeCarlo, L. T. 1997. On the meaning and use of kurtosis. Psychological Methods 2:292–307.

Diemer, J. E. 1992. Home range and movements of the tortoise Gopherus polyphemus in northern Florida. Journal of Herpetology 26:158–165.

Eubanks, J. O., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (Gopherus polyphemus). Herpetologica 59:311–321.

Fagan, W. F., P. J. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction risk in desert fishes. Ecology 83:3250–3256.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: A synthesis. Global Ecology and Biogeography 16:265–280.

Gustafson, E. J., and G. R. Parker. 1992. Relationship between land cover proportion and indices of spatial pattern. Landscape Ecology 7:101–110.

Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (Gopherus polyphemus). Herpetological Monographs 26:122–134.

Jones, J. C., and B. Dorr. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife Society Bulletin 32:456–464.

Komsta, L., and F. Novomestky. 2015. moments: Moments, cumulants, skewness, kurtosis and related tests. R package version 0.14.

Kowal, V. A, A. Schmolke, R. Kanagaraj, and D. Bruggeman. 2014. Resource selection probability functions for gopher tortoise: Providing a management tool applicable across the species' range. Environmental management 53:594–605.

Lohoefener, R., and L. Lohmeier. 1986. Experiments with gopher tortoise (Gopherus polyphemus) relocation in southern Mississippi. Herpetologica 17:37–40.

McCoy, E. D., K. A. Basiotis, K. M. Connor, and H. R. Mushinsky. 2013. Habitat selection increases the isolating effect of habitat fragmentation on the gopher tortoise. Behavioral Ecology and Sociobiology 67:815–821.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v. 4: Spatial pattern analysis program for categorical and continuous maps.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Morrison, M. L., B. Marcot, and W. Mannan. 2006. Wildlife-habitat relationships: Concepts and applications. 3rd edition. Island Press, Washington, D.C, USA.

Pelletier, D., M. Clark, M. G. Anderson, B. Rayfield, M. A. Wulder, and J. A. Cardille. 2014. Applying circuit theory for corridor expansion and management at regional scales: Tiling, pinch points, and omnidirectional connectivity. PLoS ONE 9:1–11.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. The American Naturalist 158:87–99.

Runge, M. C., J. B. Grand, and M. S. Mitchell. 2013. Structured decision making. Pages 51–72 *in* P. R. Krausman and J. W. I. Cain, editors. Wildlife Management and Conservation: Contemporary Principles and Practices. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Silvano, A. L. 2013. Incorporating long-term spatial and temporal effects in a state space model to evaluate land management alternatives for imperiled species conservation in Alabama. Thesis, Auburn University, Auburn, AL.

Smith, L. L., T. D. Tuberville, and R. A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise 2003: Final results and recommendations. Chelonian Conservation and Biology 5:326–330.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261–270.

Streng, D. R., J. S. Glitzenstein, and W. J. Platt. 1993. Evaluating effects of season of burn in longleaf pine forests: A critical literature review and some results from an ongoing long-term study. Proceedings of the Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, FL.

Tuberville, T. D., E. E. Clark, K. A. Buhlmann, and J. W. Gibbons. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (Gopherus polyphemus). Animal Conservation 8:349–358.

Tuberville, T. D., T. M. Norton, B. D. Todd, and J. S. Spratt. 2008. Long-term apparent survival of translocated gopher tortoises: A comparison of newly released and previously established animals. Biological Conservation 141:2690–2697.

Turner, M. G., R. H. Gardner, and R. V O'Neill. 2001. Landscape ecology in theory and practice. Springer, New York, New York, USA.

United States Fish and Wildlife Service [USFWS]. 2011. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List the Gopher Tortoise as Threatened in the Eastern Portion of Its Range. Federal Register 76(144):45130-45162.

United States Fish and Wildlife Service [USFWS] and Natural Resources Conservation Service [NRCS]. 2012. Gopher tortoise (Gopherus polyphemus) soil classifications for the federally listed range using the National Soil Information System database. Report, version 1.

United States Fish and Wildlife Service [USFWS], and Southeast Regional Partnership for Planning and Sustainability [SERPPAS]. 2013. 4th annual report, candidate conservation agreement for the gopher tortoise.

Chapter 3:

A Spatially Explicit Individual-based Population Projection Model to Compare Effects of Habitat and Population Management Alternatives on Gopher Tortoise Population Persistence

Introduction

Decisions about the management of wildlife must often be made in the face of uncertainty about how management actions will affect target populations. Making a defensible decision requires forecasting the potential effects of the management alternatives under consideration, a task that is often accomplished through the explicit use of modeling (Starfield 1997). Modeling, in its various forms, is a useful tool in the decision-making process that can incorporate the inherent uncertainty in predicting the outcomes of management (Conroy et al. 2008). As such, many types of models and modeling frameworks have been developed to project the future state of wildlife populations for informing management decisions.

While many modeling frameworks are available, no one method is perfectly suited to every situation. Population models have been developed for a multitude of applications, including evaluating the effects of management actions, ranking relative threats to populations, determining which demographic variables have the greatest influence on extinction risk, and identifying future research priorities (Tuberville and Gibbons 2009). A common approach is to conduct a population viability analysis (PVA), a process that seeks to project populations into the future and estimate an extinction or persistence parameter, such as time to extinction or extinction probability (Boyce 1992). The population projection can be accomplished in a number of ways, including age or stage-based matrix models (Caswell 2000), and delay or partial differential equations (Caswell et al. 1997). These types of population-based models assume that individual organisms may be aggregated together in some manner, such as treating all individuals of a particular age or sex as identical or relying on population averages (DeAngelis and Gross 1992). Population-based models, while they have a long history and are a valuable tool in ecology and management, nonetheless have their limitations.

One of the key limitations of many population-based models is the lack of a spatial component. Spatial heterogeneity is an inherent component of real-world ecological systems, and it has important consequences for survival, reproduction, and movement of organisms (Turner et al. 2001). The composition and configuration of the landscape can affect the connectivity of habitat for the species in question, which in turn can have consequences for population persistence (Fagan et al. 2002, Anzures-Dadda and Manson 2007). Additionally, heterogeneity in habitat suitability will affect a species' distribution and density on the landscape. Many non-spatial models assume that every organism in the population has an equal influence on every other organism in the population; in reality, individual organisms occupy a given location at a given time and are primarily affected by nearby organisms (DeAngelis and Gross 1992). While population-based models can be spatially explicit, such as with metapopulation models (Dunning et al. 1995), they still involve the aggregation of individuals and thus cannot account for individual organism locations and interactions, which may be particularly important for small or local populations and species with limited mobility.

An alternative method that has become increasingly popular in recent decades is the use of individual-based models (Grimm 1999). Individual, or agent-based, models can be broadly defined as those which are based on individual organisms, rather than aggregated groups (Huston et al. 1988). In a population modeling context, an individual-based model tracks individual members of the population as unique and discrete entities which have properties such as age, sex, or weight (Grimm 1999). Individual-based models incorporate variability and mechanisms at the level of individual interactions, details which may be overlooked or generalized in other population modeling frameworks (Huston et al. 1988). With these models, population-level properties such as persistence and abundance over time emerge from the combined individual behaviors of modeled organisms (DeAngelis and Gross 1992, Grimm and Railsback 2005). Individual-based models have become a widely used tool in ecology as well as many other disciplines (Grimm et al. 2006).

Individual-based models are well suited to spatially explicit modeling; while population-based spatially explicit models may be particularly appropriate for large populations, many spatially explicit models are individual-based with the locations of individuals on the landscape explicitly incorporated into the model (Dunning et al. 1995). Spatially explicit population models are particularly useful for investigating the response of organisms to habitat change, such as what might be induced by management actions (Dunning et al. 1995). One of the limitations of individual-based models, including spatially explicit ones, is that because of their complexity and the need to track individual agents, these models are computationally intensive and as such are best suited to relatively small populations.

With the ability to incorporate high levels of detail, ease of integration with spatial data, and the ability to track interactions among individuals, individual-based models are well suited for projecting relatively small populations of threatened or endangered species. One species that could benefit from such an approach is the gopher tortoise (*Gopherus polyphemus*). Gopher tortoises are medium-sized tortoises endemic to the southeastern United States (Bonin et al.

2006). The species was listed as Threatened under the Endangered Species Act in the western portion of their range (west of the Mobile and Tombigbee rivers in Alabama) in 1987 (USFWS 2011). The species was also petitioned for listing throughout its range in 2006, but listing was found to be warranted but precluded (USFWS 2011). Gopher tortoise populations are believed to be in decline throughout their range (USFWS and SERPPAS 2013), and are a species of conservation concern in all states in which they occur. Population declines are likely due to a variety of factors, including human harvest of the animals for food and pets, invasive species, disease, habitat loss, and habitat fragmentation (Smith et al. 2006). Gopher tortoises are now often found in relatively small, fragmented populations on areas of residual or restored habitat.

Gopher tortoises have well documented and specific habitat needs, and the creation or maintenance of habitat is often the goal of management for this species. They are limited in distribution by the availability of suitable habitat, which is often patchy and fragmented, and have limited dispersal capability. As such, spatially explicit modeling is an ideal choice for evaluating the effects of habitat management alternatives on gopher tortoise populations. Gopher tortoises are a burrowing species, creating burrows up to 10 meters in length (Bonin et al. 2006). These burrows also provide shelter, habitat, and protection from fire for hundreds of other species (Cox et al. 1987). The need to create burrows generally limits gopher tortoise activity to deep, sandy, well-drained soils that are suitable for digging (Auffenberg and Franz 1982). Tortoises also require an open forest canopy to allow adequate sunlight for the growth of preferred herbaceous forage and for basking, a thermoregulatory behavior (Auffenberg and Franz 1982). They are often associated with the longleaf pine (*Pinus palustris*) ecosystem, a fire-maintained, endangered forest type unique to the southeastern United States (Frost 1993).

Gopher tortoises are consistently associated with upland, open-canopy habitats and sandy soils (Boglioli et al. 2000, Jones and Dorr 2004, Baskaran et al. 2006, Kowal et al. 2014).

Perhaps not surprisingly given the threatened status of the species, a number of population models have previously been developed for the gopher tortoise. Two of the earliest gopher tortoise population modeling efforts were PVAs developed in the PopDyn population simulation program to assess the viability of small tortoise populations (Cox et al. 1987, Cox 1989). Other PVA models have been developed and used for demographic sensitivity analysis (Miller 2001), to test potential effects of reintroduction (Seigel and Dodd 2000), and to provide general management recommendations for "at risk" populations (Tuberville and Gibbons 2009). Root and Barnes (2006) developed a stage-based, spatially explicit PVA using the RAMAS GIS program, where habitat was classified as either habitat, protected habitat, or non-habitat across the state of Florida and linked in a metapopulation framework by an assigned dispersal distance.

More recent models have taken a spatially explicit and individual-based approach. Westervelt and MacAllister (2012) developed a spatially explicit individual-based population projection model for gopher tortoises in Fort Benning, Georgia. The model was developed in the NetLogo modeling environment (Wilensky 1999) and included growth and consumption of vegetation by tortoises, tortoise movement, and carrying capacity of habitat patches (Westervelt and MacAllister 2012). The population was projected for the Fort Benning area under the current landscape configuration and for hypothetical habitat configurations (circular habitat patch, uniformly distributed habitat patches) (Westervelt and MacAllister 2012). Tuberville et al. (2012) also developed an individual-based, spatially explicit population model for gopher tortoises using NetLogo. The model was developed for Fort Stewart in Georgia, and was used for demographic sensitivity testing and compared to a "traditional" PVA using the VORTEX population simulation software (Tuberville et al. 2012). These models are excellent examples of how individual based modeling can be applied to gopher tortoise populations. There is great potential to extend this framework to a habitat management decision-making context.

In the state of Alabama, gopher tortoises are a species of conservation concern and are federally listed as Threatened in the western portion of the state. Several publicly owned properties within the state are known to contain populations of gopher tortoises, ranging in size from fewer than 50 to several hundred individuals. Preserving gopher tortoise populations is often a management concern on these properties. A recent analysis done in a structured decision making framework evaluated the consequences and relative value of various forest management alternatives to wildlife and management objectives, and projected habitat conditions on several public properties in Alabama under various habitat management alternatives (Silvano 2013). With the conservation concern for gopher tortoises in Alabama and the availability of both current and projected future habitat conditions, the development of a spatially explicit individual-based population projection model would provide valuable information to managers and provide the framework for similar models to be used in future decision-making contexts.

The goal of this study was to demonstrate the utility of a stochastic, spatially explicit, individual-based gopher tortoise population projection model incorporating dynamic landscape conditions for habitat management decision making. The model was used to evaluate the effects of various population and habitat management strategies on gopher tortoise populations on selected Alabama public lands. Additionally, this study developed a stage-based, non-spatial matrix population projection model for comparison with the results of the spatially explicit, individual-based model.

Methods

Individual-based model overview

I developed an individual-based, spatially explicit, stochastic population projection model for gopher tortoises at selected public properties in Alabama. Following Tuberville et al. (2012) and Westervelt and MacAllister (2012), the model was developed in NetLogo, a free, open-source, programmable agent-based modeling environment (Wilensky 1999). The model tracks individual tortoises as they live, age, die, reproduce, and respond to changes in the landscape. The landscape is represented in a raster (cell-based) format, where each cell can hold a specified number of tortoises, based on the habitat conditions. Simulated tortoises occupy these cells, and can shift to other cells in the landscape if habitat conditions become unfavorable. Simulated tortoises are assigned unique attributes, such as age, sex, and patches (cells) they have visited, which are stored as variables unique to each individual. Each cell also has unique attributes, such as carrying capacity, which the model stores as a variable with a unique value for each cell, called patch variables. The model tracks the number of individuals in the population and their location under alternative management strategies.

Process overview

Following Tuberville et al. (2012) and Westervelt and MacAllister (2012), the individual-based model used a monthly time step. A monthly time step captures details of tortoise life history, such as timing of breeding. Unlike previously developed gopher tortoise projection models using NetLogo, my model incorporated stochasticity into the vital rates both for each iteration and for each year to capture the uncertainty surrounding estimates of these parameters and natural annual variation in these parameters. For each study site and each alternative, the model was run for 1,000 iterations, with each iteration running for 200 years (total of 2,400 monthly time steps per iteration). At the beginning of each iteration, values for survival were drawn from estimate distributions (see mortality section below). These values were used as the means for new distributions from which annual survival values were drawn at the beginning of each year (i.e., in the first month of the year; see mortality section below). Also at the beginning of the year, the habitat map changed for the first 100 years of each 200 year simulation (see habitat projection section below). The following processes occurred each month:

1. Tortoises add the patch they are on to the current list of patches they've visited (see movement section below)
2. If month = 9 (September), tortoises increase their age by one
3. Tortoises potentially die (see mortality section below)
4. Female tortoises check if there is a male within the specified radius of their current location (see reproduction section below)
5. If month = 6 (June), tortoises reproduce (see reproduction section below)
6. If month = 9 (September), hatch the eggs in the patch (see reproduction section below)
7. If month = 9 (September), grow hatchlings into juveniles (see tortoise growth section below)
8. If month ≥ 4 and ≤ 10 (from April through October), tortoises are allowed to move if needed (see movement section below)

Study areas

Two state owned sites in Alabama were chosen for the population projection: The Barbour Wildlife Management Area and adjacent Wehle Forever Wild Tract (“Barbour/Wehle”) in Barbour and Bullock counties in southeastern Alabama, and the Perdido River Wildlife Management Area (“Perdido WMA”) in Baldwin county in southwestern Alabama (Figure 3.1). Both sites are known to have gopher tortoises and are potentially important conservation areas for the species. Both sites also have stand conditions projected 100 years into the future as part of a recent analysis done in a structured decision making framework to evaluate the consequences and relative value of various forest management alternatives to management objectives (Silvano 2013). Each study site was represented as a grid of 1 ha cells. This cell size was chosen because it is small enough to capture some detail in landscape configuration, and large enough to potentially contain multiple tortoises if the habitat is suitable.

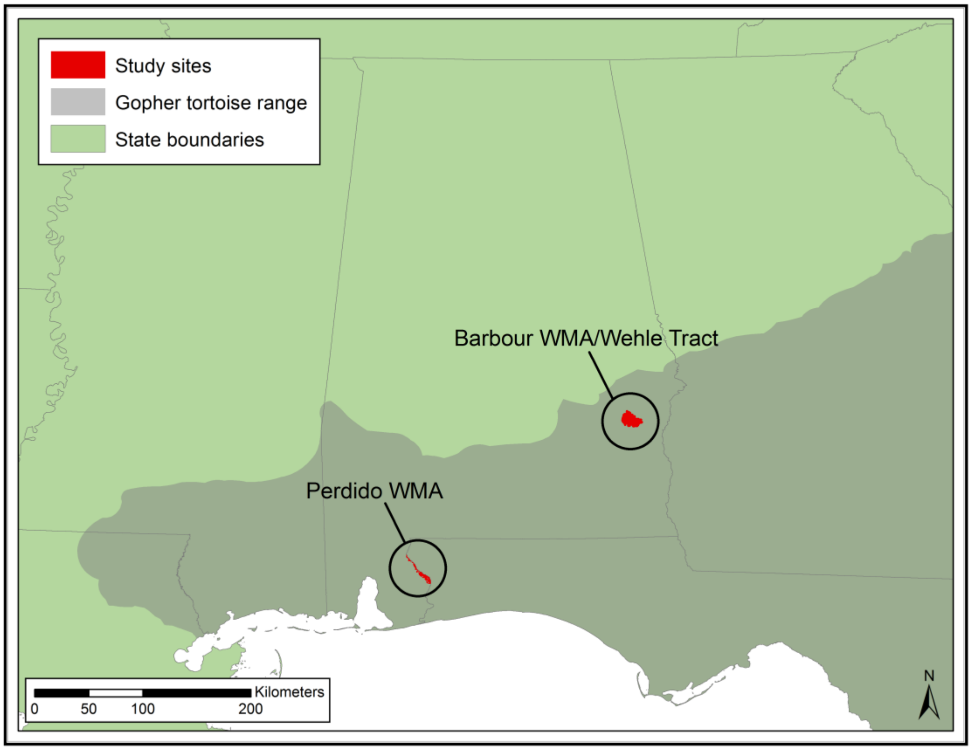


Figure 3.1. The Barbour Wildlife Management Area/Wehle Forever Wild Tract and Perdido River Wildlife Management area study sites in Alabama.

The Barbour Wildlife Management Area and Wehle Forever Wild Tract (Figure 3.2) are two adjacent properties located in the upper coastal plain region of Alabama, close to the northern edge of the gopher tortoise's range within the state. The Barbour WMA covers approximately 11,659 ha and the Wehle Forever Wild Tract covers approximately 630 ha. Barbour WMA contains a diverse array of habitat types, including longleaf and loblolly (*Pinus taeda*) pine stands of various ages and densities, mixed hardwood stands, food plots, and clearings. The Wehle Forever Wild Tract consists largely of open canopy longleaf pine.

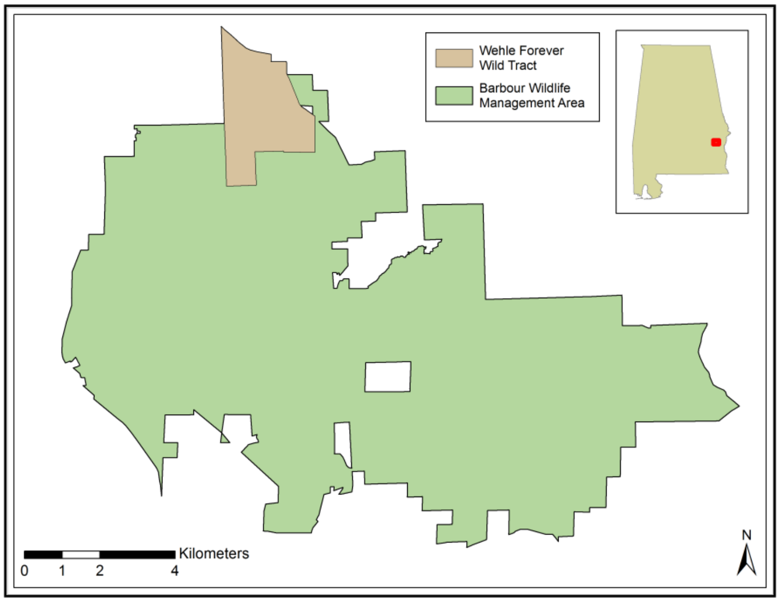


Figure 3.2. Barbour Wildlife Management Area and Wehle Forever Wild Tract in Alabama.

The gopher tortoises currently known to occur in the Barbour/Wehle area are the result of a reintroduction effort on the Wehle Tract in which 55 tortoises from southeast Alabama and West Georgia were released from 2006-2009 (E. Soehren, Alabama Department of Conservation and Natural Resources State Lands Division, personal communication). As of the summer of 2013, 13 of the 55 tortoises originally released remained on the Wehle Tract. Other surviving individuals may have moved onto the adjacent Barbour WMA, where a few tortoises are currently known to occur (E. Soehren, personal communication). While the present day gopher tortoise population in the Barbour/Wehle area is small, it provides an opportunity to conserve gopher tortoises near the northern extent of their range.

Perdido WMA is a 7,327 ha property located in the southern coastal plain region in Alabama, adjacent to the border with Florida (Figure 3.3). Much of the property contains deep, sandy soils that are suitable for gopher tortoises. The property runs along the Perdido River and includes dense timber pine stands, recent clearcuts, intermittent bogs, and some areas of longleaf pine restoration. The site supports gopher tortoises, and recent surveys estimate that the property supports 434 (266 - 711, 95% confidence interval) individuals (S. M. Hermann, Auburn University, unpublished data). Much of the property was, until recently, dominated by dense timber pine stands unsuitable for gopher tortoises. As a result, many of the tortoises found on Perdido WMA are clustered in the remaining open areas, including utility line right-of-ways. The property is currently undergoing significant changes in habitat structure, including clearcut logging of much of the area that was in dense pine stands.

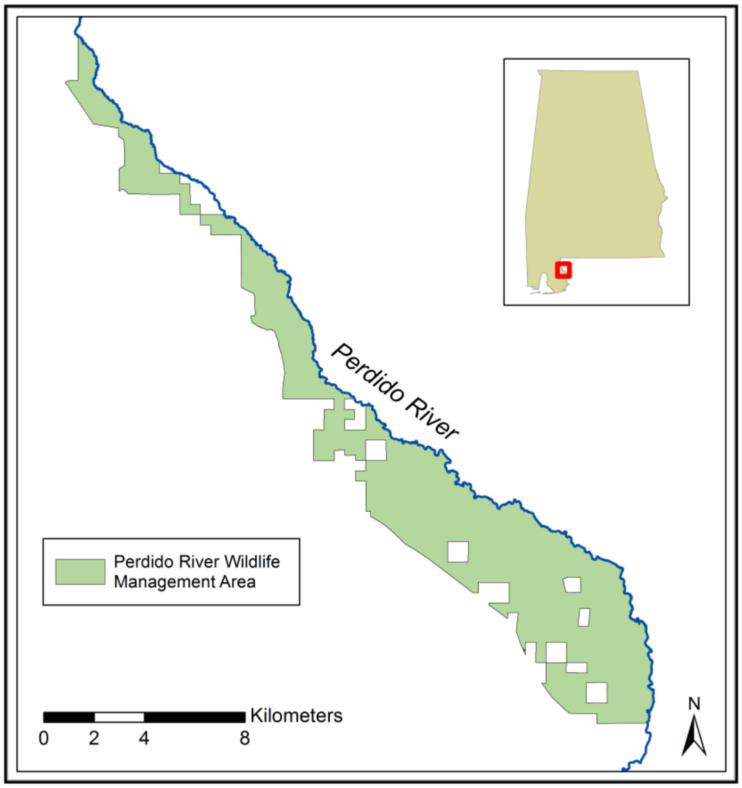


Figure 3.3. Perdido River Wildlife Management area in Alabama.

Habitat, habitat management alternatives, and habitat projection

Vegetation structure is an important component of gopher tortoise habitat. This study evaluated 11 forest management alternatives identified by Silvano (2013) (Table 3.1). These alternatives were identified with land managers and foresters from the Alabama Department of Conservation and Natural Resources (ADCNR) during four two-day workshops (Silvano 2013). A common goal identified was the conversion of even-aged forest stands to an uneven-aged structure to promote a greater diversity of wildlife species; thus, under each alternative, all forested management units were converted to uneven-aged forest (Silvano 2013). Additionally, each alternative included the presence of a Streamside Management Zone (SMZ) at least 35 ft from stream banks with >50% tree cover (Silvano 2013). Alternatives varied in the management of north facing slopes, with such slopes being converted to hardwood under some alternatives (Silvano 2013). Alternatives also varied in the type of forest managed for in floodplains (Silvano 2013). Openings (i.e., wildlife openings in forested areas) were either maintained or reforested under each alternative (Silvano 2013).

Table 3.1. Management alternatives compared in the population projections. Adapted from Silvano (2013).

Alternative	Description (text from Silvano 2013)
1	All forest types managed for uneven-age distribution. Mixed pine hardwood succeeds to upland hardwood. Openings retained in either agricultural crops or native warm-season grasses.
2	Same as alternative 1, but openings are reforested to adjacent forest type.
3	Hardwood and forested wetlands managed for uneven-age distribution. Mixed pine-hardwood stands are thinned and managed to uneven-aged hardwood. Pine forests on north-facing slopes are converted to uneven-aged hardwoods. Openings retained in either agricultural crops or native warm-season grasses.
4	Same as alternative 3, but openings are reforested to adjacent forest type.
5	All forest types managed for uneven-age distribution. Pine and upland hardwoods in floodplains are managed for flood plain forest types. Openings retained in either agricultural crops or native warm-season grasses.
6	Same as alternative 5, but openings are reforested to adjacent forest type.
7	All forest types managed for uneven-age distribution. Pine forests on north-facing slopes are converted to uneven-aged hardwoods. Pine and upland hardwoods in floodplains are managed for flood plain forest types. Openings retained in either agricultural crops or native warm season grasses.
8	Same as alternative 7, but openings are reforested to adjacent forest type.
9	All forest types except existing floodplain forests are converted or managed for uneven-aged pine. Openings retained in either agricultural crops or native warm-season grasses.
10	Same as alternative 9, but openings are reforested to adjacent forest type.
11	Prescribed fire is used to manage forest type and structure. Wildlife openings are allowed to succeed to surrounding forest type.

Silvano (2013) developed a state-space model to project stand conditions at selected public properties in Alabama from a circa 2011 baseline 100 years into the future under each of the 11 identified management alternatives. The model included transitions representing both natural (e.g., succession) and management-induced (e.g., prescribed burning) processes (Silvano 2013). The model included 25 possible states for each stand or management unit, and projections resulted in each stand or management unit being assigned a probability that it was in each of the 25 states at each time step (Silvano 2013). The Barbour WMA/Wehle Tract landscape contained 1,835 stands and management units, and the Perdido WMA contained 703 stands and management units. Because of the probabilistic nature of the model, there is some uncertainty in projected stand conditions, which increases with time. However, the habitat state with the most relevance to tortoises (uneven-aged pine) overall had a high (≥ 75%) probability of being achieved in target stands in 100 years (Silvano 2013). Thus, at the end of the 100 year projection, any suitable habitat for tortoises has most likely been established, and the remaining uncertainty in the composition of unsuitable habitat types such as hardwood stands is unlikely to impact tortoise populations significantly.

Along with vegetation conditions, soil type is an important component of gopher tortoise habitat. Thus, soil type was classified into one of five suitability categories (Highly Suitable, Moderately Suitable, Less Suitable, Marginal, and Unsuitable) according to the USFWS and NRCS (2012) classification scheme (Table 3.2) and was used in addition to the projected stand data for determining habitat quality. Highly Suitable soils represent deep, sandy, well-drained soils that are preferred by tortoises and support the highest densities of tortoise populations. Moderately Suitable soils are somewhat preferred by tortoises and have few restrictive features, and generally support average to above average population densities. Less Suitable soils contain some features that may limit the establishment or maintenance of burrows on the site, and burrow densities may be below average. Marginal soils contain limiting or restrictive features such that population density will be limited on the site; tortoises are generally expected to choose marginal soils only when other habitat factors (such as extremely dense vegetation) prohibit the use of preferred soil types. Unsuitable soils have properties that prevent the establishment and/or maintenance of tortoise burrows, such as a high water table, frequent flooding, or a high percentage of gravel fragments.

Table 3.2. Gopher tortoise soil suitability ranking criteria. Adapted from USFWS and NRCS (2012).

Suitability Ranking:	Highly Suitable	Moderately Suitable	Less Suitable	Marginal	Unsuitable
Flooding	None	None to Rare	None to Rare	None to Occasional	All Others
Ponding	None	None	None	None to Rare	All Others
Medium and coarse gravel fragments	< 15%	< 15%	< 15%	≥ 15%	> 35%
Depth to seasonal high water table	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Depth to restrictive layer	≥ 80"	≥ 60"	≥ 60"	≥ 20"	< 20"
Percent sand	≥ 70%	≥ 50%	≥ 30%	≥ 15%	< 15%
Percent clay	≤ 15%	≤ 18%	≤ 35%	≤ 60%	> 60%
Slope	≤ 15%	≤ 15%	≤ 15%	> 15%	> 35%

To incorporate habitat quality into the model, each cell was assigned a maximum number of tortoises it could hold ("carrying capacity"). More suitable habitat was assigned a higher carrying capacity, reflecting the greater tortoise densities that can be achieved in better suited habitat. Unsuitable habitat was assigned zero carrying capacity, preventing modeled tortoise individuals from occupying these habitat types. As the landscape changes through time, areas of previously suitable habitat may become unsuitable, requiring tortoises to leave those cells. If the number of tortoises within a habitat cell exceeds its carrying capacity, some individuals will shift their location to other cells (see section on tortoise movement below).

Separate carrying capacities were assigned to the various stand states and soil suitability categories (Tables 3.3 and 3.4). The final carrying capacity rasters were determined by the lowest carrying capacity of either the stand type or the underlying soil category. For example, if the stand type carrying capacity of a particular cell was 5 but the soil category carrying capacity of that cell was 1, then the final carrying capacity for that cell was 1. Thus, carrying capacity was determined by the most limiting habitat factor. These carrying capacity rasters were created using each year of the 100 year stand projection by Silvano (2013), resulting in 100 carrying capacity rasters for each of the 11 alternatives and each study area. Stand and soil data were converted to a raster format with a 100 m x 100 m (1 ha) cell size using ArcMap v. 10.3 (Environmental Systems Research Institute, Redlands, CA). The carrying capacity maps were changed at the beginning of each year for the first 100 years of the population model projection.

Estimates of tortoise density vary and depend on habitat quality, but estimates of overall population density often range from less than 1 to approximately 3 tortoises/ha (Hermann et al. 2002, Guyer et al. 2012, Ballou 2013, USFWS and SERPPAS 2013, Tuberville et al. 2014). These estimates are often for broad areas, however, such as all suitable tortoise habitat on tracts of publicly owned land. Gopher tortoises may be aggregated in some relatively small, high-quality habitat patches, such as wildlife openings with abundant herbaceous groundcover. Thus, it is not likely that each 1 ha cell of habitat on the landscape would be strictly limited to three or fewer tortoises. While Westervelt and MacAllister (2012) did limit the maximum carrying capacity of habitat in their simulation to 3 tortoises/ha, Tuberville et al. (2012) set a maximum carrying capacity of 9.7 tortoises/ha on "Priority" soil types with zero basal area of tree cover.

My model seeks to balance strictly limiting population density on the landscape and allowing more tortoises to exist within any particular 1 ha cell. Thus, the maximum carrying capacity per 1 ha cell was set to 7; this value was used for the highest soil suitability category and the two most highly suited stand states (Tables 3.3 and 3.4).

Table 3.3. Maximum number of tortoises that each cell of the carrying capacity rasters could hold based on the 25 stand state used by Silvano (2013).

State	Maximum number of tortoises per 1 ha cell (Carrying Capacity)
Open (Pine)	7
Unevenaged Pine	7
Ag (Pine)	5
Trees >12dbh pine	5
Two age pine	5
Disturbed (to Pine)	3
Seedling/Sapling pine	3
Poles/Small trees pine	3
Developed	1
Hardwood	0
Mixed Pine/Hardwood	0
Bottomland/Riparian	0
Hardwood savannah	0
Ag (Hardwood)	0
Open (Hardwood)	0
Disturbed (to Hardwood)	0
Hardwood	0
Seedling/Sapling hardwood	0
Poles/Small trees hardwood	0
Trees >12dbh hardwood	0
Two age hardwood	0
Unevenaged Hardwood	0
Water	0

Table 3.4. Maximum number of tortoises that each cell of the carrying capacity rasters could hold based on USFWS and NRCS (2012) soil suitability categories.

Soil Suitability Category	**Maximum number of tortoises per 1 ha cell (Carrying Capacity)**
Highly Suitable	7
Moderately Suitable	5
Less Suitable	3
Marginal	1
Unsuitable	0

Population augmentation alternatives

In addition to the 11 habitat management alternatives, I evaluated the effects of adding additional tortoises to each site. Relocation is a commonly employed management strategy for gopher tortoises, with the species being the target of numerous and extensive relocation/translocation efforts (Dodd and Seigel 1991). Tortoises that are displaced by situations like development (Dodd and Seigel 1991) are often candidates for relocation. Waif tortoises, i.e., tortoises originating from an unknown location which may have been moved by humans, also may require relocation. The Barbour/Wehle area was a relocation site in the past, and tortoises could potentially be moved there again in the future. Perdido WMA could also be considered as a potential relocation site in the future, particularly if habitat conditions become more favorable for tortoises. The augmentation scenarios were evaluated under each of the 11 habitat management alternatives, in addition to the 11 habitat management alternatives without augmentation.

I evaluated one population augmentation scenario for Barbour/Wehle and two for Perdido. Because the population at Barbour/Wehle is small and limited in extent, the augmentation scenario focused on adding additional tortoises to an area surrounding known burrow locations in the Wehle area. Under this scenario, 25 tortoises were added to two contiguous patches of Less Suitable and Marginal soils in the Wehle Tract area (Figure 3.4), which also encompassed the starting area for the initial tortoises in the population projection (see initialization section below). The western patch was approximately 104 ha, and the eastern patch was approximately 90 ha. Additional tortoises were added to random locations within this area in June of year 10 in the simulation. Tortoises were randomly assigned sex (with an equal probability of being either sex). Because relocated or translocated tortoises are often random individuals opportunistically taken from various sources, age was randomly assigned from an integer drawn from a uniform distribution between 5 and 60, encompassing a wide range of subadult and adult tortoise ages. Thus, the ages of reintroduced individuals were randomly assigned in each iteration.

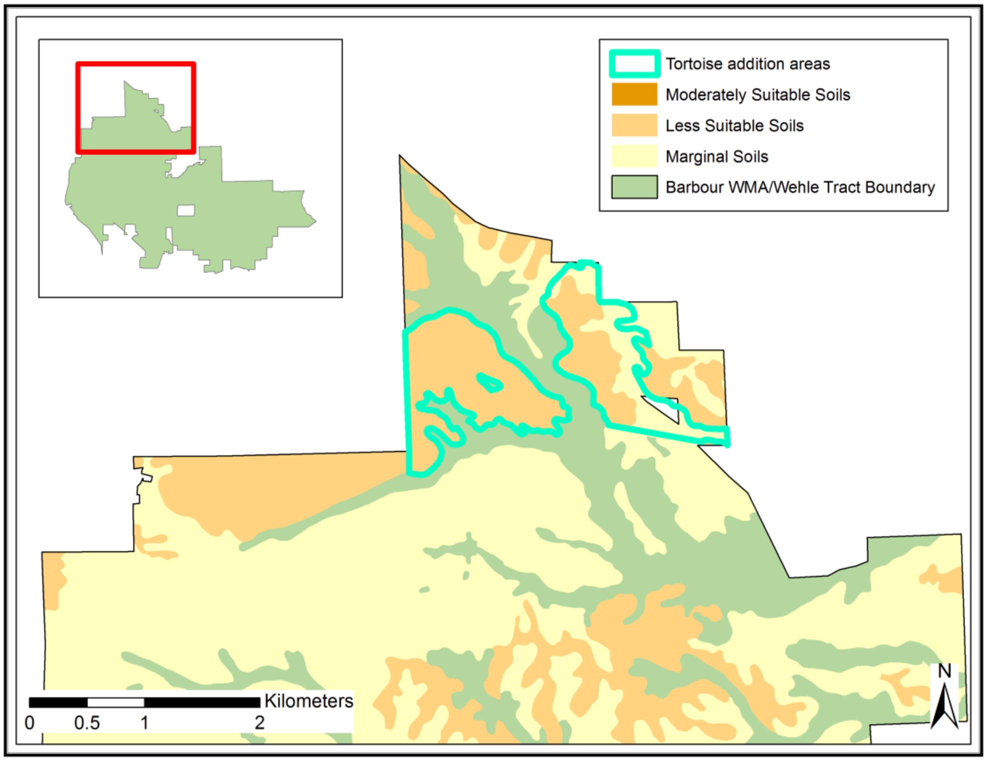


Figure 3.4. Areas where tortoises were added during population augmentation scenarios at the Barbour Wildlife Management Area and Wehle Forever Wild Tract.

For Perdido WMA, I evaluated two population augmentation scenarios. On the southern end of the Perdido WMA property, there are two relatively large contiguous patches of Highly Suitable soils. The northern patch is approximately 223 ha, while the southern patch is approximately 303 ha. These two patches were chosen for tortoise additions in the population augmentation scenarios (Figure 3.5). In one scenario, 25 tortoises were added to each patch in random locations. In the other scenario, 50 tortoises were added to the northern patch only. Thus, these scenarios compared adding 50 tortoises to a single patch vs. spreading them out evenly between two patches. Age and sex were assigned to the additional tortoises in the same manner as the Barbour/Wehle augmentation scenario. Both of the Perdido WMA augmentation scenarios added tortoises in June of year 10, as in the Barbour/Wehle augmentation scenario.

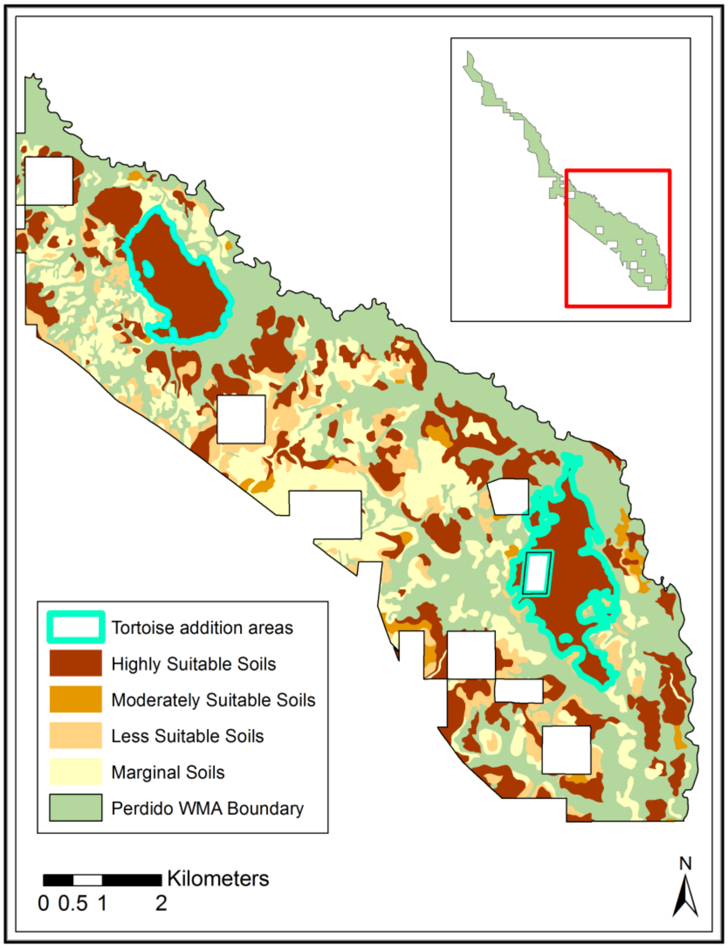


Figure 3.5. Areas where tortoises were added during population augmentation scenarios at the Perdido River Wildlife Management Area.

One important assumption behind these augmentation scenarios is that the added individuals have the same vital rates as the population they are being added to. Translocated gopher tortoises often have high dispersal rates and may travel relatively far distances post-translocation, which can result in low retention rates in translocated populations (Lohoefener and Lohmeier 1986, Burke 1989, Tuberville et al. 2005, 2008, Sasser and Soehren 2006, Ashton and Burke 2007). However, translocated individuals remaining after about 1 year post-translocation, once established, apparently have survival and retention rates similar to previously established individuals (Ashton and Burke 2007, Tuberville et al. 2008). The augmentation scenarios evaluated here thus assume that the tortoises added represent individuals that became established through a translocation or relocation effort. If such a translocation effort were to be implemented, managers would need to account for the likelihood of less than 100% retention rates of newly released individuals.

Reproduction

Reproduction in this model had two main components: egg laying and egg hatching. Gopher tortoises typically nest in the late spring and early summer, from late May and early to mid June (Landers et al. 1980, Epperson and Heise 2003). Thus, egg laying in the model occurred every June (month 6). Additionally, females only laid eggs if there was a male within a 500 m radius of their location at any time during the past year. Most mating attempts between gopher tortoises occur in the late summer and early fall, though mating attempts do occur throughout the active season (Johnson et al. 2007). Female gopher tortoises are known to store sperm (Rostal 2014), and they likely store sperm at least over the winter (Johnson et al. 2007). However, the relationship between mating events and ovulation in females remains poorly understood (Rostal 2014). Thus, I chose to limit egg laying to females that could have potentially encountered a reproductive-aged male in the past year. The 500 m radius limit prevents isolated females in the modeled landscape from breeding. While most male movements to visit female burrows are believed to be < 200 m, males have also been known to travel greater distances (e.g., 800 m) to visit females (Guyer et al. 2012). A radius of 500 m allows for the possibility of males travelling greater distances, while still preventing very isolated females from breeding.

Sexual maturity in tortoises is determined by size, and the age at which they achieve the size of maturity varies with habitat suitability and local climate (Mushinsky 2014). Aresco and Guyer (1999) estimated age at first reproduction at 20 years for pine plantations (poor quality tortoise habitat) in south-central Alabama. Males may reach sexual maturity at a smaller size and thus at a younger age than females (Landers et al. 1982). In this model, individuals were considered capable of reproduction at 20 years of age for females and 18 years of age for males.

Clutch size is expected to be positively related to female body size in gopher tortoises (Averill-Murray et al. 2014). Clutch sizes tend to be larger towards the southern portion of the gopher tortoise's range (i.e., in Florida) (Ashton et al. 2007). Unfortunately, there is no published data available on gopher tortoise clutch sizes in Alabama. One study conducted in north Florida found mean clutch sizes ranging from 4.4 to 5.33 (Perez-Heydrich et al. 2012). One Mississippi study found a mean clutch size of 4.8 (Epperson and Heise 2003). Other studies from Mississippi, Louisiana, and Georgia have found mean clutch sizes ranging from 4.5 to 7 (reviewed by Averill-Murray et al. 2014). For this study, I chose a conservative estimate of 5 eggs per female for average clutch size. For each female that had seen a male within the past year, a value was drawn from a Poisson distribution with a mean of 5 each year in June; that number was added to the total number of eggs in the cell (patch) that the female was located on. The total number of eggs in a cell was stored as a patch variable, i.e., the model stores the number of eggs in a variable unique for each patch. Values were drawn from the Poisson distribution using R v. 3.2 (R Core Team 2015) and the R-Extension for NetLogo (Thiele and Grimm 2010).

Gopher tortoise clutches typically hatch from mid to late August through September (Epperson and Heise 2003, Perez-Heydrich et al. 2012). In my model, egg hatching occurred in

September (month 9). Each patch iterated through the number of eggs it contained. If a randomly drawn number between 0 and 1 was greater than the egg mortality probability (see mortality section below), then the number of hatchlings within the patch increased by one. This process was repeated until there were no more eggs in the patch.

Tortoise growth

Tortoises increased in age in month 9 of each year, under the assumption that individuals hatched in September. Because hatchlings (tortoises less than one year old), like eggs, are considered non-mobile and do not leave the habitat cell they originate in, the number of hatchlings in each cell was stored as a patch variable. This reduced the overall number of agents tracked by the model at each time step, which reduces computation time for each run of the model. After one year, when hatchling tortoises would reach one year of age, they were sprouted from the patch as individual agents. In September, each hatchling either died or became a discrete agent based on a Bernoulli trial with the specified hatchling mortality probability. Each survivor would become an individual with age 1 and a randomly assigned sex (where there is an equal chance of being male or female), and the number of hatchlings in the patch was reduced by 1. This process repeated until there were no more hatchlings in the patch. While gopher tortoise sex is determined by the temperature of the incubation environment (Rostal and Wibbels 2014), the overall sex ratio for the simulated population (and thus survivors of the hatchling state) is assumed to be 1:1.

Mortality

To capture variability in mortality probability at various life stages, different survival probabilities were assigned to tortoises based on age (Table 3.4). Egg survival (i.e., nest survival) can be highly variable but is generally low, with predation being a major cause of mortality (Landers et al. 1980, Epperson and Heise 2003, Smith et al. 2013). Smith et al. (2013) assessed nest survival across three years at a site in southwestern Georgia, and found nest survival in unprotected nests as 34.93% (± 10.34% SE) and in protected nests as 66.41% (± 9.65% SE), where nests were protected via fences excluding mid-sized mammalian predators. It is unknown what the nest predation levels may be on either the Barbour/Wehle area or the Perdido WMA, though nests are likely subjected to a wide variety of predators. Mean survival probability of eggs for this study was set at 0.4, with significant yearly variation.

Mortality is high during the first year of life for gopher tortoises, often exceeding 90% (Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006, Perez-Heydrich et al. 2012). The survival probability of 0.128 used in this study is based on the meta-analysis and field study conducted by Perez-Heydrich et al. (2012). There is very little information on the survival of gopher tortoises past the first year of life, in the juvenile stage. Gopher tortoises in the juvenile stage (1-4 years old) have relatively soft carapaces and plastrons (Landers et al. 1982), making them vulnerable to predation (Wilson 1991). One study was conducted on tortoises of this age class in west-central Florida, and found bimonthly survival rates of 0.69 (0.62-1.0, 95% confidence interval), 0.89 (0.88-1.0, 95% confidence interval), and 0.74 (0.67-1.0, 95% confidence interval), with survival of 1.0 for all other bimonthly periods (Wilson 1991). Like juveniles, the subadult age class also has very limited survival data available. Tuberville et al. (2008) assessed the long-term (over 12 years) survival of a translocated population of tortoises on St. Catherine's Island, Georgia, and found that sexually immature tortoises, which included "subadults" and "juveniles" but did not distinguish between the two, had a survival of 0.84 ± 0.05, which was lower than the 0.98 ± 0.01 survival estimate for adults. Adult gopher tortoises are believed to have very high survival, though there are few long term studies available. In addition to the Tuberville et al. (2008) translocation survival study, Ashton and Burke (2007) found a 98.5% retention rate of adult tortoises between 2 and 17 years post-relocation in southern Florida. Tuberville et al. (2014) estimated adult survival at 94.6% ± 3.9% for males and 98.0% ± 2.8% for females at the Conecuh National Forest in south-central Alabama, and at 86.8% ± 3.8% for males and 95.5% ± 2.2% for females at the Green Grove site on the Jones Ecological Research Center in southwestern Georgia.

Two levels of uncertainty and variability were incorporated into survival probabilities: scientific uncertainty about long-term average survival and natural year-to-year variation. The former was incorporated by randomly drawing a mean long-term survival value held fixed for each iteration; the latter was incorporated by randomly drawing survival rates from a distribution with the selected long-term mean each year of the iteration. For each iteration, a mean survival value for that iteration was drawn from a beta distribution with shape parameters derived from the means and replicate standard deviations in Table 3.4. At the beginning of each year, an annual survival probability was drawn from a beta distribution with shape parameters derived from the mean survival value of the replicate and the annual standard deviations in Table 3.4. The annual survival probability was converted to a monthly probability, under the assumption that survival is equal across months. At each time step for each tortoise, a random number was drawn between 0 and 1; if this value was less than the probability of mortality corresponding to that tortoise's age, the tortoise would die. Shape parameters were calculated and values were drawn from beta distributions in R using the R-Extension for NetLogo.

Table 3.4. Mean survival probabilities and variation for replicates used in the population projection model.

Tortoise Age	Mean Survival Probability	Standard deviation for replicates	Standard deviation for years	Key References
Egg	0.4	0.05	0.1	Smith et al. (2013)
Hatchling (< 1 year)	0.128	0.05	0.1	Perez-Heydrich et al. (2012)
Juvenile (1-4 years)	0.5	0.07	0.07	Wilson (1991)
Subadult (5-14 years)	0.9	0.05	0.05	Tuberville et al. (2008)
Adult (15 years)	0.97	0.02	0.01	Tuberville et al. (2014)

Movement

As described above, individual tortoises occupied 1 ha cells that were assigned a carrying capacity based on the habitat suitability. Tortoises would only move from a cell if the number of tortoises in that cell increased above the carrying capacity or if the changing habitat conditions resulted in a decrease in carrying capacity of the cell below the number of tortoises residing in it. Burrow abandonment in tortoises is known to be related to habitat conditions (Aresco and Guyer

1999*b*, Jones and Dorr 2004). Because density estimates are usually based on older age classes, this procedure was limited to subadults and adults. If the number of tortoises in a cell increased above carrying capacity, the youngest tortoise at least five years of age was moved from the cell. This tortoise would assess its eight neighboring cells, and move to the one with the most space available (where space is carrying capacity minus the number of tortoises five years of age or older). If none of the surrounding neighbors had space, the tortoise would randomly choose one of the eight neighboring cells to move to. It would then again check for neighbors with available space and either move to the neighbor with the most space if available, or move to a randomly chosen neighboring cell. Thus, a tortoise was allowed to move twice within a single time step if it did not find a cell with space on the first try. If the tortoise was randomly choosing a cell to move to (i.e., none had space available), its choices would be limited to cells it had not occupied within the past year. This was to prevent tortoises from randomly moving back to cells known to be unsuitable. A list of patches visited was maintained for each tortoise and cleared at the end of each year. If a tortoise randomly chose to move to a cell outside of the study area, it would have a 6% chance of dying (to simulate leaving the property altogether) and a 94% chance it would return to the property on a neighboring cell. The relatively low chance of "dying" (leaving the property) prevents large numbers of tortoises from dying if they happen to reside near the edge of the property, but still allows for the possibility that an individual may move off the study area. Juvenile tortoises (1-4 years old) were only allowed to move if the cell they were on had a carrying capacity of zero, in which case they followed the same procedure described above. Movement occurred only during the active season for gopher tortoises (from April through October). If a tortoise was on unsuitable habitat (carrying capacity of zero) in November it would die, as tortoises cannot overwinter in unsuitable habitat.

Initialization

For the Barbour/Wehle area, the model was initiated with 16 tortoises at 20 years of age (adults); three more than the 13 from the reintroduction effort that were known to occur on the Wehle Tract as of 2013 (E. Soehren, personal communication), to account for the likelihood that some individuals were undetected by surveys. It is not clear whether reproduction is occurring at this site; thus, no hatchlings, juveniles, or subadults were created for the initialization. Additionally, while the tortoises known to occur on this site are adults, the exact age of these individuals is unknown, making more accurate assignment of age difficult. The starting population of tortoises was placed randomly within contiguous patches of Less Suitable soils in the Wehle Tract area, in cells that also had a carrying capacity > 0, encompassing the known locations of tortoises as of 2013 and the original release locations of the translocation efforts (Figure 3.6). The starting area was 156 ha in size. Individuals were randomly assigned sex, with an equal probability of being male or female.

Figure 3.6. Potential starting cells for the initial tortoise population at the Barbour Wildlife Management Area and Wehle Forever Wild Tract study area.

At Perdido WMA, recent (2015) line transect density surveys estimated the tortoise population size at 434 (266-711, 95% confidence interval) individuals (S. M. Hermann, unpublished data). To capture the uncertainty in the initial population size, the number of individuals in the starting population was drawn from a normal distribution with a mean of 434 and a standard deviation of 113.52 for each iteration. Following Tuberville et al. (2012), tortoises in the starting population were assigned age based on the absolute value of a random number drawn from a normal distribution with a mean of 0 and a standard deviation of 30. Thus, the age distribution of the starting population had greater frequencies of younger individuals, with tortoises with older ages being less frequent. However, because line transect burrow surveys for gopher tortoises primarily estimate the population size of older age classes (because very young tortoises have a low detection probability), if the randomly drawn age was less than 5 the age would be drawn again for that tortoise. At the start of each iteration, the starting population followed the reproduction, egg hatching, and hatchling growing procedures instantaneously to produce an initial population of hatchlings, eggs, and juveniles. As with the Barbour/Wehle site, a 1:1 sex ratio of the population was assumed, and individuals were randomly assigned sex with an equal probability of being male or female. The initial population of tortoises on Perdido WMA was randomly distributed on contiguous patches of Highly Suitable soils 5 ha in size or larger that had non-zero carrying capacity under initial landscape conditions (Figure 3.7). The potential starting area covered 1,647 ha.

