RED WOLF CONSERVATION IN THE FACE OF CLIMATE CHANGE

by

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EXECUTIVE SUMMARY

The red wolf (*Canis rufus*), the world's most endangered canid, was once abundant across the southeastern USA. When it was hunted to near extinction, the U.S. Fish and Wildlife Service (USFWS) began the Red Wolf Recovery Program (RWRP), capturing, breeding, and reintroducing the species to the wild in eastern North Carolina. The program was a conservation success story, with the wild population reaching 130 in 2006, but has since declined significantly, and now there are only between 8 and 20 wild red wolves left. If recovered, the red wolf could help restore southeastern predator/prey ecosystem dynamics and redeem former ranges that coyotes have taken over. Red wolves likely keep meso-predators in check, which in turn allows the meso-predator's prey to reach sustainable levels. The RWRP faces threats from hybridization with coyotes, sea-level rise, urbanization, vehicle collisions, and hunting.

With all these pressures, the program has prioritized the identification of additional sites for reintroduction, hence the goal of my project: to determine appropriate sites for reintroduction, especially considering climate change effects. I used the following models to assess site suitability: (1) based on established site suitability factors, (2) with sea-level rise incorporated, and (3) with sea-level rise and urbanization. Potential sites were federal and state protected areas surrounded by a 30-mile buffer and meeting certain criteria.

For Model 1, I used site suitability variables (habitat type, prey abundance, livestock concentration, amount of hunting, age of residents), reclassified each attribute for each variable based on its suitability for the red wolf, and weighed each variable according to its importance for survival. I put these reclassified and weighed variables into a tool in GIS that created a suitability landscape, giving the 'overall picture' of suitability at each location in the historic range. I then calculated the average suitability score for each site, and ranked the sites according to their scores. For Model 2, I removed sites that had 10% or more of their area projected to overlap with 1 meter of sea-level rise, and re-ranked the sites. For Model 3, I removed sites that had 10% or more of their area projected to overlap with at least 50% probability of projected urbanization in 2100, and ranked the remaining sites.

In Model 1, I found the top three sites to be (1) Croatan National Forest (NF), (2) Okefenokee National Wildlife Refuge (NWR), and (3) the current site, Alligator River/Pocosin Lakes NWRs. These sites had average to very good deer abundance, and habitat types included cultivated crop areas, woody wetlands, shrubs and herbaceous wetlands. Croatan NF and AR/PL NWR are surrounded by water and contain rare pocosin wetland habitat. Okefenokee NWR is an important swamp and serves as headwaters for two

rivers. Croatan NF is more coastal and hosts estuarine birds; it also contains pine forests. The buffered area for Okefenokee NWR is the largest usable area of these three because Croatan NF and AR/PL NWR are so close to the coast.

In Model 2, I removed 8 sites affected by sea-level rise, and the top sites began to shift farther inland. They were (1) Okefenokee NWR, (2) Bienville NF, and (3) Hoosier NF. Bienville NF has excellent deer abundance and a variety of habitat types, most of which are fairly suitable, such as mixed forest (oak-hickory and pine) and cultivated cropland; but it also has some low intensity development (less suitable). Hoosier NF has average deer abundance and very suitable habitat with a mixture of deciduous forests, pasture, and croplands. It also has karst systems and hills, and is nearby rural communities. All three of these top sites have wetlands (and are of comparable size, around 200 thousand acres.

In Model 3, I removed 16 sites affected by urbanization, and found the top sites to be (1) Homochitto NF, (2) De Soto NF, and (3) West Virginia and Virginia Protected Areas (WV and VA PAs).These three top sites have either excellent deer abundance and moderate-highly suitable habitat (i.e., Homochitto NF), or average deer abundance and highly suitable habitat (i.e., De Soto NF and WV and VA PAs). Homochitto NF has a diversity of habitat types seen in a gradient from cultivated crops and woody wetlands near the Mississippi River Delta to deciduous and mixed forest, shrubs, and evergreen forest and grassland moving east. De Soto NF also has a diversity of ecosystems, including pine and hardwood forests, vast grasslands, and frequently flooded swamps; it has a rolling terrain. VA and WV PAs are much more mountainous. This site has much more deciduous forest/pasture areas, with some mixed forest and cultivated crops. It is also much larger, about three times the size of the other top sites from this model, made up of many smaller protected areas.