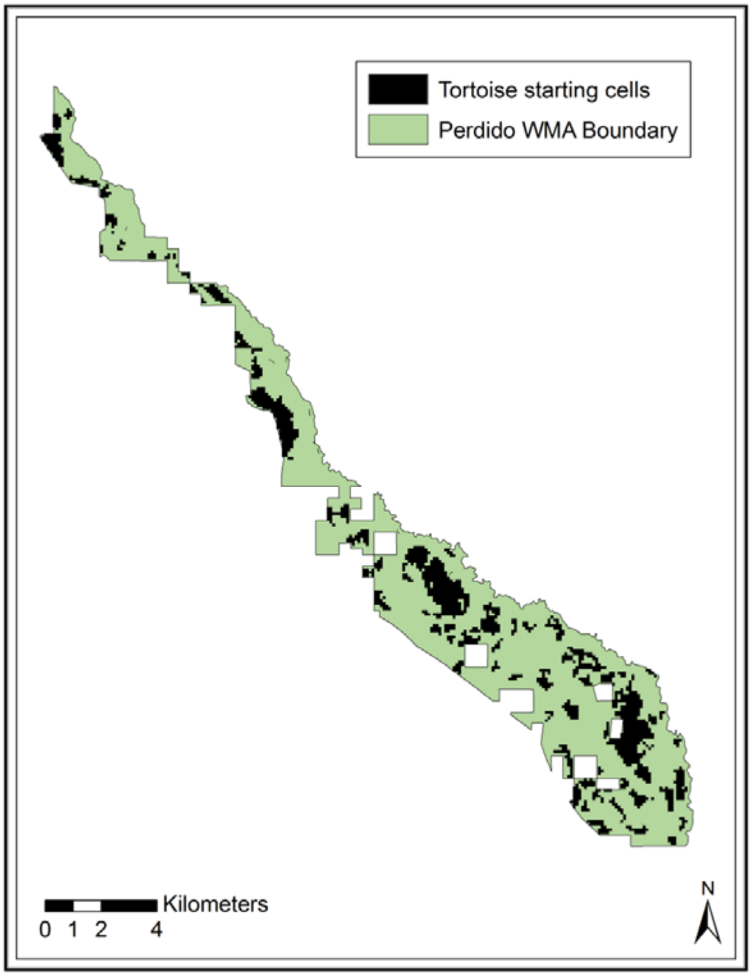


Figure 3.7. Potential starting cells for the initial tortoise population at the Perdido River Wildlife Management Area study area.

Analysis

Data analysis was done using R v. 3.2, and output spatial data was summarized using ArcMap v. 10.3. For each iteration of the population projection, an output raster map was generated at the 100 and 200 year time steps with each cell of the output raster given a value of 1 if it was occupied by at least one tortoise age 1 or older (juveniles and older), and a 0 otherwise. These rasters were added for each alternative, thus showing the number of times (out of the 1,000 iterations of the model) that a given cell of the landscape was occupied by at least one tortoise after 100 and 200 years. All analyses on population size included the total population of tortoises tracked individually by the model as agents (not stored as patch variables), thus including all individuals at least one year of age and older. For each iteration, the population size at 100 and 200 years was compared to the starting population size of that iteration; the mean percent change between these time steps and the initial population size was then calculated by averaging across all iterations for each alternative. Extinction probability after 100 and 200 years was calculated as the number of iterations in which population size reached fewer than 2 individuals (age 1 or older) by those time steps, out of the total number of iterations, for each alternative.

Matrix population model

I developed a stage-based stochastic matrix population projection model in R v. 3.2 to compare with the results of the individual-based spatially explicit model. Tortoises were divided into one of five stages, corresponding to the age classes with different survival probabilities in the individual-based model: eggs, hatchlings (< 1 year old), juveniles (1 - 4 years old), subadults

(5 - 19 years old), and adults (≥ 20 years old). The model was run for 200 yearly time steps and 10,000 iterations. Survival values were derived in much the same way as in the individual-based model. For each iteration, a mean survival probability for the iteration was drawn from a beta distribution created with the mean and standard deviations for replicates presented in Table 4. At each time step, the mean survival for the replicate and the annual standard deviations presented in Table 4 were used to create another beta distribution from which the annual survival for that time step was drawn. Because juveniles and subadults stay in their age class for multiple time steps before advancing to the next stage, survival probabilities for these age classes were converted to probabilities of surviving and staying in the age class and probabilities of surviving and advancing to the next age class using the equations provided in Crouse et al. (1987). The number of eggs produced each year was drawn from a Poisson distribution with a mean of 5, multiplied by half the adult population at that time step (assuming a 1:1 sex ratio and all females breed in a given year). Only adults (≥ 20 years of age) produced eggs.

The transition matrix consisted of annual survival probabilities and fecundity, and was multiplied by the population vector at each time step. Two initial (starting) populations were tested. The larger starting population consisted of 250 adults, 125 subadults, 125 juveniles, 250 hatchlings, and 500 eggs - a large enough population to be considered viable under the current estimate of a minimum viable population for gopher tortoises (250 adults) (Gopher Tortoise Council 2013). The second starting population consisted of 16 adults - the same as the starting population in the Barbour WMA individual-based projections. Extinction probability, defined as the number of times the population reached fewer than 2 individuals (juveniles or older) out of the 10,000 iterations, was calculated at the 100 and 200 year time steps. Population size of each age class was also recorded for every time step.

Results

At both study areas, under all habitat management alternatives and population augmentation scenarios tested, there was a significant decline in total tortoise abundance over time, approaching zero tortoises after 200 years (Figures 3.8 - 3.12), corresponding to declines of over 90% of initial population sizes. For both study areas and all population augmentation scenarios, different habitat management alternatives resulted in similar mean population sizes (Figures 3.8 - 3.12, Tables 3.6 - 3.10). The greatest differences between habitat management alternatives were typically seen around year 50 (Figures 3.8 - 3.12), but differences appeared relatively minor. The only population increase observed was at the Barbour/Wehle study area under the population augmentation scenario, where the population initially increased following the addition of tortoises at year 10 under all habitat management scenarios, but then declined substantially by year 100 (Figure 3.9).

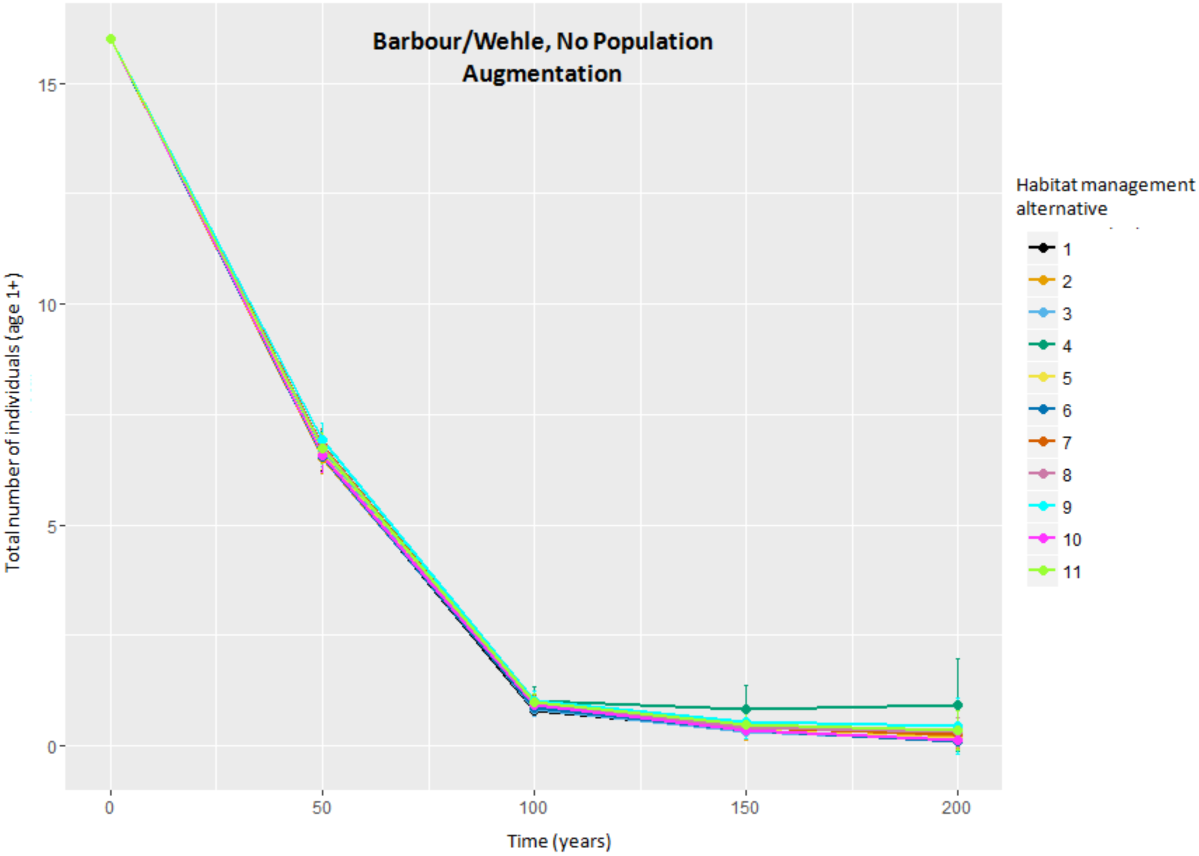


Figure 3.8. Mean and 95% confidence intervals for total population size (tortoises 1 year of age and older) under 11 habitat management alternatives at selected time points corresponding to 50 years, 100 years, 150 years, and 200 years at the Barbour Wildlife Management Area/Wehle Forever Wild Tract study area under the no population augmentation scenario.

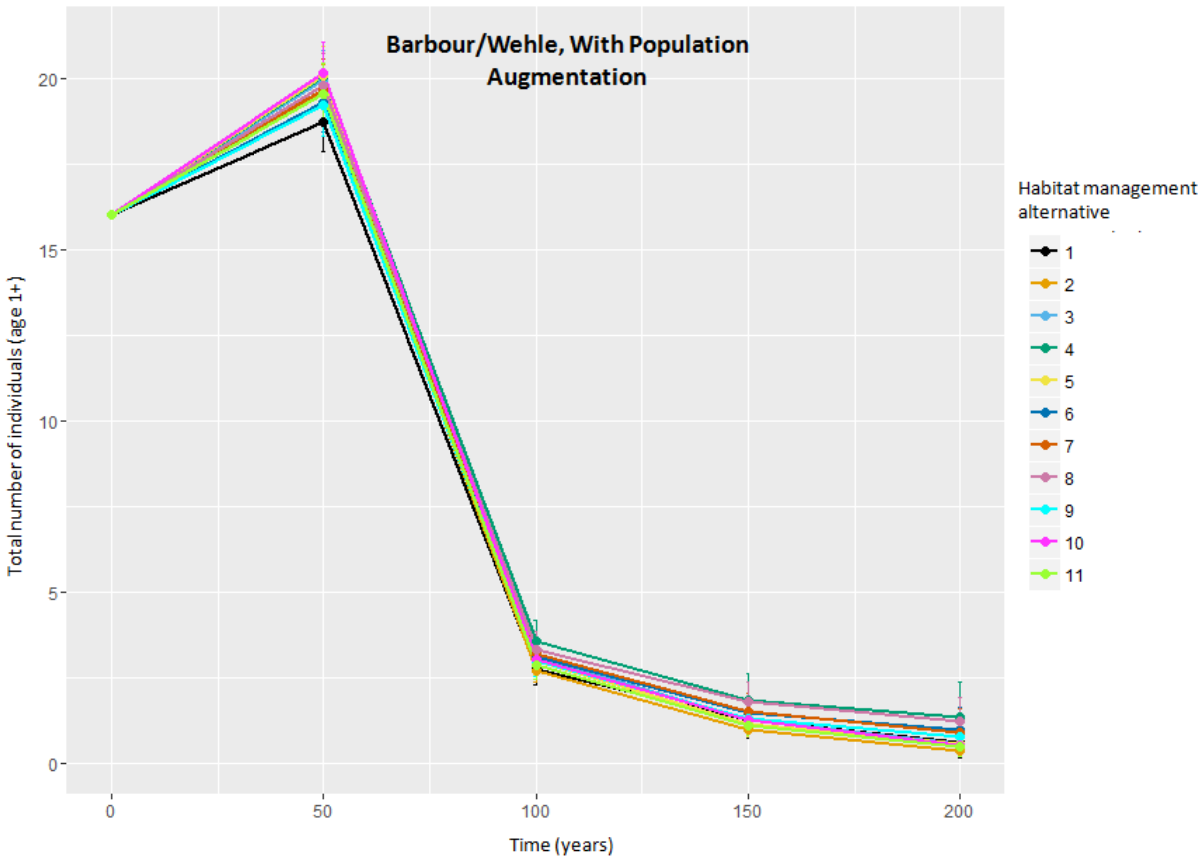


Figure 3.9. Mean and 95% confidence intervals for total population size (tortoises 1 year of age and older) under 11 habitat management alternatives at selected time points corresponding to 50 years, 100 years, 150 years, and 200 years at the Barbour Wildlife Management Area/Wehle Forever Wild Tract study area under the population augmentation scenario (25 additional tortoises added in year 10).

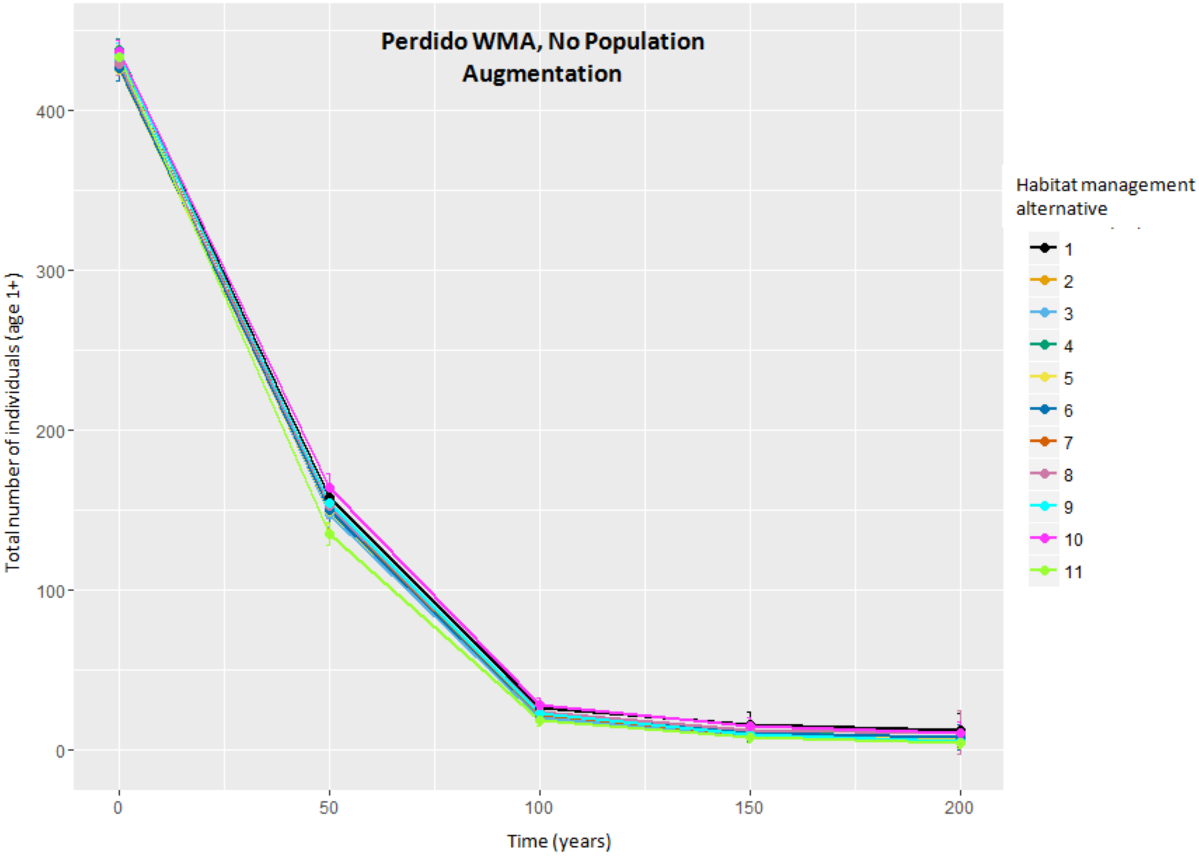


Figure 3.10. Mean and 95% confidence intervals for total population size (tortoises 1 year of age and older) under 11 habitat management alternatives at selected time points corresponding to 50 years, 100 years, 150 years, and 200 years at the Perdido River Wildlife Management Area study area under the no population augmentation scenario.

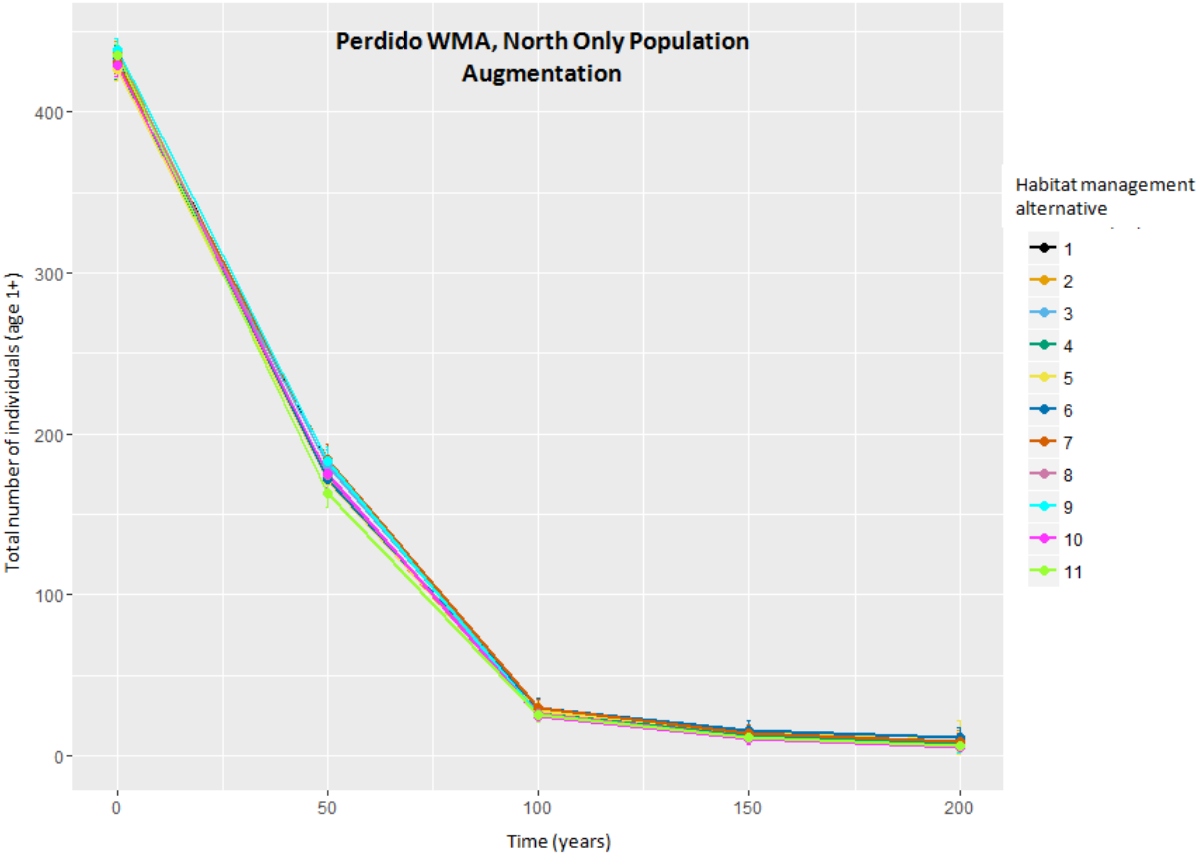


Figure 3.11. Mean and 95% confidence intervals for total population size (tortoises 1 year of age and older) under 11 habitat management alternatives at selected time points corresponding to 50 years, 100 years, 150 years, and 200 years at the Perdido River Wildlife Management Area study area under the North population augmentation scenario (50 tortoises added to the northern reintroduction area in year 10).

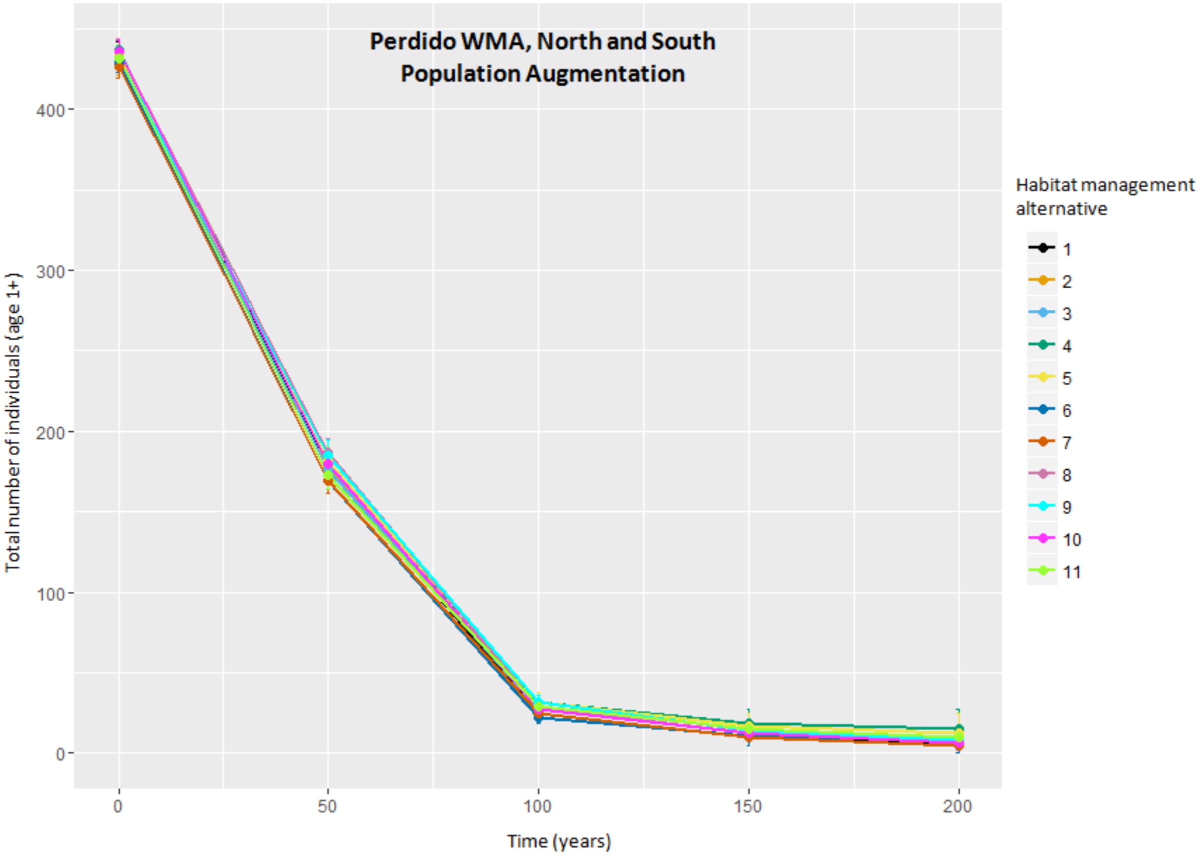


Figure 3.12. Mean and 95% confidence intervals for total population size (tortoises 1 year of age and older) under 11 habitat management alternatives at selected time points corresponding to 50 years, 100 years, 150 years, and 200 years at the Perdido River Wildlife Management Area study area under the North and South population augmentation scenario (25 tortoises added to the northern reintroduction area and 25 tortoises added to the southern reintroduction area in year 10).

Table 3.6. Initial population size, population size after 100 years, population size after 200 years, and percent change from the initial population size with standard errors (SE) for the Barbour Wildlife Management Area/Wehle Forever Wild Tract study area under 11 habitat management alternatives and the no population augmentation scenario. Population sizes include all tortoises 1 year of age and older.

Barbour/Wehle, Without Population Augmentation					
Alternative	Initial Population Size	Population Size After 100 Years (SE)	Percent Change (SE)	Population Size After 200 Years (SE)	Percent Change (SE)
1	16	0.81 (0.07)	-94.95 (0.46)	0.16 (0.05)	-98.99 (0.34)
2	16	0.92 (0.12)	-94.26 (0.77)	0.21 (0.14)	-98.68 (0.86)
3	16	0.82 (0.07)	-94.88 (0.44)	0.14 (0.04)	-99.16 (0.26)
4	16	1.02 (0.15)	-93.60 (0.96)	0.92 (0.54)	-94.24 (3.38)
5	16	0.89 (0.08)	-94.46 (0.51)	0.15 (0.06)	-99.09 (0.35)
6	16	0.84 (0.08)	-94.73 (0.48)	0.09 (0.03)	-99.47 (0.16)
7	16	0.94 (0.10)	-94.11 (0.60)	0.26 (0.10)	-98.39 (0.60)
8	16	0.91 (0.10)	-94.34 (0.62)	0.31 (0.17)	-98.06 (1.06)
9	16	1.01 (0.12)	-93.70 (0.75)	0.44 (0.33)	-97.24 (2.05)
10	16	0.92 (0.08)	-94.25 (0.53)	0.11 (0.04)	-99.29 (0.22)
11	16	0.97 (0.10)	-93.91 (0.63)	0.35 (0.23)	-97.83 (1.41)

Table 3.7. Initial population size, population size after 100 years, population size after 200 years, and percent change from the initial population size with standard errors (SE) for the Barbour Wildlife Management Area/Wehle Forever Wild Tract study area under 11 habitat management alternatives and the population augmentation scenario (25 tortoises added in year 10). Population sizes include all tortoises 1 year of age and older.

Barbour/Wehle, With Population Augmentation					
Alternative	Initial Population Size	Population Size After 100 Years (SE)	Percent Change (SE)	Population Size After 200 Years (SE)	Percent Change (SE)
1	16	2.75 (0.23)	-82.81 (1.45)	0.60 (0.24)	-96.23 (1.49)
2	16	2.69 (0.18)	-83.18 (1.09)	0.34 (0.08)	-97.89 (0.51)
3	16	3.11 (0.22)	-80.59 (1.36)	0.55 (0.11)	-96.58 (0.71)
4	16	3.56 (0.30)	-77.78 (1.89)	1.32 (0.53)	-91.74 (3.28)
5	16	2.99 (0.21)	-81.30 (1.31)	0.56 (0.20)	-96.51 (1.24)
6	16	3.09 (0.29)	-80.70 (1.78)	0.95 (0.34)	-94.06 (2.15)
7	16	3.19 (0.24)	-80.04 (1.50)	0.89 (0.36)	-94.47 (2.25)
8	16	3.29 (0.27)	-79.47 (1.70)	1.22 (0.35)	-92.39 (2.18)
9	16	2.97 (0.23)	-81.47 (1.44)	0.76 (0.23)	-95.27 (1.46)
10	16	3.02 (0.20)	-81.10 (1.28)	0.50 (0.11)	-96.89 (0.68)
11	16	2.86 (0.21)	-82.11 (1.32)	0.47 (0.14)	-97.09 (0.88)

Table 3.8. Initial population size, population size after 100 years, population size after 200 years, and percent change from the initial population size with standard errors (SE) for the Perdido Wildlife Management Area study area under 11 habitat management alternatives and the no population augmentation scenario. Population sizes include all tortoises 1 year of age and older.

Perdido WMA, Without Population Augmentation					
Alternative	Average Initial Population Size (SE)	Population Size After 100 Years (SE)	Percent Change (SE)	Population Size After 200 Years (SE)	Percent Change (SE)
1	436.09 (3.61)	27.03 (2.73)	-93.79 (0.77)	12.22 (5.75)	-96.63 (1.98)
2	430.36 (3.54)	21.93 (1.83)	-95.15 (0.39)	4.77 (1.30)	-98.97 (0.29)
3	430.95 (3.60)	20.45 (1.74)	-95.29 (0.39)	5.77 (2.53)	-98.62 (0.62)
4	437.26 (3.50)	24.25 (2.08)	-94.58 (0.47)	7.52 (2.15)	-98.25 (0.53)
5	424.98 (3.46)	24.20 (2.01)	-94.50 (0.43)	6.75 (2.23)	-98.52 (0.44)
6	425.68 (3.63)	22.14 (2.29)	-95.00 (0.47)	8.42 (4.13)	-98.24 (0.81)
7	434.35 (3.66)	22.69 (1.80)	-94.87 (0.39)	5.56 (1.91)	-98.76 (0.43)
8	428.53 (3.60)	23.90 (2.53)	-94.41 (0.61)	10.96 (6.89)	-97.23 (1.72)
9	434.62 (3.68)	23.42 (1.96)	-94.80 (0.39)	5.66 (2.09)	-98.88 (0.36)
10	436.16 (3.64)	28.07 (2.52)	-93.70 (0.58)	10.60 (3.87)	-97.57 (0.89)
11	433.12 (3.69)	18.56 (1.62)	-95.91 (0.35)	4.34 (1.50)	-99.03 (0.37)

Table 3.9. Initial population size, population size after 100 years, population size after 200 years, and percent change from the initial population size with standard errors (SE) for the Perdido Wildlife Management Area study area under 11 habitat management alternatives and the North population augmentation scenario (50 tortoises added to northern reintroduction area in year 10). Population sizes include all tortoises 1 year of age and older.

Perdido WMA, North Only Population Augmentation					
Alternative	Average Initial Population Size (SE)	Population Size After 100 Years (SE)	Percent Change (SE)	Population Size After 200 Years (SE)	Percent Change (SE)
1	433.66 (3.65)	28.04 (2.17)	-93.65 (0.49)	6.86 (2.80)	-98.44 (0.63)
2	436.71 (3.77)	26.21 (2.39)	-93.93 (0.52)	9.09 (3.55)	-97.98 (0.77)
3	432.03 (3.45)	27.81 (1.99)	-93.71 (0.43)	5.59 (1.23)	-98.74 (0.27)
4	427.41 (3.63)	27.19 (2.03)	-93.51 (0.49)	7.05 (1.77)	-98.29 (0.42)
5	426.40 (3.61)	27.79 (2.81)	-93.56 (0.65)	11.16 (5.41)	-97.40 (1.29)
6	434.43 (3.67)	29.94 (2.87)	-93.10 (0.65)	10.99 (3.15)	-97.38 (0.77)
7	430.80 (3.67)	29.72 (2.47)	-93.17 (0.55)	8.87 (2.66)	-97.95 (0.55)
8	435.20 (3.47)	25.89 (2.19)	-94.20 (0.45)	5.92 (1.72)	-98.73 (0.35)
9	438.44 (3.50)	25.22 (2.12)	-94.36 (0.45)	5.61 (2.18)	-98.78 (0.45)
10	429.17 (3.63)	24.57 (1.94)	-94.39 (0.41)	5.26 (1.53)	-98.85 (0.32)
11	434.78 (3.62)	25.39 (2.07)	-94.21 (0.45)	6.18 (1.96)	-98.61 (0.41)

Table 3.10. Initial population size, population size after 100 years, population size after 200 years, and percent change from the initial population size with standard errors (SE) for the Perdido Wildlife Management Area study area under 11 habitat management alternatives and the North and South population augmentation scenario (25 tortoises added to the northern reintroduction area and 25 tortoises added to the southern reintroduction area in year 10). Population sizes include all tortoises 1 year of age and older.

Perdido WMA, North and South Augmentation					
Alternative	Average Initial Population Size (SE)	Population Size After 100 Years (SE)	Percent Change (SE)	Population Size After 200 Years (SE)	Percent Change (SE)
1	435.04 (3.69)	24.58 (1.78)	-94.27 (0.44)	5.27 (1.86)	-98.60 (0.59)
2	428.41 (3.48)	27.75 (2.21)	-93.57 (0.48)	6.70 (2.25)	-98.55 (0.43)
3	433.25 (3.54)	27.62 (2.29)	-93.68 (0.48)	8.02 (2.57)	-98.29 (0.49)
4	436.74 (3.48)	31.39 (3.12)	-92.62 (0.76)	15.37 (6.11)	-96.12 (1.65)
5	433.48 (3.53)	31.53 (3.02)	-92.87 (0.64)	12.46 (6.21)	-97.25 (1.29)
6	429.30 (3.36)	21.99 (1.86)	-94.91 (0.41)	8.07 (4.14)	-98.24 (0.89)
7	426.45 (3.55)	24.75 (1.85)	-94.11 (0.43)	4.71 (1.21)	-98.87 (0.27)
8	436.32 (3.72)	27.79 (2.30)	-93.62 (0.54)	7.88 (3.10	-98.11 (0.80)
9	431.84 (3.70)	31.23 (2.49)	-93.03 (0.51)	8.17 (1.77)	-98.25 (0.39)
10	435.85 (3.57)	26.91 (2.02)	-93.80 (0.45)	5.99 (1.53)	-98.64 (0.35)
11	431.80 (3.63)	29.29 (2.62)	-93.28 (0.60)	10.19 (3.49)	-97.67 (0.75)

Extinction probability, where extinction is defined here as fewer than 2 individuals age 1 or older remaining in the population, was high for both properties (averaged across all 11 habitat management alternatives) for both population augmentation and no augmentation scenarios (Table 3.11). Extinction probability for a given time step was calculated as the number of times a population reached extinction, out of the total number of iterations, for that time step. For the Barbour/Wehle area, extinction probability was > 60% after 100 years, and > 95% after 200 years (Table 3.11). However, extinction probability was lower under the population augmentation scenario, particularly at 100 years (64% with augmentation vs. 85% probability of extinction without augmentation). The Perdido WMA population had comparatively low extinction probability after 100 years under all scenarios, less than 35% (Table 3.11). Both population augmentation strategies, adding tortoises to the north augmentation area only and adding them to both the north and south areas, had similar extinction probabilities, though both were slightly lower than the no augmentation scenario (Table 3.11).

Table 3.11. Extinction probability averaged across all iterations including all 11 habitat management alternatives for the Barbour Wildlife Management Area and Wehle Forever Wild Tract study area and the Perdido River Wildlife Management Area study area. Extinction probability is defined here as the number of times the population reached fewer than 2 individuals out of the total number of iterations of the model at a given time step. Small differences among scenarios are meaningful given the high precision with which scenario extinction probabilities are estimated via simulation. For example, the maximum 95% confidence interval for this data, based on a binomial distribution and 11,000 total trials (i.e. iterations, 1,000 for each alternative) is approximately ± 0.01.

	Barbour/Wehle		**Perdido WMA**		
	No Augmentation	Population Augmentation	No Augmentation	North Augmentation	North and South Augmentation
Extinction Probability, 100 years	0.85	0.64	0.34	0.30	0.29
Extinction Probability, 200 years	0.98	0.96	0.89	0.87	0.87

Because of the consistent declines in populations, few cells of the simulated landscape were occupied by tortoises (juveniles and older) at the 100 and 200 year time steps. Cells that were occupied were generally limited to the starting area cells and close neighbors. After 200 years, fewer cells tended to be occupied and cells were occupied less often than at shorter time steps (e.g., 100 years). For both sites, population augmentation appeared to increase the probability of cells being occupied at later time steps (Figures 3.13 - 3.22). There was some difference among habitat management alternatives in the distribution of cells that were occupied at least once across the landscape. For example, at Perdido WMA, habitat management alternative 11 (minimum management scenario) had a more limited distribution of occupied cells than alternative 9 (all forest types except existing floodplain converted to uneven-aged pine; Figure 3.23).

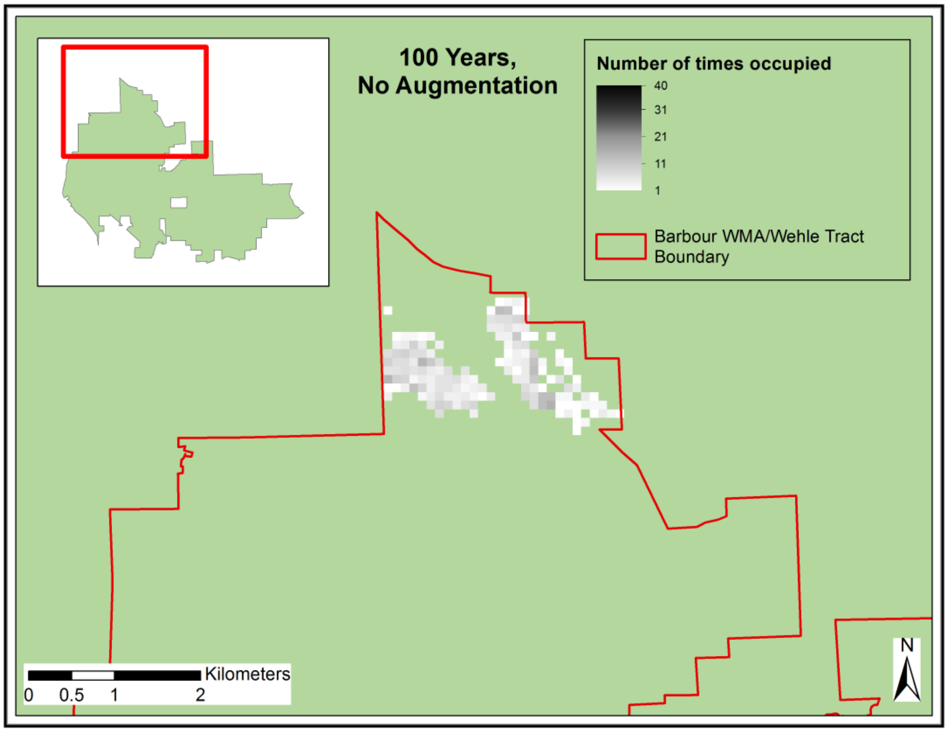


Figure 3.13. Number of times cells of the simulated Barbour Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 100 years of the no population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 100 year time step.

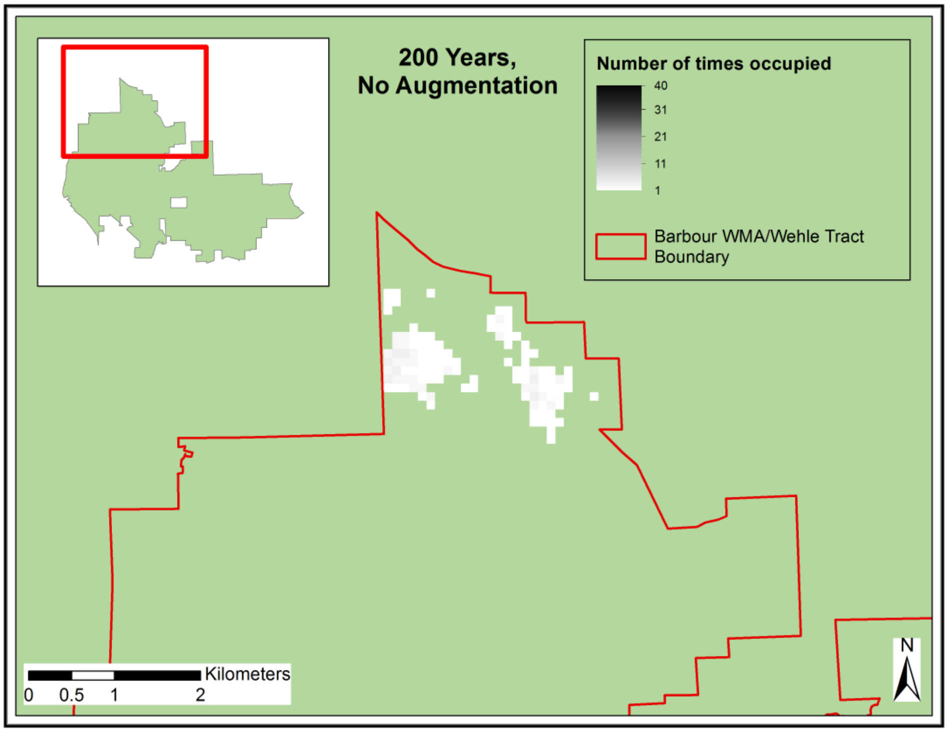


Figure 3.14. Number of times cells of the simulated Barbour Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 200 years of the no population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 200 year time step.

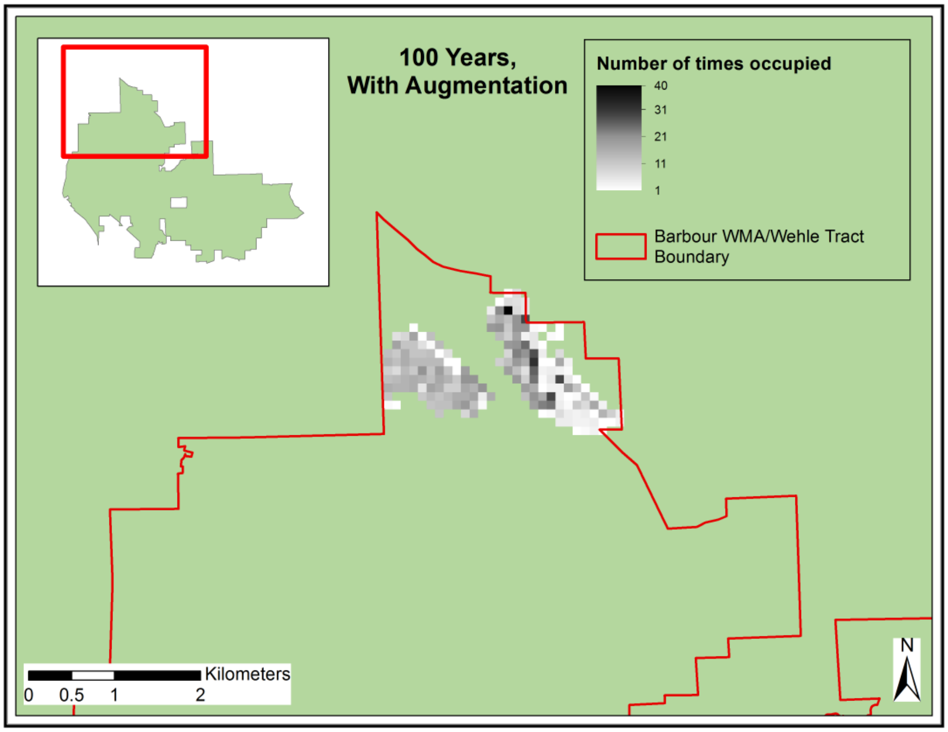


Figure 3.15. Number of times cells of the simulated Barbour Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 100 years of the population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 100 year time step.

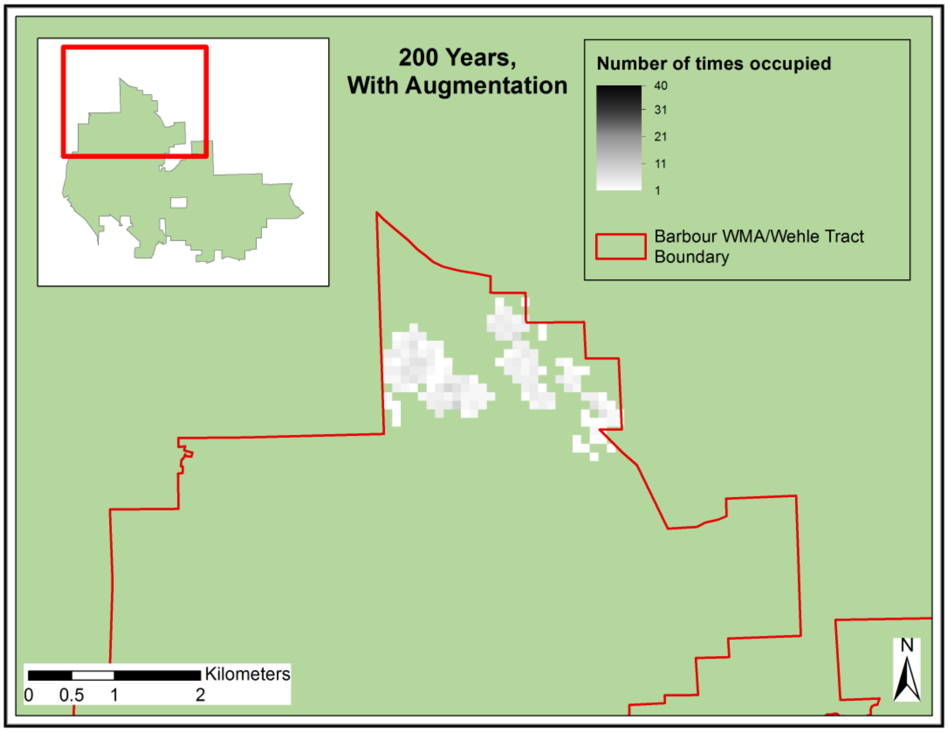


Figure 3.16. Number of times cells of the simulated Barbour Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 200 years of the population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 200 year time step.

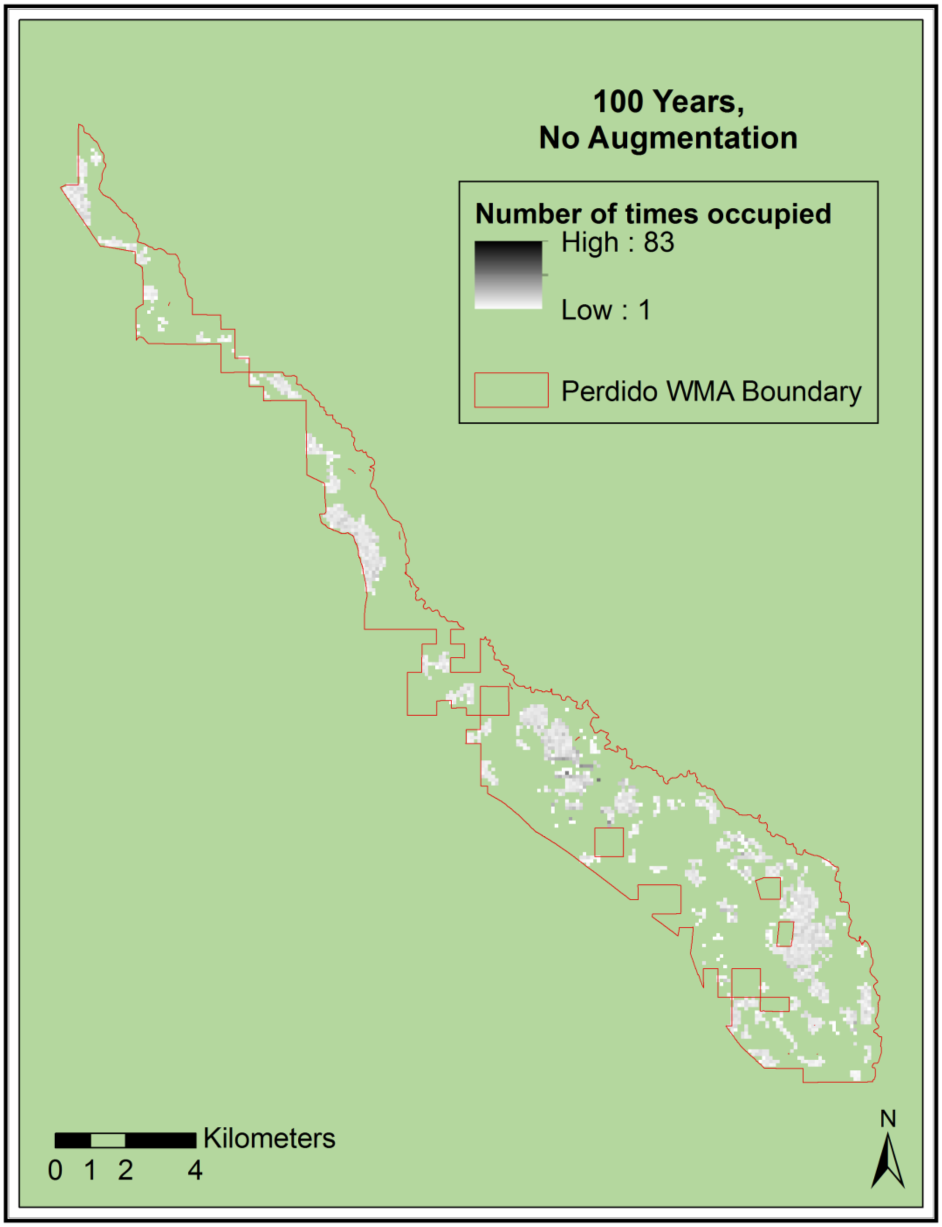


Figure 3.17. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 100 years of the no population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 100 year time step.

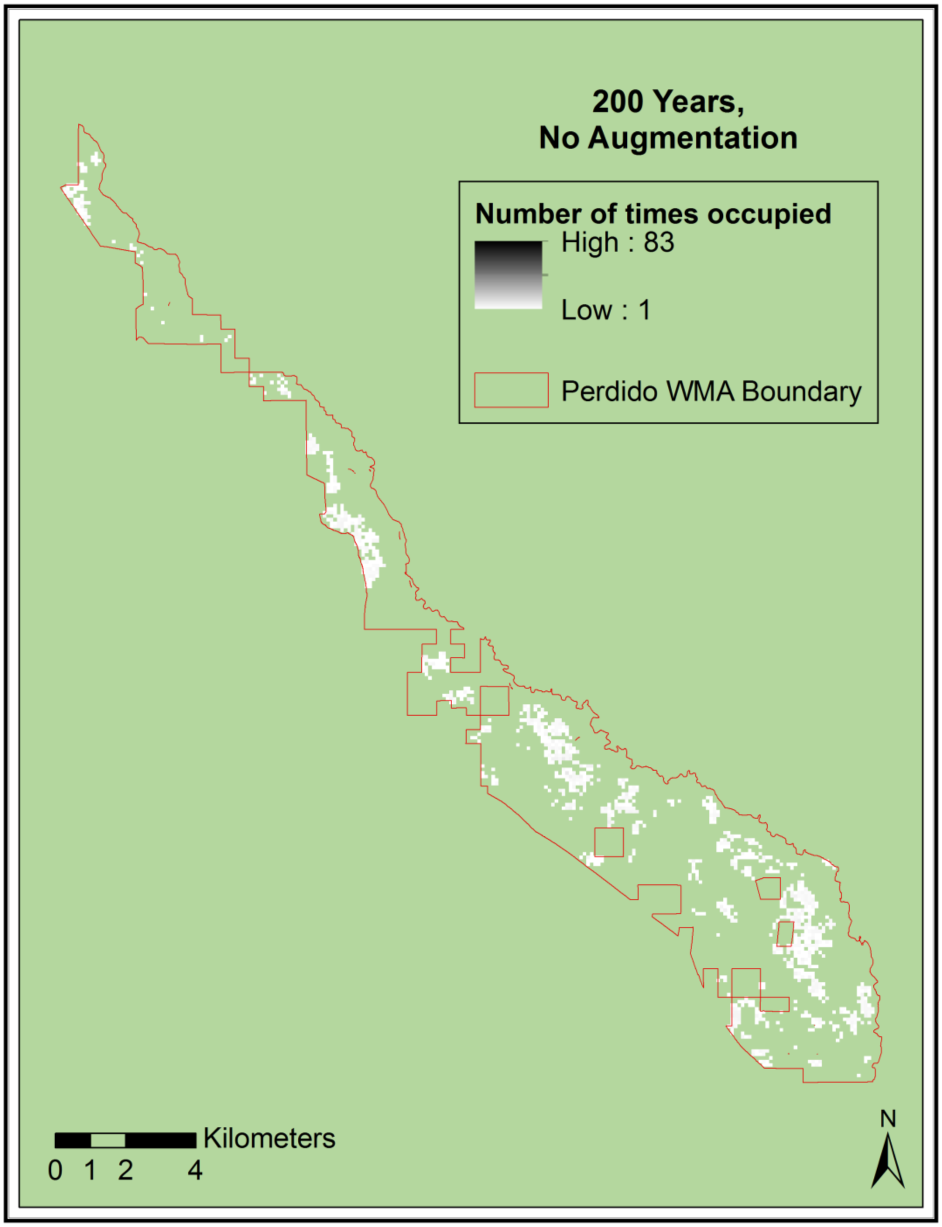


Figure 3.18. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 200 years of the no population augmentation scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 200 year time step.

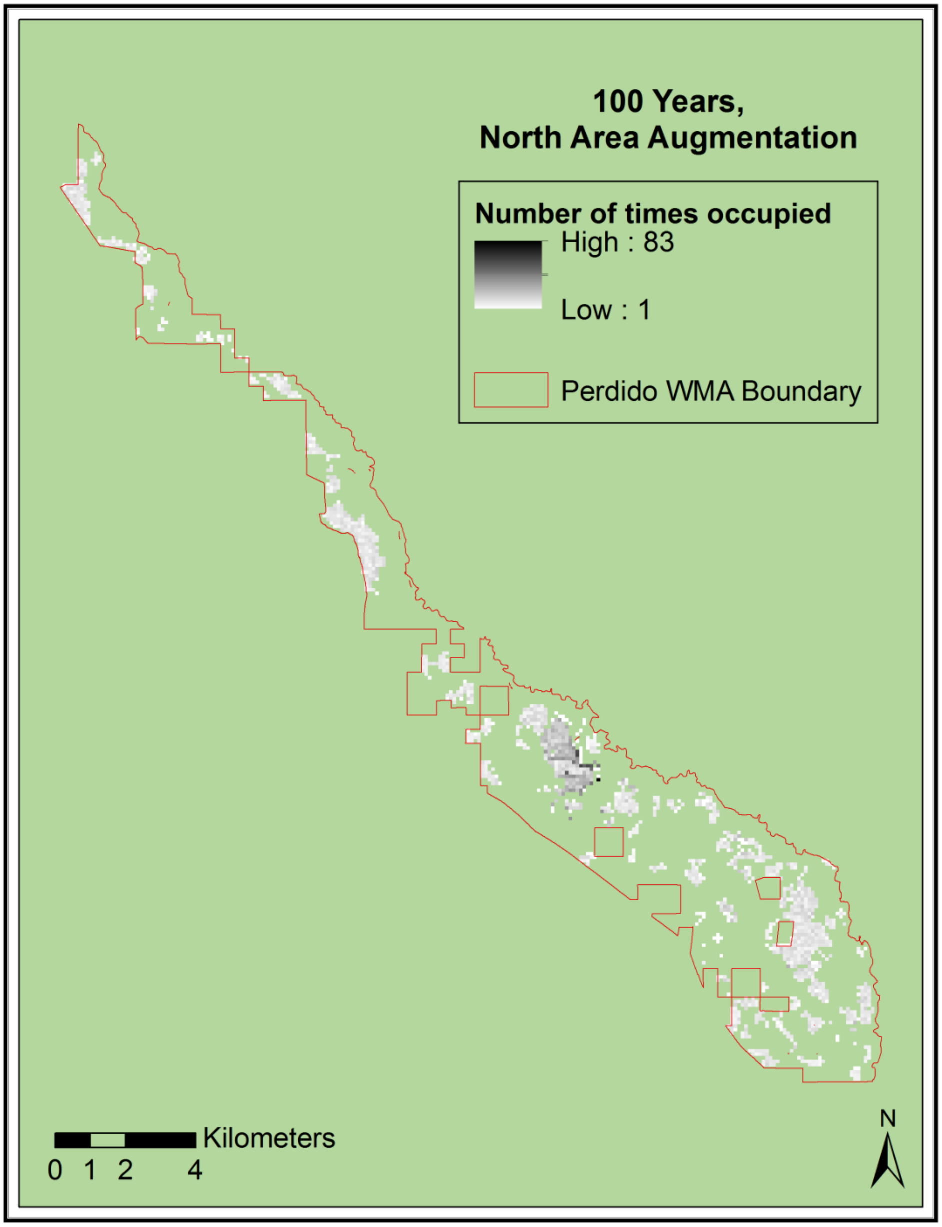


Figure 3.19. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 100 years of the population augmentation in the northern patch scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 100 year time step.

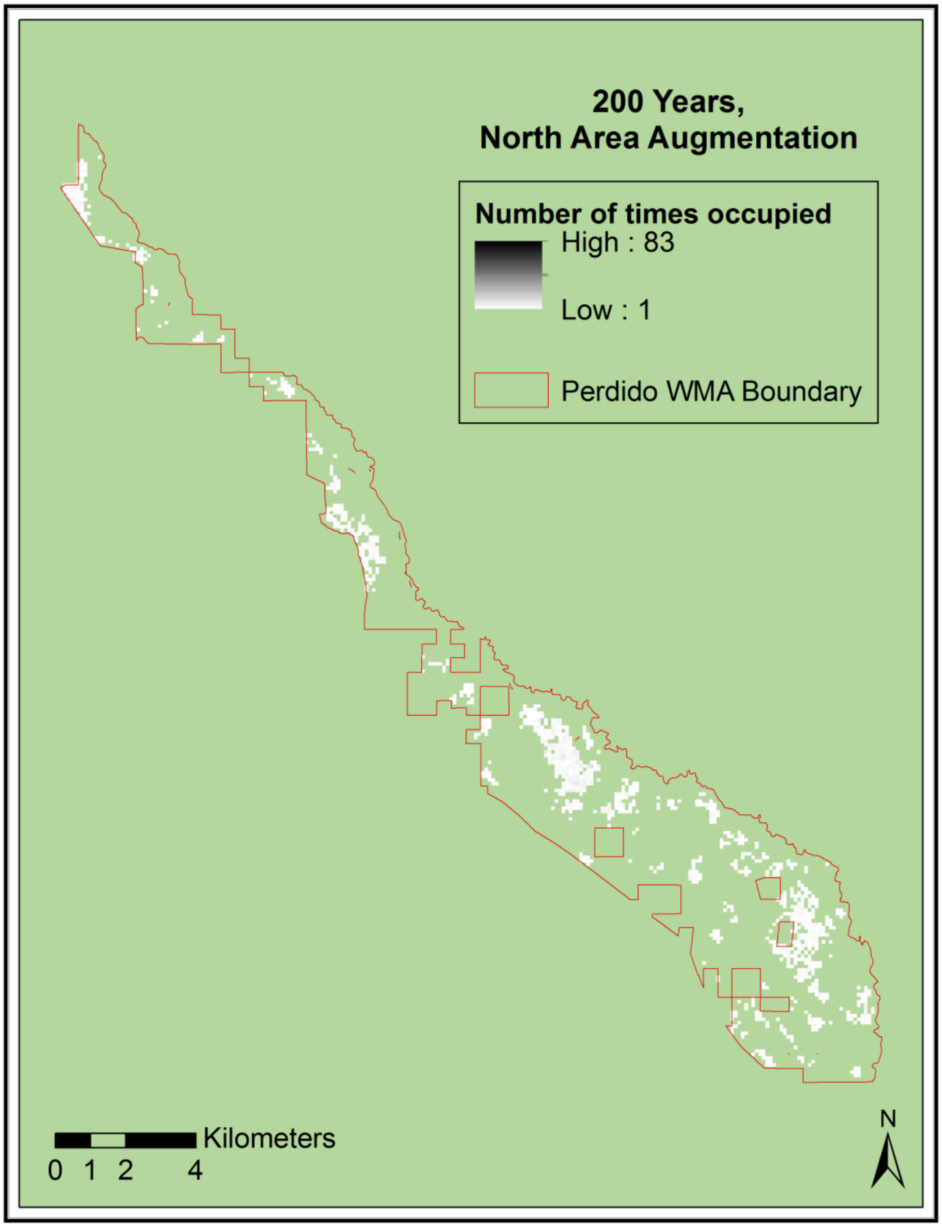


Figure 3.20. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 200 years of the population augmentation in the northern patch scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 200 year time step.

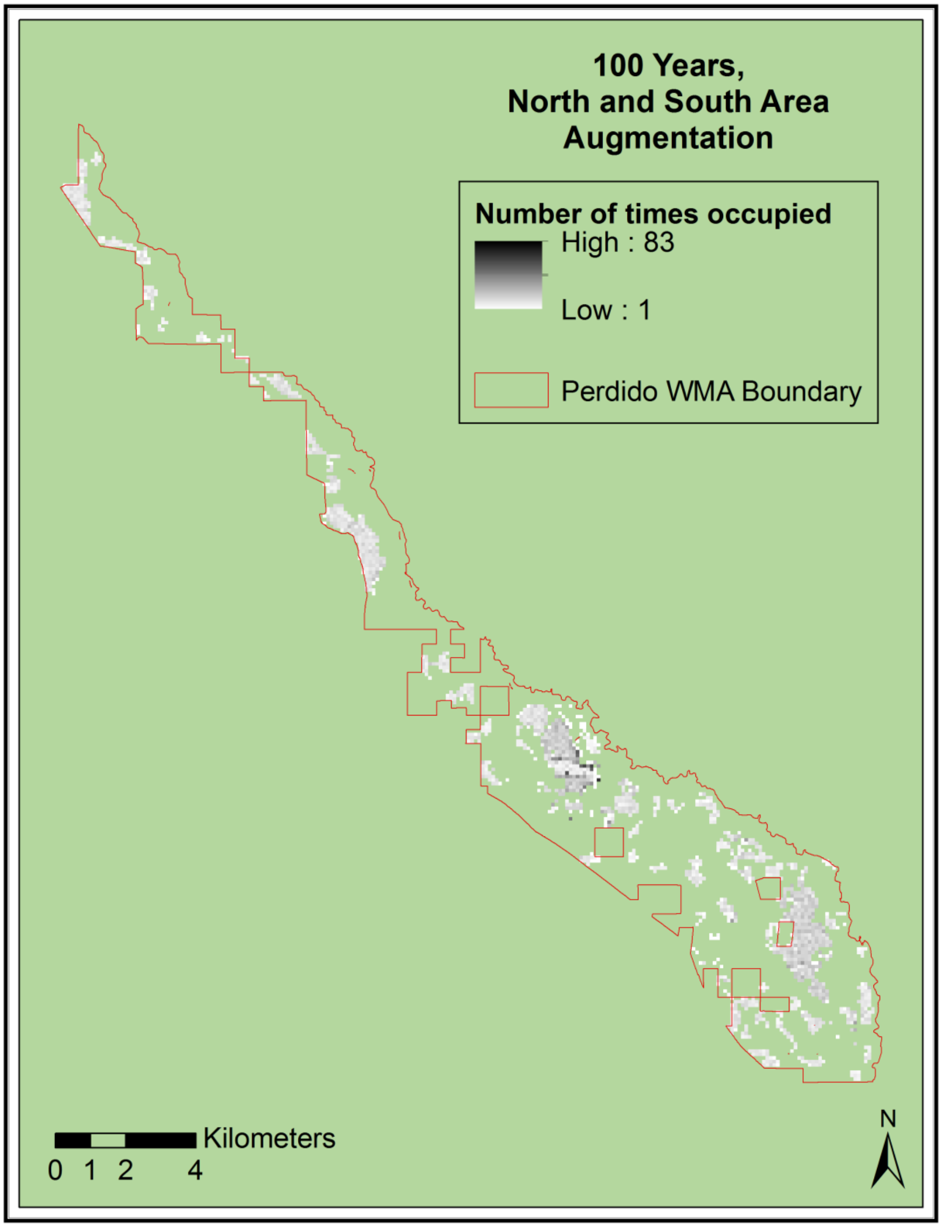


Figure 3.21. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 100 years of the population augmentation in the northern and southern patches scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 100 year time step.

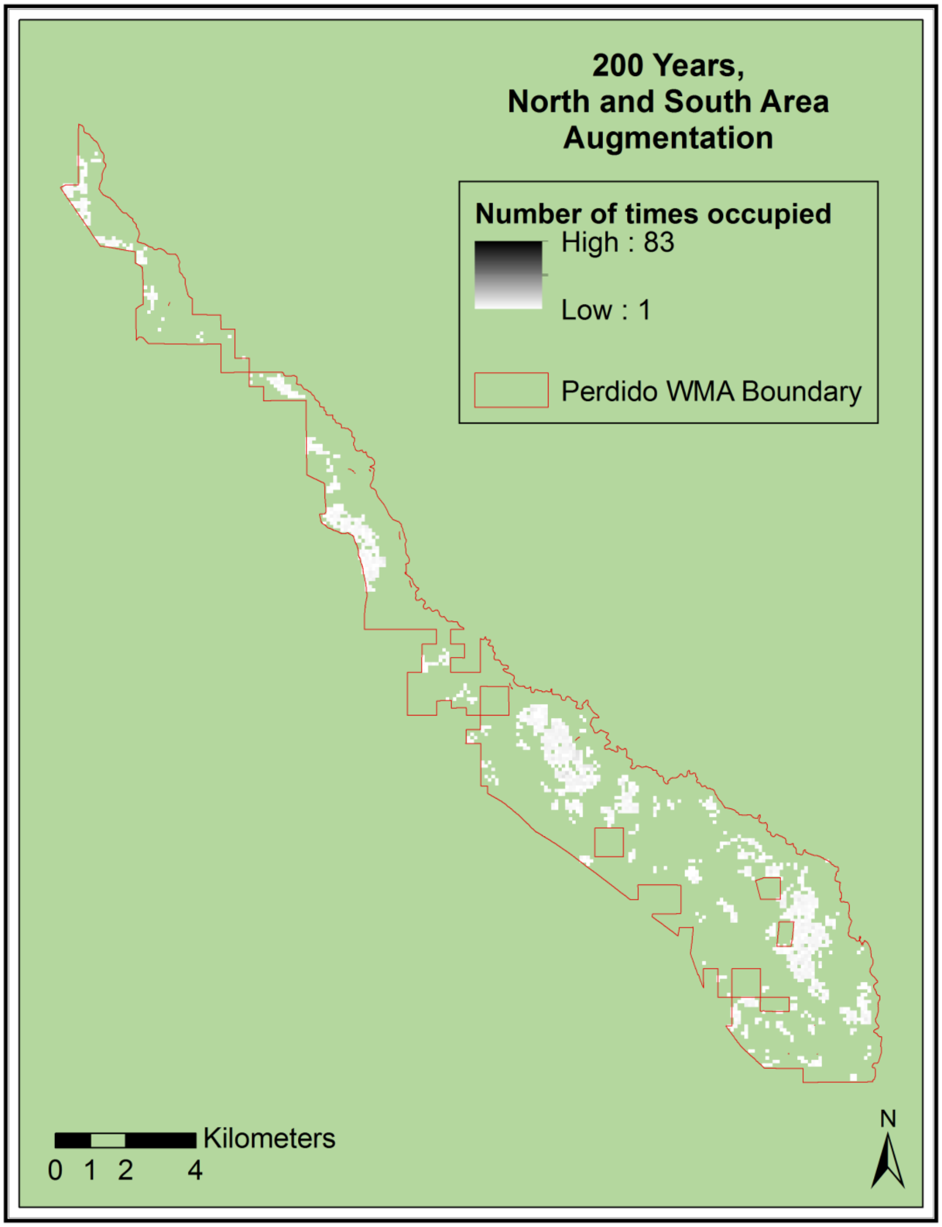


Figure 3.22. Number of times cells of the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (one year of age or older) after 200 years of the population augmentation in the northern and southern patches scenario during the 1,000 iterations of the population projection. Results shown are for habitat management alternative 9 (most of the landscape managed for uneven-aged pine). Cells not shown were never occupied at the 200 year time step.

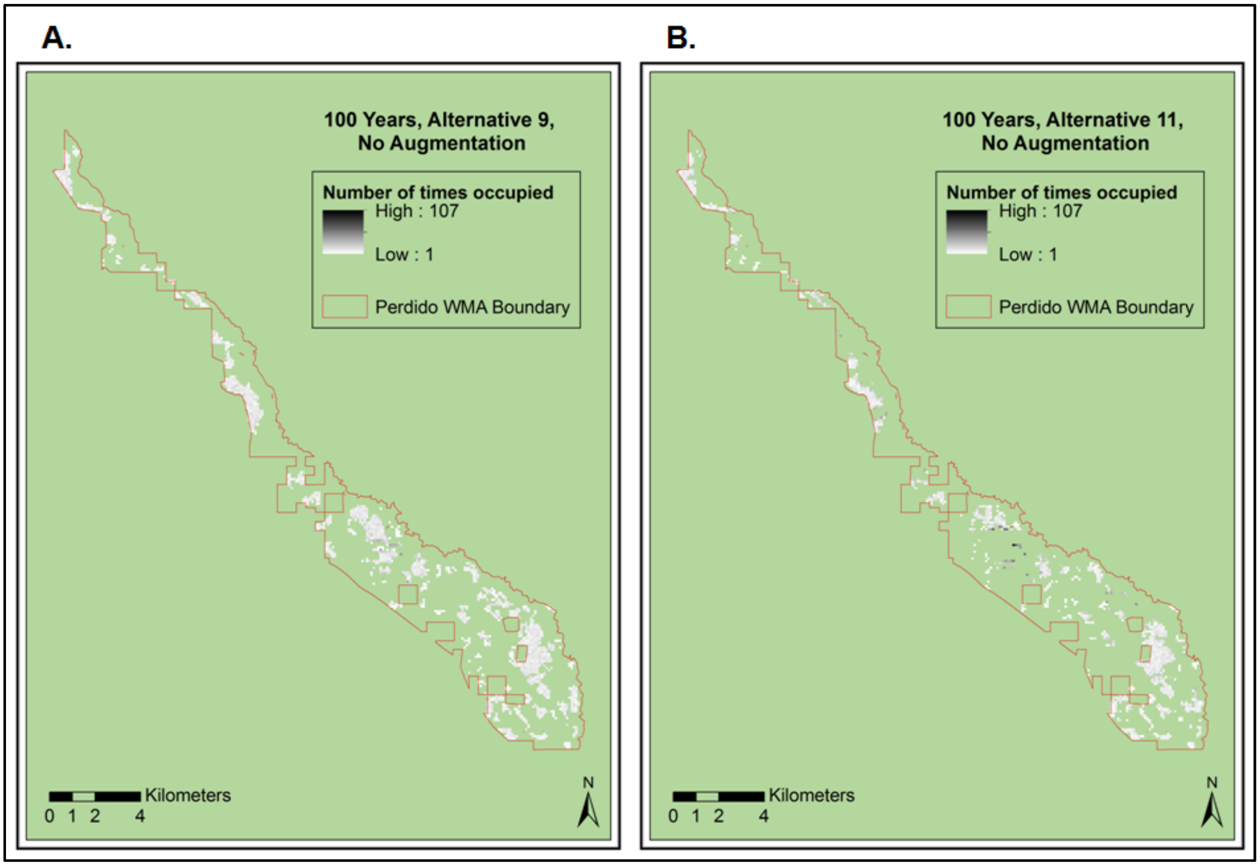


Figure 3.23. Number of times cells in the simulated Perdido River Wildlife Management Area landscape were occupied by at least one tortoise (1 year of age or older) out of the 1,000 iterations of the population projection. Cells not shown were not occupied under any iteration at these time steps. A: After 100 years with no population augmentation under habitat management alternative 9 (manage for uneven-aged pine in most of the landscape). B: After 100 years with no population augmentation under habitat management alternative 11 (minimum management).

The matrix population model, similar to the individual-based model, projected population declines with both starting population sizes tested (Table 3.12). On average, the population size decreased by over 70% by year 100 (Table 3.12). With the larger starting population size, extinction probability was lower at both 100 and 200 years than it was at either study site or any management scenario under the individual-based model (Table 3.10). For the smaller (16 adults) initial population, the extinction probability from the matrix projection was 0.50 at 100 years and 0.77 after 200 years, compared to 0.64 - 0.85 after 100 years and 0.96 - 0.98 after 200 years in the individual-based Barbour WMA projections with the same starting population size (Table 3.11). The percent change from the initial population size (for both initial population sizes examined) was almost always lower with the matrix model than with the individual-based model under all alternatives and augmentation scenarios, with the exception being change from initial population for Barbour/Wehle with population augmentation at 100 years (Tables 3.6 - 3.10, Table 3.12).

Table 3.12. Mean population size, mean percent change from initial population size, standard errors (SE), and extinction probability at 100 and 200 years from the matrix population projection model. Population size includes all individuals 1 year of age and older. Extinction probability is defined as the number of times the population contained fewer than 2 individuals (age 1 and older) at the given time step out of the total number of iterations.

Initial Population Size (ages 1+)	Time	Mean Population Size (SE)	Mean Percent Change from Initial Population Size (SE)	Extinction Probability
500	100 Years	82.83 (1.16)	-83.43 (0.23)	0.11
500	200 Years	47.69 (1.63)	-90.46 (0.33)	0.43
16	100 Years	4.22 (0.058)	-73.64 (0.36)	0.50
16	200 Years	2.31 (0.079)	-85.56 (0.49)	0.77

Discussion

Under all scenarios examined, there were consistent and significant declines in the tortoise populations at both study areas with the individual-based model. There are numerous possibilities as to why declines might have occurred, which are discussed below. The matrix stage-based model also showed significant declines in tortoise population sizes over time using the same vital rates (survival and fecundity). The population declines observed with the matrix model suggest that the vital rates used are at least partially responsible for the observed simulated population declines, rather than characteristics of the individual-based spatially explicit models alone, such as distribution of tortoises on the landscape or movement. Nevertheless, the individual-based model showed greater population declines than the matrix model, and the smaller initial population size (16 adult individuals) tested with the matrix model had a lower probability of extinction than the Barbour WMA individual-based projection (with the same initial population size), suggesting that other factors may be involved in the individual-based population declines.

It is possible that the life history parameters used in this model resulted in declining populations because they may have been estimated from declining populations. Gopher tortoise populations are considered to be in decline across their range (USFWS and SERPPAS 2013), and it is quite possible that many studies are conducted on declining populations. Tuberville et al. (2012) found that the initial life history parameter values they tried in their individual-based spatially explicit model, which they estimated from the literature, resulted in a declining population. They calibrated their model accordingly by adjusting juvenile survival (Tuberville et al. 2012). Similarly, Tuberville and Gibbons (2009) found that they needed to increase juvenile survivorship above estimates they had derived from the literature to obtain a stable population in their gopher tortoise population model in program VORTEX. Tortoise life history parameters, particularly survival of juveniles, is still poorly understood. Further research on survivorship, both from long-term field studies and from further simulation experiments, is necessary to broaden our understanding of gopher tortoise population dynamics. It is possible that human alteration of the ecosystem, such as habitat alteration and facilitating the spread of predators such as red imported fire ants, coyotes, and raccoons has altered tortoise vital rates from their historical levels. If the current estimates of survival used in this study are accurate, then gopher tortoise populations are unlikely to be viable in the long term.

Despite the influence of vital rates, the individual-based model projected greater declines than the matrix model, suggesting that vital rates alone may not be sufficient to explain the declines. Less favorable population outcomes in the individual-based model are to be expected, because the model accounts for some population processes that are ignored in the matrix model. First, some mortality was allowed to occur in the individual-based model if a simulated tortoise moved outside of the study area boundaries, to account for the possibility of an individual moving off of the property. Second, if a tortoise was on unsuitable habitat and was unable to get to an area of suitable habitat before winter, it would die. Finally, the individual-based model accounted for the locations of individuals and prevented isolated individuals from breeding. The matrix model assumed no heterogeneity or changes in habitat conditions and did not account for individuals emigrating from the population. It also could not account for the distribution of individuals across the landscape and the proximity of tortoises to one another, which are important considerations for tortoise populations. Omitting these details, such as was done in the matrix model, may be misleading for small, local populations like those in this study where individual interactions with the landscape and other individuals have important consequences for the population as a whole.

Another aspect of the individual-based model that may have contributed to projected declines is the very limited movement/dispersal for tortoises in the model. Tortoises would only move to new cells on the landscape if they had to, i.e., if there were too many tortoises in that cell by way of population growth or decreasing habitat suitability, and they would choose the first available patch they found. Dispersal and movements in gopher tortoises are poorly understood. Rarely, tortoises have been recorded moving relatively long distances and establishing burrows in new locations (Eubanks et al. 2003). Additionally, tortoises in reality may seek out other tortoises if they are moving to a new location, a behavior that was not included in my model. Greater dispersal capability or more detailed movement behaviors that involve seeking out other individuals where possible may have allowed populations at these study areas to aggregate to smaller groups of cells, thus limiting isolation and providing extra breeding opportunities which may have bolstered population growth.

A related potential reason for tortoise decline is the density of the starting populations. Tortoises were randomly located within the starting area boundaries in my model. In reality, tortoises are often found clustered near each other, forming social groups. While this is difficult to achieve on a simulated landscape, greater clustering of tortoises in the starting or augmentation populations may have helped prevent isolation of tortoises and thus increased the population growth rate.

Another possibility is that the tortoise populations at Barbour/Wehle and Perdido WMA are not viable populations (i.e., likely to persist in the long term). This is particularly relevant in the case of the Barbour/Wehle population, which is very small, even if some individuals are added. Currently, the estimate for a minimum viable population of gopher tortoises is 250 individuals at a density of at least 0.4 tortoises per ha (Gopher Tortoise Council 2013), which is far more tortoises than the Barbour/Wehle population could possibly contain. In the case of Perdido WMA, the initial population was drawn from a distribution with a mean of 434 tortoises, which exceeds the 250 individual minimum viable population guideline. However, tortoises were randomly placed within approximately 1,647 ha of potential starting area. 434 tortoises on 1,647 ha of property averages to 0.26 tortoises per ha, which is below the 0.4 tortoises per ha minimum density guideline. While some individuals may by chance be randomly placed closer or further from others in the model initialization, and while the starting conditions of the model were reasonable given current knowledge about the property, it is possible that the Perdido WMA population may not be viable due (in part) to low density.

An additional consideration is the incorporation of stochasticity in my model. The large annual variability in some parameters such as nest and hatchling survivorship may result in relatively small populations, such as those in this study, randomly bouncing to extinction. This level of stochasticity was not included in previous individual based spatially explicit gopher tortoise population models (Tuberville et al. 2012, Westervelt and MacAllister 2012). Incorporation of stochastic elements is necessary, however, both to incorporate uncertainty about the true value of life history parameters and to cover the natural range of annual variation that exists in the real world.

I did not find significant differences between the 11 habitat management alternatives included in this study in terms of effects on the overall population. This could be linked to the declining nature of the populations, whereby they rarely or never reach the carrying capacity of the cells in which they are located and exist at low densities, so availability of habitat is not a concern. For the Barbour/Wehle area, the starting area for the initial tortoise population occurred on an area of the property that is already more or less suitable for gopher tortoises, and the suitability of this area is not likely to change under any of the alternatives examined. This is less applicable to the Perdido WMA population, since the starting area encompassed areas that had the potential to shift to unsuitable or less suitable states over time (e.g., floodplain forest, hardwood). However, due to the declining nature of the population and relatively low density of individuals, this may not have affected the few individuals remaining in the population at the time.

While population augmentation did not result in a rescue of either the Barbour/Wehle or Perdido WMA populations, it did appear to reduce the probability of extinction. Combined with other management options, population augmentation may be a useful strategy to help preserve either of these populations if properly implemented. However, successful translocation of gopher tortoises is difficult. Translocated tortoises typically have high rates of dispersal off of the release site in the short term (Lohoefener and Lohmeier 1986, Burke 1989, Tuberville et al. 2005, 2008, Sasser and Soehren 2006, Ashton and Burke 2007). Penning tortoises for relatively long time spans (e.g., 1 year) may decrease post-release dispersal (Tuberville et al. 2005), but this requires significant amounts of planning and time. Additionally, gopher tortoises are social animals and appear to develop distinct social groups within larger populations (Guyer et al. 2014). Thus, translocating individuals has the potential to disrupt the social structure of both the translocated and the recipient population. Population augmentation strategies, if implemented, must be done with great care.

There do appear to be some differences among some of the habitat management alternatives in their effects on the distribution of tortoises on the landscape. Habitat management alternative 11 (minimum management) seemed to restrict tortoises to fewer cells on the landscape than the other alternatives at Perdido WMA. If populations were increasing on either of these properties, there would likely be greater implications of the various habitat management alternatives, as there would be more tortoises available to colonize suitable habitat. Nonetheless, changing habitat conditions may have important consequences for remaining tortoises.

Conversion of areas occupied by tortoises to unsuitable habitat may result in tortoises being forced to abandon burrows or congregate in smaller remaining areas of habitat. Additionally, changing habitat conditions may affect the connectivity of suitable habitat, which could result in subpopulations or groups of tortoises becoming more isolated from each other, which could ultimately affect population persistence.

Because both the individual-based spatially explicit and matrix stage-based models resulted in declining populations, further analyses utilizing different vital rate estimates are warranted. While the estimates used in this study are based on current understanding of gopher tortoise life history, tortoise vital rates, particularly survival, are not well understood. While future field studies will be invaluable to furthering our knowledge of such parameters, exploring the effects of hypothetical parameter values on the models developed in this study is warranted. In particular, evaluating the habitat management alternatives under an otherwise stable or growing population may help elucidate what effects such alternatives may have on a population. The use of hypothetical vital rates or starting population sizes/configurations can be used to test outcomes under various hypotheses of tortoise life history.

The models developed in this study have the potential to be useful in a number of other situations. First, this type of model could be developed for other existing tortoise populations, particularly for sites that are believed to be of high importance for tortoise conservation. For example, the Conecuh National Forest in south-central Alabama contains one of the largest known populations of tortoises in the state on public lands. A spatially explicit individual-based model for the Conecuh National Forest population of tortoises could help managers assess the viability of the population as a whole and potentially identify areas on the property where tortoises may be at risk in the long term. This type of approach could be applied to other species as well, particularly for relatively small populations where the spatial distribution of habitat is a concern. Finally, there is the potential to include multiple species in a single individual-based model, which may be useful where species interactions are important. For example, a model could be developed incorporating gopher tortoises, their burrow locations, and one of the many commensal species that utilize tortoise burrows. Such a model could provide information on the dynamics of the commensal species while explicitly accounting for gopher tortoise population dynamics.

This study provides valuable insight into how our current understanding of gopher tortoise life history plays out on the landscape. While the models used inherently include some assumptions and simplifications, they nonetheless highlight the potential implications of relatively small populations subjected to stochastic conditions. Additionally, this work highlights potential areas for future research, both in the field and in model development. More long term field studies are needed to accurately assess average survival for gopher tortoises of various age classes, particularly the younger age classes. Population models can help evaluate whether life history parameters derived from field studies are likely to result in stable populations. Targeted models built for specific properties and management scenarios, like the one presented in this study, can help inform decisions about management strategies. Finally, this model is a stepping stone for more complex models to be built in the future to better simulate the intricacies of tortoise behavior. For example, future models could develop better tortoise placement algorithms to create more realistically clustered starting populations or more realistic movement scenarios. There is great potential to build informative individual-based spatially explicit models that reveal more detail about population dynamics than may be achieved by other modeling methods. With the ever-increasing accessibility of high powered computer processing, available memory, and storage, it is possible to build increasingly complex models. While no model is ever expected to fully approximate reality, and even the simplest models can provide incredibly useful and valuable information, the possibility of complex and detailed models is an exciting frontier worthy of further exploration.

Literature Cited

Anzures-Dadda, A., and R. H. Manson. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69–76.

Aresco, M. J., and C. Guyer. 1999*a*. Growth of the tortoise Gopherus polyphemus in slash pine plantations of southcentral Alabama. Herpetologica 55:499–506.

Aresco, M. J., and C. Guyer. 1999*b*. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26–35.

Ashton, K. G., R. L. Burke, and J. N. Layne. 2007. Geographic variation in body and clutch size of gopher tortoises. Copeia 2:355–363.

Ashton, K. G., and R. L. Burke. 2007. Long-term retention of a relocated population of gopher tortoises. Journal of Wildlife Management 71:783–787.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (Gopherus polyphemus). Pages 95–126 *in* R. B. Bury, editor. North American tortoises: Conservation and ecology (Wildlife Research Report 12). U.S. Fish and Wildlife Service, Washington, D.C., USA.

Averill-Murray, R. C., L. J. Allison, and L. L. Smith. 2014. Nesting and reproductive output among North American tortoises. Pages 110–117 *in* D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland, USA.

Ballou, A. R. 2013. Aspects of gopher tortoise (Gopherus polyphemus) populations in Georgia: Status, landscape predictors, juvenile movements, and burrow use. Thesis, University of Georgia, Athens, GA.

Baskaran, L. M., V. H. Dale, R. A. Efroymson, and W. Birkhead. 2006. Habitat modeling within a regional context: An example using gopher tortoise. American Midland Naturalist 155:335–351.

Boglioli, M. D., W. K. Michener, and C. Guyer. 2000. Habitat selection and modification by the gopher tortoise, Gopherus polyphemus, in Georgia longleaf pine forest. Chelonian Conservation and Biology 3:699–705.

Bonin, F., B. Devaux, and A. Dupre. 2006. Turtles of the world. P. C. H. Pritchard, editor. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology, Evolution, and Systmatics 23:481–506.

Burke, R. L. 1989. Florida gopher tortoise relocation: Overview and case study. Biological Conservation 48:295–309.

Butler, J. A., and S. Sowell. 1996. Survivorship and predation of hatchling and yearling gopher tortoises, Gopherus polyphemus. Journal of Herpetology 30:455–458.

Caswell, H., R. M. Nisbet, A. M. de Roos, and S. Tuljapurkar. 1997. Structured-population models: Many methods, a few basic concepts. Pages 3–17 *in* S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, freshwater, and terrestrial systems. Chapman and Hall, New York, New York, USA.

Caswell, H. 2000. Matrix population models: Construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Conroy, M. J., R. J. Barker, P. W. Dillingham, D. Fletcher, A. M. Gormley, and I. M. Westbrooke. 2008. Application of decision theory to conservation management: Recovery of Hector's dolphin. Wildlife Research 35:93–102.

Cox, J., D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (Gopherus polyphemus) populations found on lands slated for large-scale development in Florida. Nongame Wildlife Program Technical Report No. 4. Office of Environmental Services, Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Cox, J. 1989. Survival characteristics of small gopher tortoise populations and their possible influence on relocation efforts. J. E. Diemer, D. R. Jackson, J. L. Landers, J. N. Layne, and D. A. Wood, editors. Gopher tortoise relocation symposium proceedings.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

DeAngelis, D. L., and L. J. Gross, editors. 1992. Individual-based models and approaches in ecology: Populations, communities, and ecosystems. Chapman and Hall, New York, New York, USA.

Dodd, C. K., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336–350.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: Current forms and future uses. Ecological Applications 5:3–11.

Epperson, D. M., and C. D. Heise. 2003. Nesting and hatchling ecology of gopher tortoises (Gopherus polyphemus) in southern Mississippi. Journal of Herpetology 37:315–324.

Eubanks, J. O., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (Gopherus polyphemus). Herpetologica 59:311–321.

Fagan, W. F., P. J. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction risk in desert fishes. Ecology 83:3250–3256.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 *in*. Proceedings of the Tall Timbers Fire Ecology Conference.

Gopher Tortoise Council. 2013. Gopher tortoise minimum viable population and minimum reserve size working group report.

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jørgensen, W. M. Mooij, B. Müller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rüger, E. Strand, S. Souissi, R. A. Stillman, R. Vabø, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198:115–126.

Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, New Jersey, USA.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? Ecological Modelling 115:129–148.

Guyer, C., S. M. Hermann, and V. M. Johnson. 2014. Social behaviors of North American tortoises. Pages 102–109 *in* D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland, USA.

Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (Gopherus polyphemus). Herpetological Monographs 26:122–134.

Hermann, S. M., C. Guyer, J. H. Waddle, and M. G. Nelms. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, Gopherus polyphemus. Biological Conservation 108:289–298.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. Bioscience 38:682–691.

Johnson, V. M., C. Guyer, and M. D. Boglioli. 2007. Phenology of attempted matings in gopher tortoises. Copeia 2007:490–495.

Jones, J. C., and B. Dorr. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife Society Bulletin 32:456–464.

Kowal, V. A., A. Schmolke, R. Kanagaraj, and D. Bruggeman. 2014. Resource selection probability functions for gopher tortoise: Providing a management tool applicable across the species' range. Environmental management 53:594–605.

Landers, J. L., J. A. Garner, and W. A. McRae. 1980. Reproduction of gopher tortoises (Gopherus polyphemus) in southwestern Georgia. Herpetologica 36:353–361.

Landers, L. J., A. W. McRae, and J. A. Garner. 1982. Growth and maturity of the gopher tortoises in southwestern Georgia. Bulletin of the Florida State Museum, Biological Sciences 27:81 – 110.

Lohoefener, R., and L. Lohmeier. 1986. Experiments with gopher tortoise (Gopherus polyphemus) relocation in southern Mississippi. Herpetologica 17:37-40.

Miller, P. S. 2001. Preliminary population viability assessment for the gopher tortoise (Gopherus polyphemus) in Florida. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Mushinsky, H. R. 2014. Growth patterns of North American tortoises. Pages 53–59 *in* D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Baltimore, Maryland, USA.

Perez-Heydrich, C., K. Jackson, L. D. Wendland, and M. B. Brown. 2012. Gopher tortoise hatchling survival: Field study and meta-analysis. Herpetologica 68:334–344.

Pike, D. A., and R. A. Seigel. 2006. Variation in hatchling tortoise survivorship at three geographic localities. Herpetologica 62:125–131.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Root, K. V, and J. Barnes. 2006. Risk assessment for a focal set of rare and imperiled wildlife in Florida. FWC Contract No. 03111 Final Report.

Rostal, D. C., and T. Wibbels. 2014. Embryonic development, hatching success, and temperature-dependent sex determination in North American tortoises. Pages 46–52 *in* D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland, USA.

Rostal, D. C. 2014. Reproductive physiology of North American tortoises. Pages 37–45 *in* D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland, USA.

Sasser, M., and E. C. Soehren. 2006. Gopher tortoise relocation initiative on the Forever Wild Wehle Tract in Bullock County, Alabama: A conservation restoration project for a high priority species. Final Report Submitted to Wildlife Section, Wildlife and Freshwater Fisheries Division, Alabama Department of Consevation and Natural Resources.

Seigel, R., and C. Dodd. 2000. Manipulation of turtle populations for conservation: Halfway technologies or viable options? Pages 218–238 *in* M. Klemens, editor. Turtle Conservation. Smithsonian Institution Press, Washington, D.C., USA.

Silvano, A. L. 2013. Incorporating long-term spatial and temporal effects in a state space model to evaluate land management alternatives for imperiled species conservation in Alabama. Thesis, Auburn University, Auburn, AL.

Smith, L. L., D. A. Steen, L. M. Conner, and J. C. Rutledge. 2013. Effects of predator exclusion on nest and hatchling survival in the gopher tortoise. The Journal of Wildlife Management 77:352–358.

Smith, L. L., T. D. Tuberville, and R. A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise 2003: Final results and recommendations. Chelonian Conservation and Biology 5:326–330.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261–270.

Thiele, J. C., and V. Grimm. 2010. NetLogo meets R: Linking agent-based models with a toolbox for their analysis. Environmental Modelling and Software 25(8):972–974.

Tuberville, T. D., K. M. Andrews, J. D. Westervelt, H. E. Balbach, J. Macey, and L. Carlile. 2012. Using demographic sensitivity testing to guide management of gopher tortoises at Fort Stewart, Georgia: A Comparison of individual-based modeling and population viability analysis approaches. Pages 109–131 *in* J. D. Westervelt and G. L. Cohen, editors. Ecologist-Developed Spatially Explicit Dynamic Landscape Models, Modeling Dynamic Systems. Springer US, Boston, Massachusetts, USA.

Tuberville, T. D., E. E. Clark, K. A. Buhlmann, and J. W. Gibbons. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (Gopherus polyphemus). Animal Conservation 8:349–358.

Tuberville, T. D., J. W. Gibbons, and H. E. Balbach. 2009. Estimating viability of gopher tortoise populations. Final Report. Contruction Engineering Research Laboratory, U.S. Army Corps of Engineers, Washington, D.C.

Tuberville, T. D., T. M. Norton, B. D. Todd, and J. S. Spratt. 2008. Long-term apparent survival of translocated gopher tortoises: A comparison of newly released and previously established animals. Biological Conservation 141:2690–2697.

Tuberville, T. D., B. D. Todd, S. M. Hermann, W. K. Michener, and C. Guyer. 2014. Survival, demography, and growth of gopher tortoises (Gopherus polyphemus) from three study sites with different management histories. The Journal of Wildlife Management 78:1151–1160.

Turner, M. G., R. H. Gardner, and R. V O'Neill. 2001. Landscape ecology in theory and practice. Springer, New York, New York, USA.

Westervelt, J. D., and B. MacAllister. 2012. Forcasting gopher tortoise (Gopherus polyphemus) distribution and long-term viability at Fort Benning, Georgia. Pages 85–107 *in* J. D. Westervelt and G. L. Cohen, editors. Ecologist-Developed Spatially Explicit Dynamic Landscape Models, Modeling Dynamic Systems. Springer US, Boston, Massachusetts, USA.

Wilensky, U. 1999. NetLogo. Center for connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

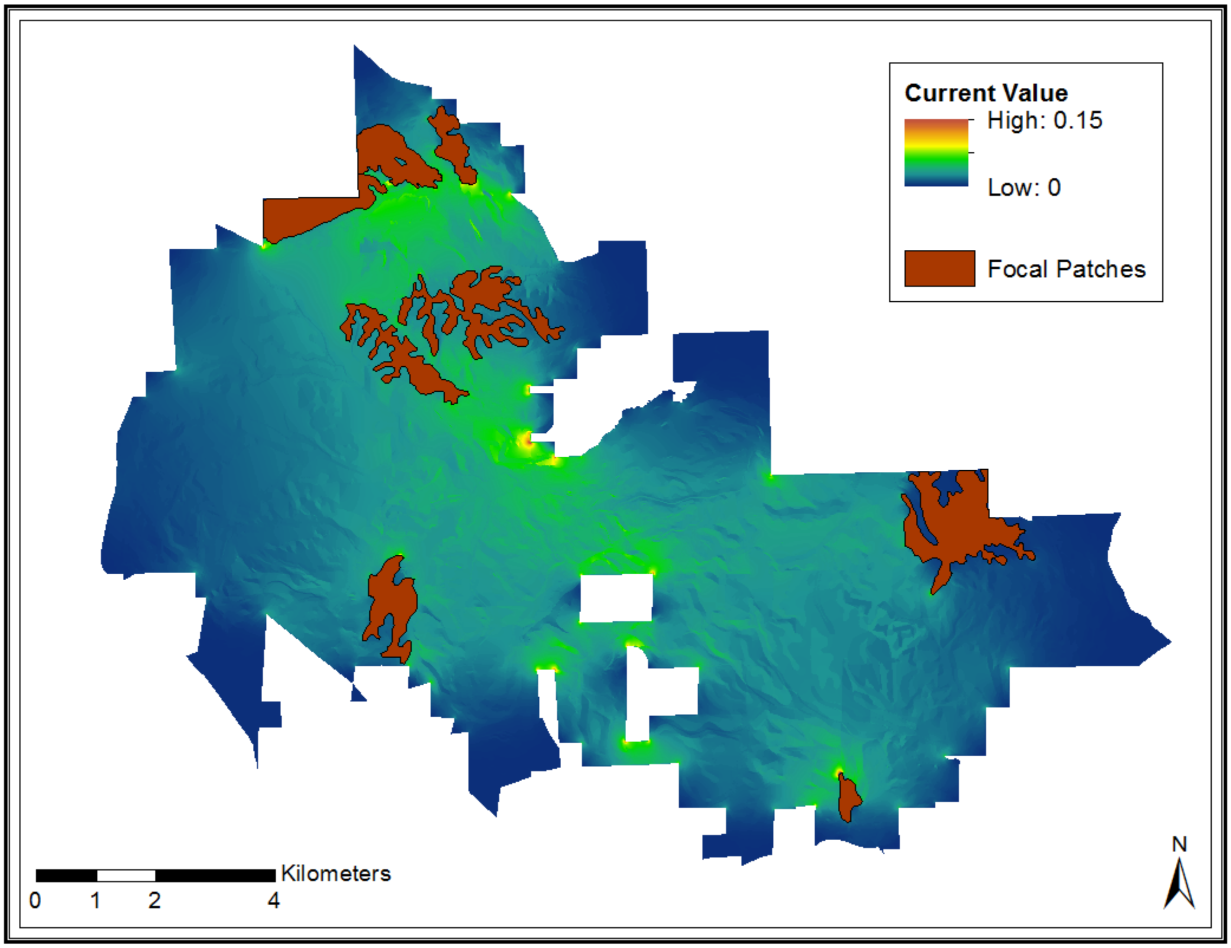
Wilson, D. 1991. Estimates of survival for juvenile gopher tortoises, Gopherus polyphemus. Journal of Herpetology 25:376–379.

United States Fish and Wildlife Service [USFWS]. 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list the gopher tortoise as threatened in the eastern portion of its range. Federal Register 76(144):45130-45162.

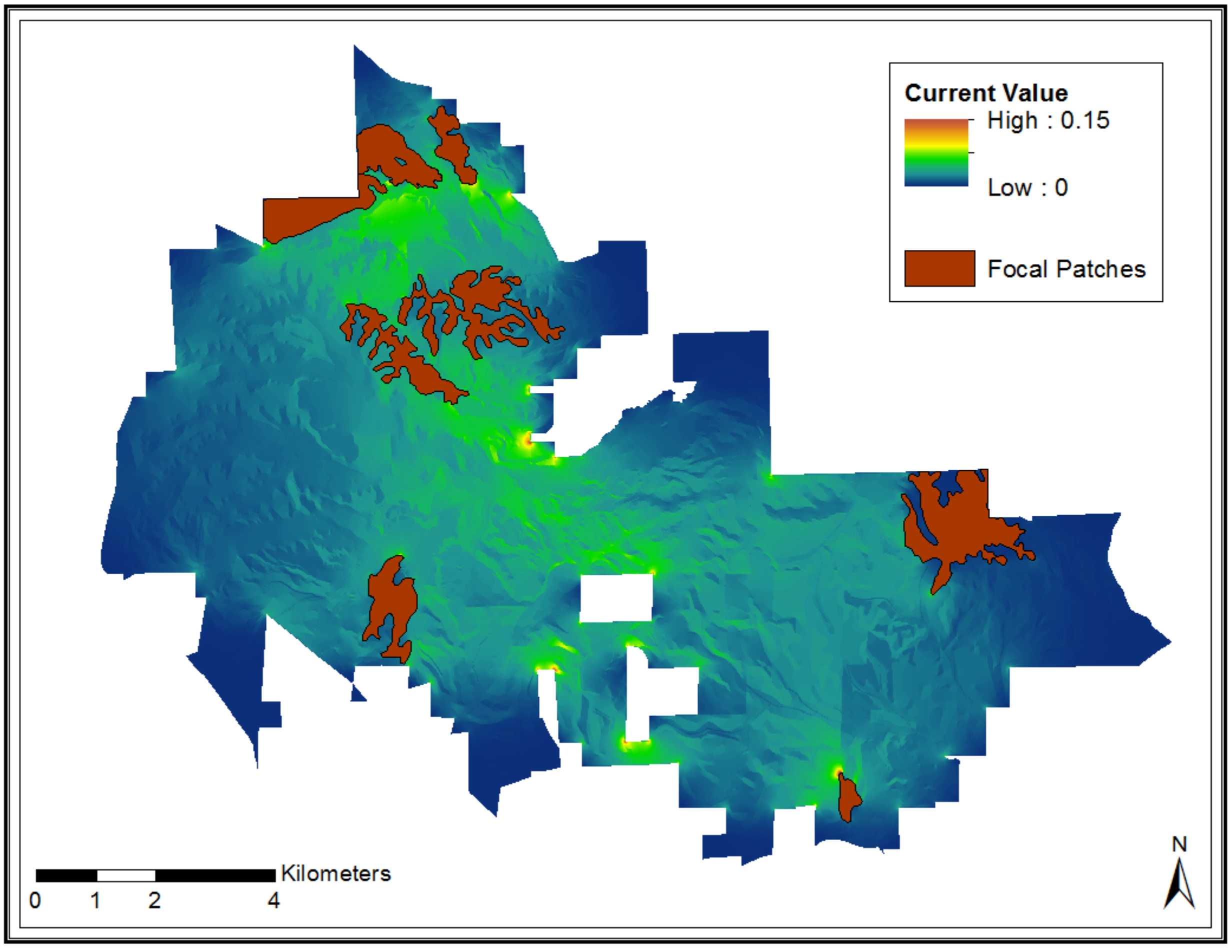
United States Fish and Wildlife Service [USFWS] and Natural Resources Conservation Service [NRCS]. 2012. Gopher tortoise (Gopherus polyphemus) soil classifications for the federally listed range using the National Soil Information System database. Report, version 1.

United States Fish and Wildlife Service [USFWS], and Southeast Regional Partnership for Planning and Sustainability [SERPPAS]. 2013. 4th annual report, candidate conservation agreement for the gopher tortoise.

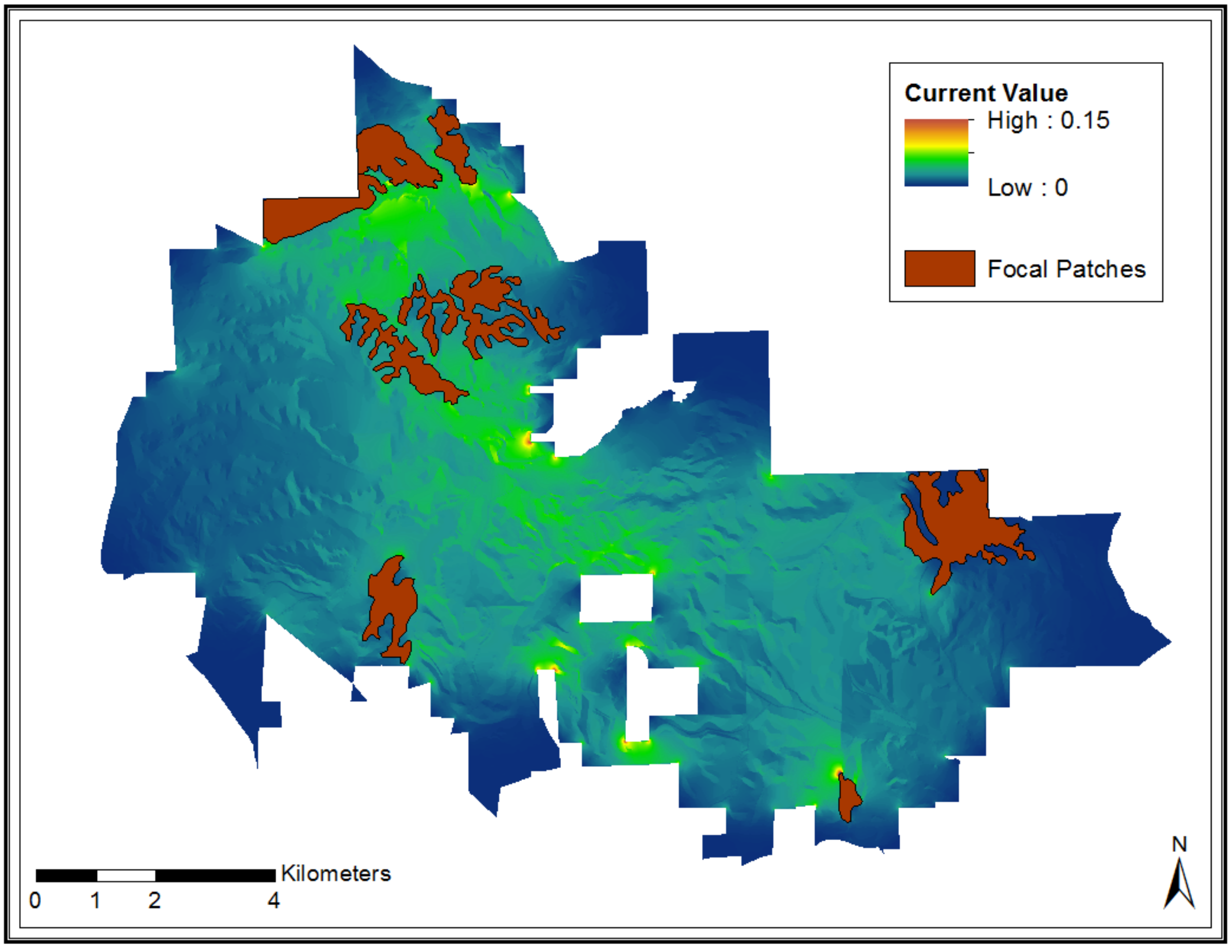
Appendix 1. Current flow for each habitat management alternative under each set of resistance values for each study site for initial landscape conditions and the most probable conditions after the 100 year habitat projection.