Overall, I found that when sea-level rise and urbanization are integrated into site prioritization, the most suitable areas shift away from the coast and towards more rural cores. Although their site suitability scores are slightly lower, I expect top sites from Models 2 and 3 to be more sustainable in the future. The suitability characteristics differed between sites, but all top sites in all 3 models had at least average to high deer abundance and habitat suitability variables, which were the most important variables for survival. There are strengths and weaknesses for each of the sites I analyzed, but the current site is highly threatened by sea-level rise and cascading effects. I recommend that the USFWS reintroduce red wolves to some of these additional suitable sites soon to help this critically endangered species build resilience to eminent threats and to help improve the landscape for wildlife, natural systems, and people. This project was completed with the support of my client, Dr. Ron Sutherland with the Wildlands Network.

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Introduction

The Problem

Canis rufus (red wolf) is a species native to the United States, and critically endangered (Phillips 2018). Historically, red wolves were very common, with population estimates in the tens of thousands, and their range was the entire southeastern United States (Hinton 2013). However, this range was severely constrained due to hunting by European settlers, predator control programs in the U.S., and abundant coyotes, and by the 1970s only about 100 individuals remained (Hinton 2013). The US Fish and Wildlife Service (USFWS) began a captive breeding intervention program as the species became extinct in the wild, and in 1987 released 8 individuals into the wild at the Alligator River National Wildlife Refuge (Hinton 2013). The population grew to 130 in 2006, but then declined and now in 2022 between 8 and 20 individuals remain (USFWS 2022). The overall focus of this program has been on establishing the wild population and maintaining the breeding populations in captivity. However, the viability of survival of the red wolf in the wild in the face of climate change is not yet well understood.

The primary threats to this species are habitat loss, conflict with humans (Hinton 2013), and hybridization with coyotes (Gese 2015). Lack of resources besides habitat could also severely impact their survival, especially lack of available prey (National Geographic). It is now illegal to kill a red wolf (USFWS 2021), but illegal hunting still occurs (Hinton 2015). A likely reason for this is that landowners want to protect their property and shoot a wolf that ventures onto it, often mistaking it for a coyote. While it is illegal to kill red wolves, a resolution almost passed in 2018 allowing landowners to kill them on their property. Gunshot wounds remain their primary cause of death (USFWS 2022), but it is difficult to enforce accountability for those responsible (USFWS 2014). Vehicle collisions around the reintroduction site are another leading cause of mortality (USFWS 2022, R. Sutherland pers. com.). What was once a conservation success story is now in dire need of action to avoid the extinction of the 'All-American' red wolf.

Importance

Like many wildlife conservation issues, humans have had a major influence on the red wolf, including involvement in habitat loss, captive breeding, reintroduction, and management, and direct conflicts that still occur. Besides the intrinsic value of conserving this endemic species, the red wolf as an apex predator could restore the southeast's balanced predator/prey ecosystem dynamics, as well as redeem some of their former ranges that coyotes have taken over (Childs pers. comm.). It is hypothesized that red wolves help keep meso-predators, like racoon, in check which in turn allows the racoon's prey (such as quail) to recover. We have not seen deer population suffer as a result of reintroduction, which was a concern from the public. This is also an excellent case study on a long-term management program to essentially save a species from extinction.

Literature Review

The red wolf was listed as "threatened with extinction" in 1967. The Endangered Species Act (ESA) required the USFWS to take action, and it began its red wolf recovery work in 1973, capturing 14 individuals (believed to be all that remained) from the wild that were used to breed new pups. The wolf was declared functionally extinct in the wild in 1980, and as the captive population grew, these individuals were distributed to partner agencies, including zoos and museums around the USA, to participate in captive breeding (named the Red Wolf Species Survival Plan [SSP] program). This was done to maintain the existence of the genetic material of the red wolf, encourage more genetic diversity, and increase the number of individuals. These captive breeding programs supplied individuals to be released back into the wild and served as a 'genetic bank'. As the SSP has been ongoing for almost 50 years, it is the longest program of its kind. There are now about 43 partner sites and 245 captive individuals (USFWS 2022).

The first wolves were reintroduced to the wild in 1987 at Alligator River National Wildlife Refuge (NWR). This is referred to as a nonessential experimental population (NEP). Since then, the USFWS has been tracking habitat use, pack behavior and reproduction, disease and mortality, and conflict with humans. Based on the Service's judgment, additional wolves from the captive breeding program are introduced when there is an adequate gap in the wild established population (e.g., a newly matured wolf needs a mate, or a member of the pack dies, USFWS 2018) or to supplement the population. A second NEP was established in Great Smoky Mountains National Park from 1992 to 1998, but the wolves there moved to habitat outside the park, and pup survival was low. Therefore, the NEP was terminated, and Alligator River is the only site currently (Hinton et al. 2013).