Current flow using resistance set 1 under initial landscape conditions (circa 2011) at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



Current flow using resistance set 1 after 100 years under management alternative 1 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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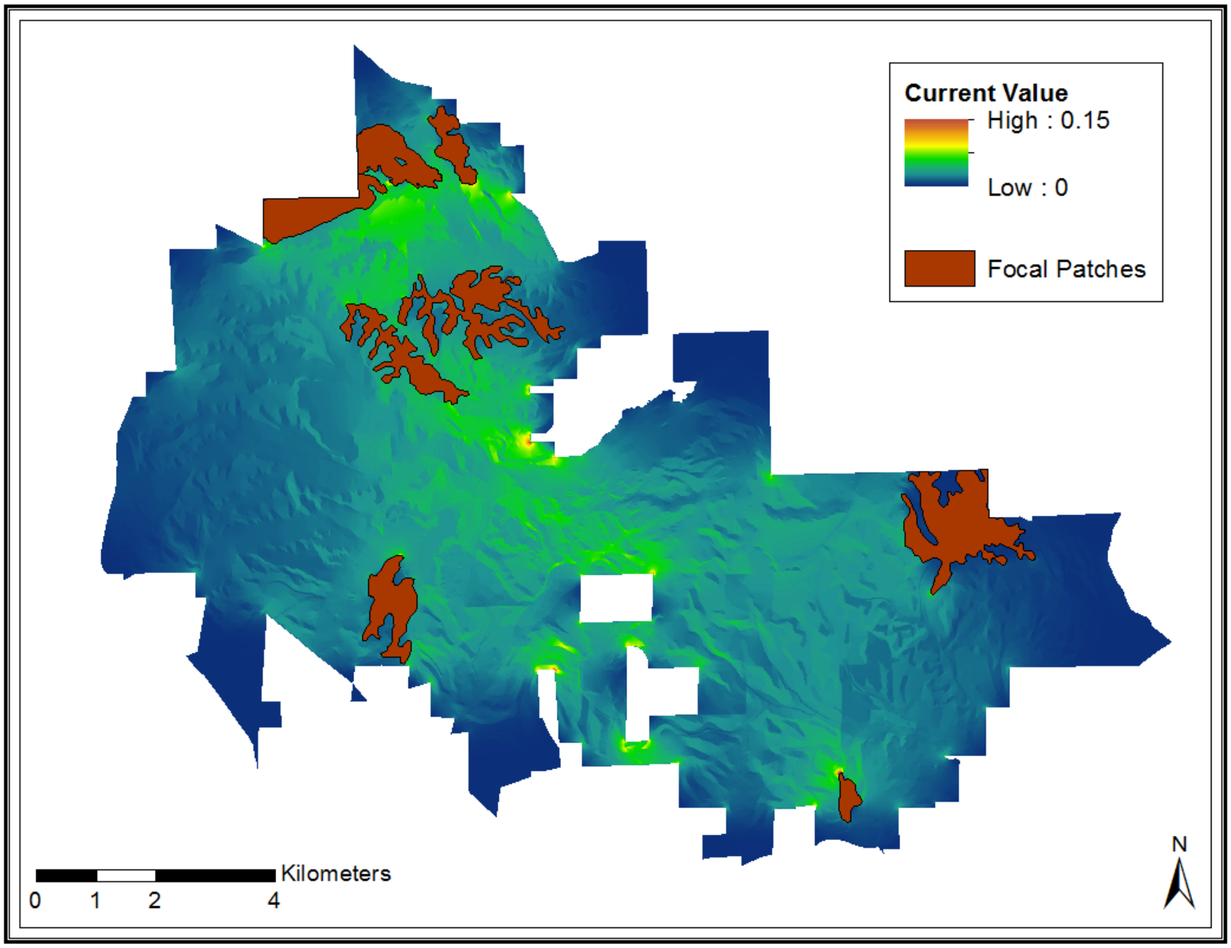

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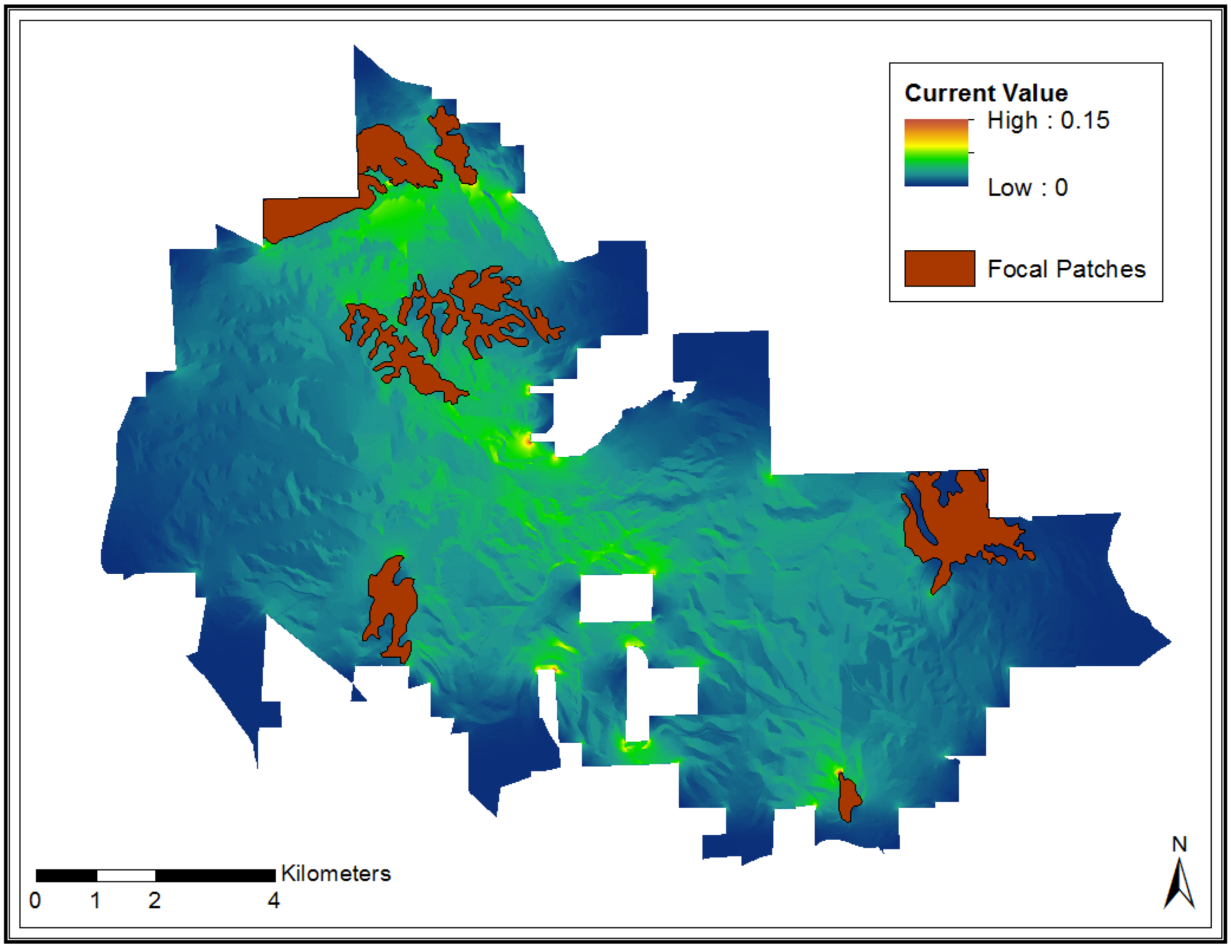

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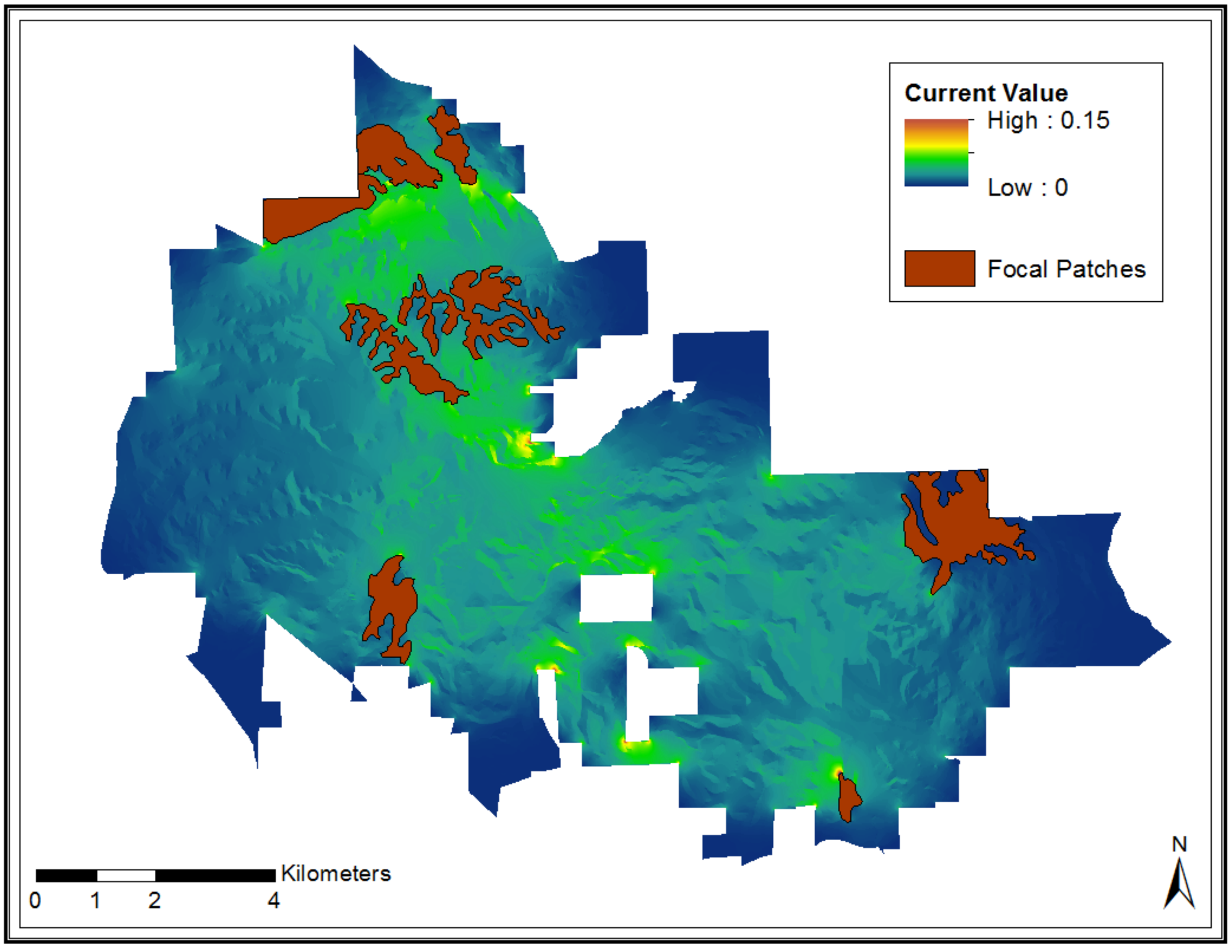

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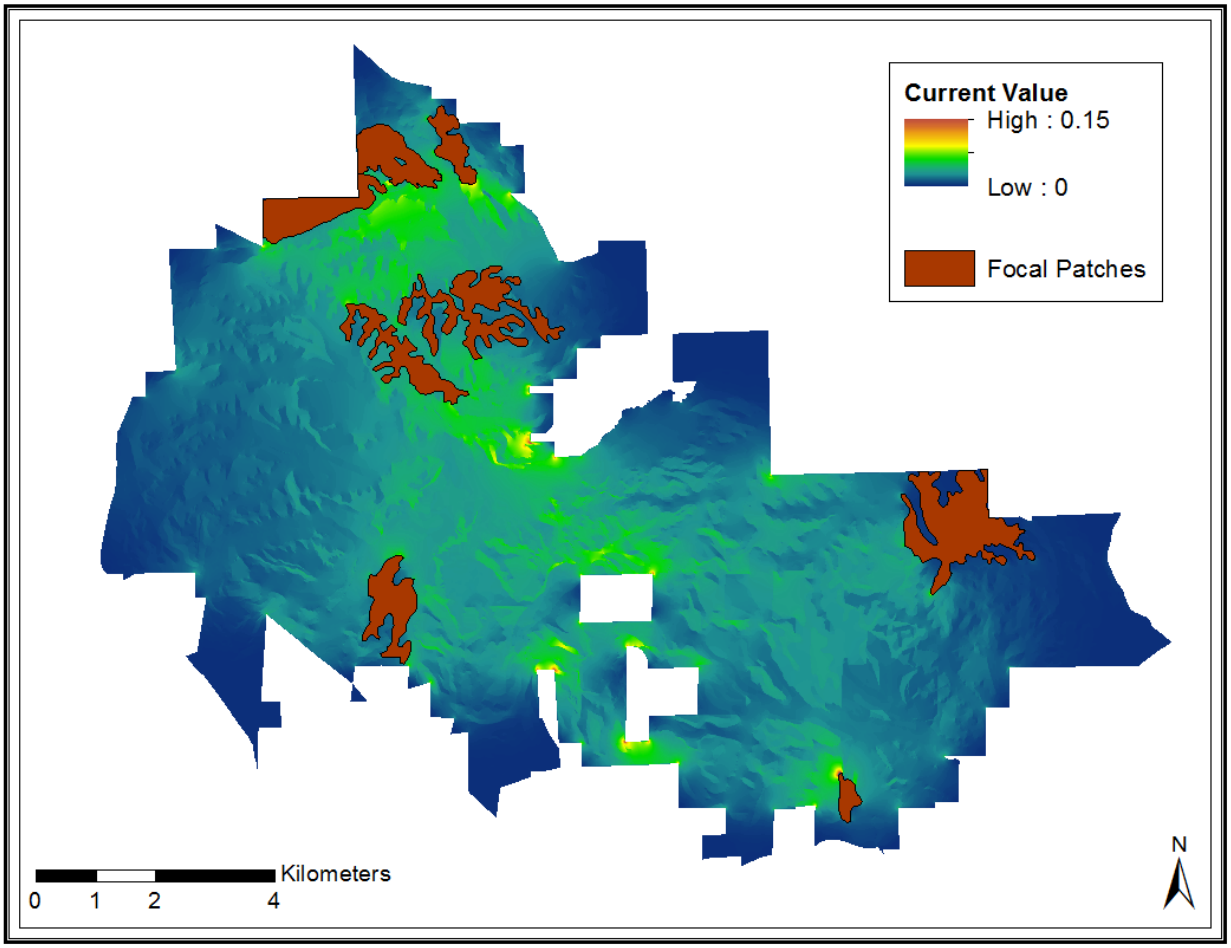
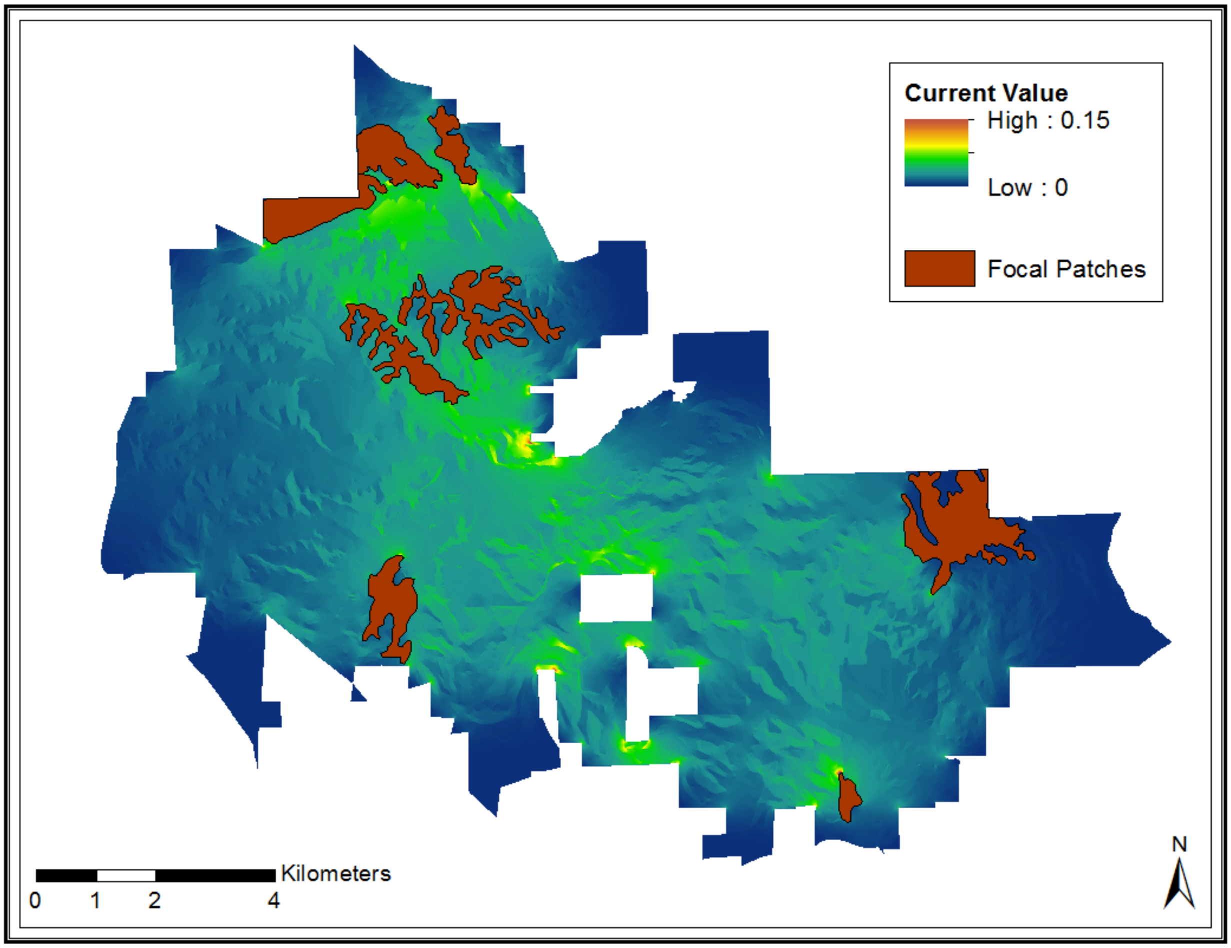


Current flow using resistance set 1 after 100 years under management alternative 6 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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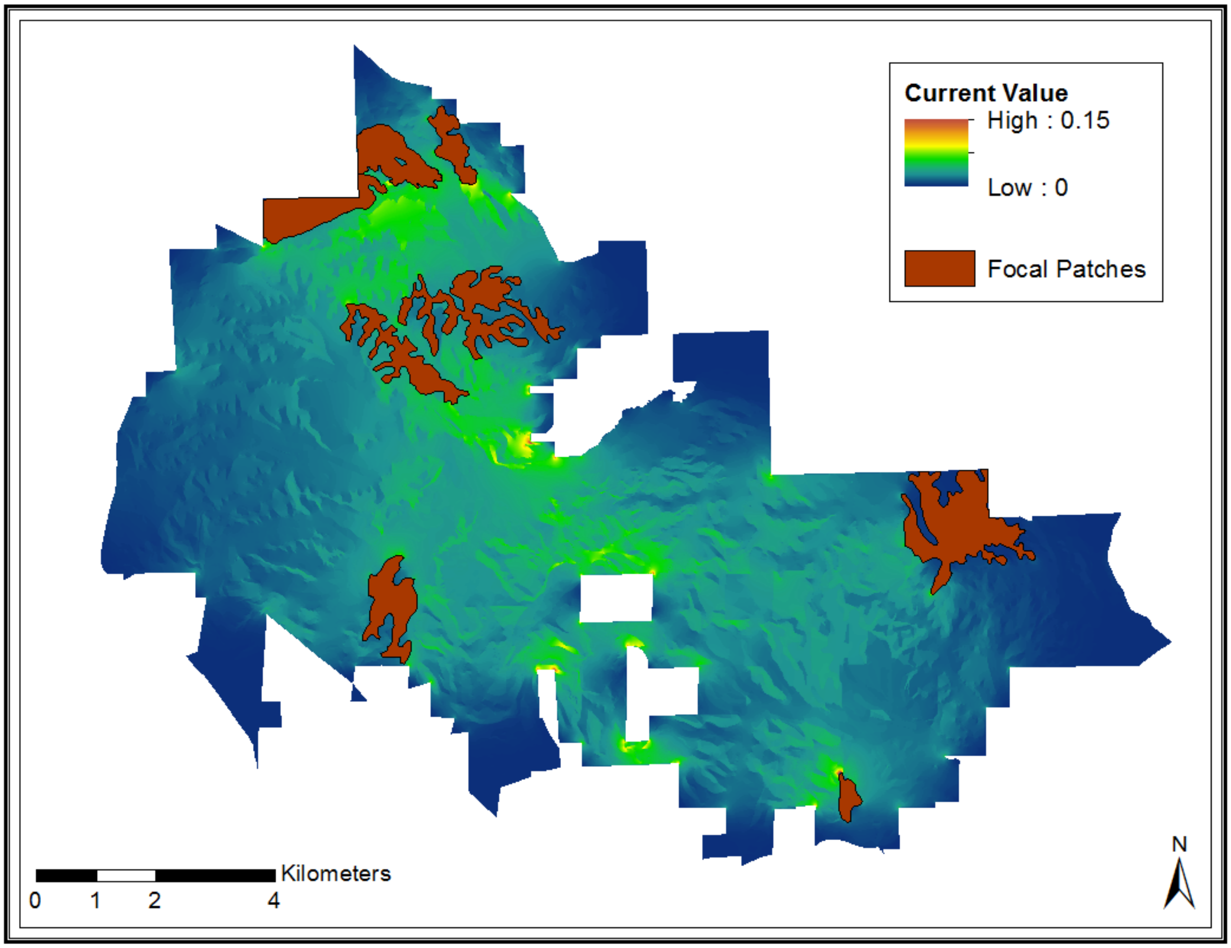
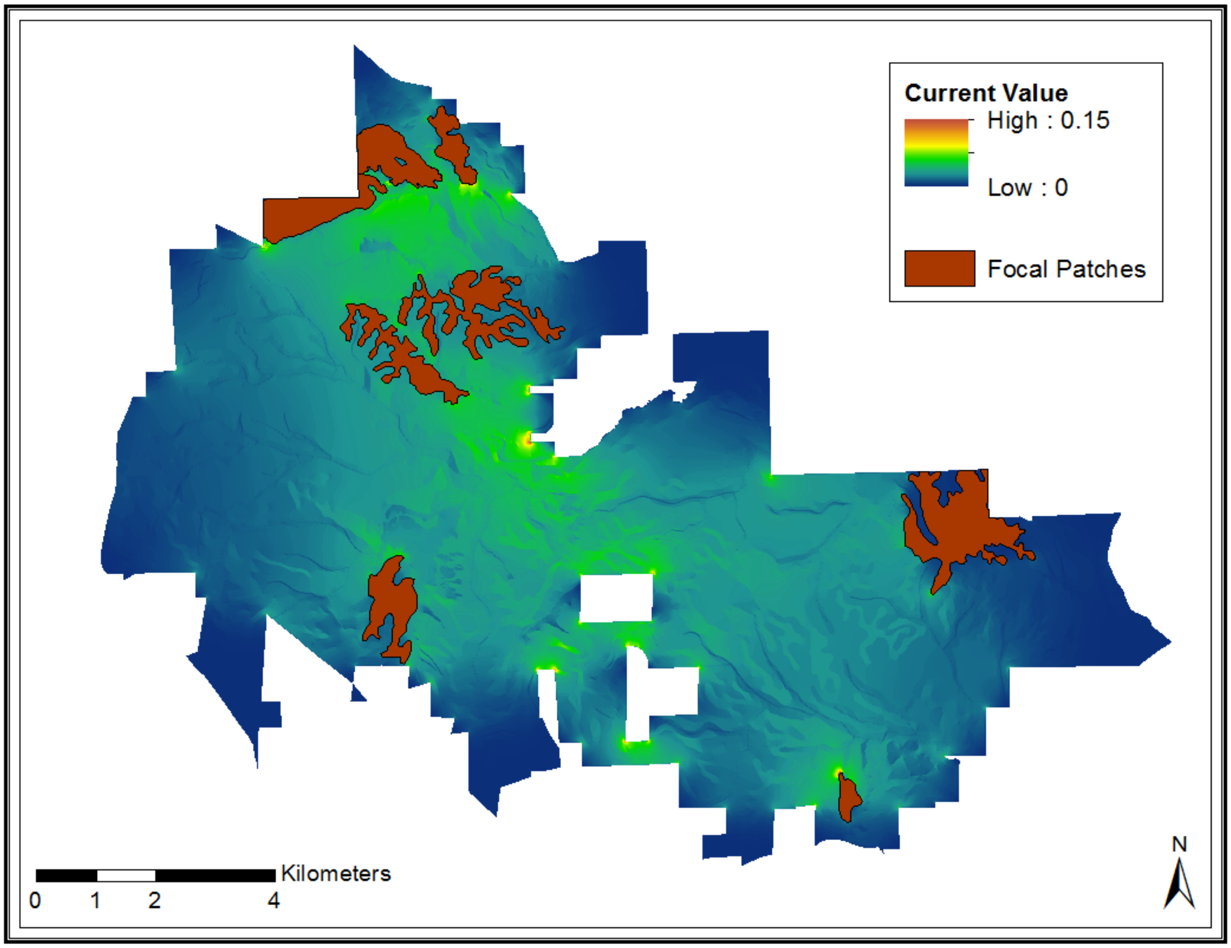


Current flow using resistance set 1 after 100 years under management alternative 8 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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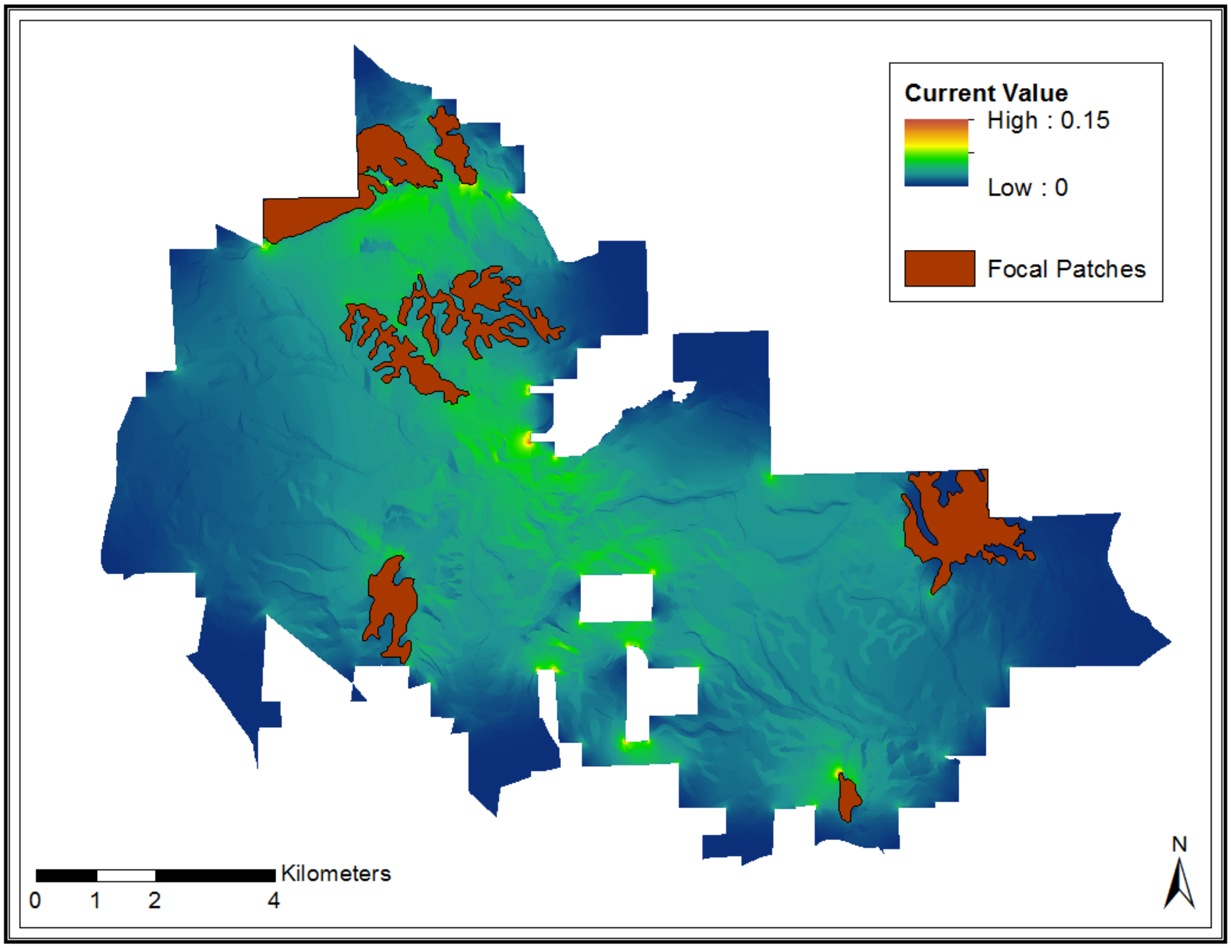

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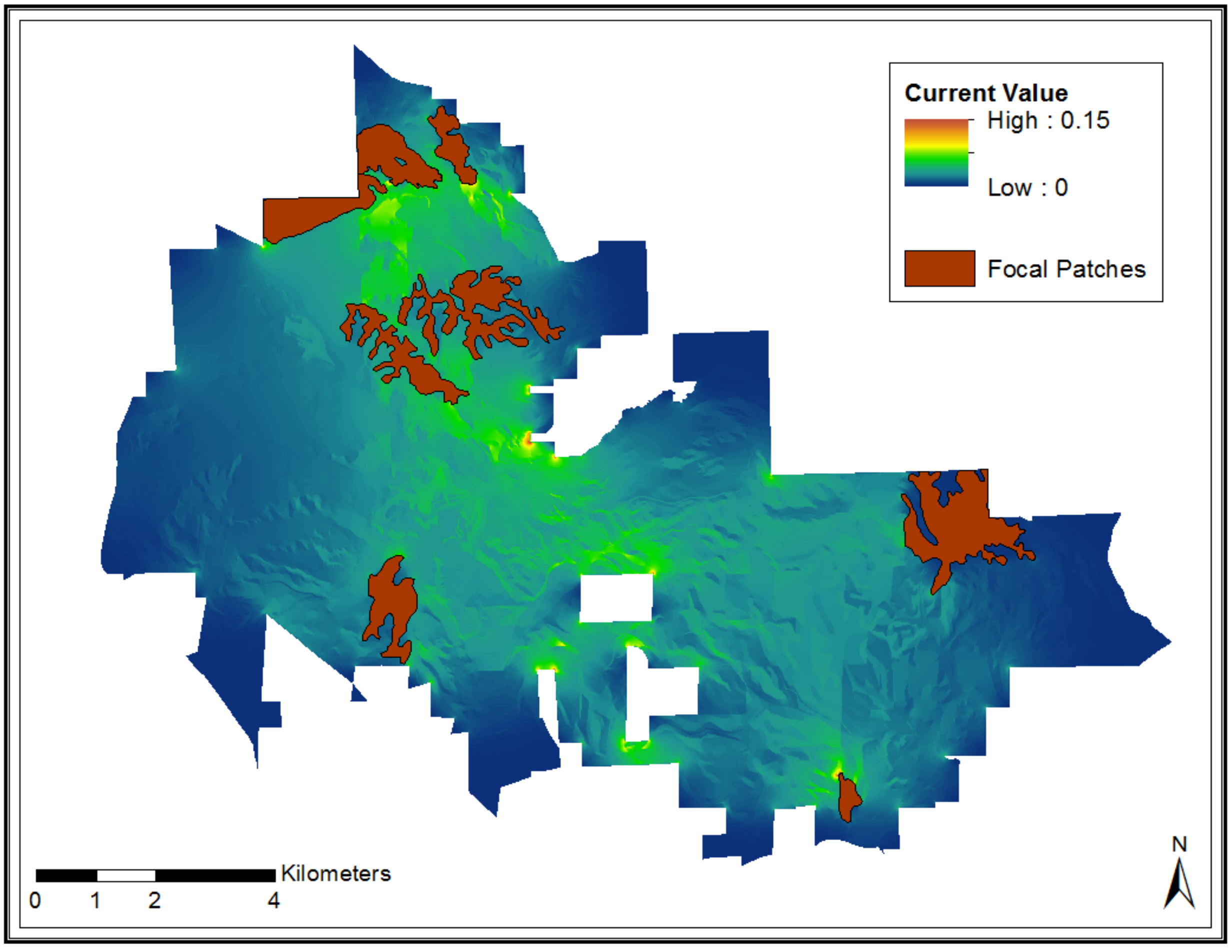
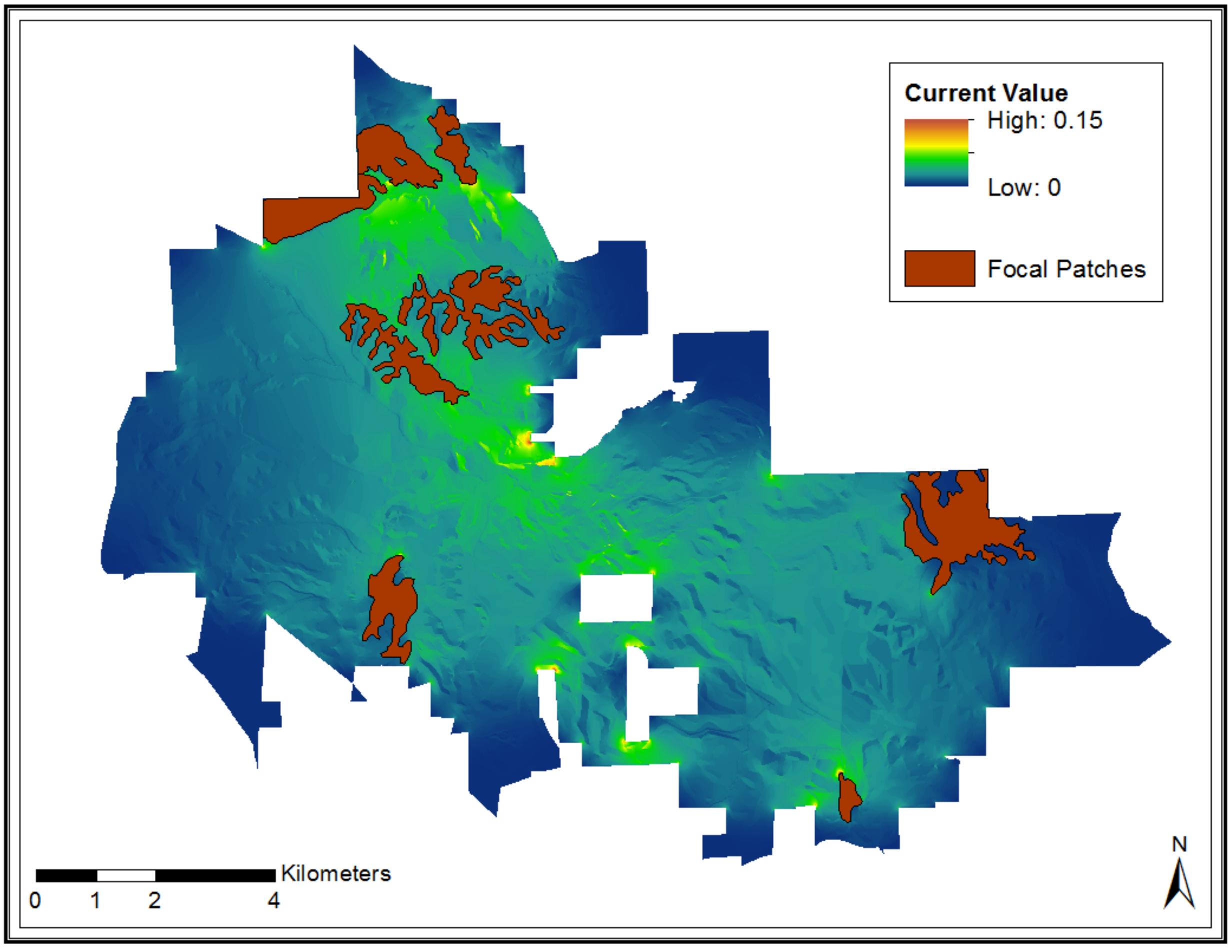
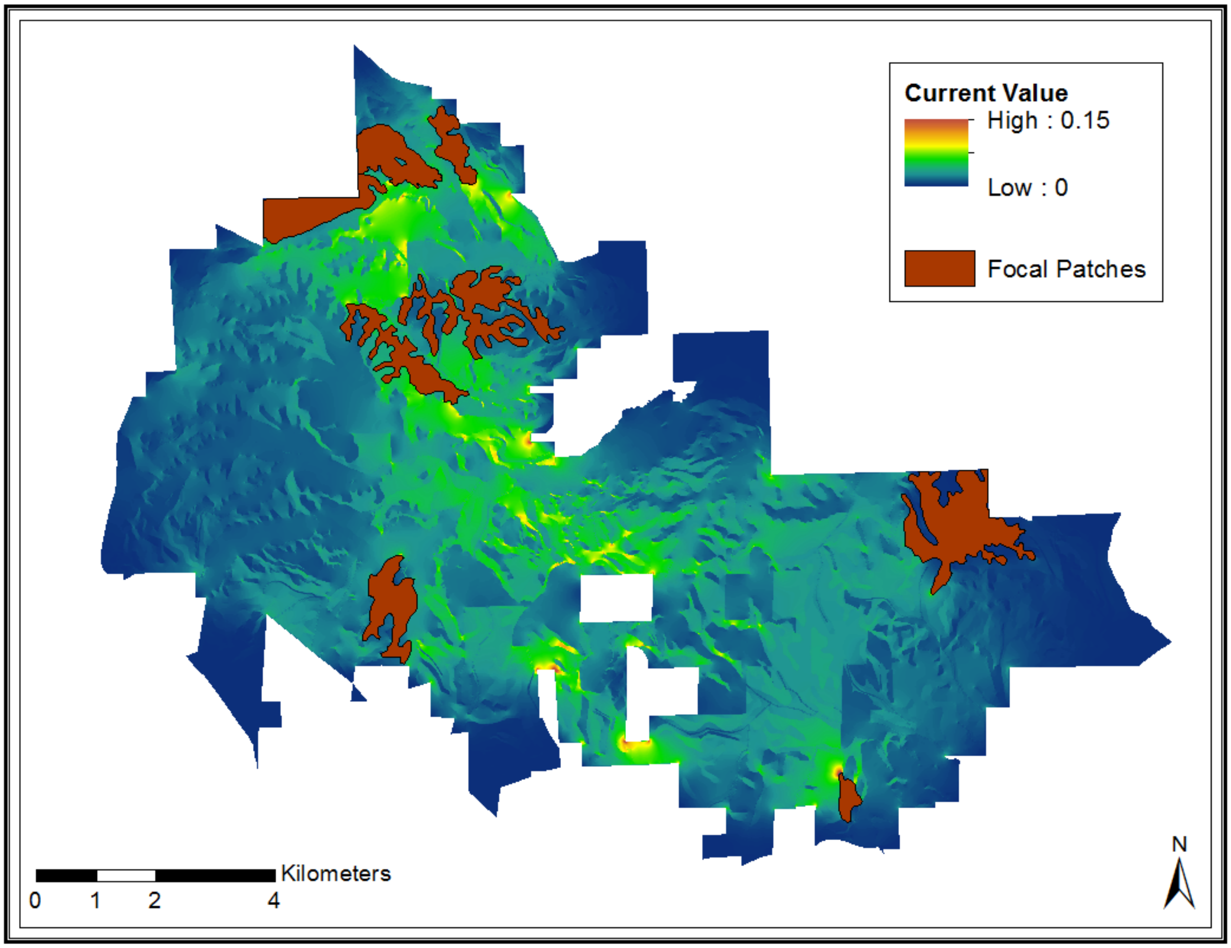


Current flow using resistance set 1 after 100 years under management alternative 11 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



Current flow using resistance set 2 under initial landscape conditions (circa 2011) at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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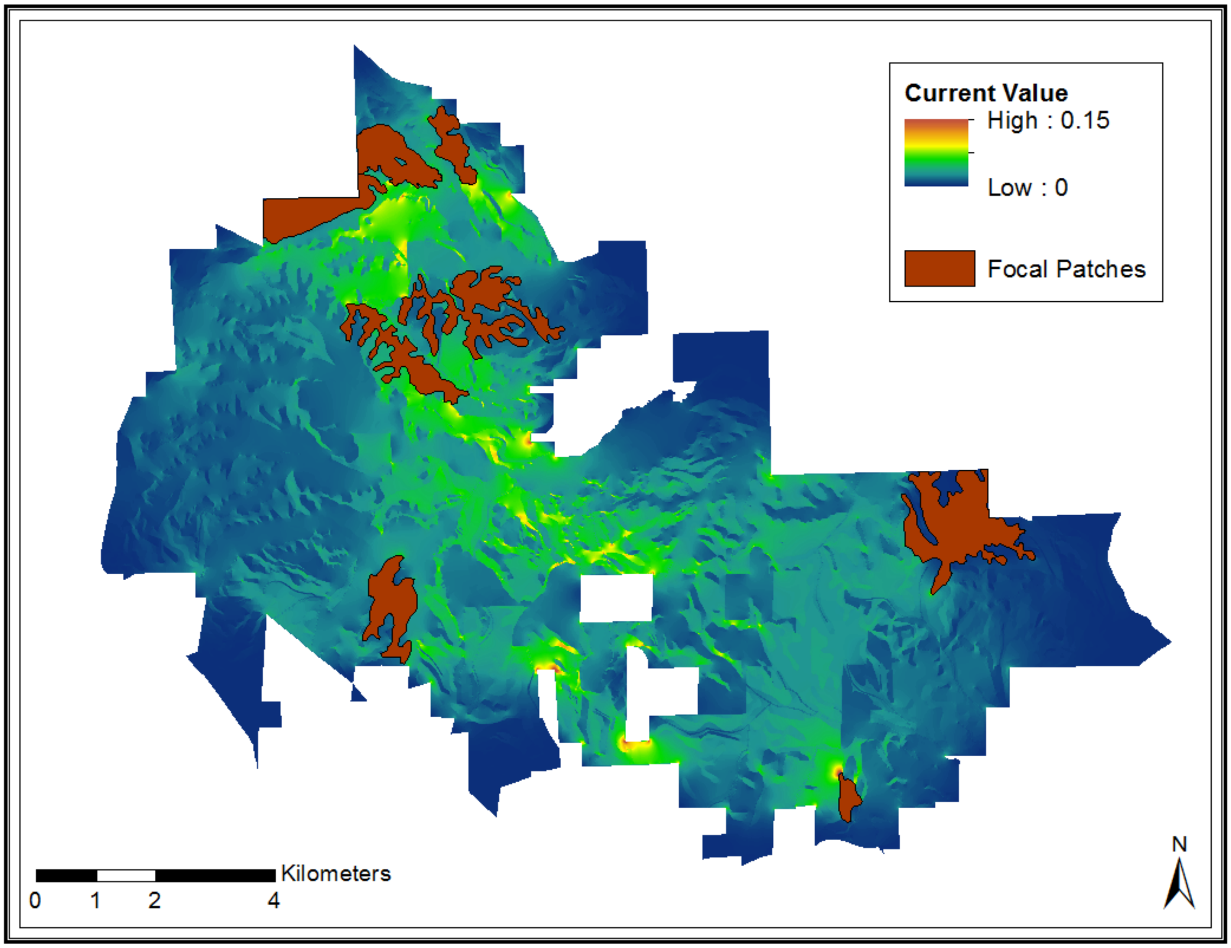

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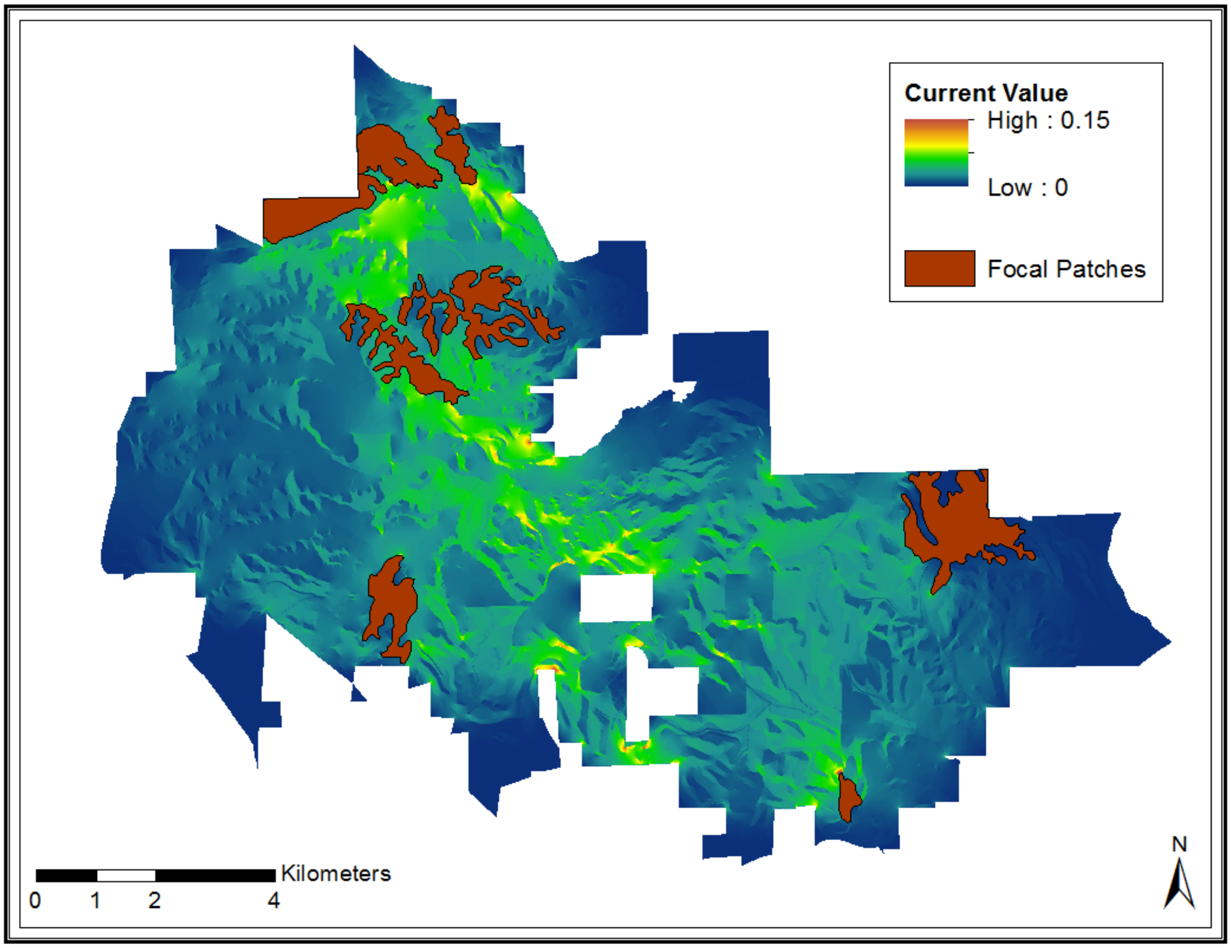
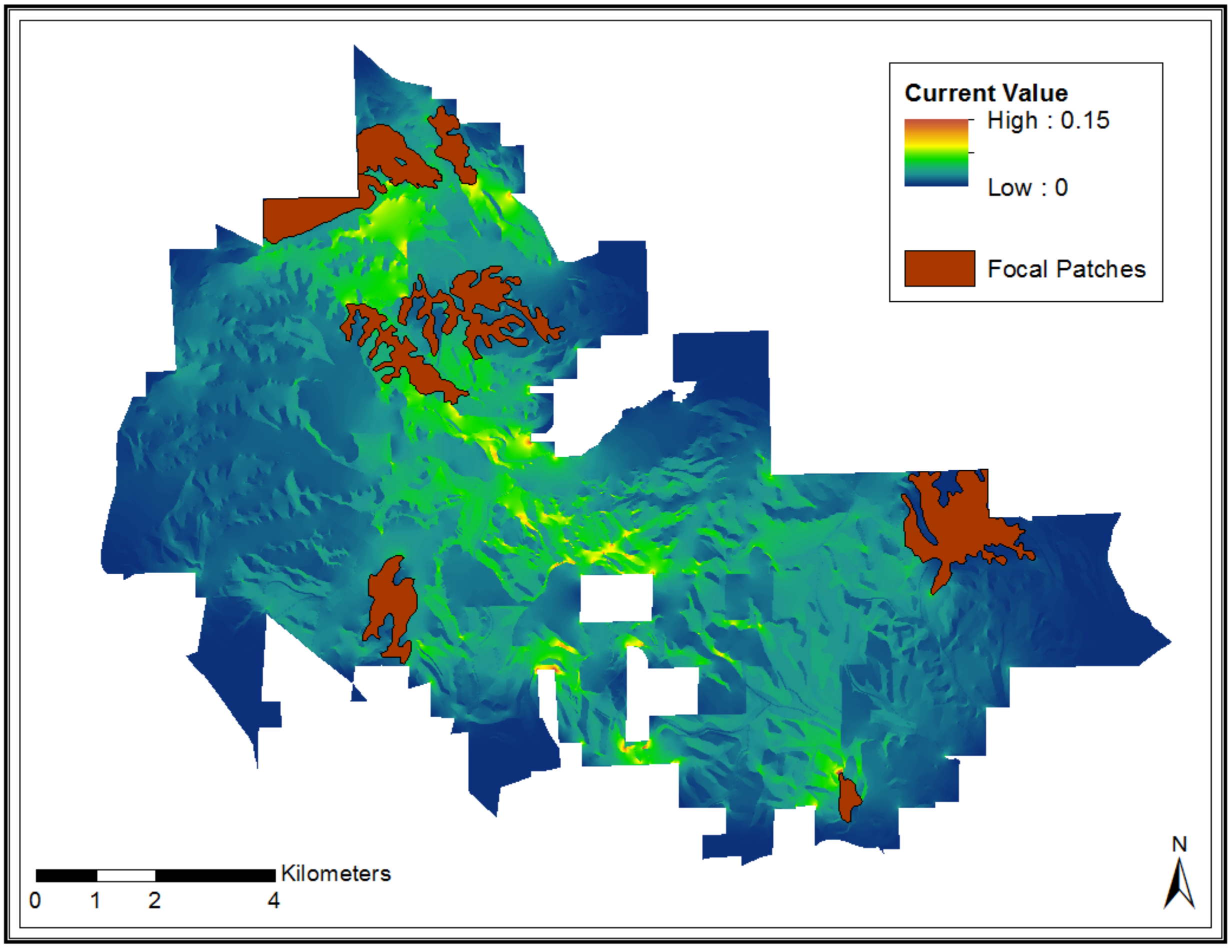


Current flow using resistance set 2 after 100 years under management alternative 3 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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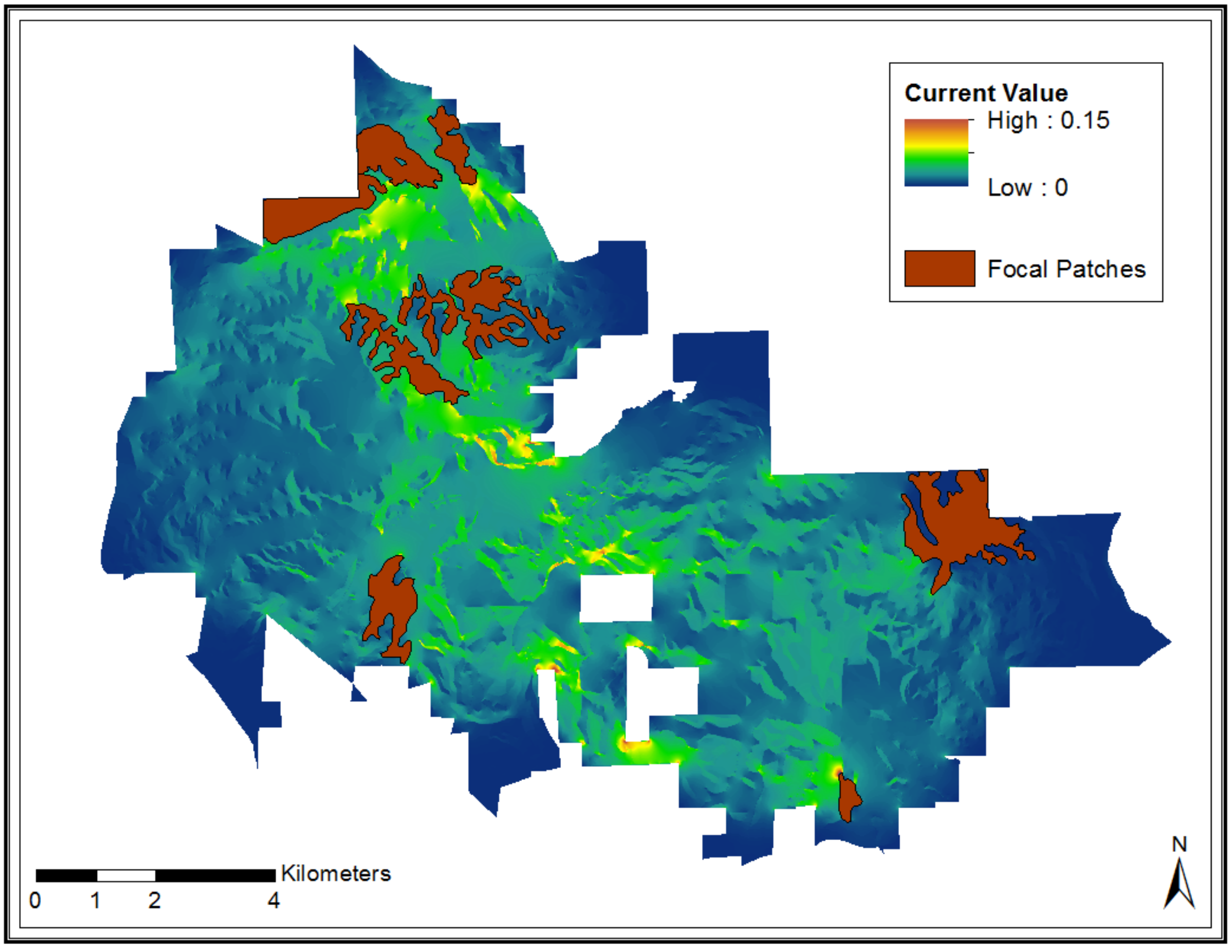

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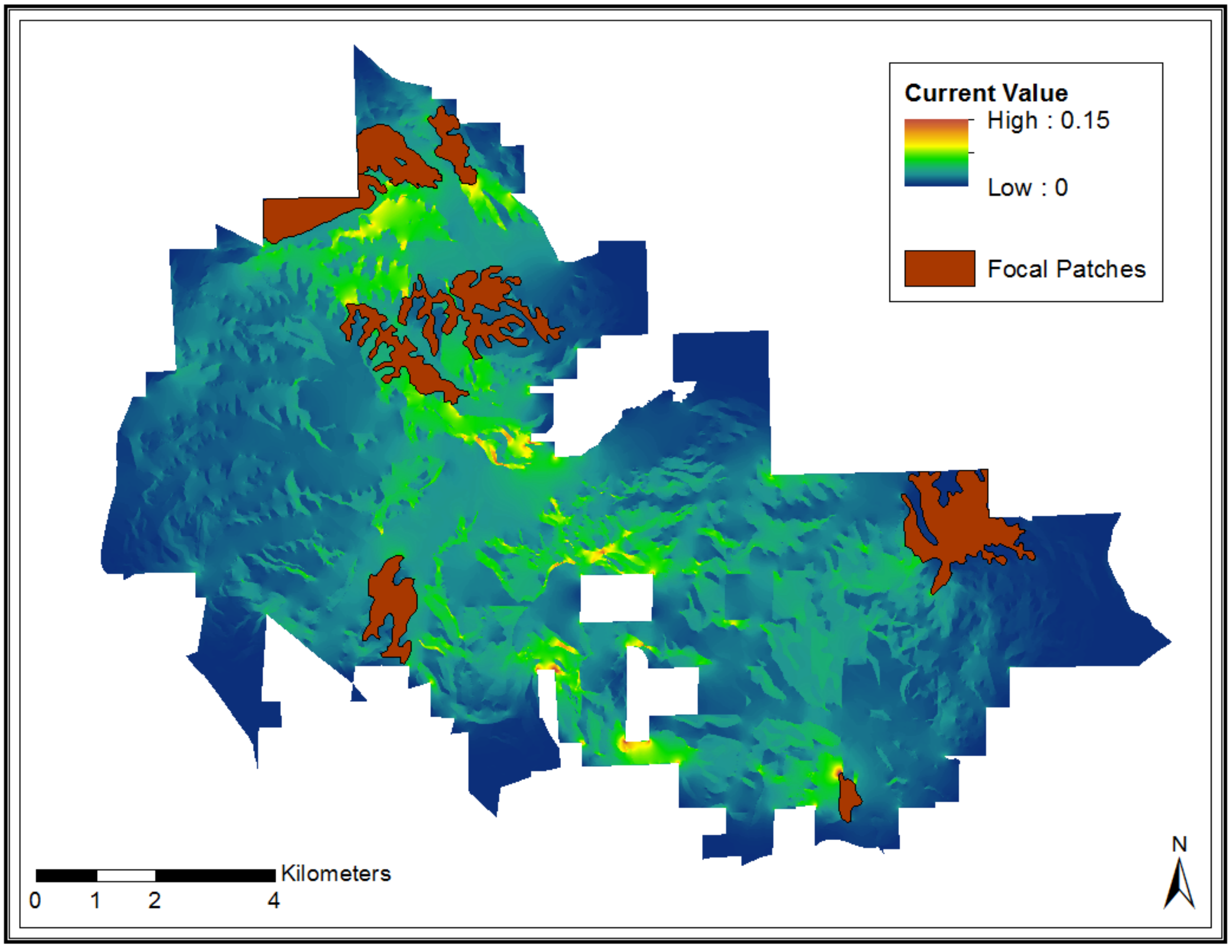
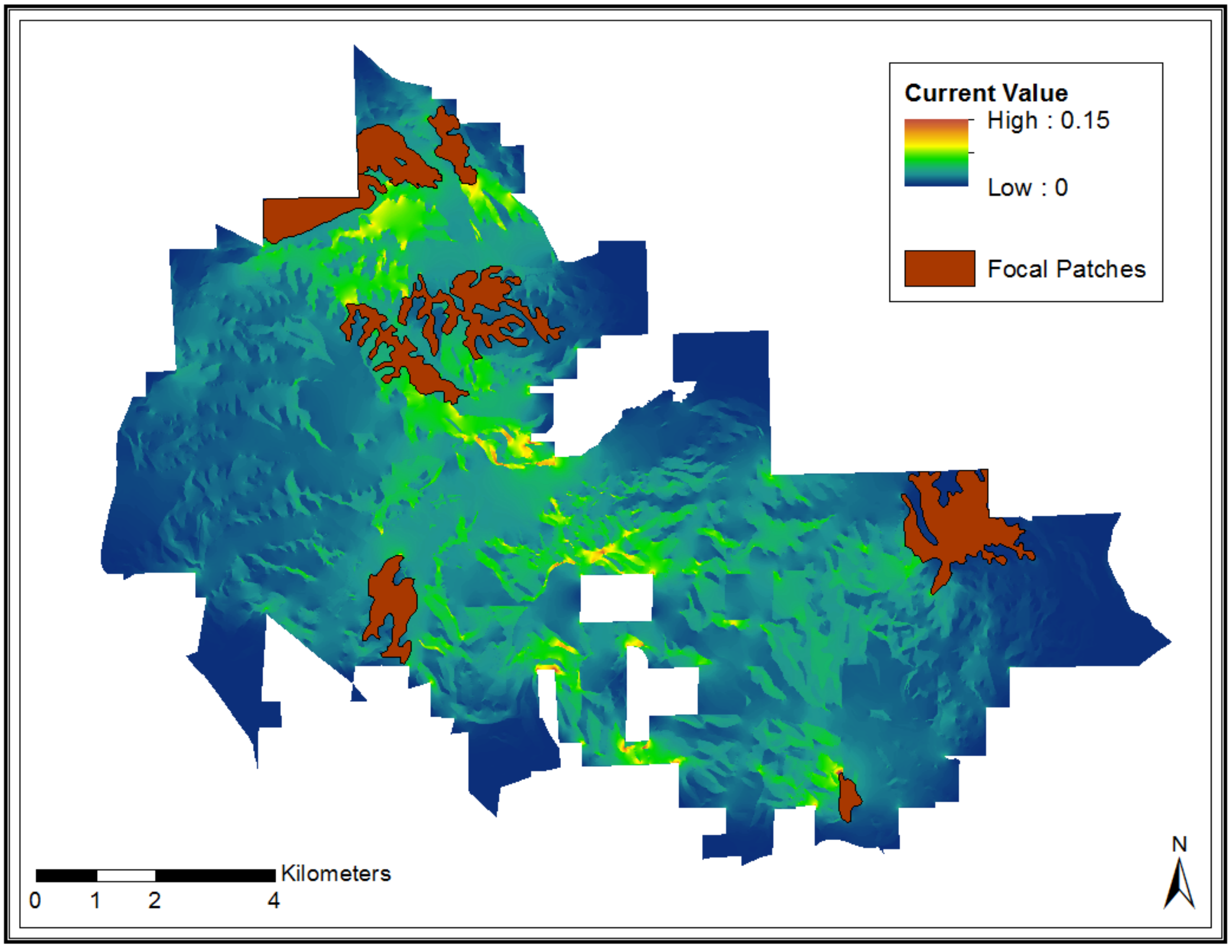


Current flow using resistance set 2 after 100 years under management alternative 6 at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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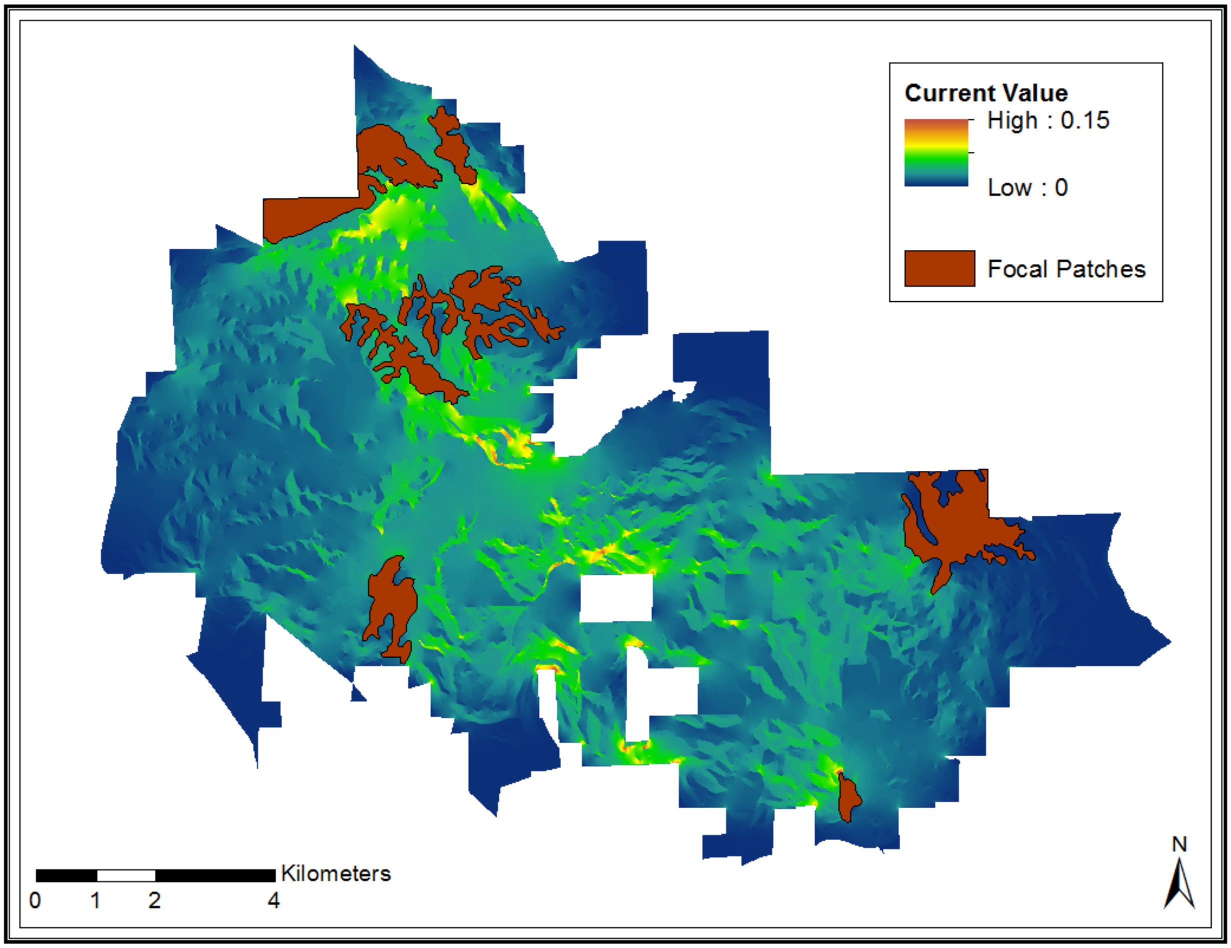

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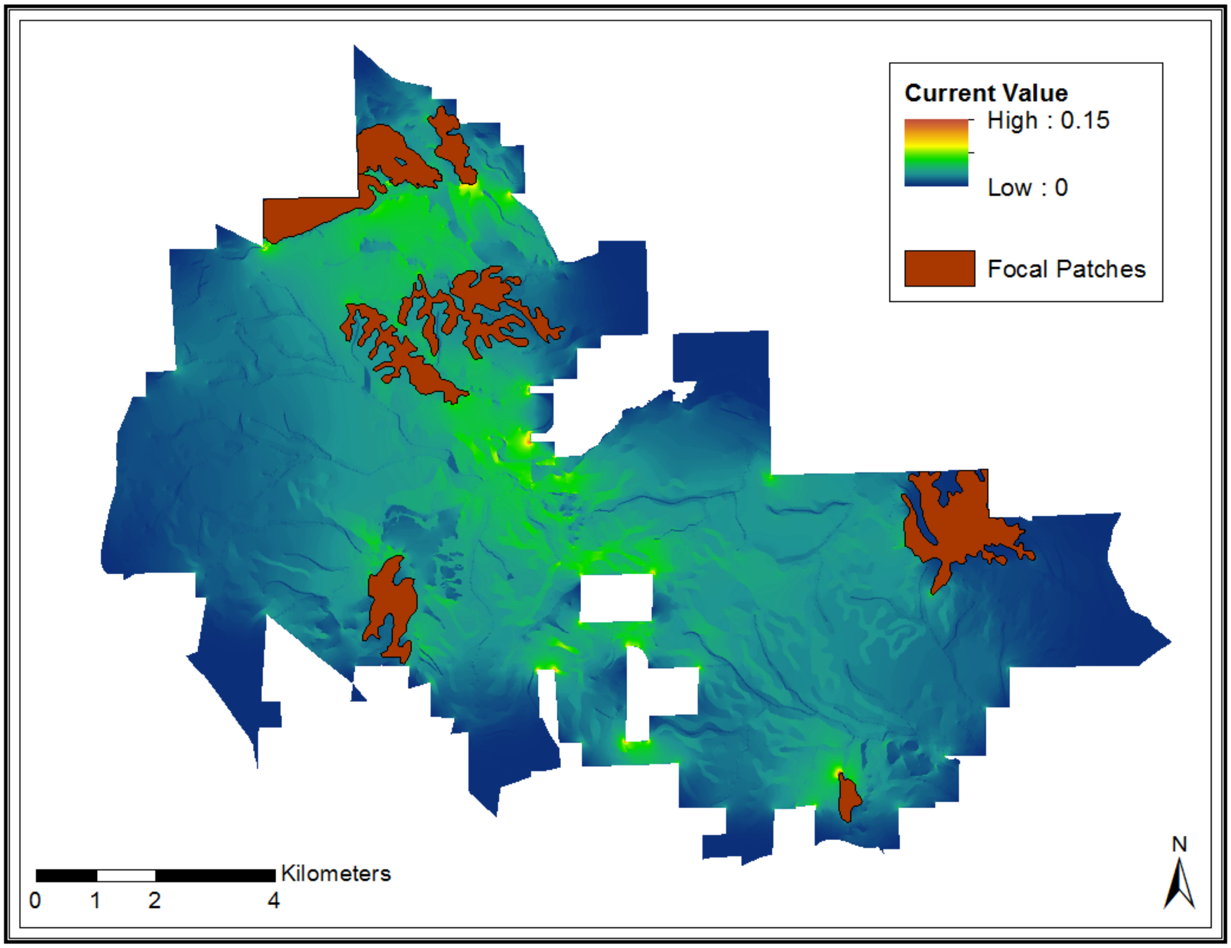

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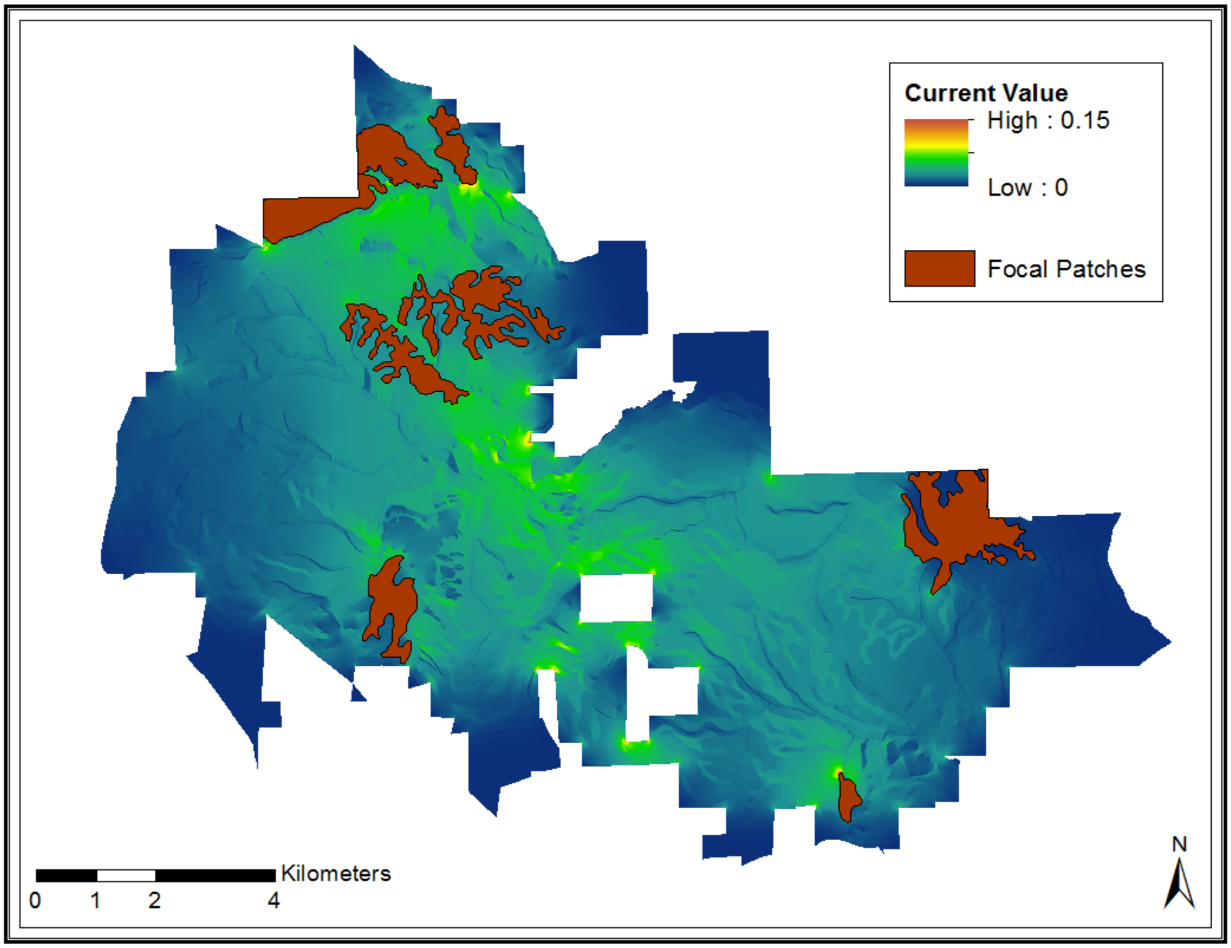

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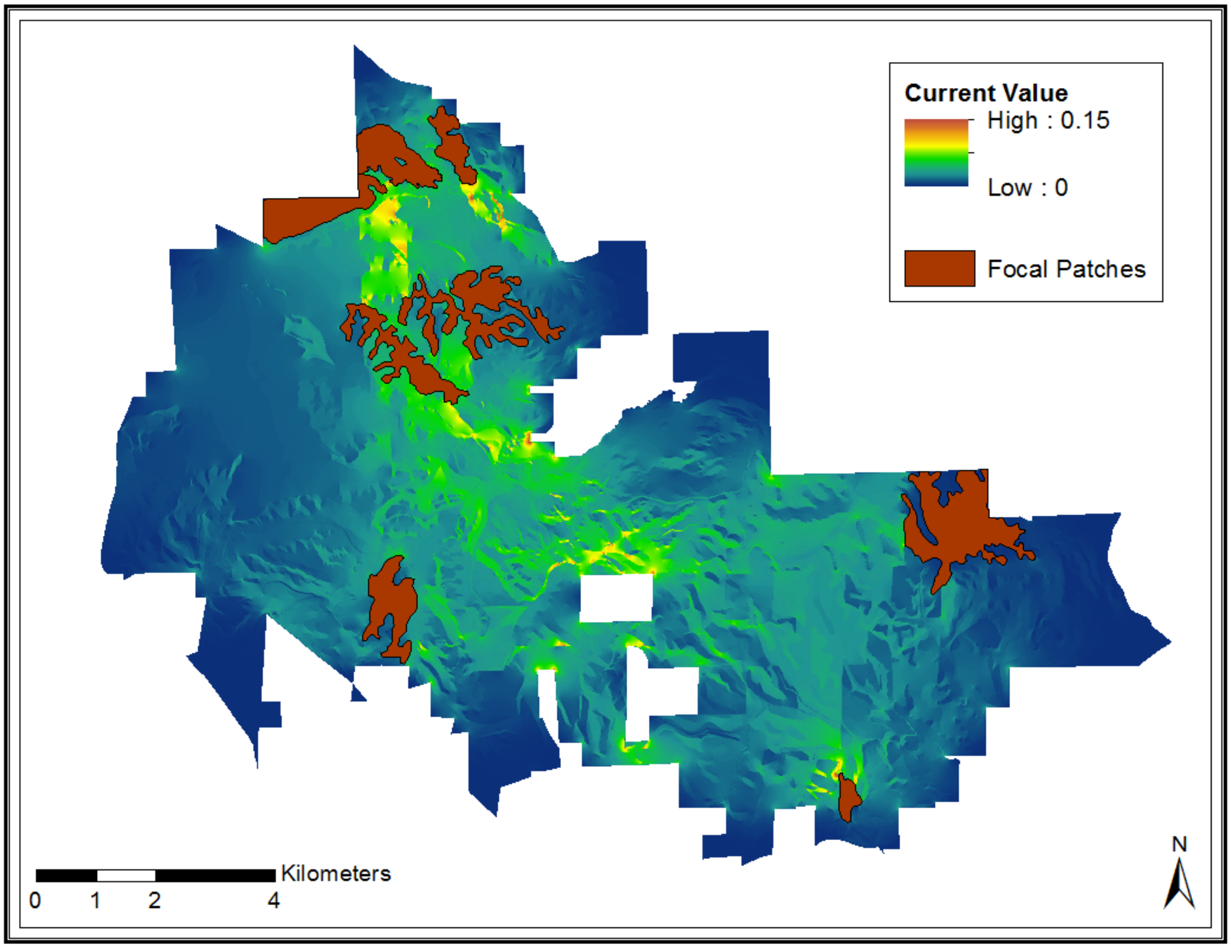

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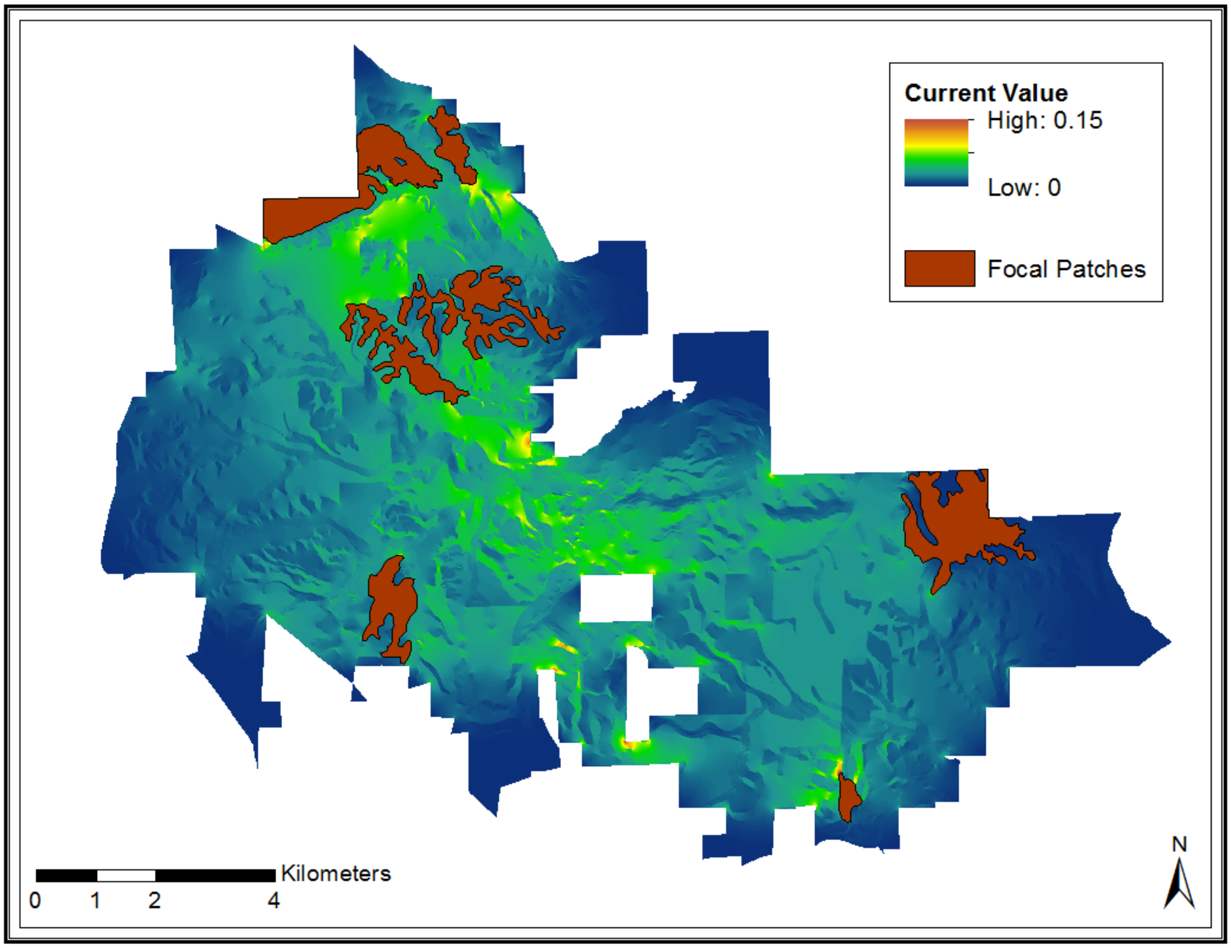
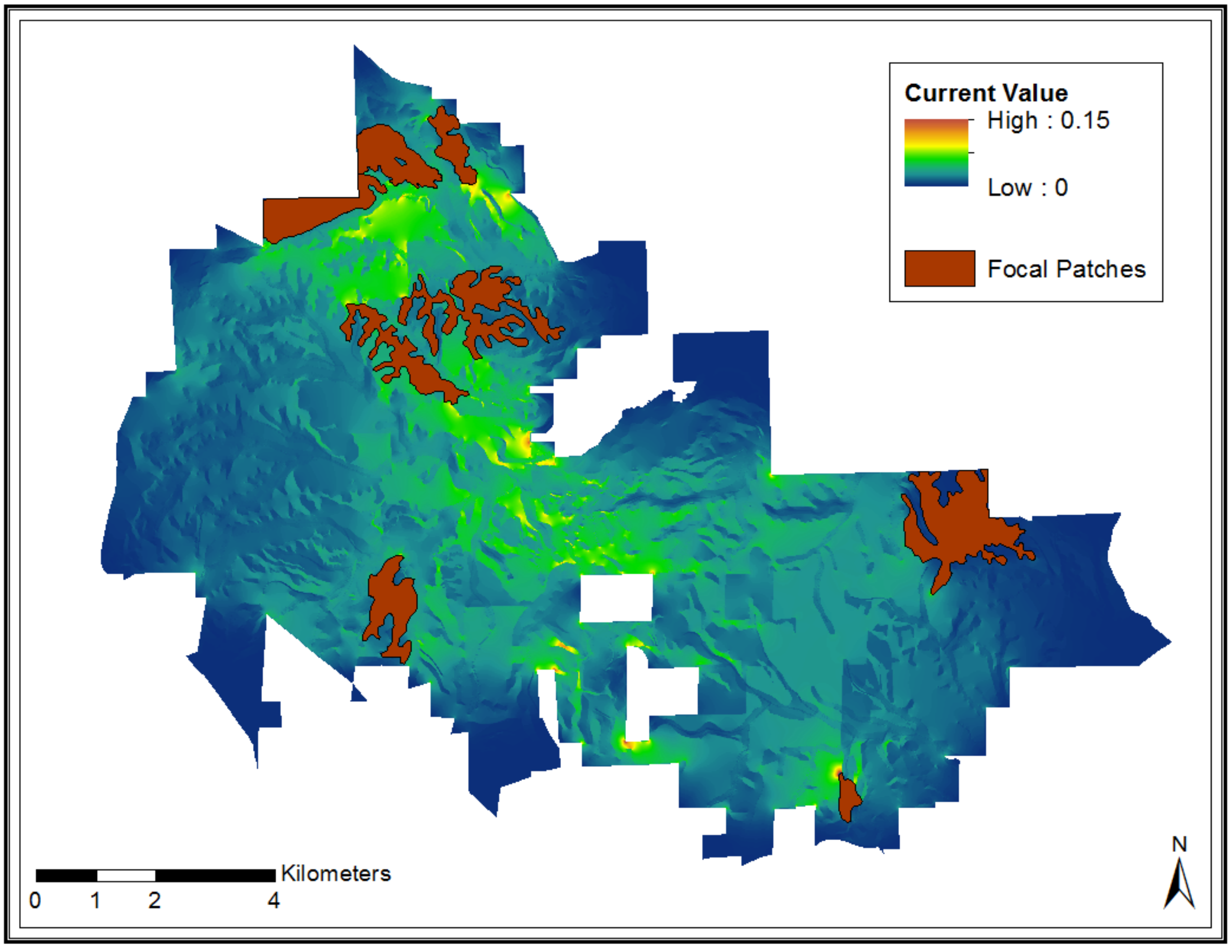


Current flow using resistance set 3 under initial landscape conditions (circa 2011) at Barbour Wildlife Management Area and Wehle Forever Wild Tract.



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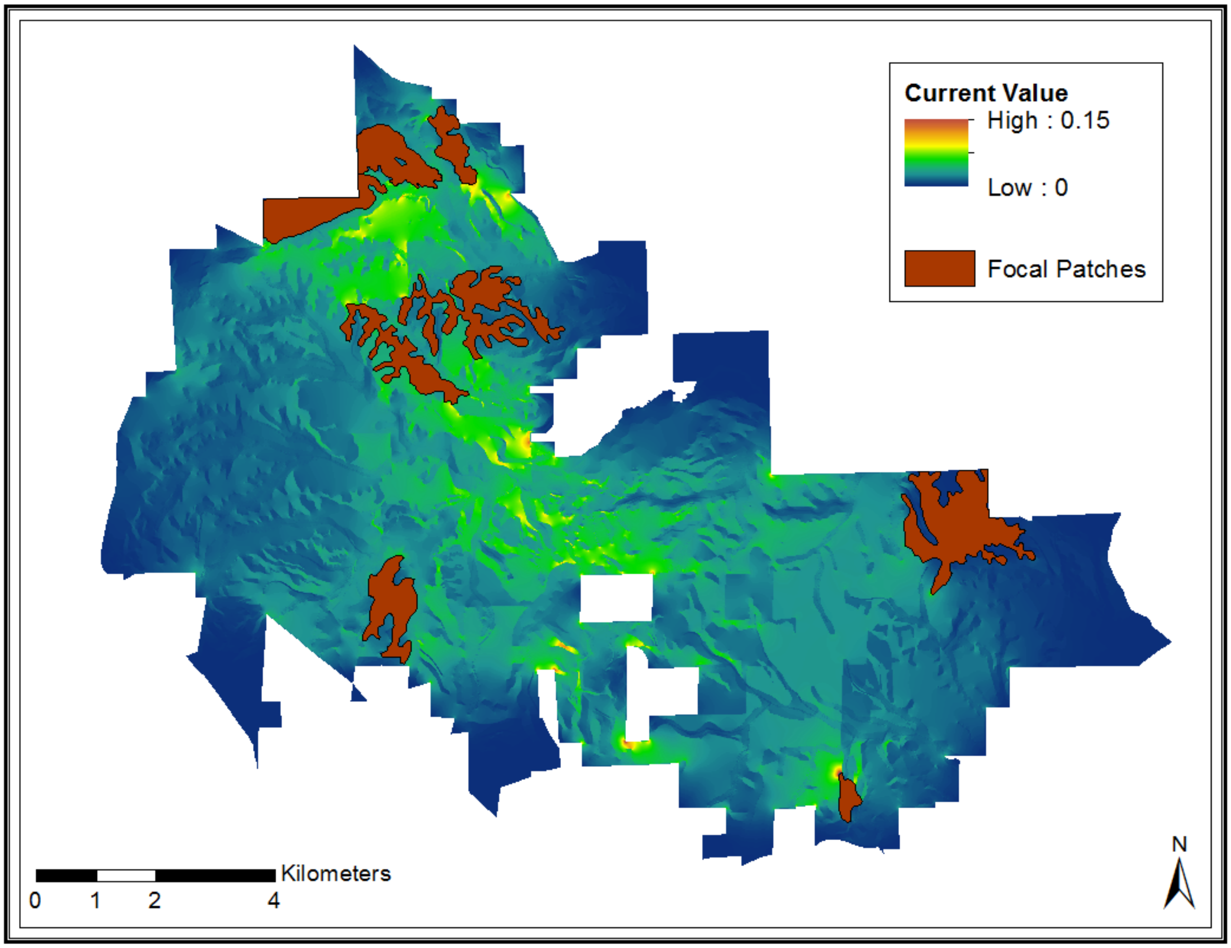

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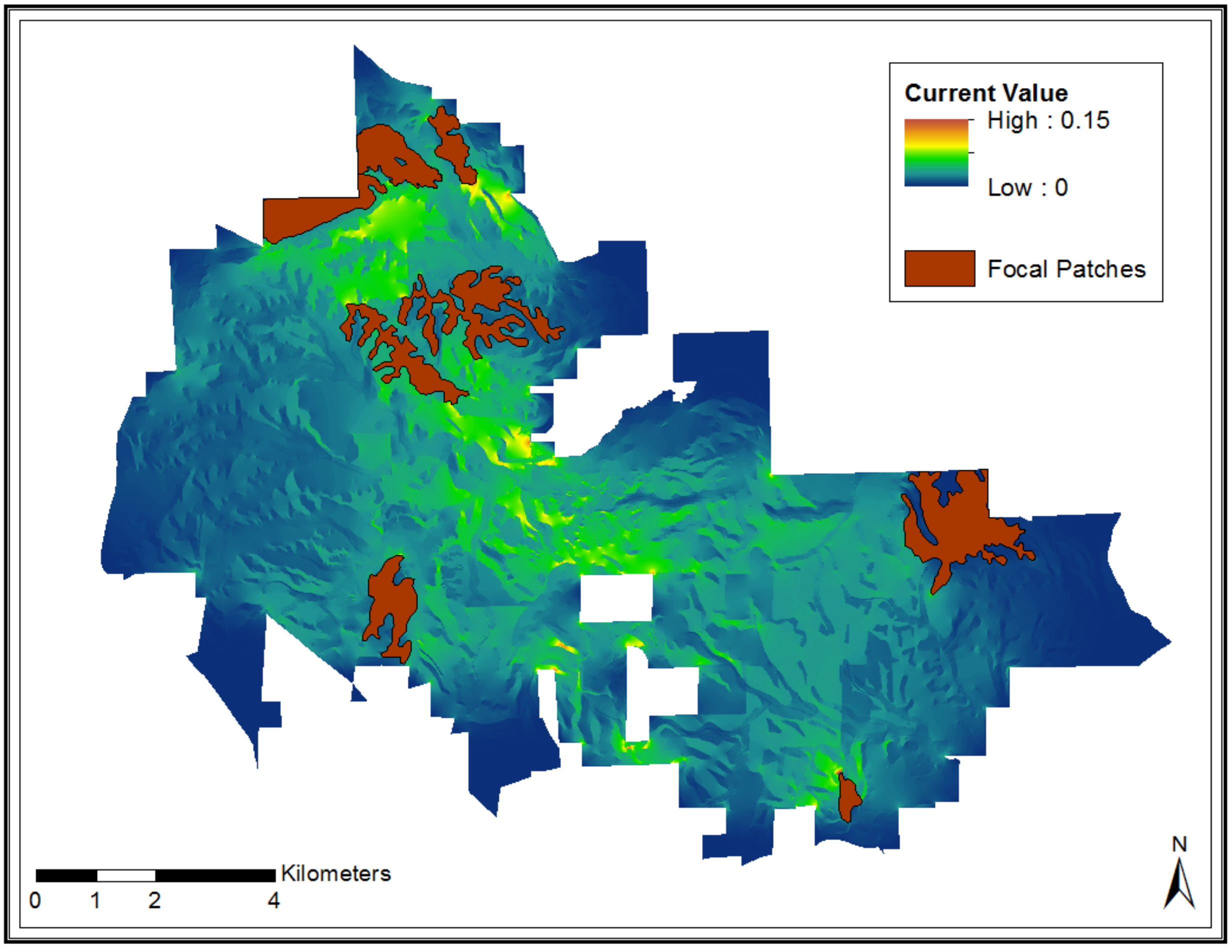

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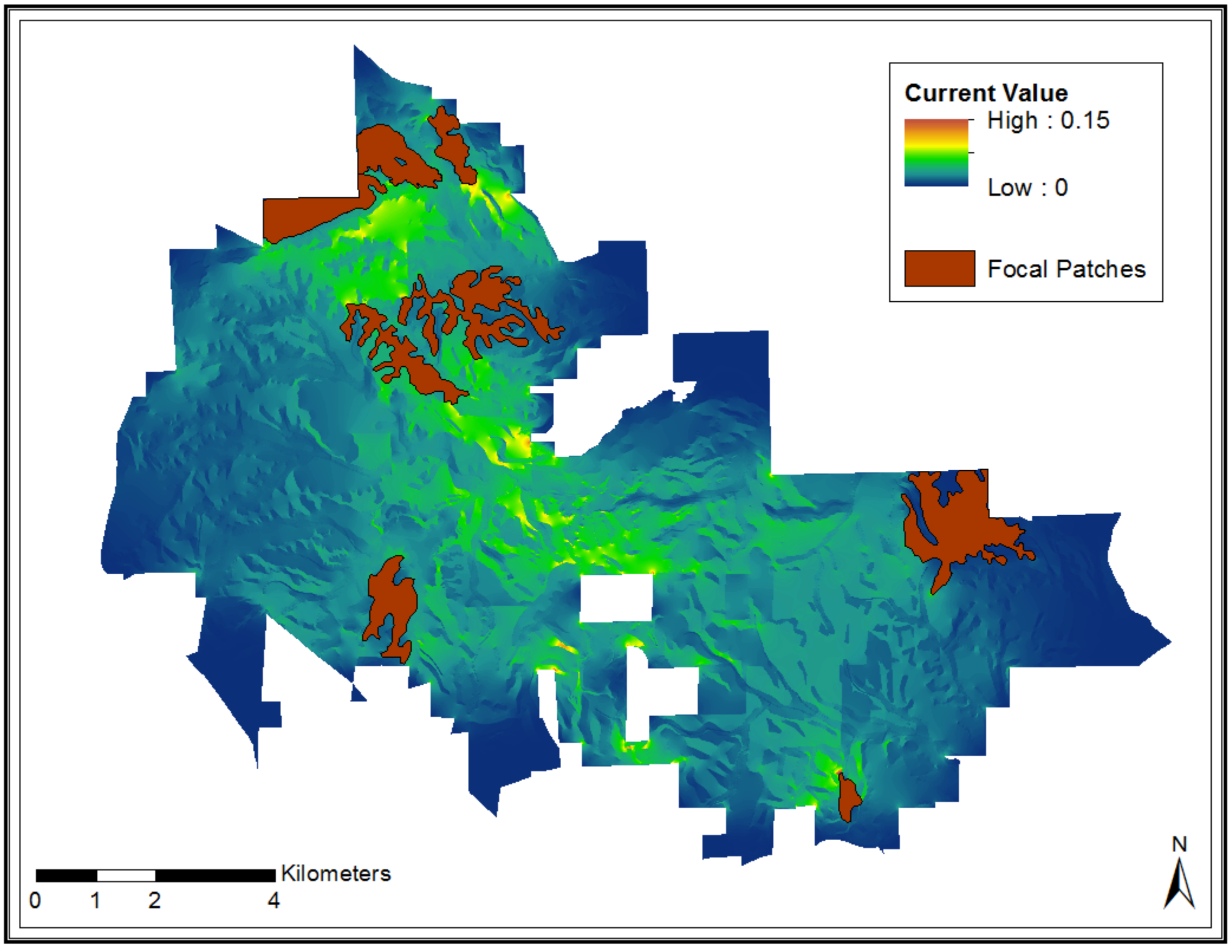

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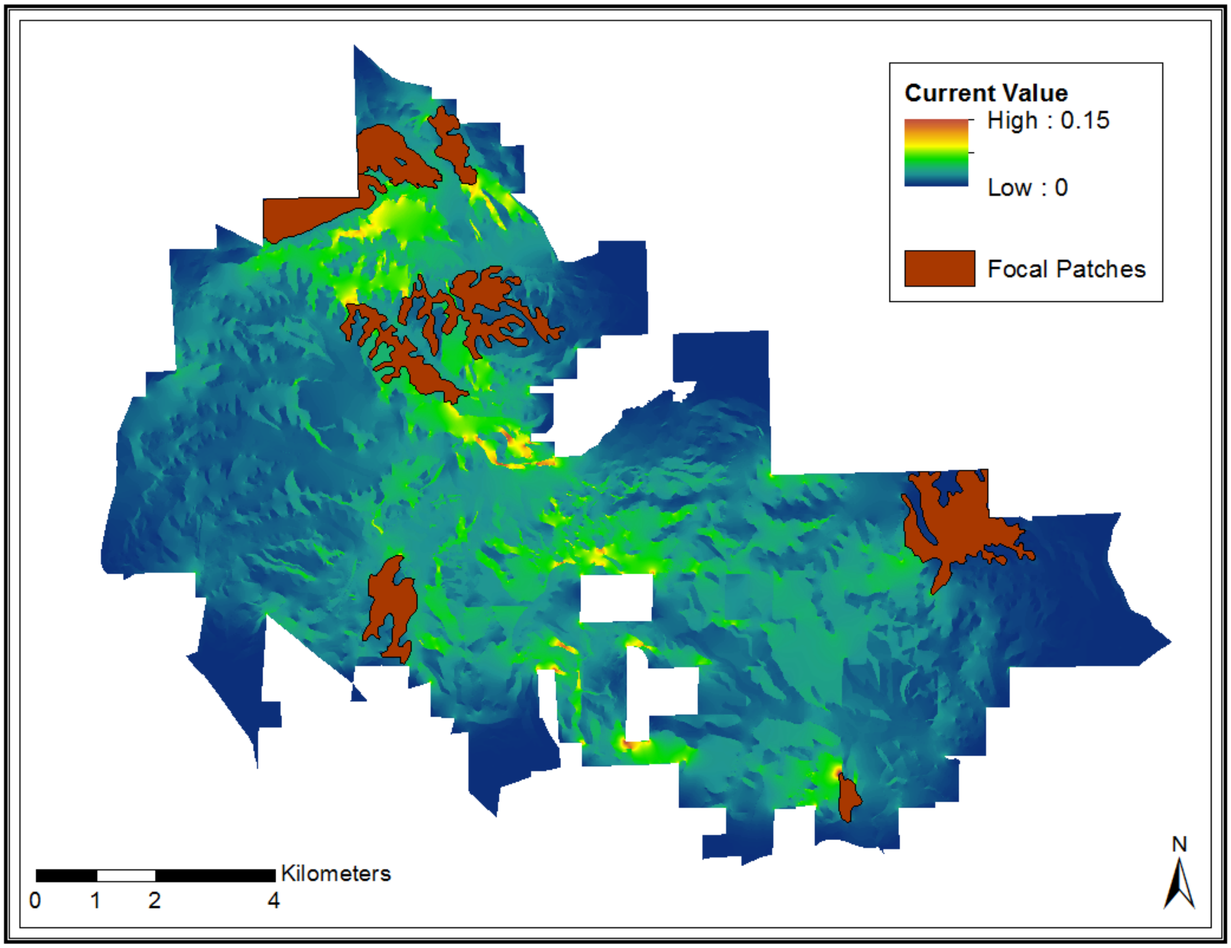

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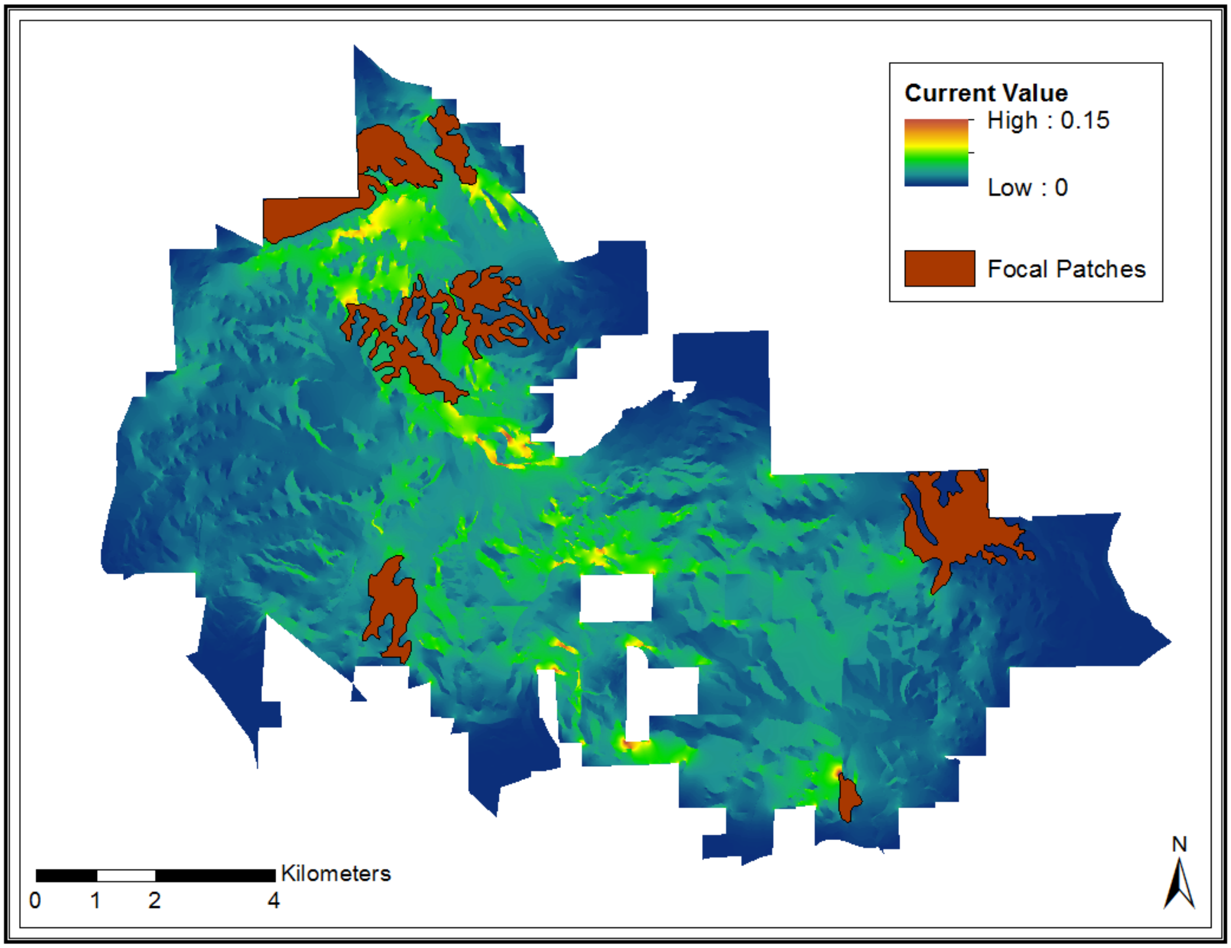

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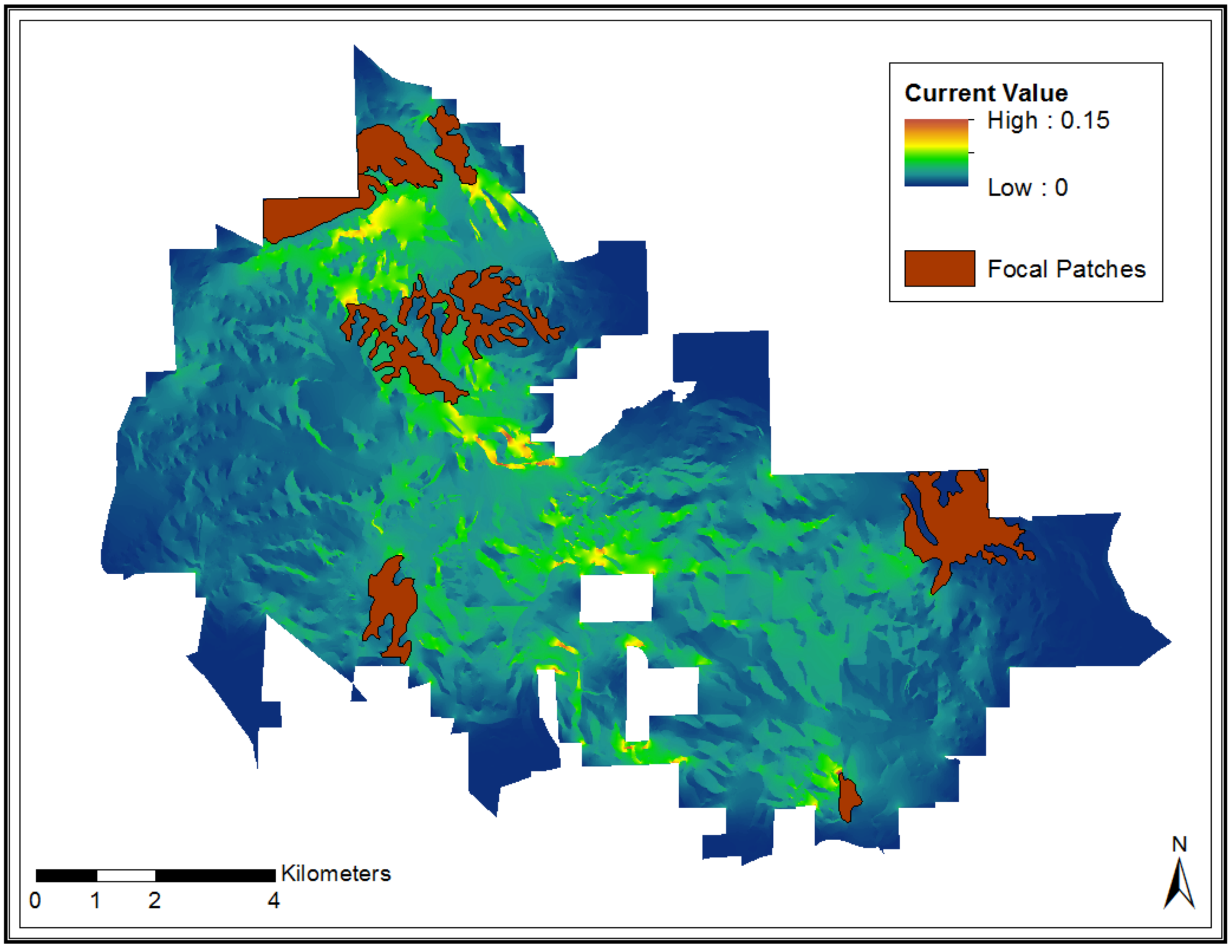