Besides acclimating older individuals into the NEP, the Service sometimes introduces pups from captive breeding through pup fostering. For this to occur, a litter in the wild population needs to be born around the same time as a litter in a captive population. One or more pups from the captive litter are placed with the wild litter to be raised along with them. This supplements genetic diversity and the number of individuals in the NEP. Pup fostering had not occurred from 2014 to 2021 (Madison pers. comm.), but in May 2021, the first group of pup fosters in 7 years were successfully introduced to and accepted by a wild mother (Ramos 2021).

Another canid closely related to the red wolf, the coyote (*Canis latrans*), has diluted red wolf genetic material, expanded to overtake most of the wolf's original habitat, and influenced people's perceptions and behaviors toward the wolves (Gese et al. 2015). Research has been conducted to verify that the red wolf is, in fact, a separate species from the coyote, and to determine strategies to lessen interbreeding (Bohling and Waits 2015, Gese et al. 2015). The USFWS also sterilizes and marks coyotes in the Alligator River area, not only to prevent breeding with red wolves but also to prevent them breeding at all in the area, which decreases their competition with wolves (Madison pers. comm.).

The USFWS and others would like to expand the red wolf reintroduction program to more sites (USFWS 2018, 2022). As such, research has been done to determine priority sites for wolf reintroduction around the southeast United States (Dellinger et al. 2013, Desmul 2013, O'Neal 2018). With numerous threats from humans, climate change (especially sea-level rise), and other canids, habitat connectivity has also been analyzed and projected to decrease overall in the south Atlantic states (Leonard et al 2016). Within the state of North Carolina, analyses showed that additional suitable habitat patches relatively close to the current population (Croatan National Forest) would incur the least cost for the wolves to travel (Desmul 2013). However, it is unclear if and when the wild wolves would travel and whether migration would be facilitated by management. It appears most likely that management would place wolves in new sites; they would not travel there independently.

Some of the most significant regulations regarding wild red wolves involve private landowners and their rights to shoot predators on their land (Hinton et al. 2018). Red wolves are not constrained to the limits of the refuges in the NEP; they do venture onto private property and are sometimes shot as they are likely misidentified as coyotes threatening the landowner or resources on their property. Recent research has found gunshot wounds are a common cause of mortality in red wolves (Hinton et al. 2017); and although landowners are not permitted to shoot a wolf on their property, some of the local community has urged for a resolution to legalize this, which almost passed in 2016 (SELC 2021). Gunshot mortality risk is now the greatest threat to the red wolf's expansion (Sutherland pers. comm., USFWS 2022).

Overall, there have been many changes to the red wolf management program in the past few years. The USFWS and many non-profit agencies that advocate for the red wolf have disagreed on how best to manage the species, and a recent (2021) lawsuit required the Service to revise the wolf's management plan. This revised plan was released on March 1, 2021, and called for one adult pair to be released into the wild population in summer 2021 (USFWS 2021). In that year, several adult wolves were released into the NEP; however, most, if not all, were killed by vehicle collisions and gunshot wounds (USFWS 2022). The Service would like to implement the reintroduction program on additional sites in the future, but the timeframe, requirements, and feasibility for this are unclear. As of February 2022, identifying future reintroduction sites is a priority for the Red Wolf Recovery Program (USFWS), and this project contributes to that effort. With red wolf numbers struggling on the Albemarle Peninsula, and ever-present threats from sea level rise, extreme climate events, human conflict, habitat loss, and hybridization, we need to strategically plan and implement actions that are required to ensure the species survives in the wild while using our resources efficiently.

Habitat

With a historic range covering the entire southeastern United States, the red wolf was able to live in many habitat types, including coastal prairie, forest, marsh, and swamp (Dellinger et al 2010, NWF 2022). Habitat loss was a major reason for the wolf's decline before management interventions (NWF 2022). This habitat loss was associated with European colonization, destruction of natural habitats to build human developments, agricultural and industrial lands, and increased urbanization. While the red wolf populations drastically declined after 1900 (Wayne and Jenks 1991), coyotes established themselves in the southeast, taking advantage of decreased competition from red wolves and a greater tolerance for human-influenced landscapes (Lockyear et al 2016, NWF 2022).

The southeast continues to face loss of wildlife habitat due to sea-level rise and urbanization, which pose serious threats to red wolves. Sea-level rise is one of the greatest climate change-related risks to the southeastern coast of the U.S. (Terando et al 2014). The area in which the NEP is located is especially vulnerable to sea-level rise (Desmul 2013) due to its low-lying nature (NWF 2022), the potential for high variation in flood extent (Poulter and Halpin 2008), and extensive artificial drainage networks (Poulter et al 2008).