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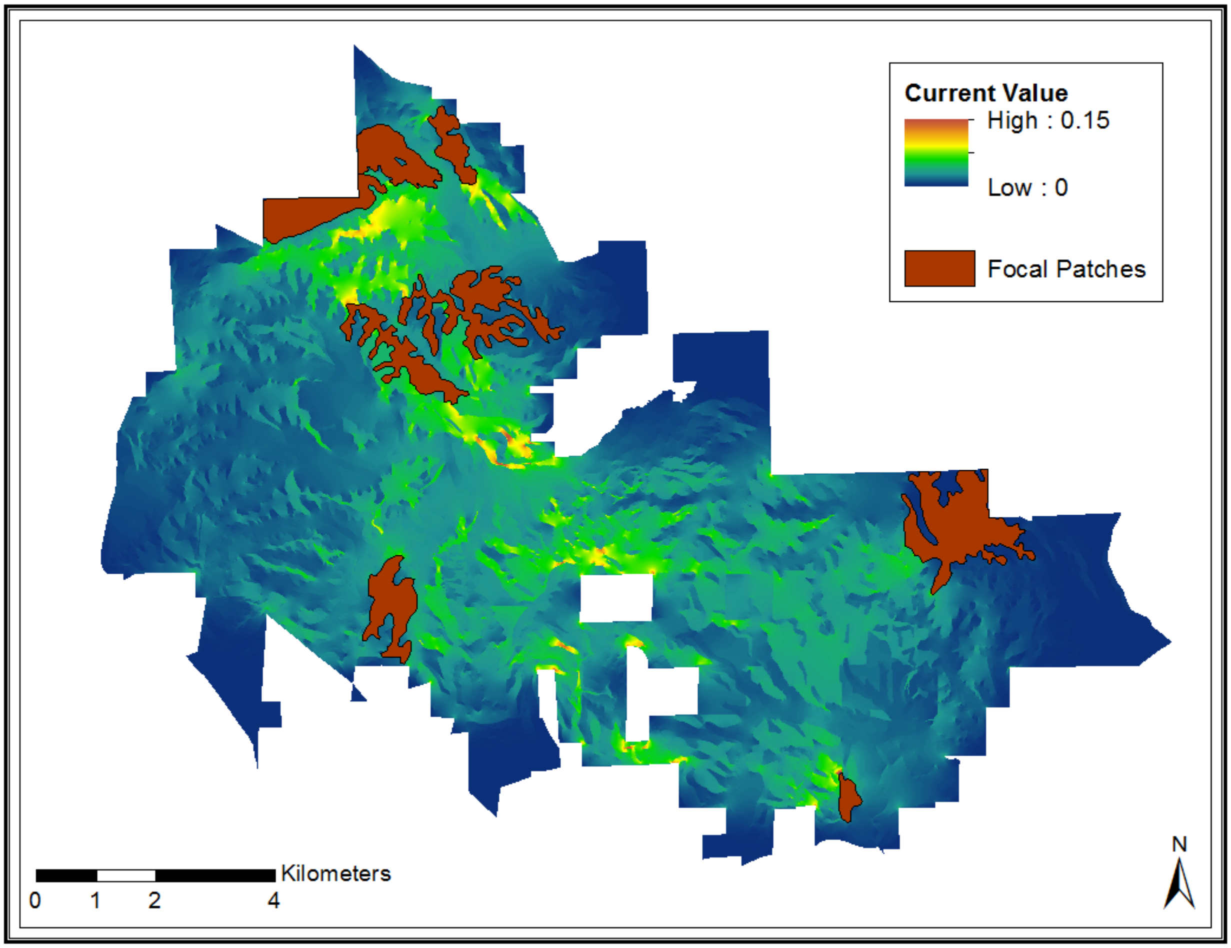

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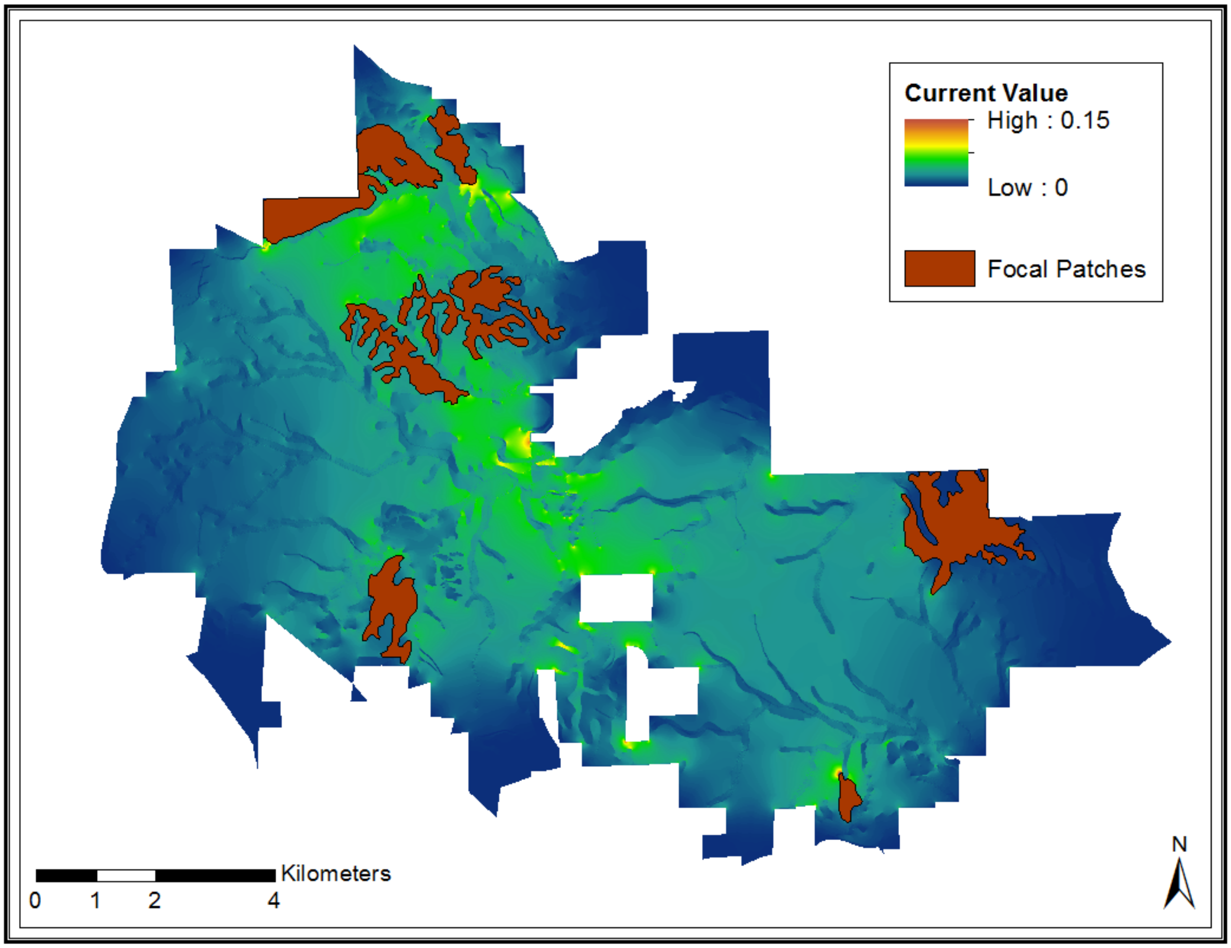

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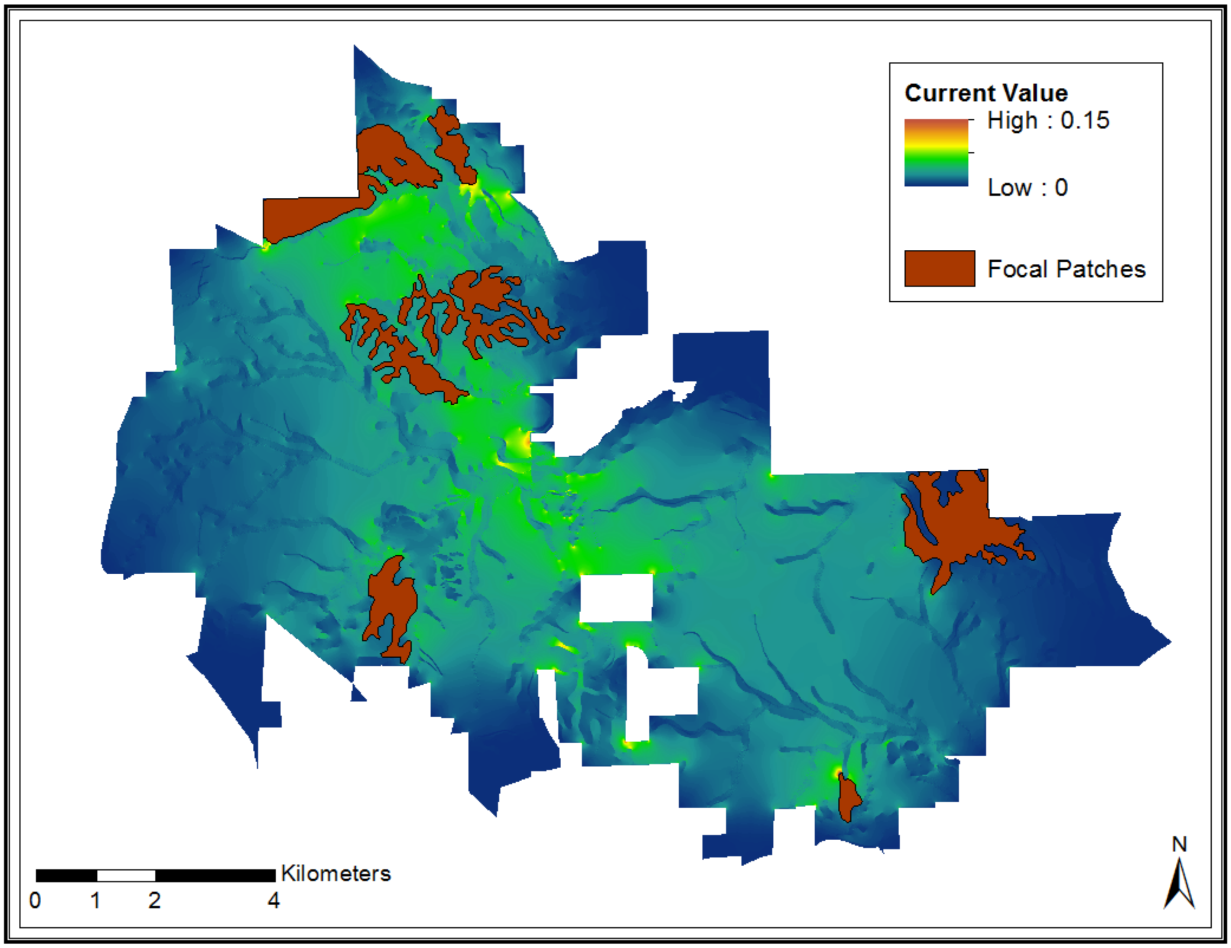

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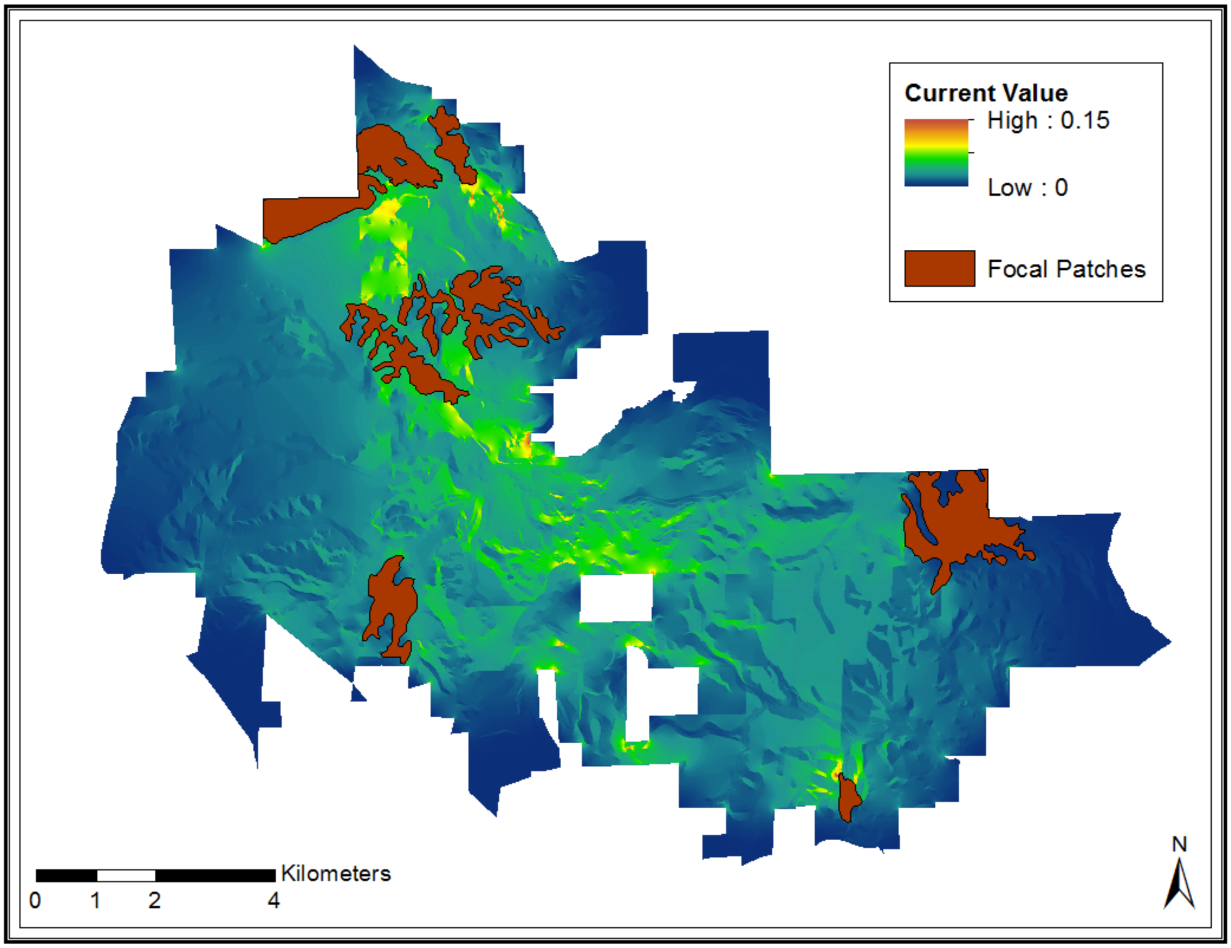

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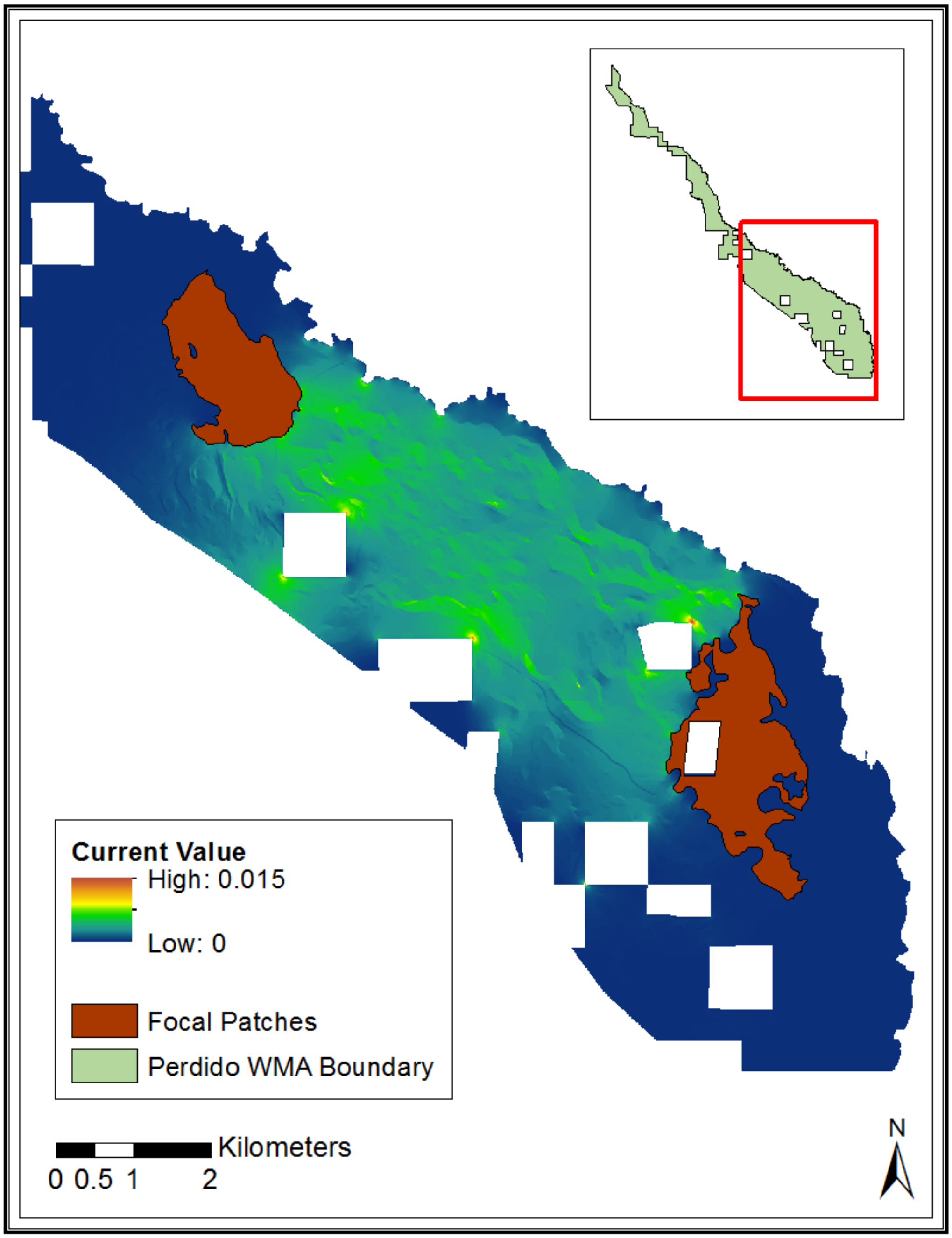
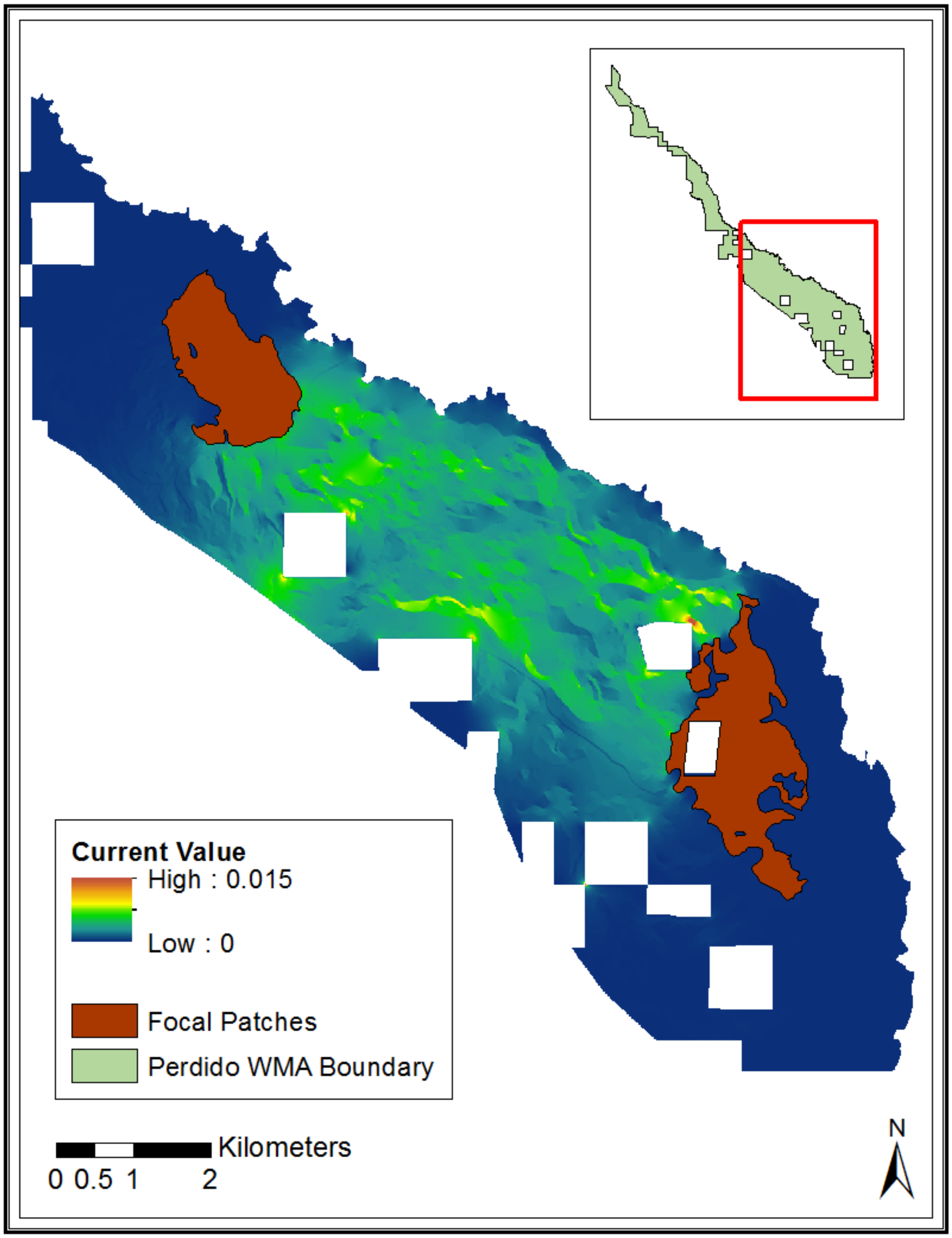
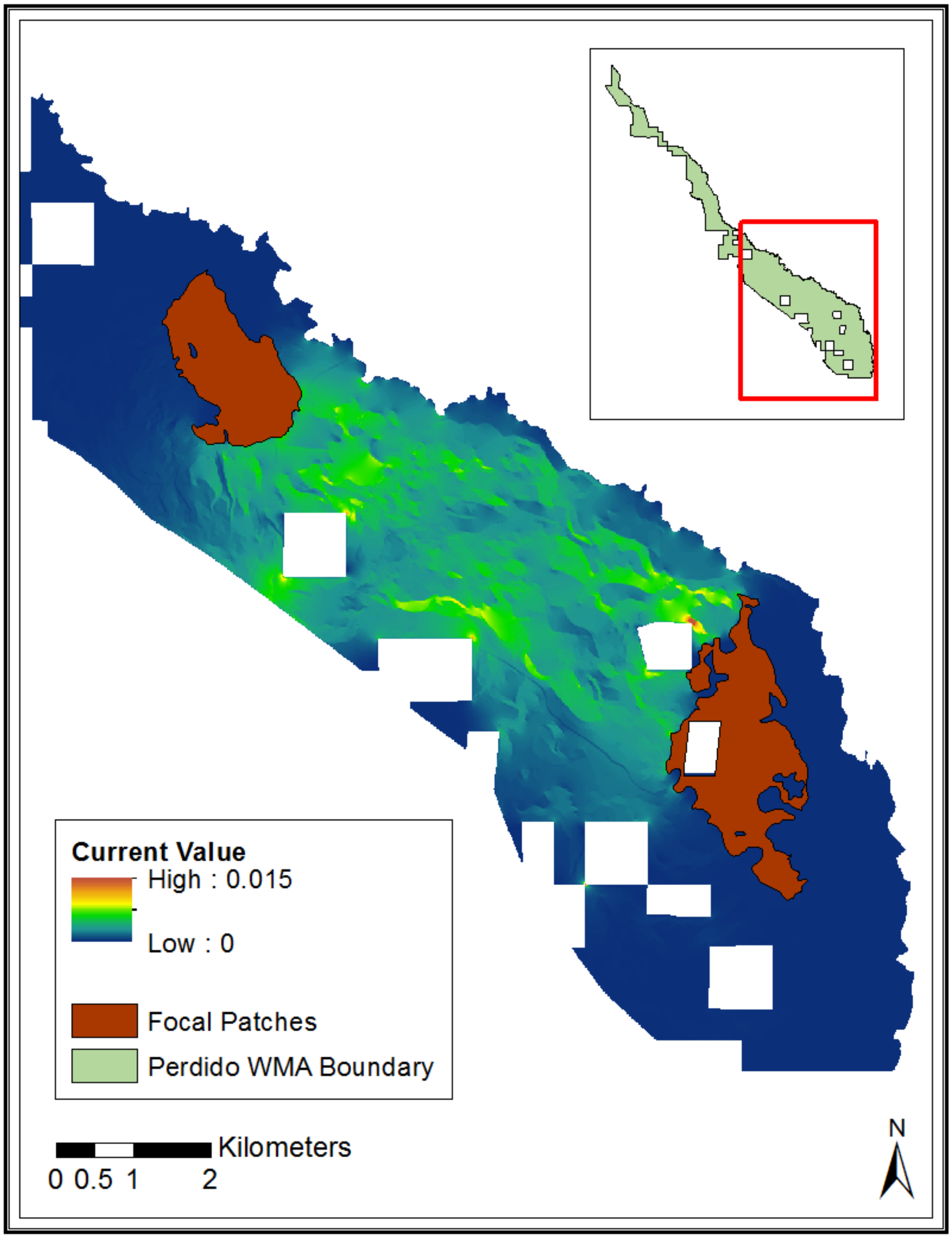


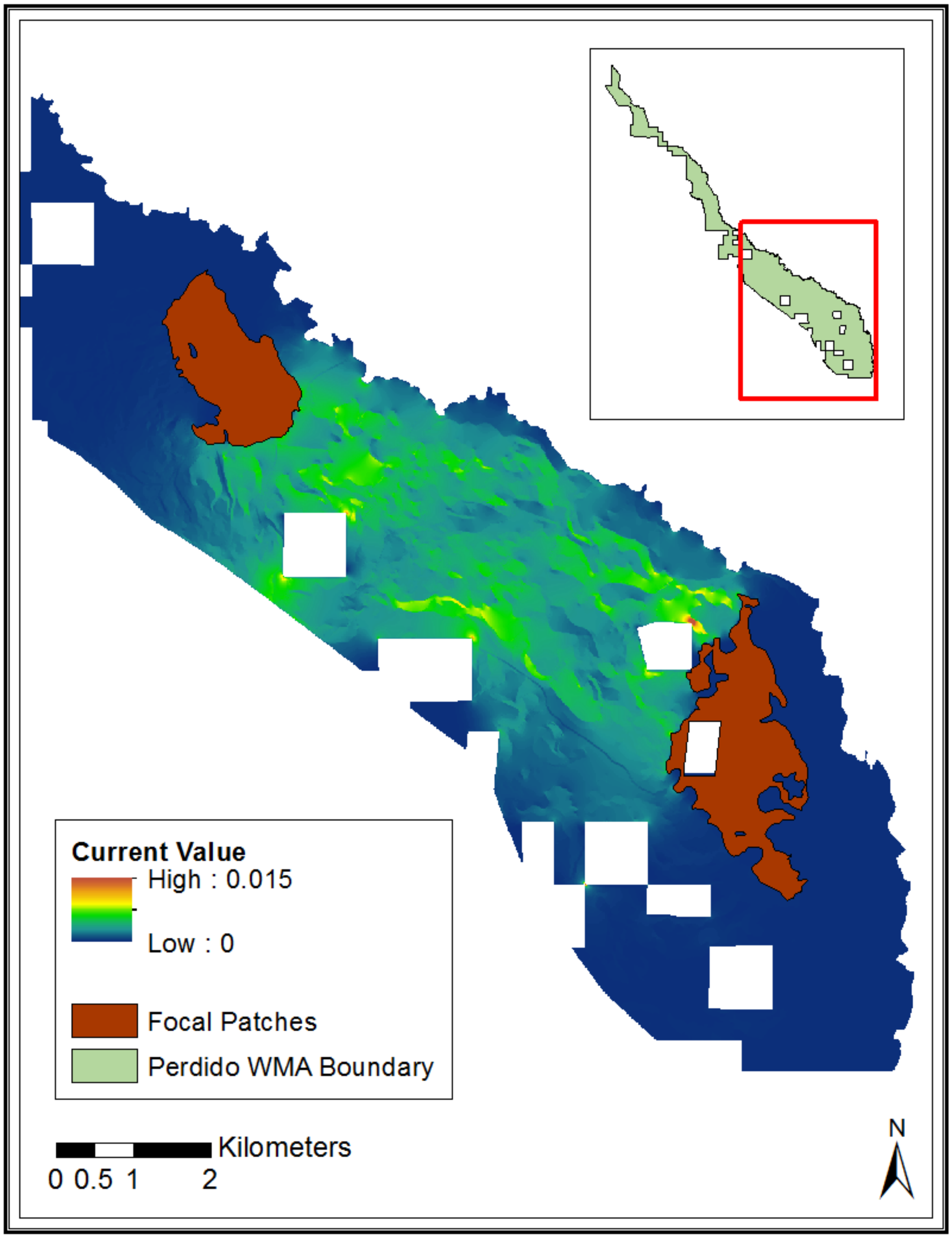
Current flow using resistance set 1 under initial landscape conditions (circa 2011) at Perdido Wildlife Management Area.



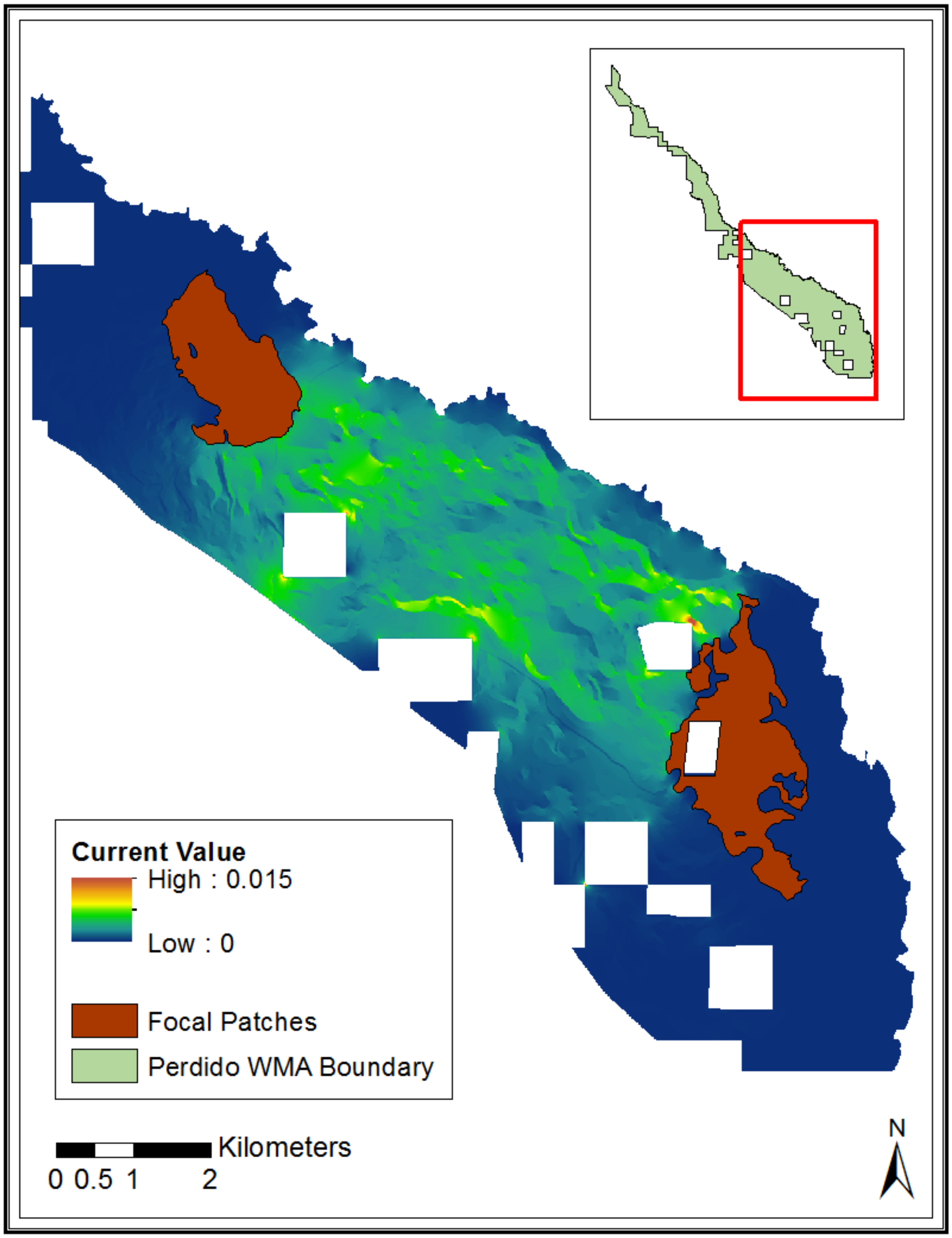
Current flow using resistance set 1 after 100 years under management alternative 1 at Perdido Wildlife Management Area.



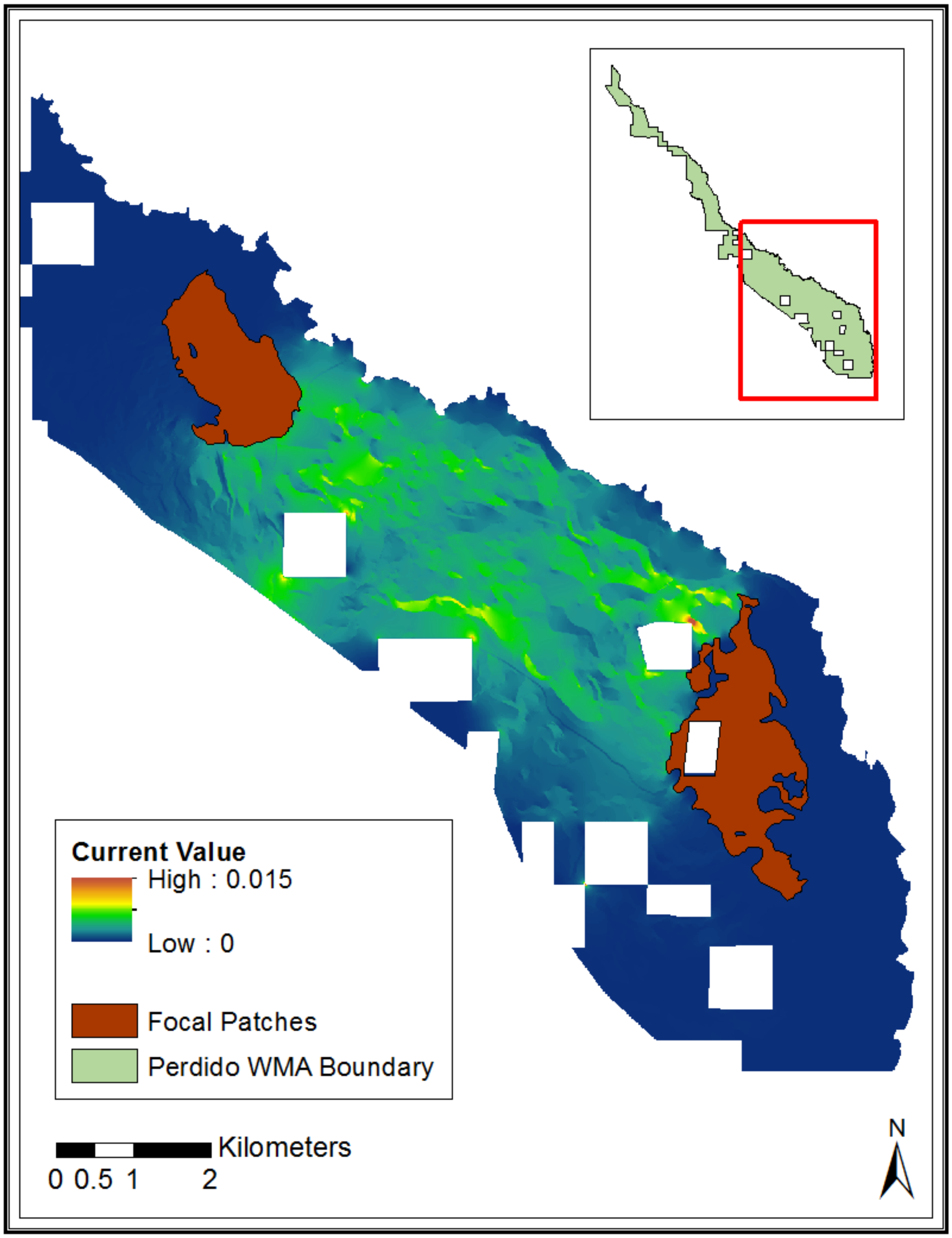
Current flow using resistance set 1 after 100 years under management alternative 2 at Perdido Wildlife Management Area.



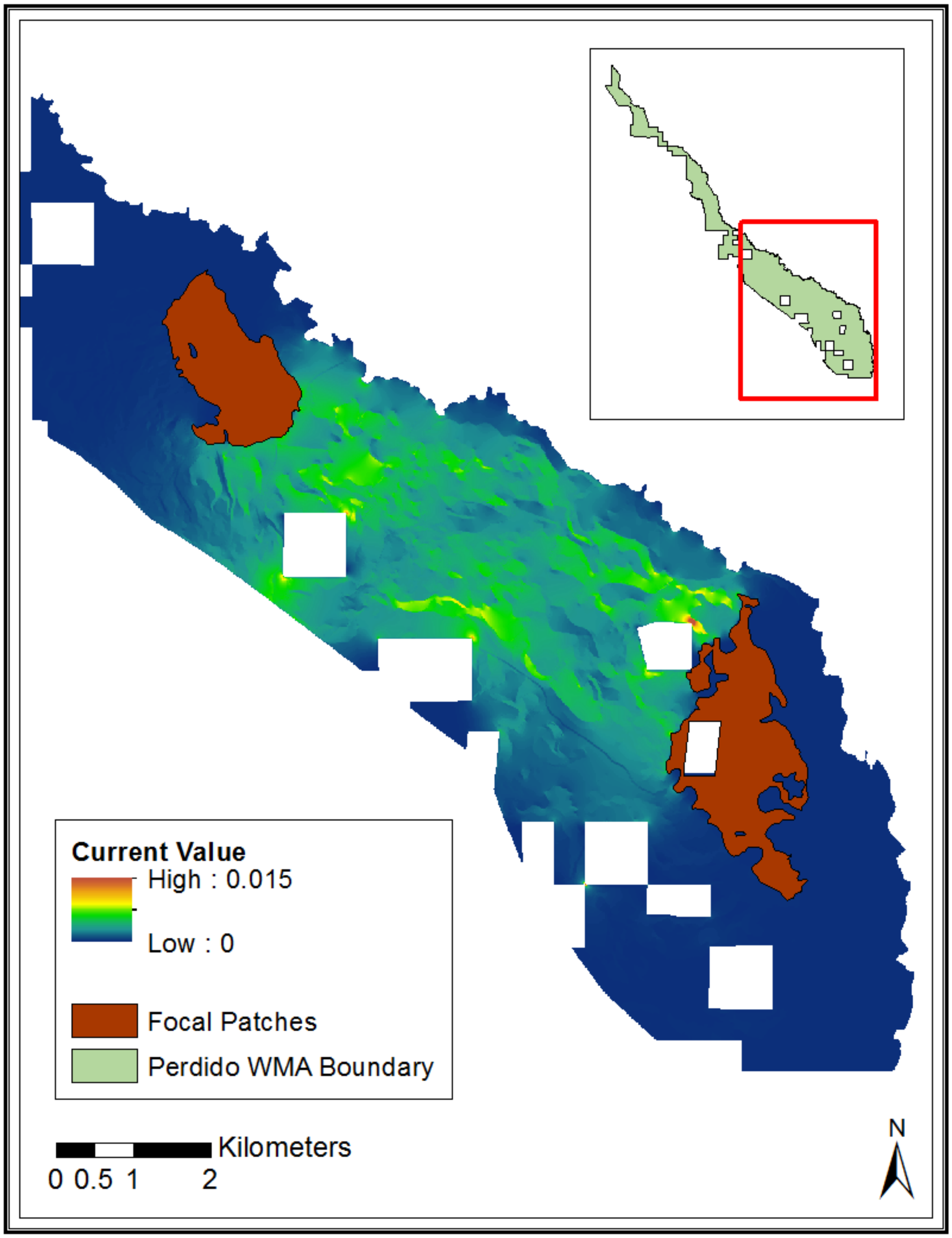
Current flow using resistance set 1 after 100 years under management alternative 3 at Perdido Wildlife Management Area.



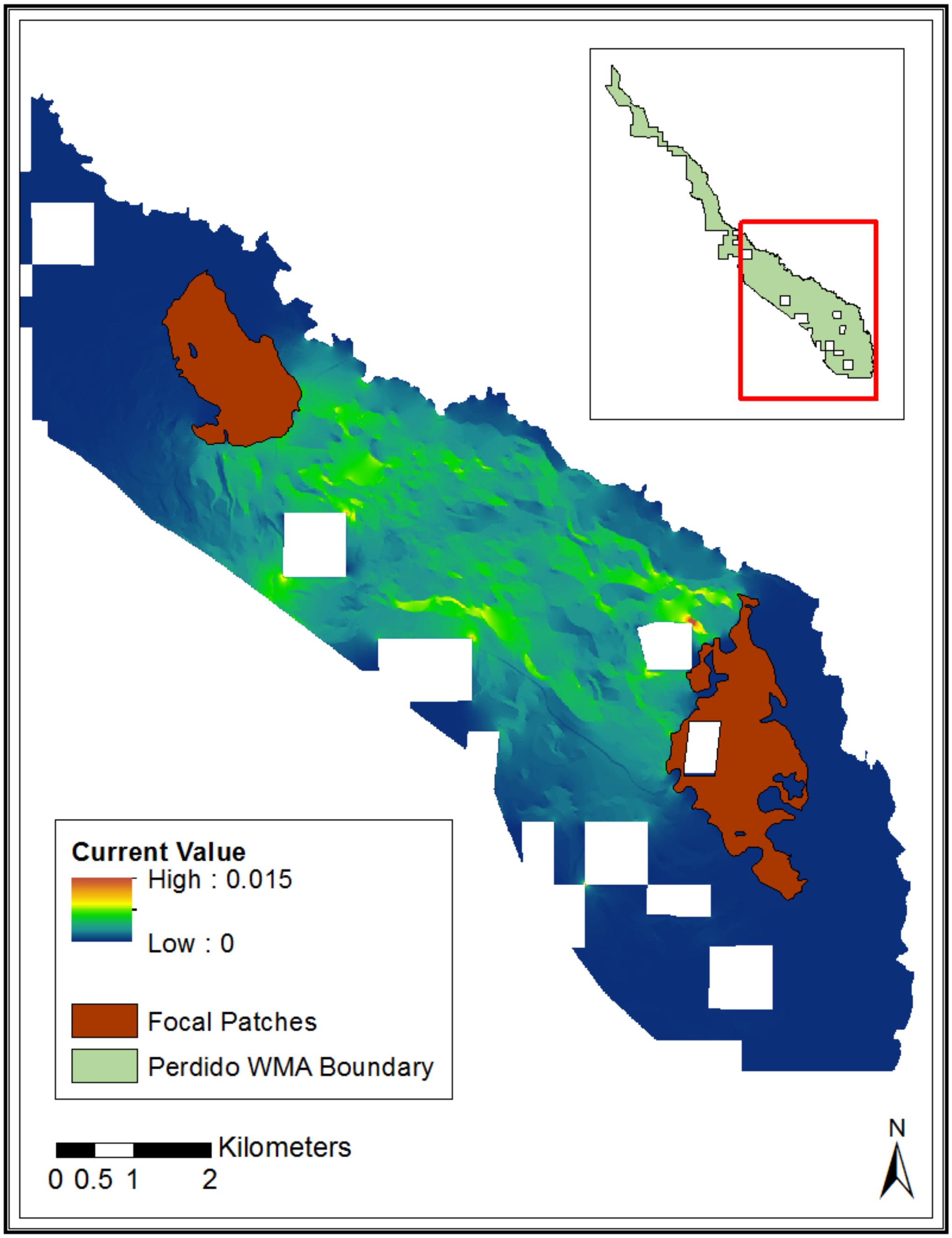
Current flow using resistance set 1 after 100 years under management alternative 4 at Perdido Wildlife Management Area.



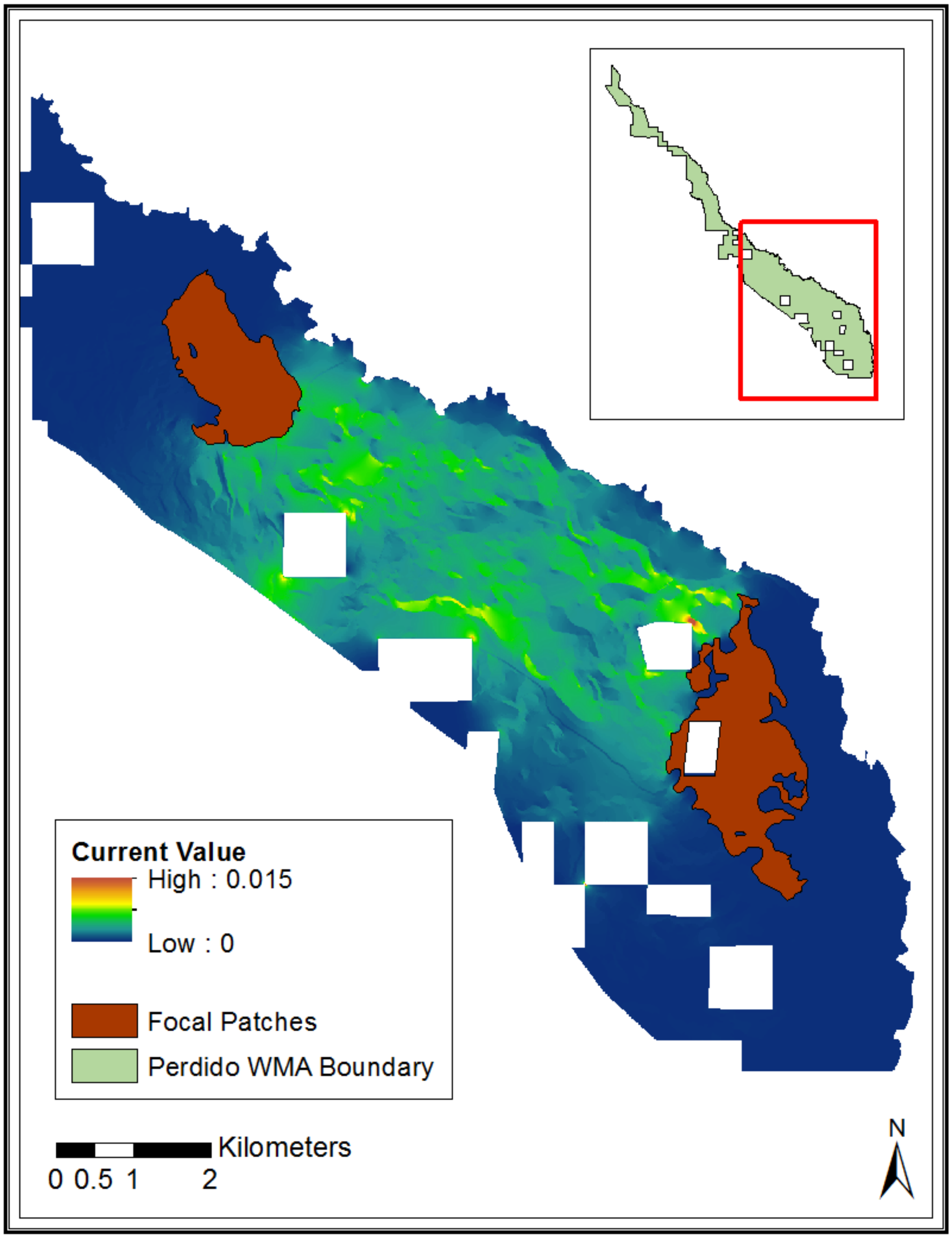
Current flow using resistance set 1 after 100 years under management alternative 5 at Perdido Wildlife Management Area.



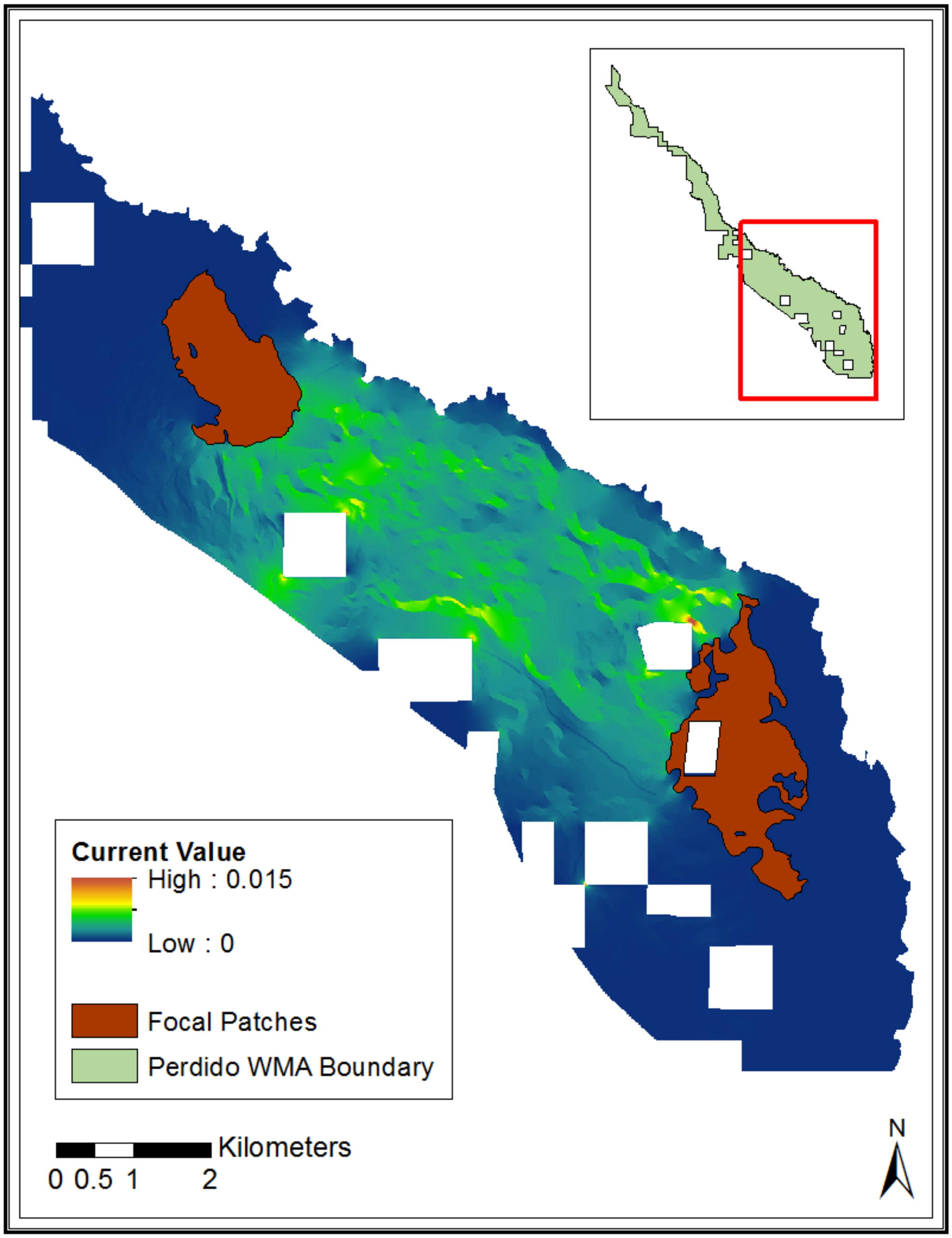
Current flow using resistance set 1 after 100 years under management alternative 6 at Perdido Wildlife Management Area.



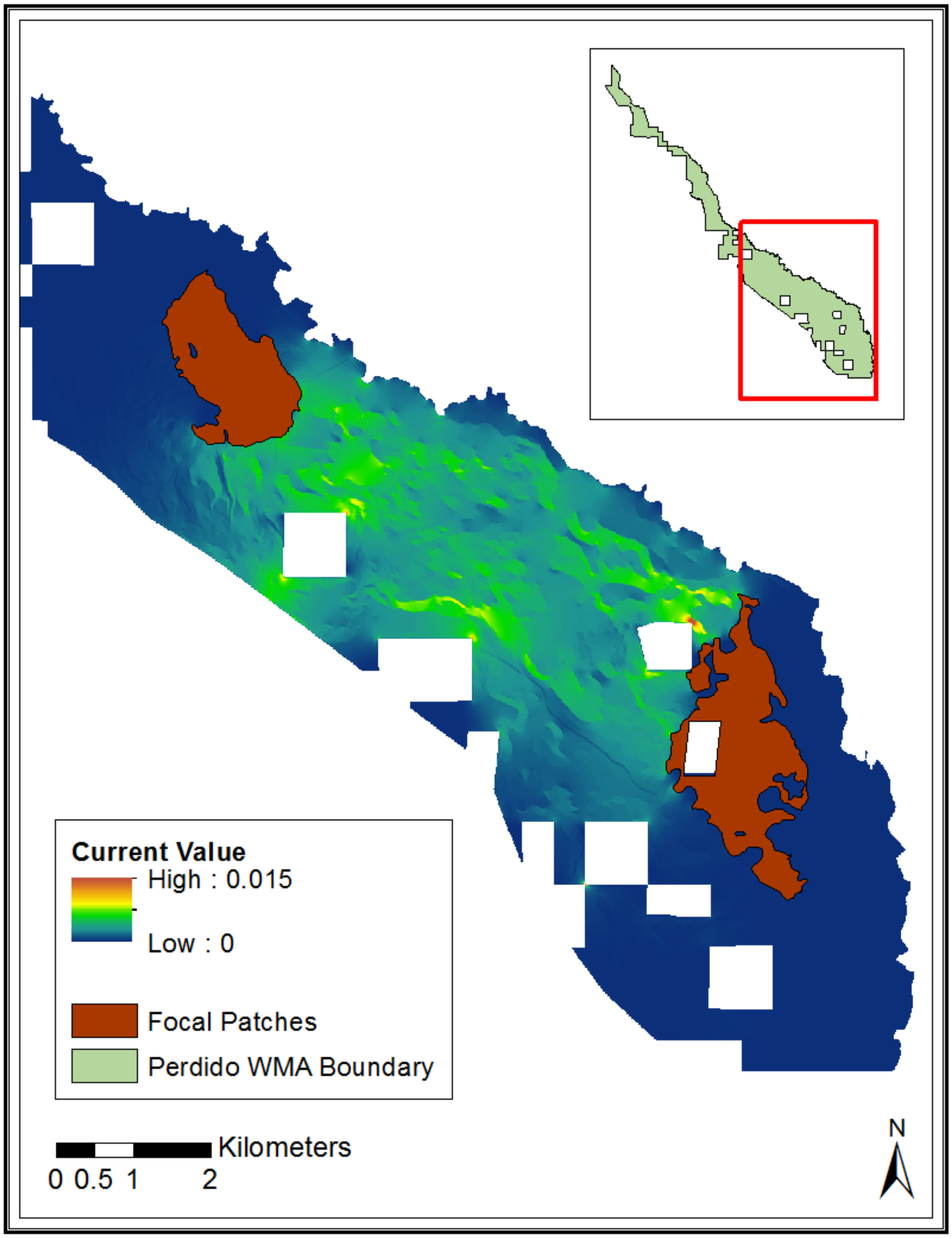
Current flow using resistance set 1 after 100 years under management alternative 7 at Perdido Wildlife Management Area.



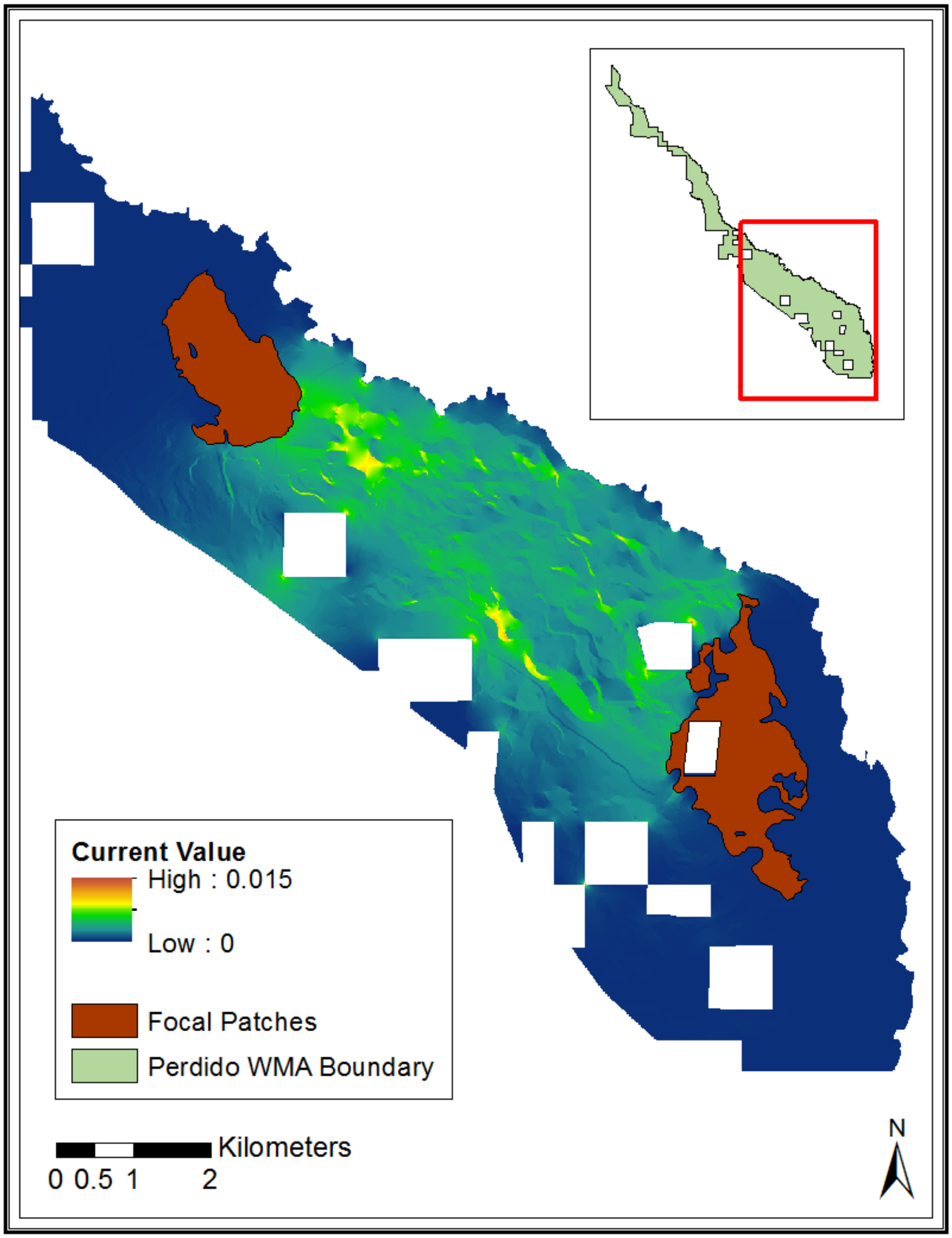
Current flow using resistance set 1 after 100 years under management alternative 8 at Perdido Wildlife Management Area.



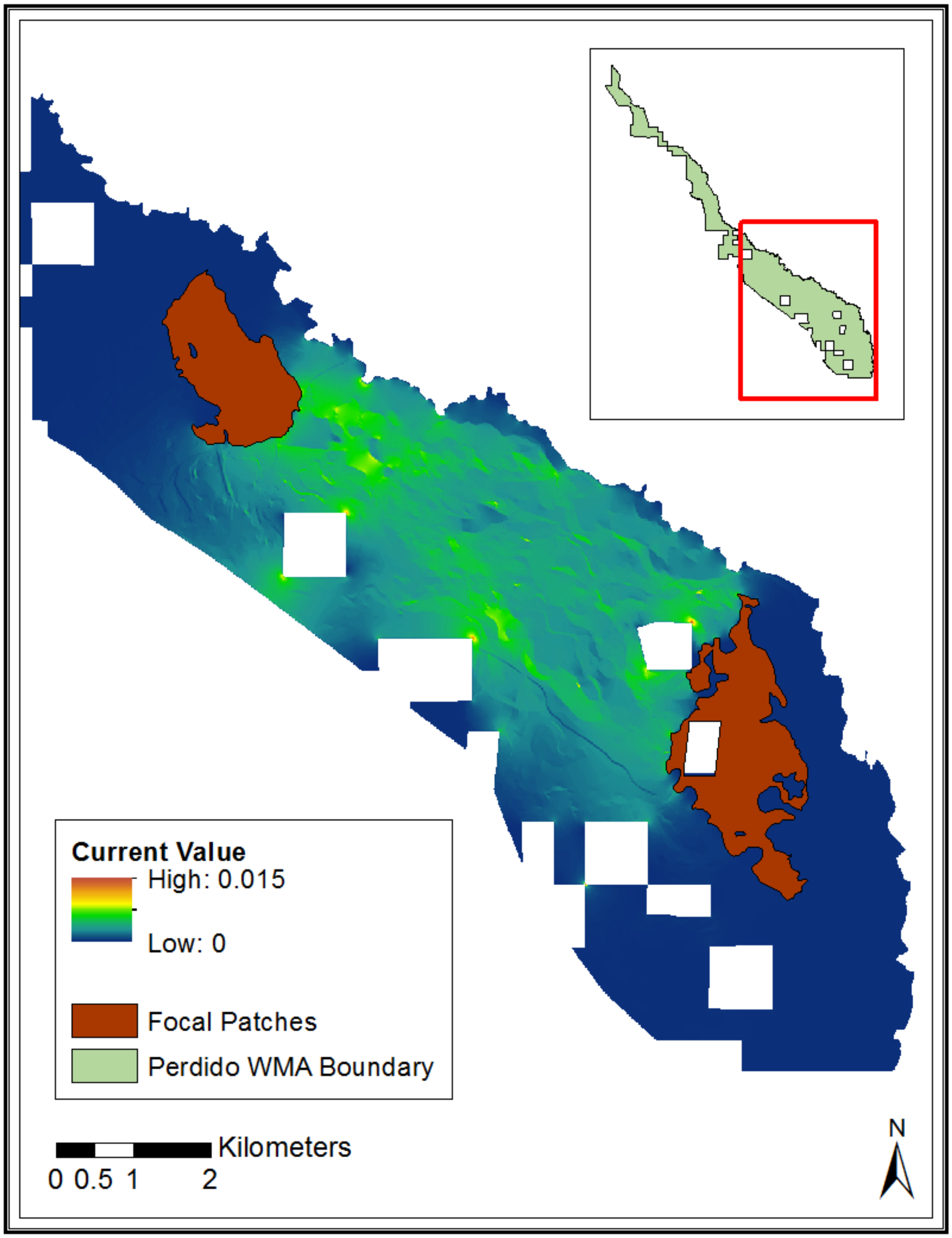
Current flow using resistance set 1 after 100 years under management alternative 9 at Perdido Wildlife Management Area.



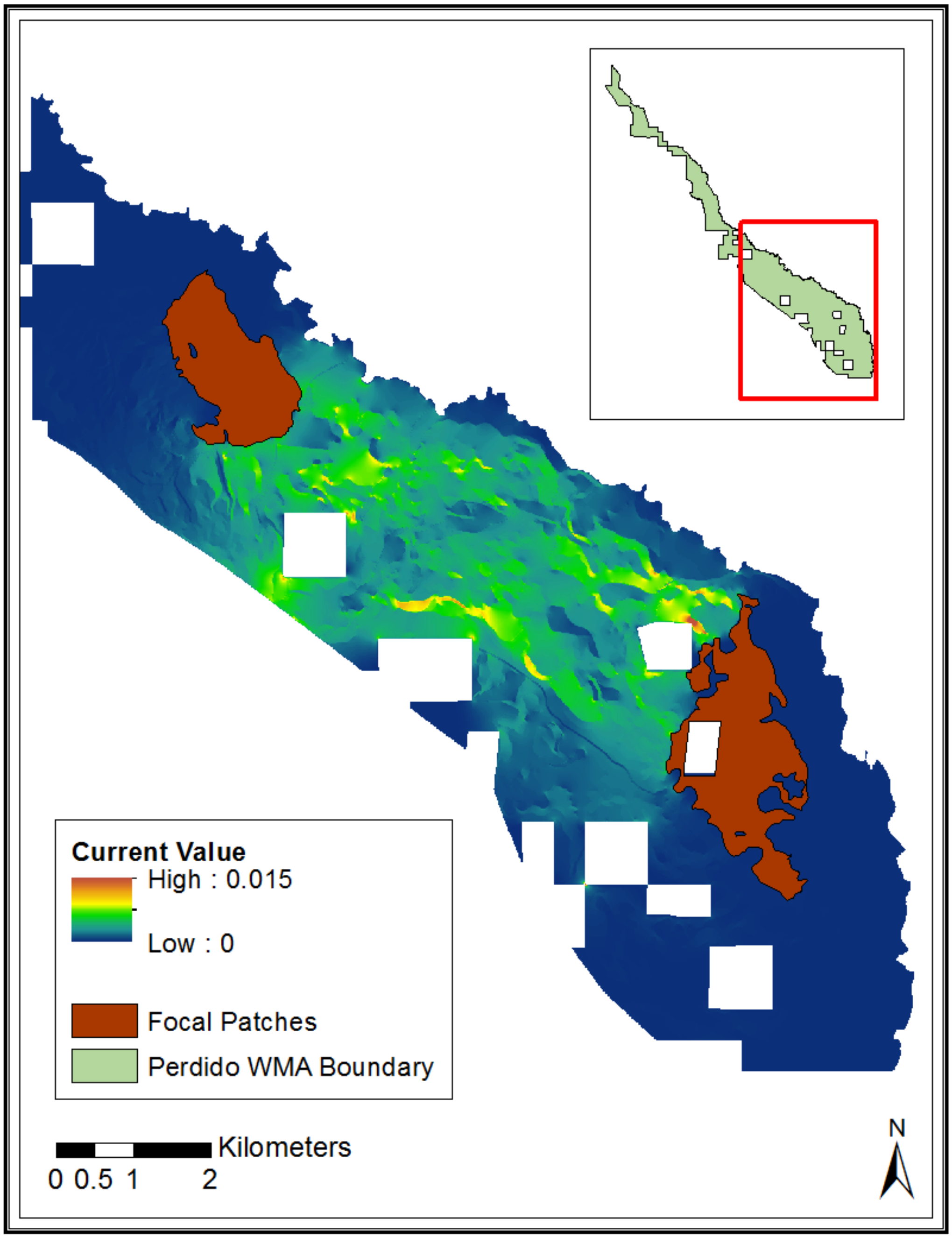
Current flow using resistance set 1 after 100 years under management alternative 10 at Perdido Wildlife Management Area.



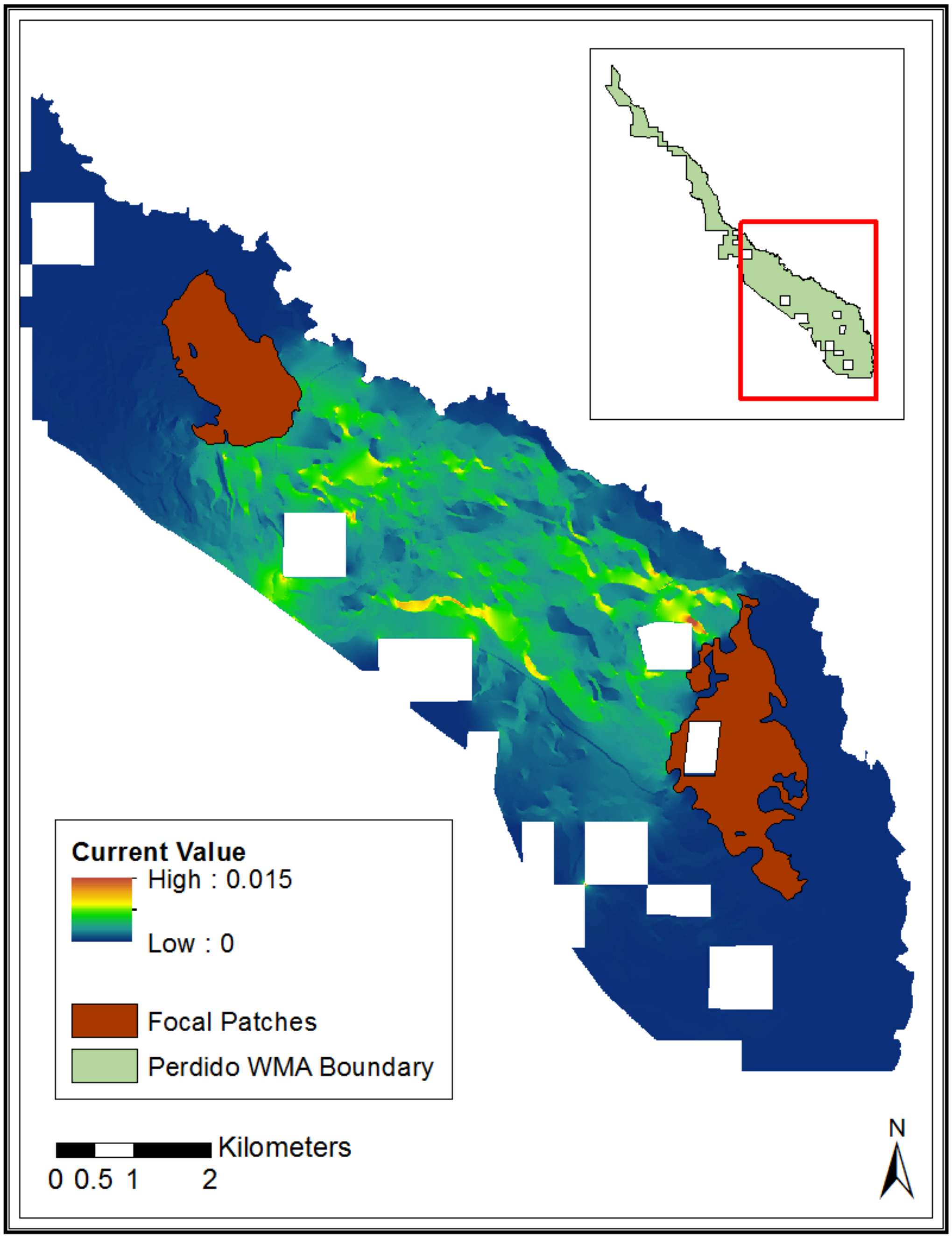
Current flow using resistance set 1 after 100 years under management alternative 11 at Perdido Wildlife Management Area.



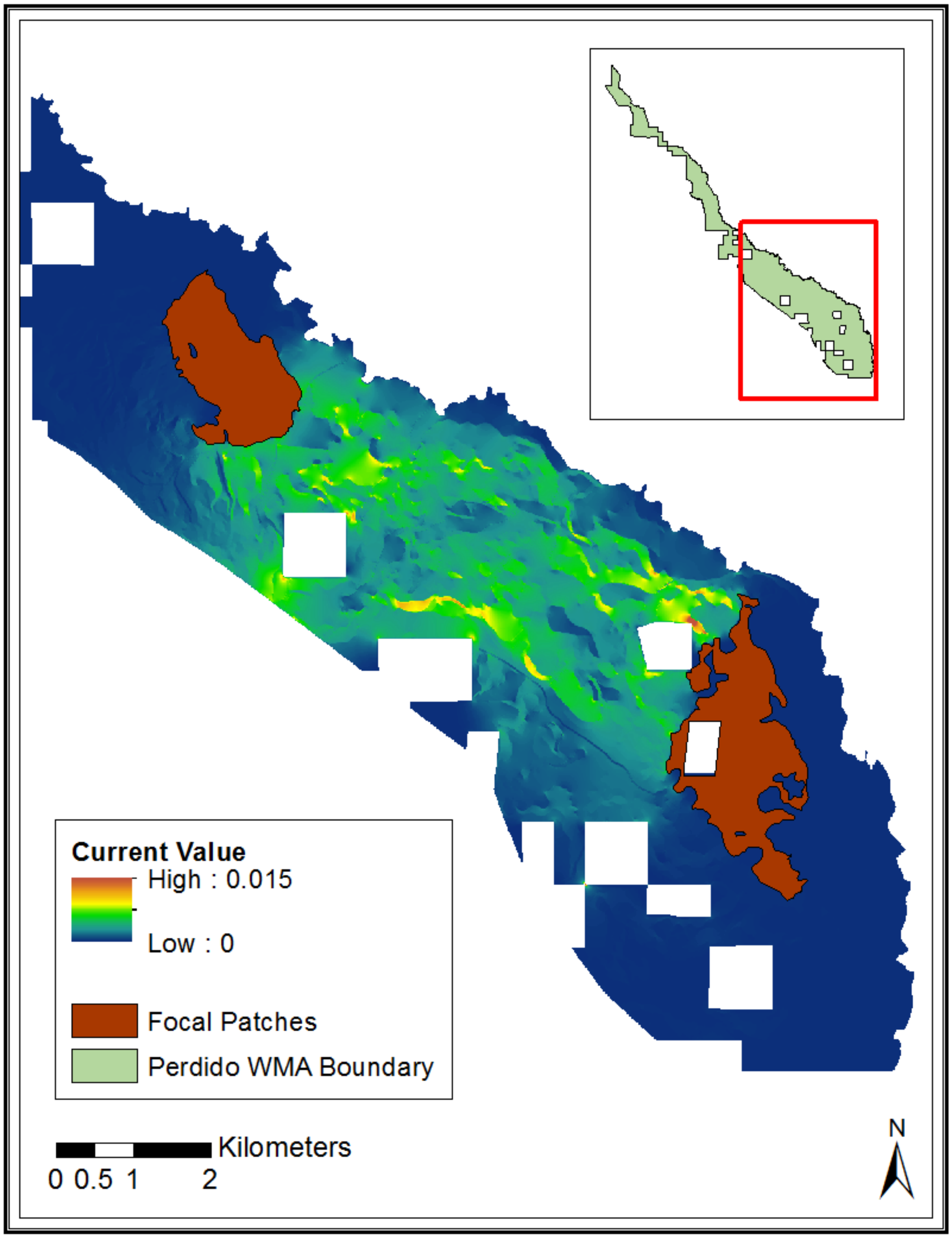
Current flow using resistance set 2 under initial landscape conditions at Perdido Wildlife Management Area.



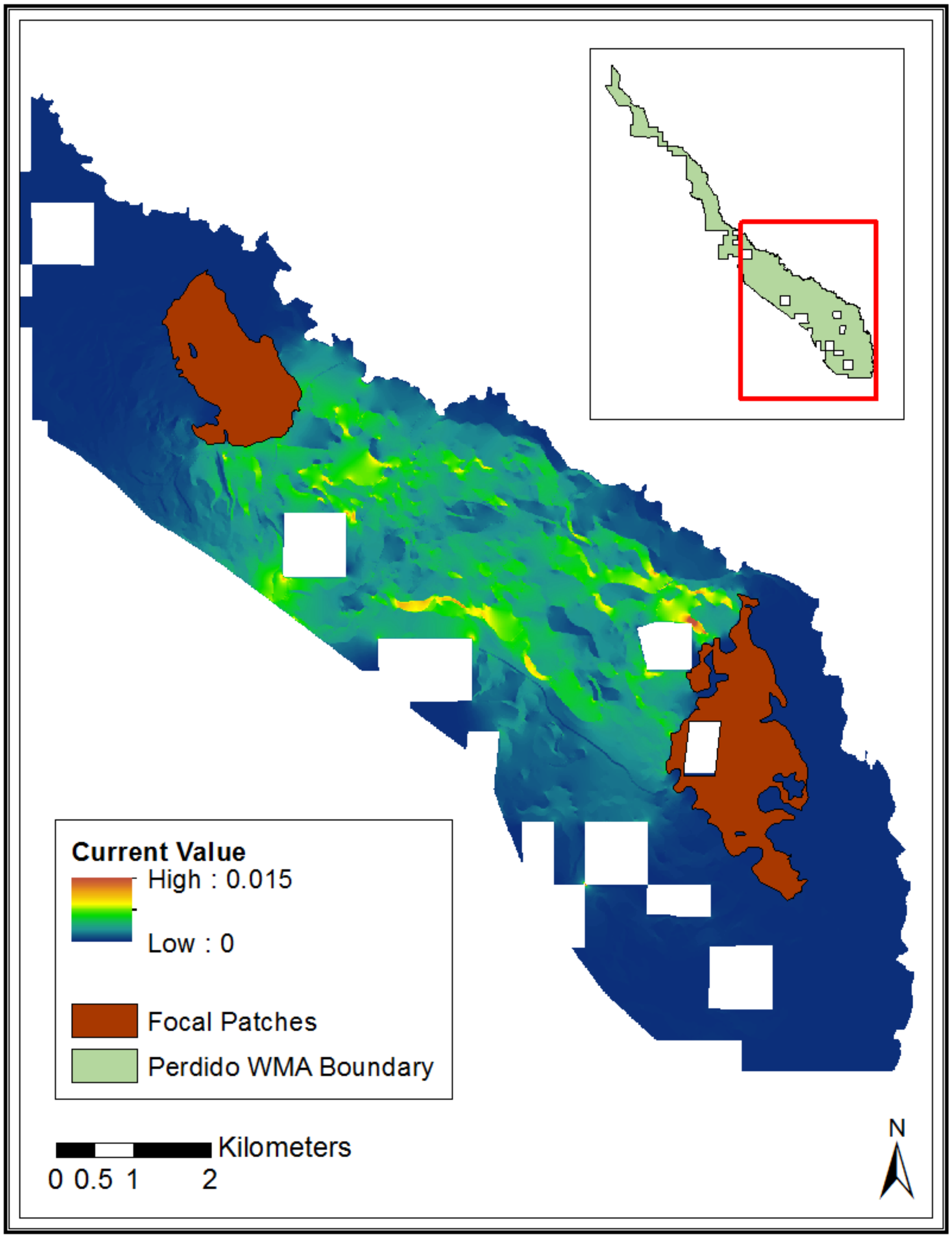
Current flow using resistance set 2 after 100 years under management alternative 1 at Perdido Wildlife Management Area.



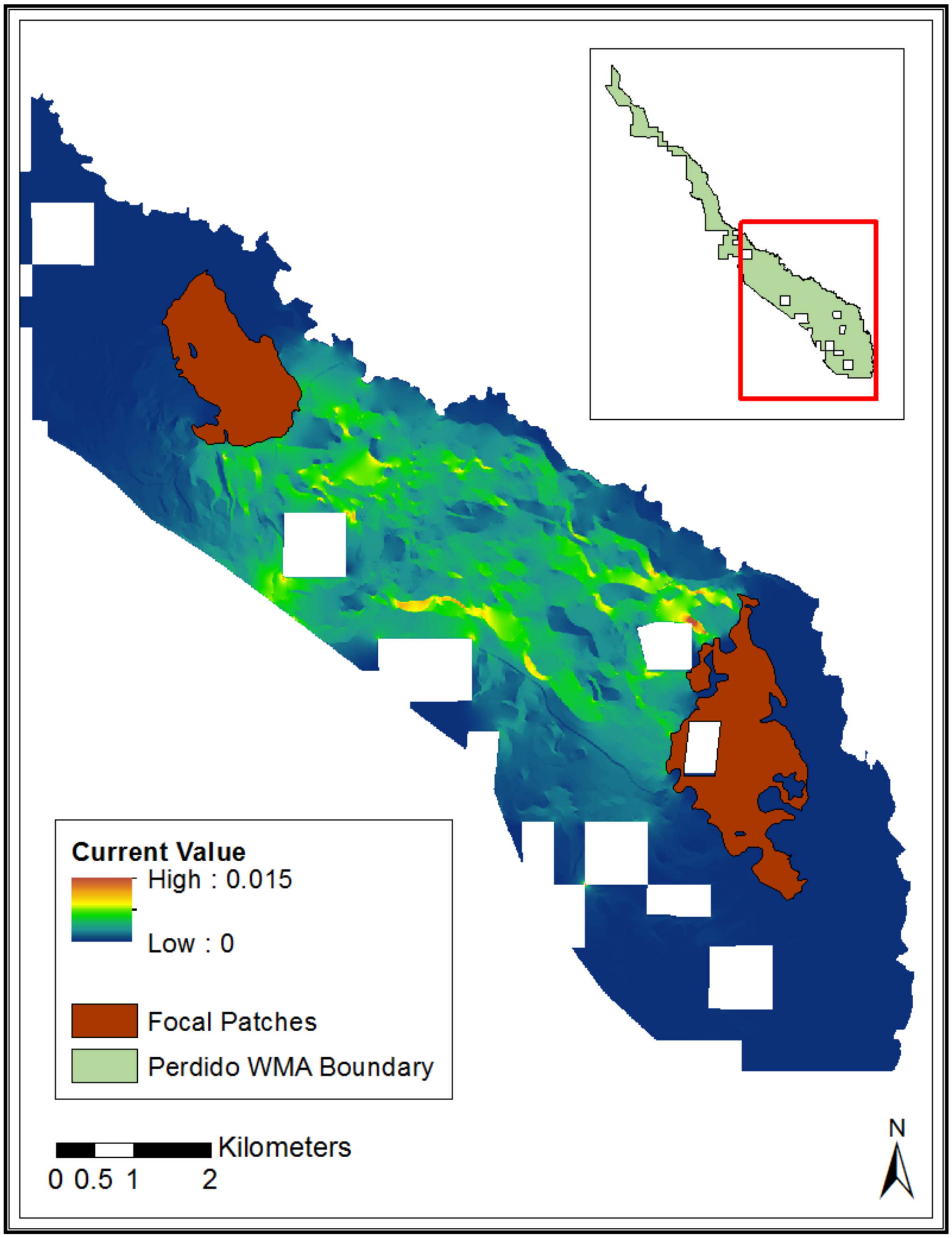
Current flow using resistance set 2 after 100 years under management alternative 2 at Perdido Wildlife Management Area.



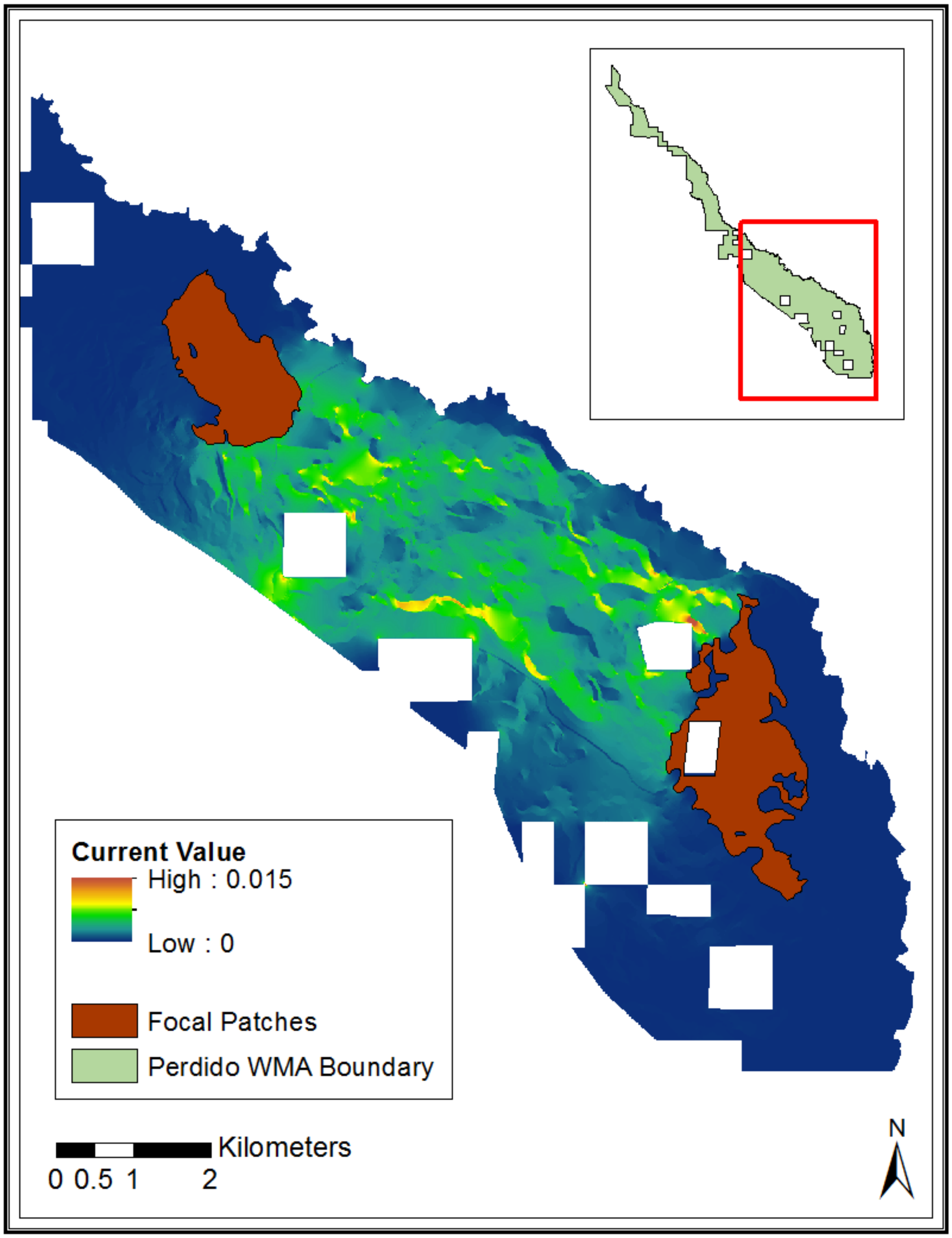
Current flow using resistance set 2 after 100 years under management alternative 3 at Perdido Wildlife Management Area.



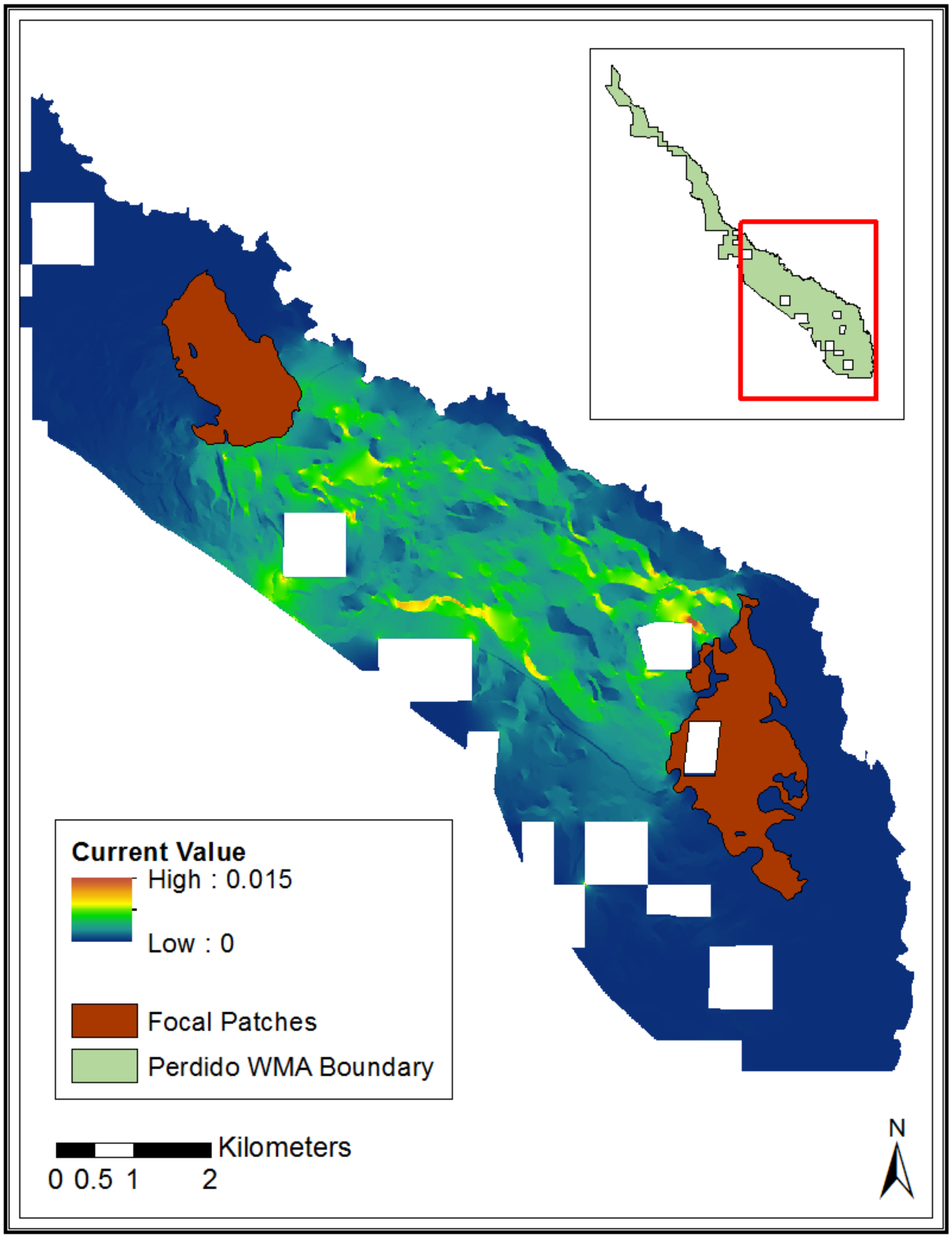
Current flow using resistance set 2 after 100 years under management alternative 4 at Perdido Wildlife Management Area.



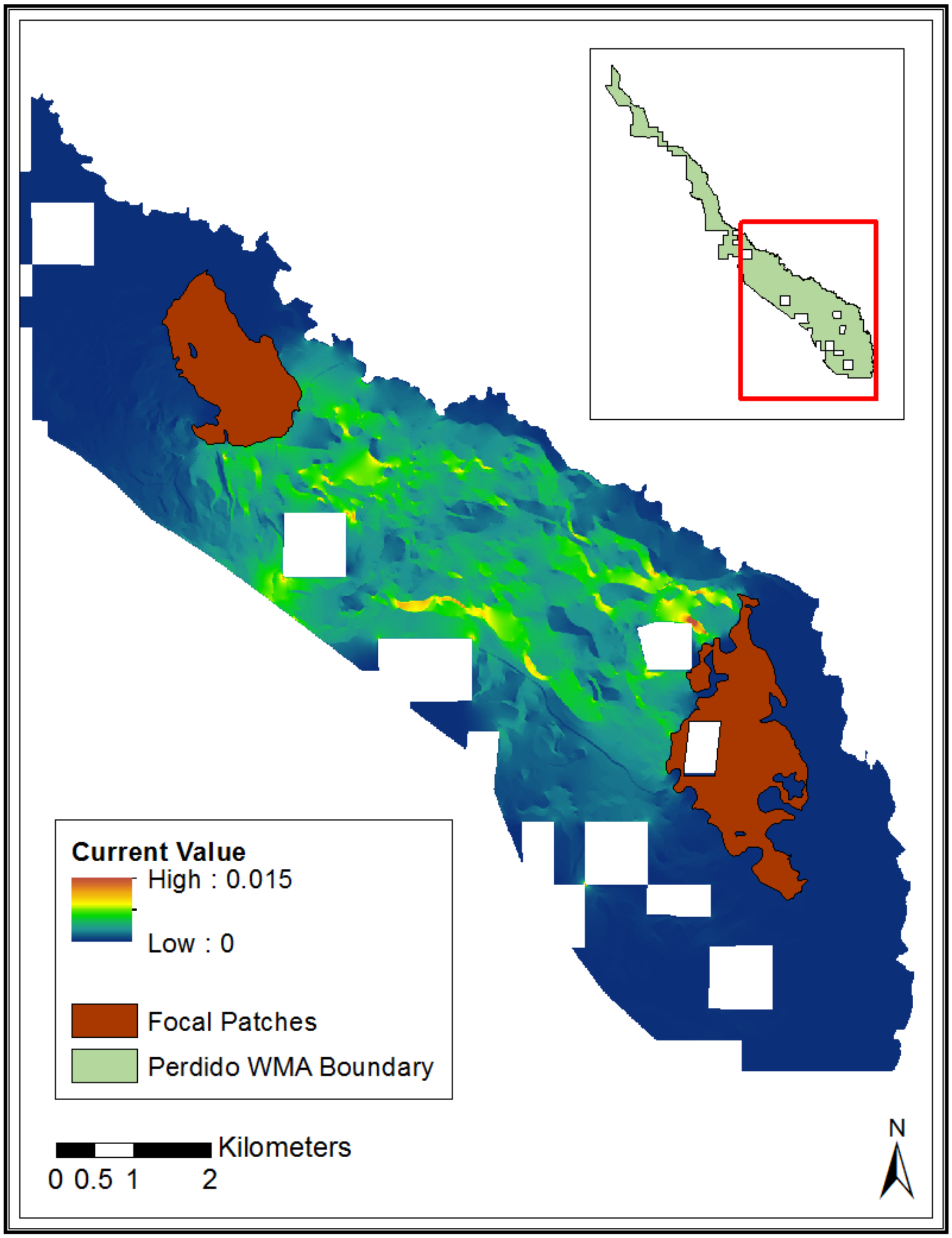
Current flow using resistance set 2 after 100 years under management alternative 5 at Perdido Wildlife Management Area.



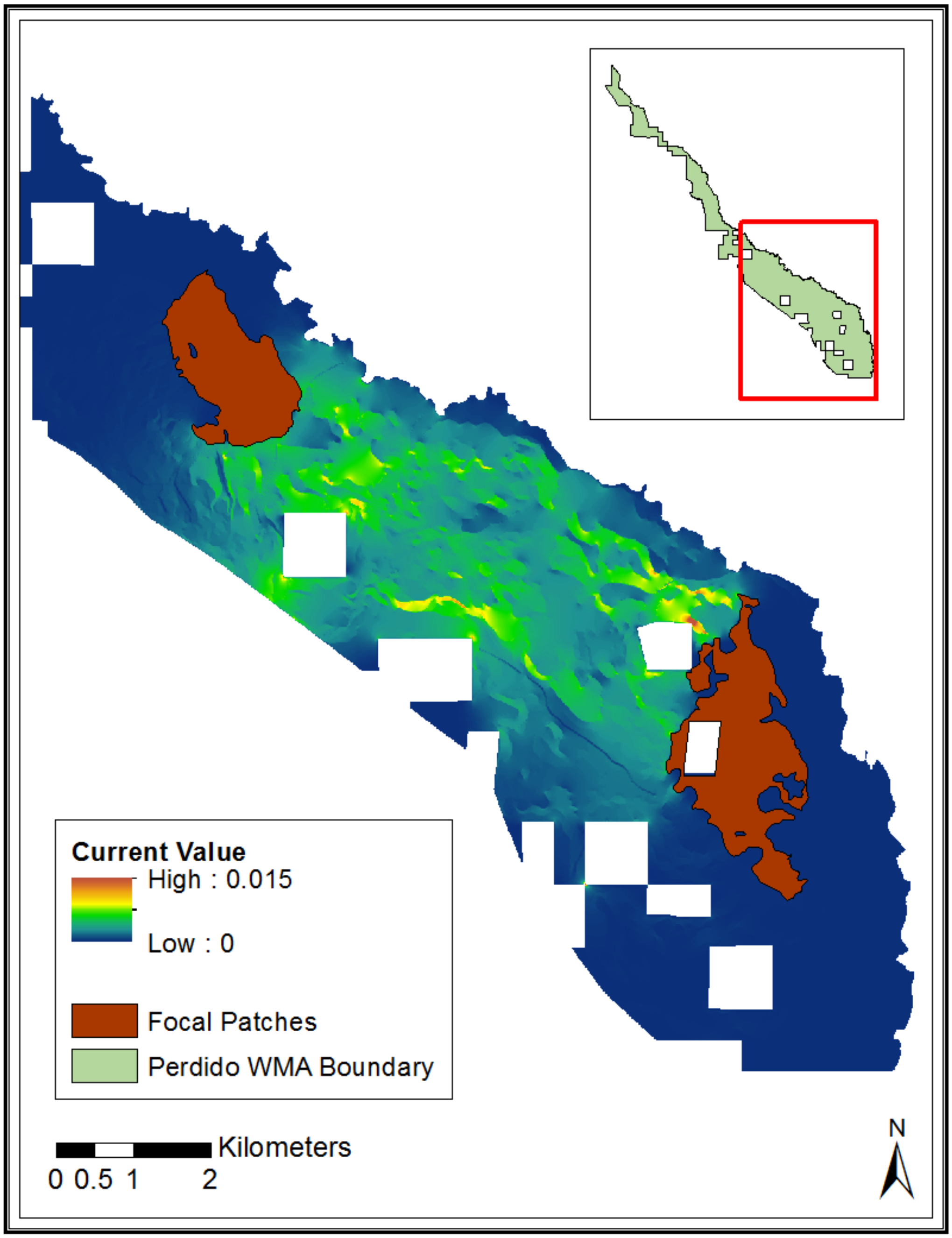
Current flow using resistance set 2 after 100 years under management alternative 6 at Perdido Wildlife Management Area.



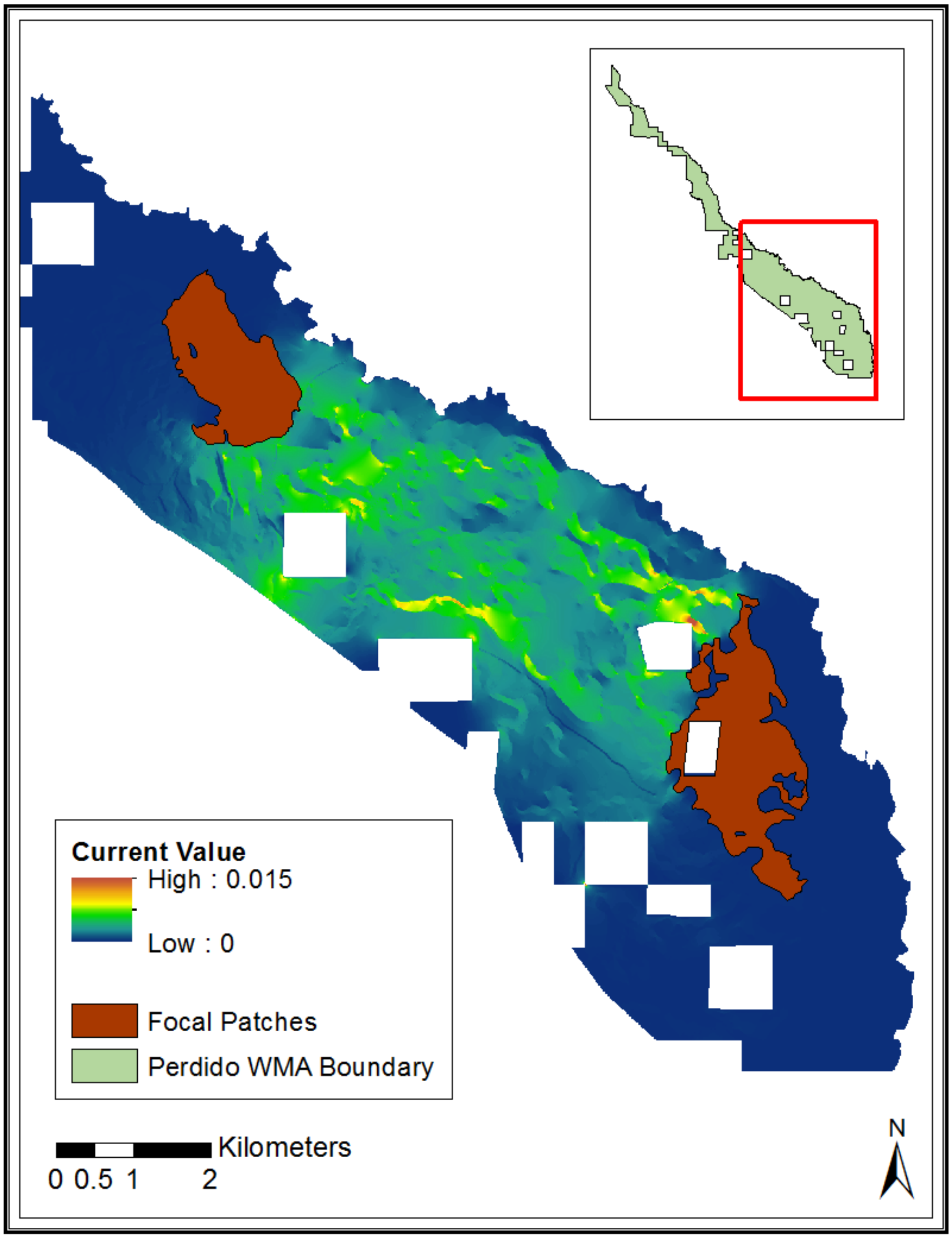
Current flow using resistance set 2 after 100 years under management alternative 7 at Perdido Wildlife Management Area.



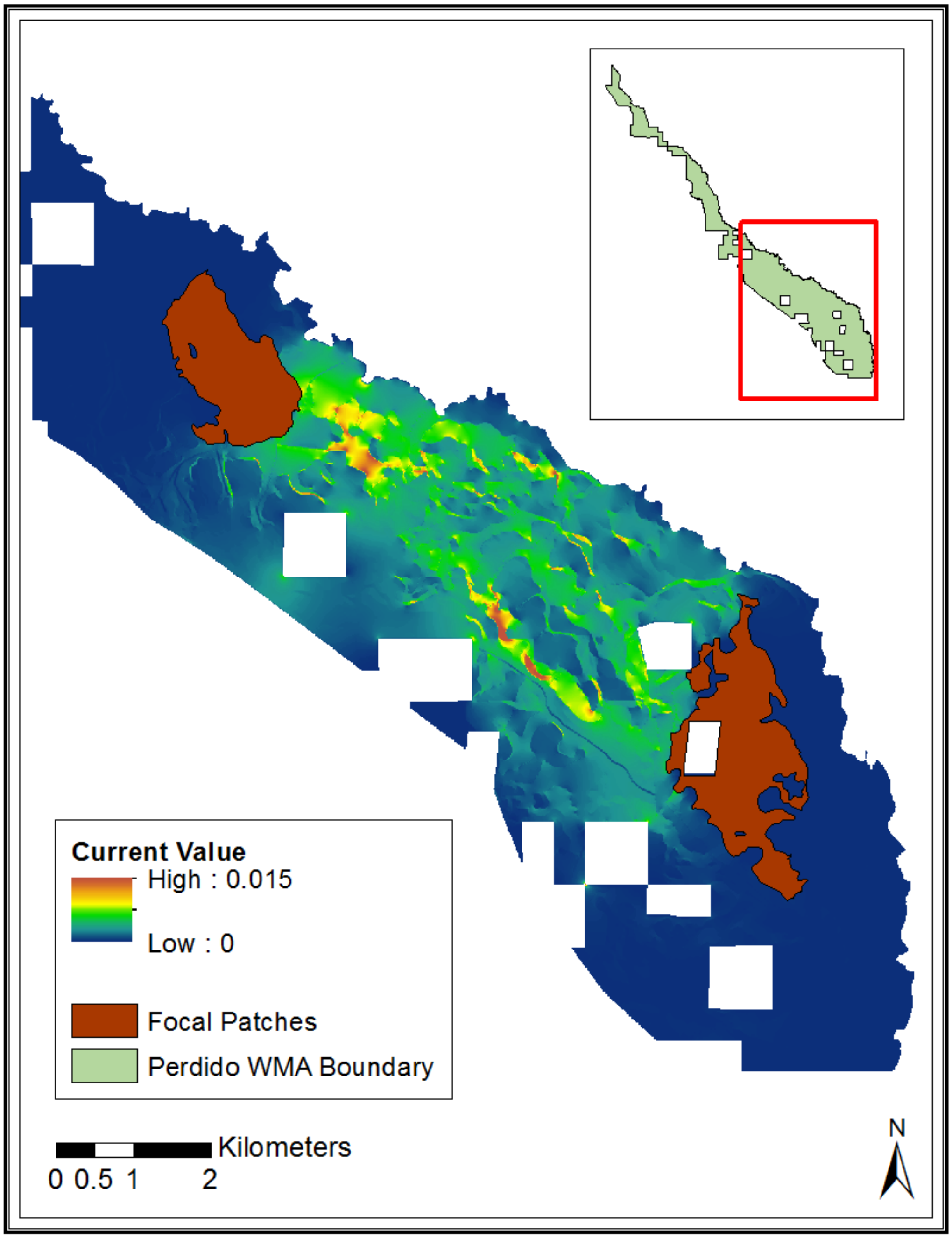
Current flow using resistance set 2 after 100 years under management alternative 8 at Perdido Wildlife Management Area.



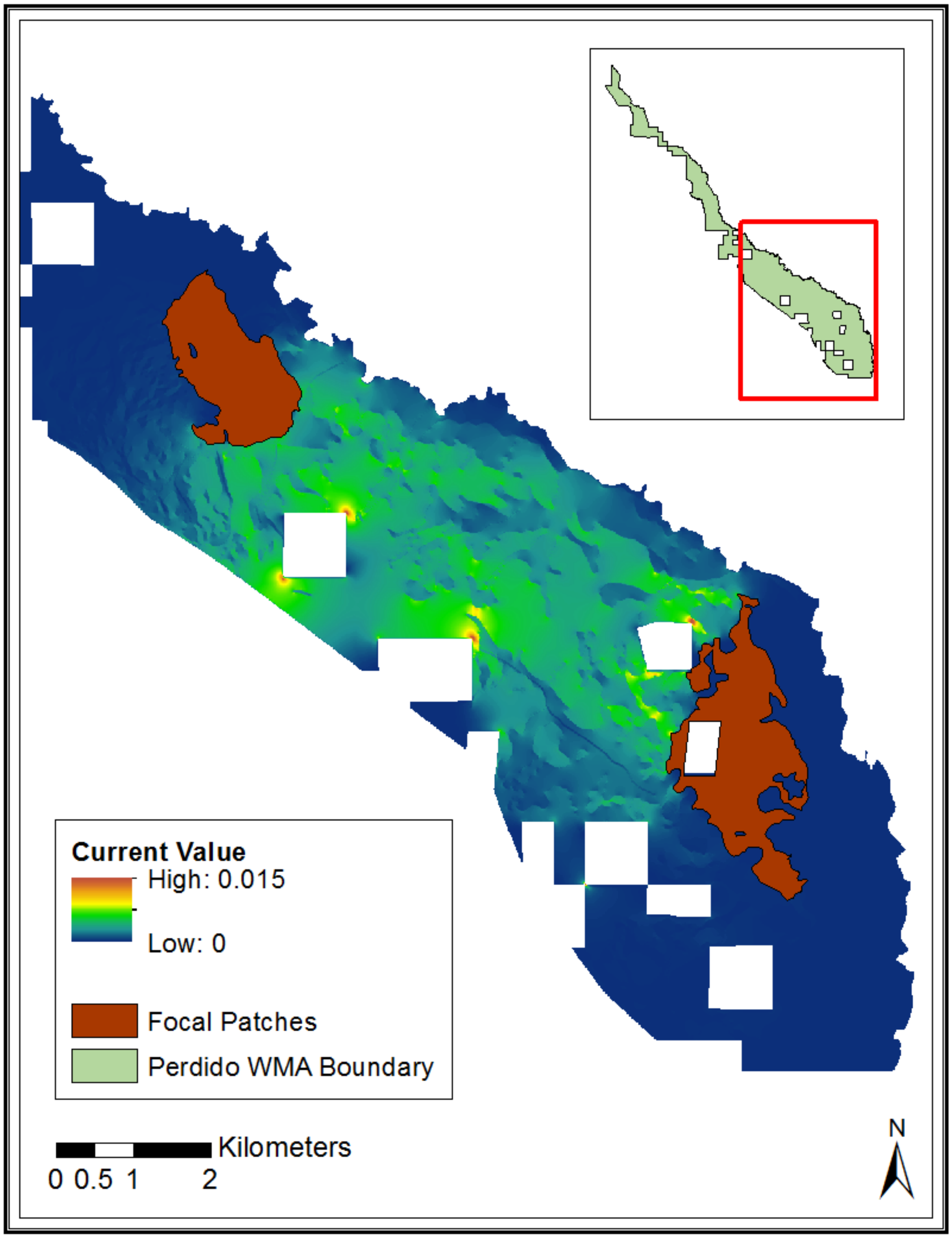
Current flow using resistance set 2 after 100 years under management alternative 9 at Perdido Wildlife Management Area.



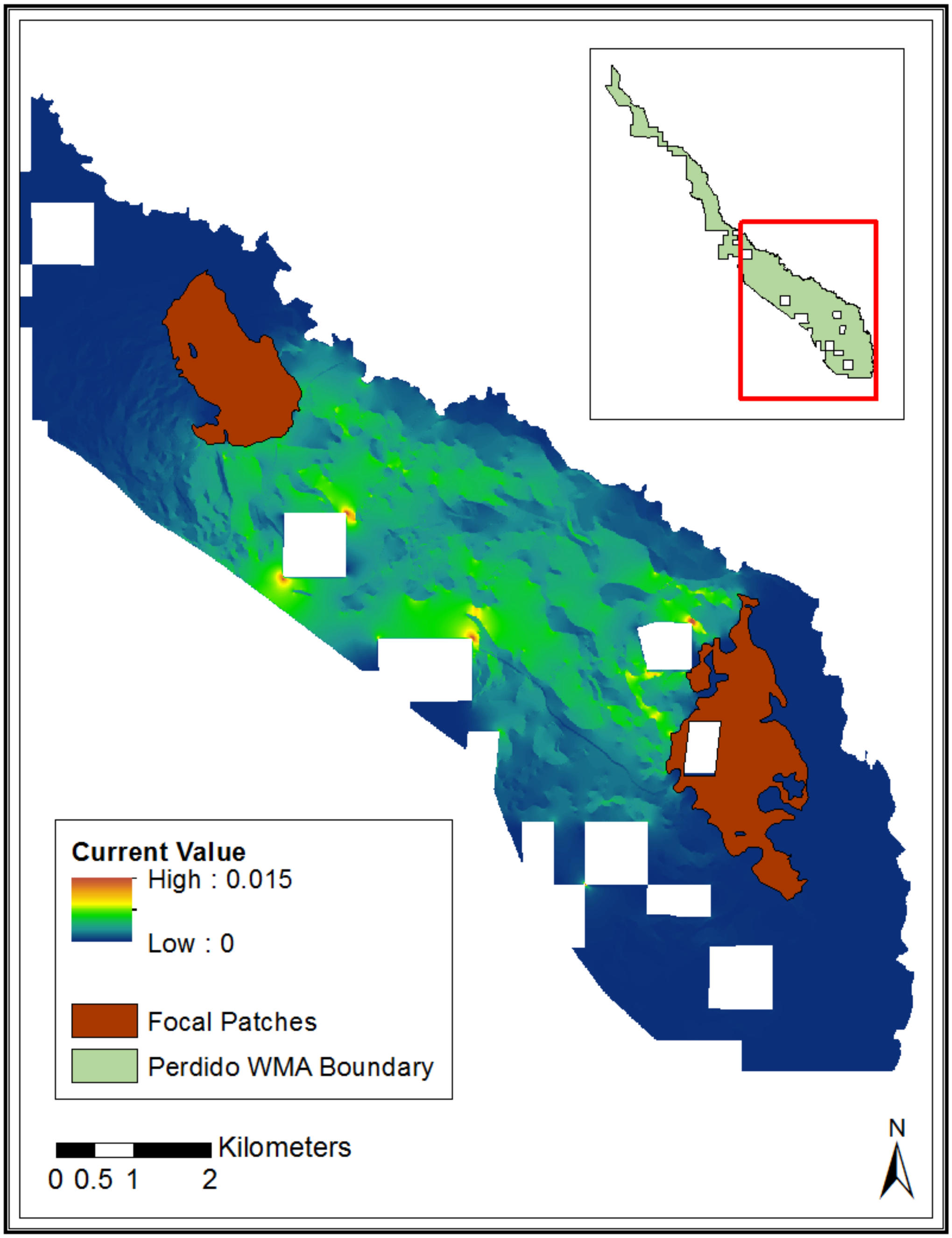
Current flow using resistance set 2 after 100 years under management alternative 10 at Perdido Wildlife Management Area.



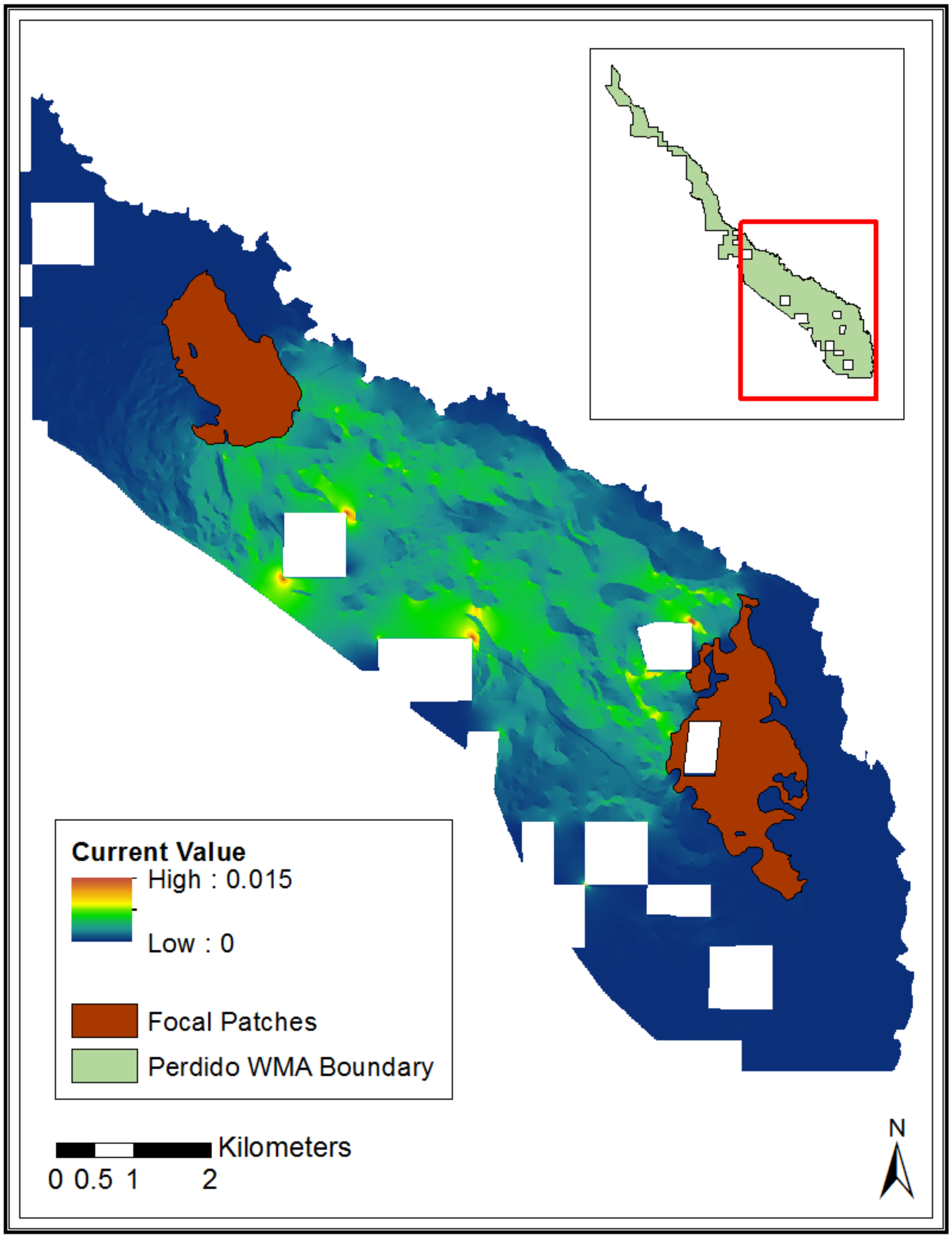
Current flow using resistance set 2 after 100 years under management alternative 11 at Perdido Wildlife Management Area.



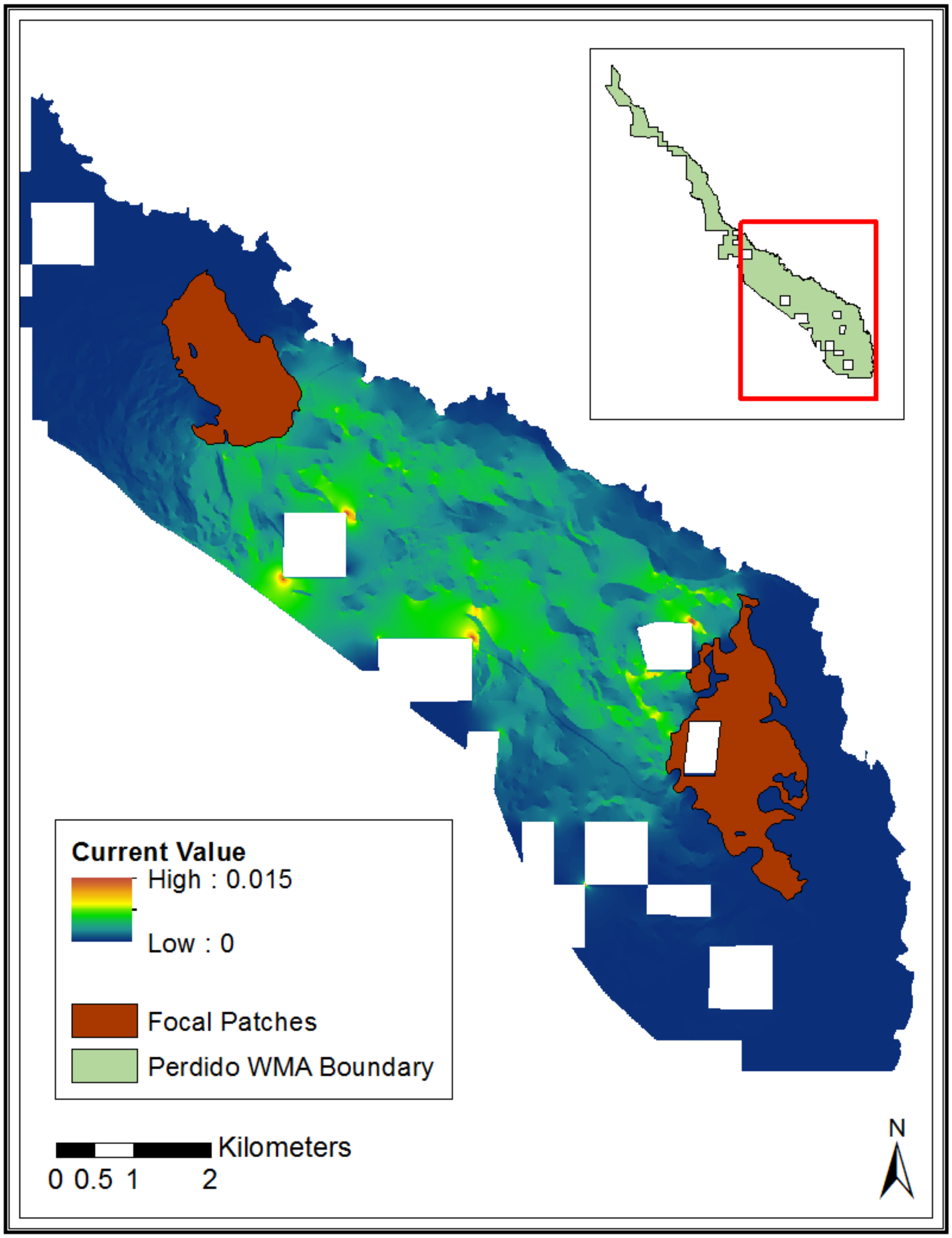
Current flow using resistance set 3 under initial landscape conditions (circa 2011) at Perdido Wildlife Management Area.



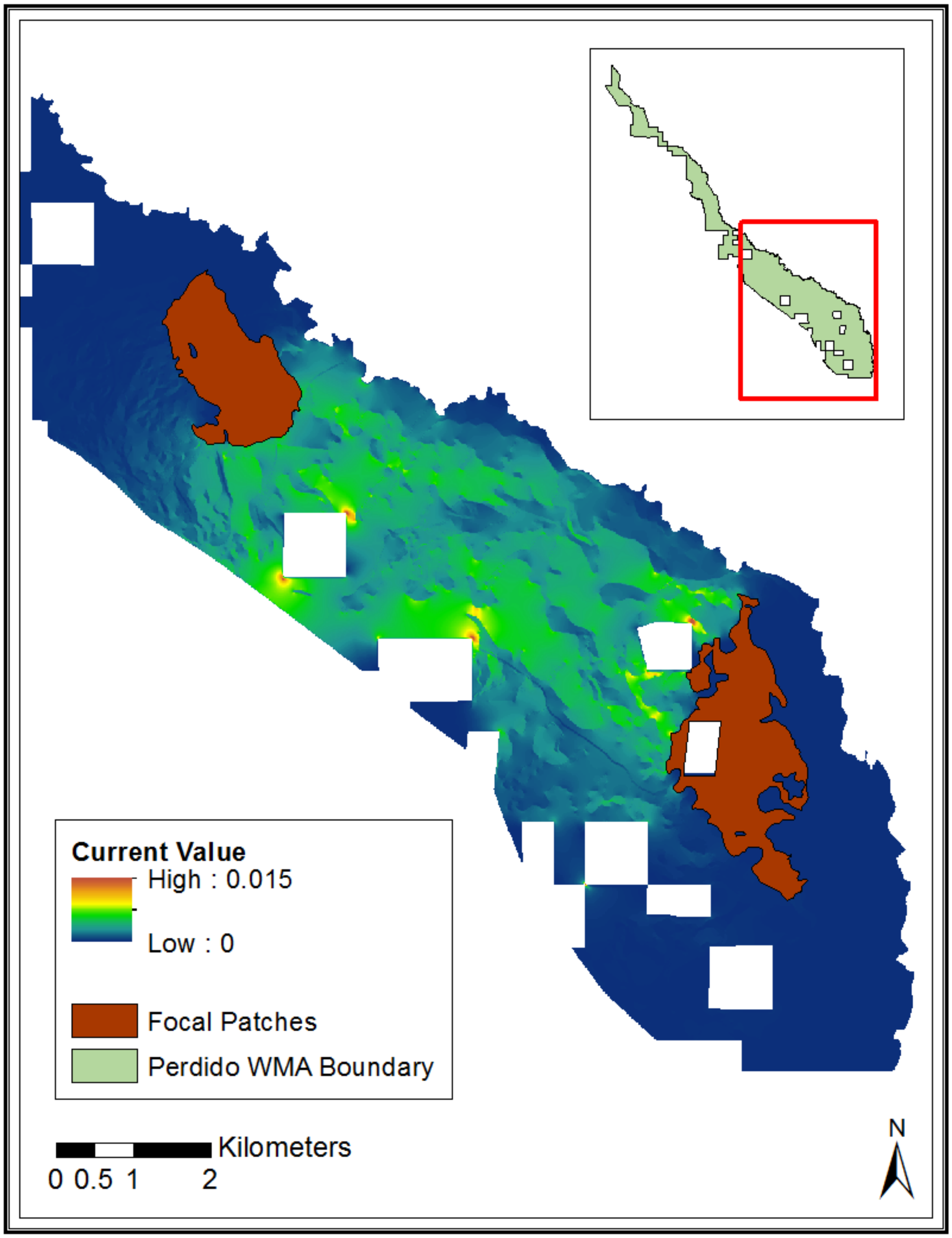
Current flow using resistance set 3 after 100 years under management alternative 1 at Perdido Wildlife Management Area.



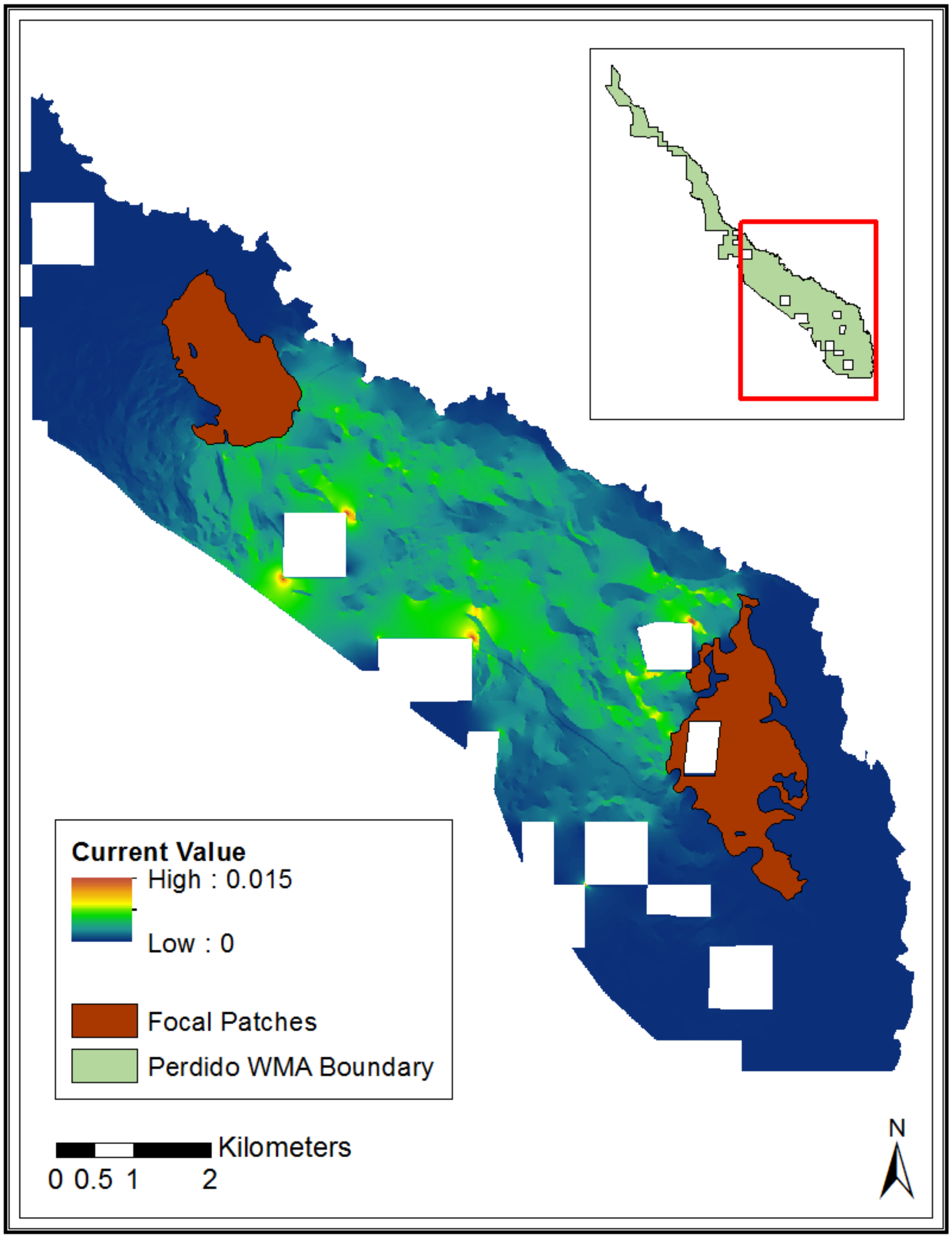
Current flow using resistance set 3 after 100 years under management alternative 2 at Perdido Wildlife Management Area.



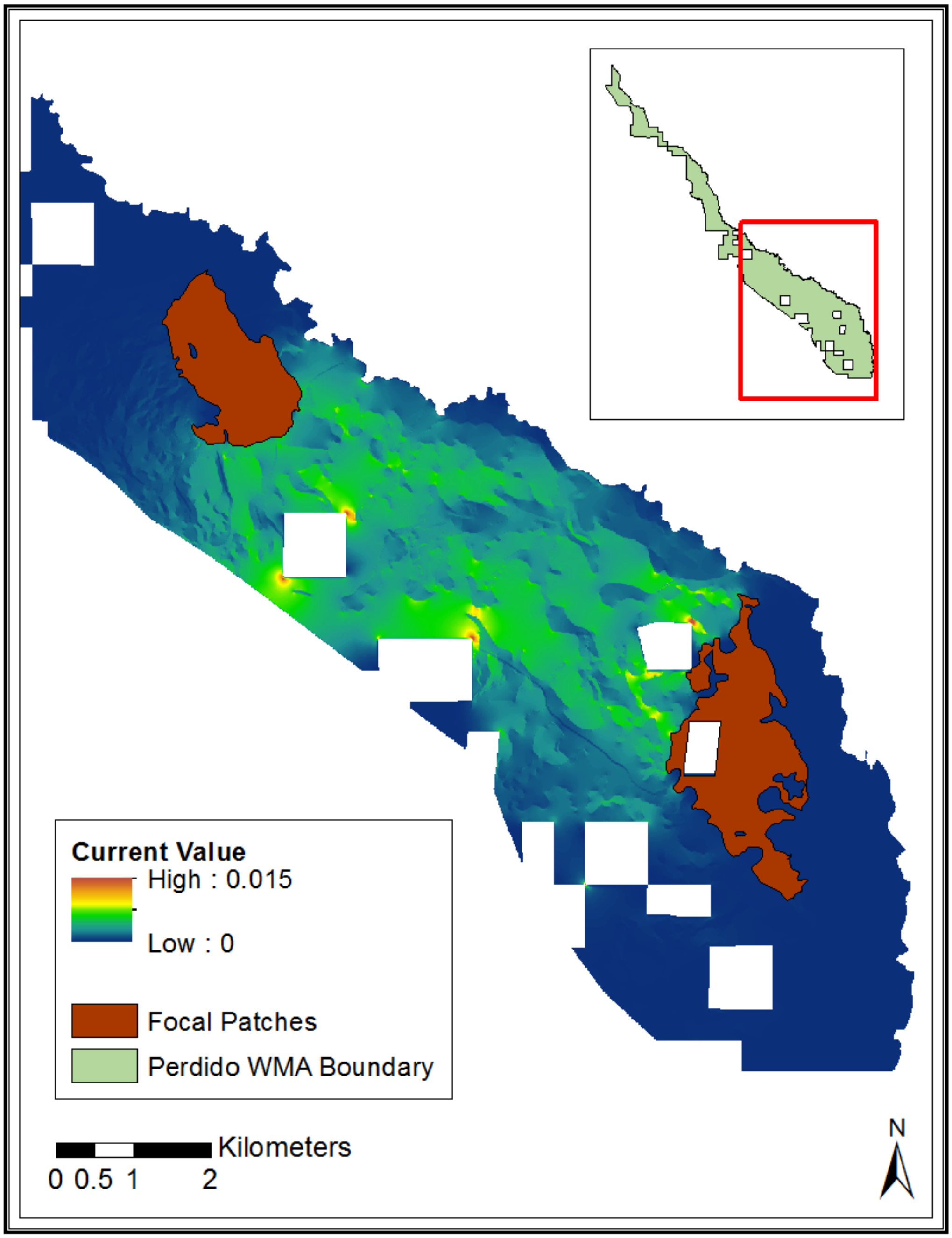
Current flow using resistance set 3 after 100 years under management alternative 3 at Perdido Wildlife Management Area.



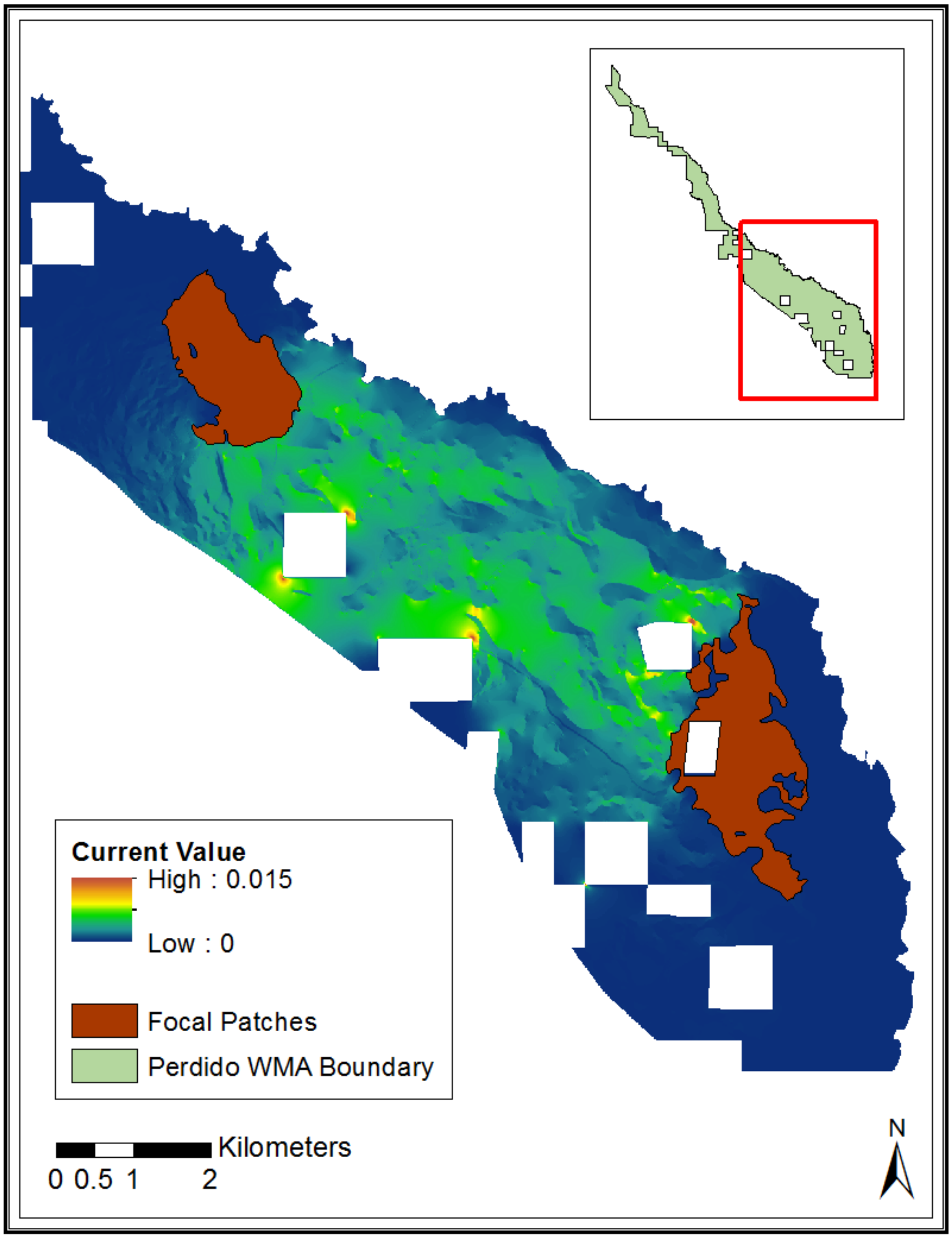
Current flow using resistance set 3 after 100 years under management alternative 4 at Perdido Wildlife Management Area.



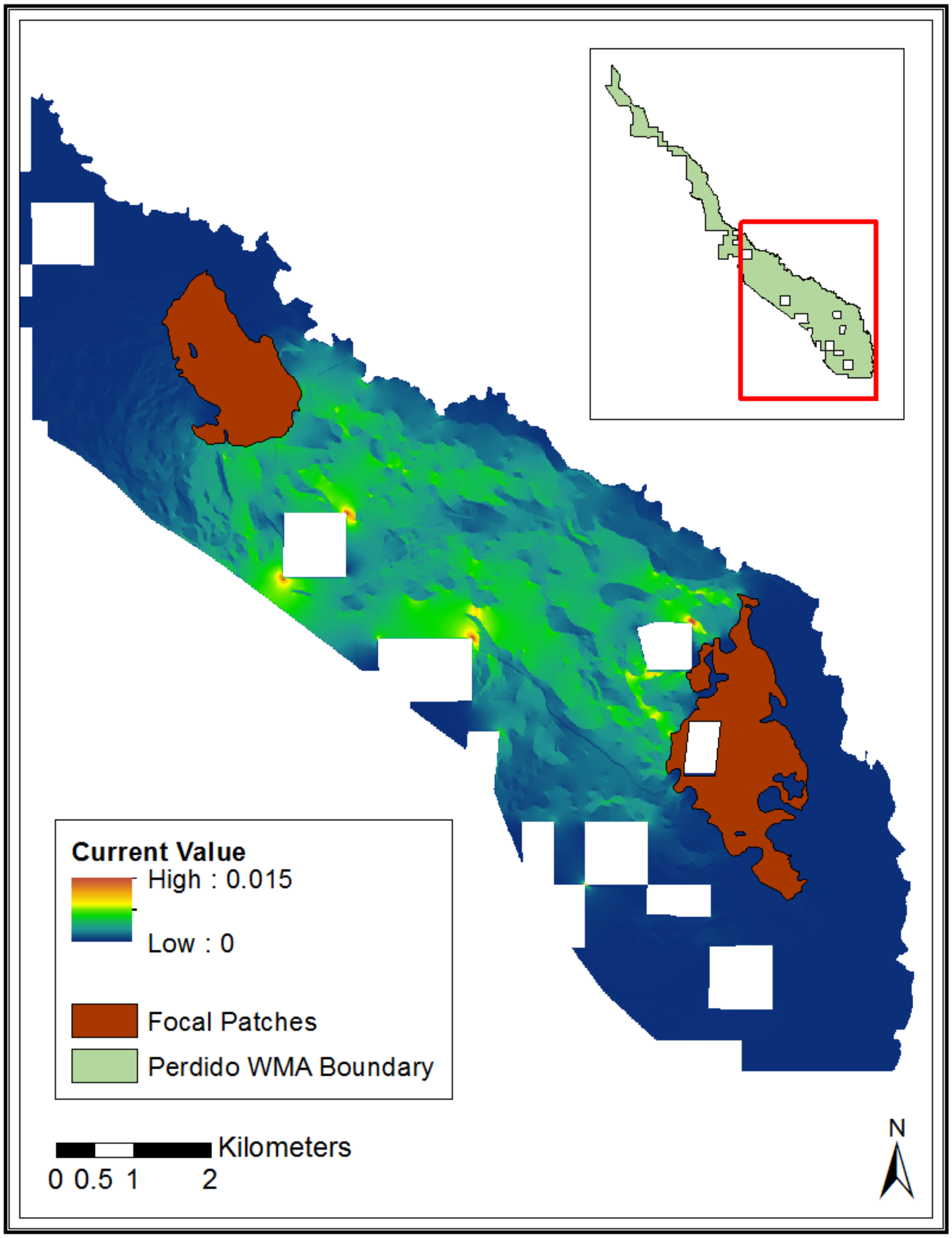
Current flow using resistance set 3 after 100 years under management alternative 5 at Perdido Wildlife Management Area.



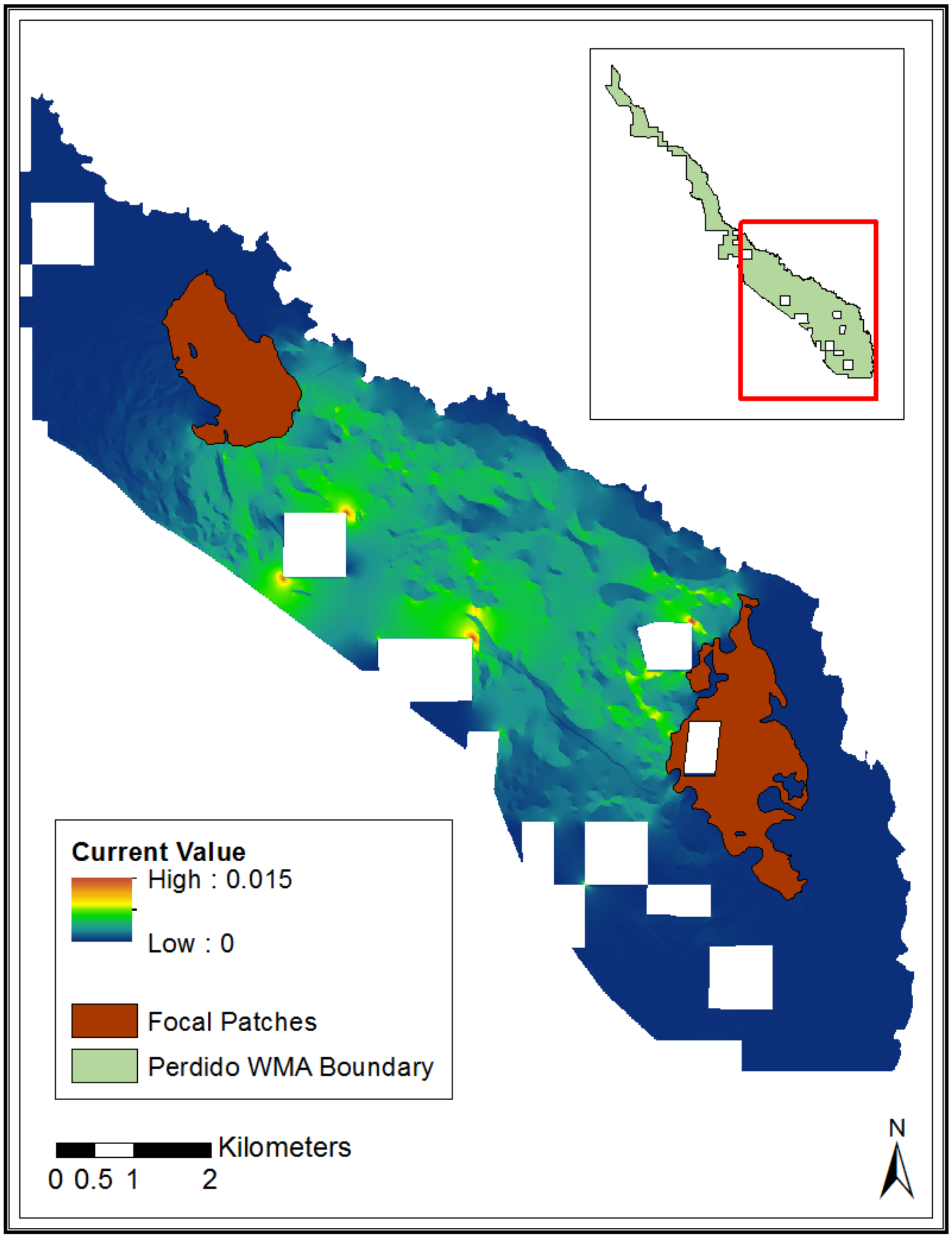
Current flow using resistance set 3 after 100 years under management alternative 6 at Perdido Wildlife Management Area.



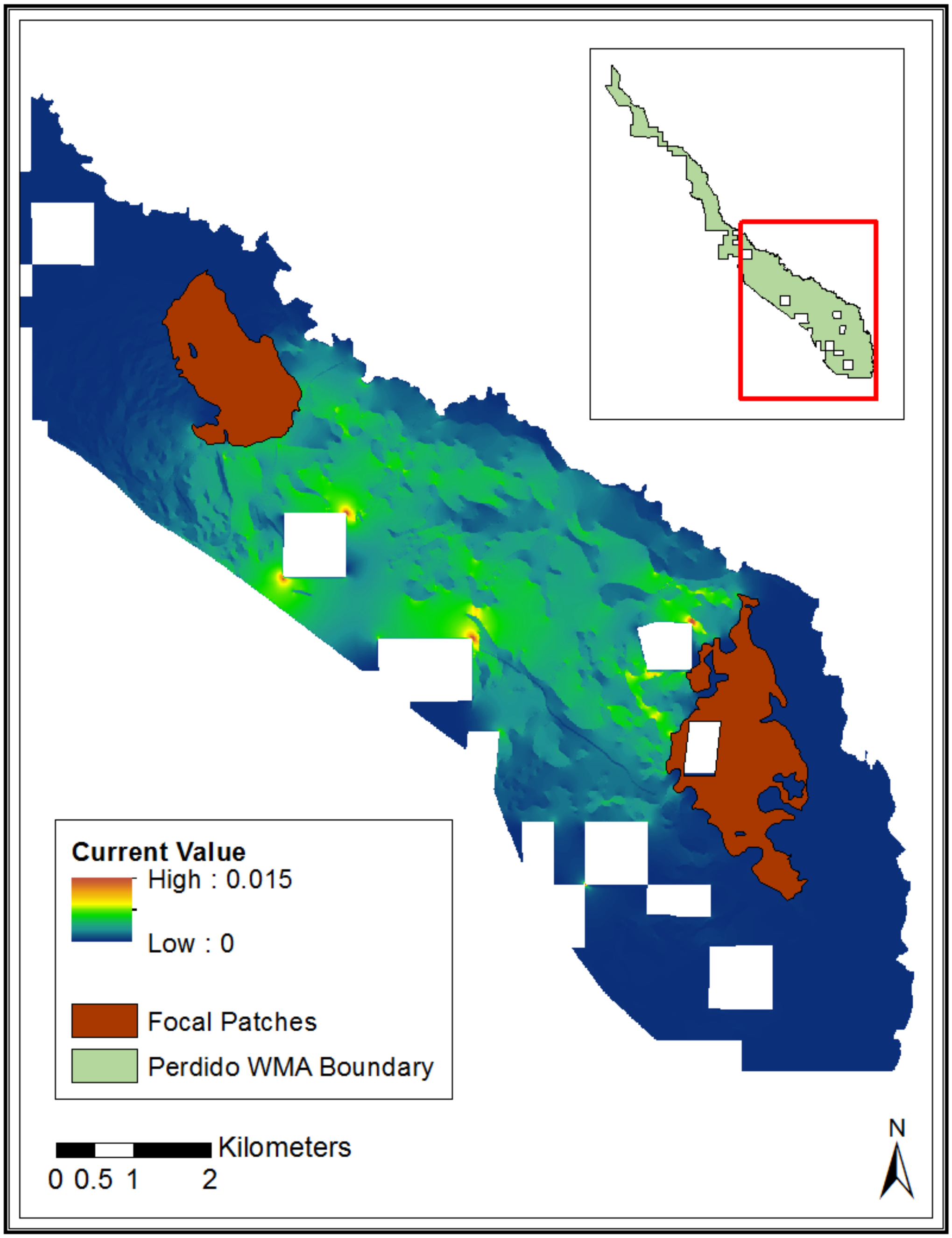
Current flow using resistance set 3 after 100 years under management alternative 7 at Perdido Wildlife Management Area.



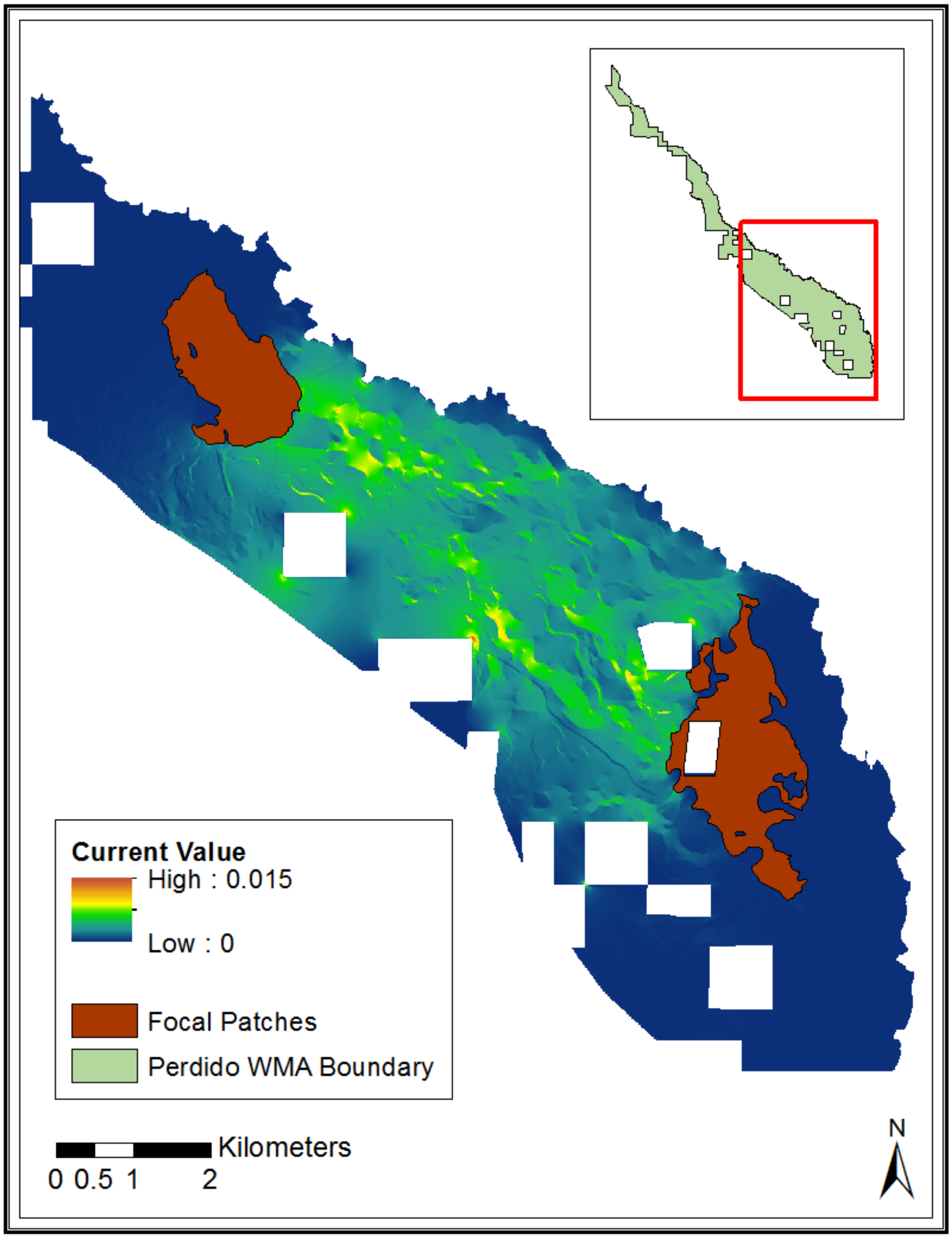
Current flow using resistance set 3 after 100 years under management alternative 8 at Perdido Wildlife Management Area.



Current flow using resistance set 3 after 100 years under management alternative 9 at Perdido Wildlife Management Area.



Current flow using resistance set 3 after 100 years under management alternative 10 at Perdido Wildlife Management Area.



Current flow using resistance set 3 after 100 years under management alternative 11 at Perdido Wildlife Management Area.

Appendix 2. Skewness and kurtosis values for the histograms of the current map values for each study site, alternative, and year.

Skewness and kurtosis values using resistance set 1 at Barbour Wildlife Management Area and Wehle Forever Wild Tract for all alternatives and years.

Alternative	Year	Skewness	Kurtosis
Initial State	**0**	0.61	4.03
1	**25**	0.71	3.92
1	**50**	0.72	4.08
1	**100**	0.72	4.08
2	**25**	0.70	3.88
2	**50**	0.72	4.04
2	**100**	0.72	4.04
3	**25**	0.69	3.80
3	**50**	0.69	3.91
3	**100**	0.69	3.91
4	**25**	0.68	3.76
4	**50**	0.69	3.87
4	**100**	0.69	3.87
5	**25**	0.73	4.12
5	**50**	0.75	4.27
5	**100**	0.75	4.27
6	**25**	0.73	4.08
6	**50**	0.75	4.23
6	**100**	0.75	4.23
7	**25**	0.72	4.06
7	**50**	0.73	4.17
7	**100**	0.73	4.17
8	**25**	0.71	4.02
8	**50**	0.73	4.13
8	**100**	0.73	4.13
9	**25**	0.57	3.56
9	**50**	0.54	4.03
9	**100**	0.54	4.03
10	**25**	0.56	3.52
10	**50**	0.54	3.99
10	**100**	0.54	3.99
11	**25**	0.64	3.87
11	**50**	0.72	4.01
11	**100**	0.73	3.99

Skewness and kurtosis values using resistance set 2 at Barbour Wildlife Management Area and Wehle Forever Wild Tract for all alternatives and years.

Alternative	**Year**	**Skewness**	**Kurtosis**
Initial State	**0**	0.74	4.18
1	**25**	1.06	4.53
1	**50**	1.16	4.98
1	**100**	1.16	4.98
2	**25**	1.06	4.54
2	**50**	1.17	5.02
2	**100**	1.17	5.02
3	**25**	1.04	4.41
3	**50**	1.14	4.80
3	**100**	1.14	4.80
4	**25**	1.04	4.41
4	**50**	1.14	4.82
4	**100**	1.14	4.82
5	**25**	1.22	5.47
5	**50**	1.26	5.70
5	**100**	1.26	5.70
6	**25**	1.21	5.43
6	**50**	1.26	5.68
6	**100**	1.26	5.68
7	**25**	1.21	5.48
7	**50**	1.26	5.70
7	**100**	1.26	5.70
8	**25**	1.20	5.43
8	**50**	1.25	5.67
8	**100**	1.25	5.67
9	**25**	0.76	3.60
9	**50**	0.76	6.97
9	**100**	0.76	6.97
10	**25**	0.76	3.58
10	**50**	0.76	6.97
10	**100**	0.76	6.97
11	**25**	0.79	4.42
11	**50**	1.18	5.51
11	**100**	1.31	5.77

Skewness and kurtosis values using resistance set 3 at Barbour Wildlife Management Area and Wehle Forever Wild Tract for all alternatives and years.

Alternative	Year	Skewness	Kurtosis
Initial State	**0**	0.99	4.86
1	**25**	1.05	4.78
1	**50**	1.06	4.79
1	**100**	1.06	4.79
2	**25**	1.05	4.76
2	**50**	1.05	4.76
2	**100**	1.05	4.76
3	**25**	1.03	4.62
3	**50**	1.03	4.62
3	**100**	1.03	4.62
4	**25**	1.02	4.60
4	**50**	1.03	4.60
4	**100**	1.03	4.60
5	**25**	1.17	5.32
5	**50**	1.29	5.79
5	**100**	1.29	5.79
6	**25**	1.15	5.26
6	**50**	1.28	5.70
6	**100**	1.28	5.70
7	**25**	1.16	5.22
7	**50**	1.29	5.77
7	**100**	1.29	5.77
8	**25**	1.14	5.16
8	**50**	1.28	5.68
8	**100**	1.28	5.68
9	**25**	0.83	6.08
9	**50**	0.83	5.96
9	**100**	0.83	5.96
10	**25**	0.82	6.05
10	**50**	0.83	5.93
10	**100**	0.83	5.93
11	**25**	1.16	5.24
11	**50**	1.19	5.36
11	**100**	1.18	5.41

Skewness and kurtosis values using resistance set 1 at Perdido Wildlife Management Area for all alternatives and years.

Alternative	Year	Skewness	Kurtosis
Initial State	**0**	1.37	3.89
1	**25**	1.55	4.76
1	**50**	1.65	5.48
1	**100**	1.65	5.48
2	**25**	1.55	4.76
2	**50**	1.65	5.48
2	**100**	1.65	5.48
3	**25**	1.55	4.76
3	**50**	1.65	5.48
3	**100**	1.65	5.48
4	**25**	1.55	4.76
4	**50**	1.65	5.48
4	**100**	1.65	5.48
5	**25**	1.55	4.76
5	**50**	1.65	5.48
5	**100**	1.65	5.48
6	**25**	1.55	4.76
6	**50**	1.65	5.48
6	**100**	1.65	5.48
7	**25**	1.55	4.76
7	**50**	1.65	5.48
7	**100**	1.65	5.48
8	**25**	1.55	4.76
8	**50**	1.65	5.48
8	**100**	1.65	5.48
9	**25**	1.52	4.63
9	**50**	1.62	5.31
9	**100**	1.62	5.31
10	**25**	1.52	4.62
10	**50**	1.62	5.31
10	**100**	1.62	5.31
11	**25**	1.52	4.55
11	**50**	1.51	4.53
11	**100**	1.65	5.32

Skewness and kurtosis values using resistance set 2 at Perdido Wildlife Management Area for all alternatives and years.

Alternative	Year	Skewness	Kurtosis
Initial State	**0**	1.40	3.92
1	**25**	1.88	6.71
1	**50**	1.98	7.54
1	**100**	1.98	7.54
2	**25**	1.88	6.71
2	**50**	1.98	7.54
2	**100**	1.98	7.54
3	**25**	1.88	6.71
3	**50**	1.98	7.54
3	**100**	1.98	7.54
4	**25**	1.88	6.71
4	**50**	1.98	7.54
4	**100**	1.98	7.54
5	**25**	1.88	6.71
5	**50**	1.98	7.54
5	**100**	1.98	7.54
6	**25**	1.88	6.71
6	**50**	1.98	7.54
6	**100**	1.98	7.54
7	**25**	1.88	6.71
7	**50**	1.98	7.54
7	**100**	1.98	7.54
8	**25**	1.88	6.71
8	**50**	1.98	7.54
8	**100**	1.98	7.54
9	**25**	1.78	6.15
9	**50**	1.88	6.95
9	**100**	1.88	6.95
10	**25**	1.78	6.15
10	**50**	1.88	6.95
10	**100**	1.88	6.95
11	**25**	1.60	4.94
11	**50**	1.99	7.50
11	**100**	2.67	12.84

Skewness and kurtosis values using resistance set 3 at Perdido Wildlife Management Area for all alternatives and years.

Alternative	Year	Skewness	Kurtosis
Initial State	**0**	1.66	5.39
1	**25**	1.69	5.52
1	**50**	1.69	5.52
1	**100**	1.69	5.52
2	**25**	1.69	5.52
2	**50**	1.69	5.52
2	**100**	1.69	5.52
3	**25**	1.69	5.52
3	**50**	1.69	5.52
3	**100**	1.69	5.52
4	**25**	1.69	5.52
4	**50**	1.69	5.52
4	**100**	1.69	5.52
5	**25**	1.69	5.52
5	**50**	1.69	5.52
5	**100**	1.69	5.52
6	**25**	1.69	5.52
6	**50**	1.69	5.52
6	**100**	1.69	5.52
7	**25**	1.69	5.52
7	**50**	1.69	5.52
7	**100**	1.69	5.52
8	**25**	1.69	5.52
8	**50**	1.69	5.52
8	**100**	1.69	5.52
9	**25**	1.65	5.37
9	**50**	1.65	5.37
9	**100**	1.65	5.37
10	**25**	1.65	5.37
10	**50**	1.65	5.37
10	**100**	1.65	5.37
11	**25**	1.80	6.24
11	**50**	1.71	5.53
11	**100**	1.71	5.53