In the southeast, the reach of urban extent grows as people expand into suburban areas. This increases the amount of fragmentation on the natural landscape and lends to more urban-adapted species. It also exacerbates other threats that wildlife face such as the urban heat island effect, invasive species, and human-wildlife conflict (Terrando et al 2014). Large carnivores such as wolves can be especially sensitive to land-use change because they have relatively long generation times and require large home ranges. With increasing human land use, wildlife must adapt to survive by either using smaller natural areas or using a "mosaic" of natural and human-altered landscapes (Dellinger et al 2012).

Habitat loss due to sea-level rise and urbanization both pose pressures on red wolf survival, exacerbating habitat loss from other sources. "Core" habitat areas are predicted to become lower in number and smaller in area (Leonard et al 2016), and sea-level rise will likely require wolves to retreat inland, but pathways allowing them to do this could also be removed by both sea-level rise and urbanization (Desmul 2013). Connectivity pathways are expected to shift to the north and inland (Leonard et al 2016). Intermittent inundation in the NEP makes it difficult for wolves to move and discourages the presence of prey (Dellinger et al 2012).

While research is relatively young, studies have begun to better understand red wolf use of habitat in the face of these threats, especially related to human landscapes. Recent studies have shown an overwhelming preference for agricultural fields, likely because of the high abundance of deer, the main prey species, in those areas, and possibly lower pest and parasite risk (Hinton and Chamberlain 2010, Dellinger et al 2012). Wolves also preferred secondary roads, likely due to easy mobility and high visibility. However, when human density was high, wolves tended to avoid the preferred 'rural' human landscape and use more forested areas. This likely represents a trade-off between high visibility/mobility and conflict with humans. This suggests that a 'mosaic' habitat is ideal, and that smaller, connected habitats interspersed with low-intensity human development are better-suited for red wolves than larger protected areas untouched by humans (Dellinger et al 2012).

Client

Dr. Ron Sutherland is the Chief Scientist with the Wildlands Network, a nonprofit organization that focuses on reconnecting, restoring, and rewilding North America. Dr. Sutherland researches and advocates for red wolves and served as the client for Shane O'Neal's MP in 2018. He is currently working on field projects using camera traps to observe wolf occurrence and behaviors, and an additional project studying the red wolf's effects on small game species in the NEP, including quail.

Objective

This MP work seeks to answer the following overarching question: What are appropriate sites for red wolf reintroduction given projected climate change effects?

With the following sub-questions:

(1) Which sites are suitable without considering sea-level rise or urbanization?
(2) How is the suitability of reintroduction sites affected by sea-level rise?
(3) How is the suitability of reintroduction sites affected by sea-level rise and urbanization?

Materials and methods

Research Approach

I answered these questions by conducting analyses in GIS. I used previously conducted red wolf MPs on site prioritization (O'Neal 2018) and sea-level rise and connectivity (Desmul 2013) to base the framework of these research methods. This allowed the work to be synergistic, and using similar methods made things consistent.

To answer the question (1) Which sites are suitable without considering sea-level rise or urbanization? I updated site prioritization data (O'Neal 2018) and conducted a site suitability analysis.

To answer question (2) How is the suitability of reintroduction sites affected by sea-level rise? I used modeled projected sea-level rise (Desmul 2013, Poulter and Halpin 2008, NOAA 2022), and integrated it into the site suitability analysis.

To answer question (3) How is the suitability of reintroduction sites affected by sea-level rise and urbanization? I incorporated projected urbanization (SLEUTH model, Terando et al 2014) in addition to sea-level rise into the site suitability analysis.

For each model, I ranked the potential sites based on their suitability for reintroduction and compared the three scenarios. I also made management recommendations for red wolf recovery.

Additionally, I assisted with field projects run by Wildlands Network during the summer 2021 field season at the NEP. This fieldwork involved quail surveys for a study of wolf effects on prey species and camera trapping. The USFWS Red Wolf team does field projects including field monitoring, GPS and camera tracking, and feeding captive wolves that I had planned to assist with parts of; however, we were not able to collaborate. These field data will contribute to future studies supplementing this body of knowledge.

Data Collection

The study area was the historic range of the red wolf, comprising the entire southeastern United States (O'Neal 2018). The NEP consists of Alligator River National Wildlife Refuge (ARNWR), Pocosin Lakes National Wildlife Refuge (PLNWR), and adjacent counties, eastern North Carolina (totaling approx. 6,000 km^2) and is the only place where red wolves currently live in the wild (FWS 2018). However, canids with remnant admixed red wolf DNA have recently been discovered in Louisiana and Texas in 2018 (Hinton et al 2018), and studies are underway to better understand various characteristics of these "ghost canids" and how they can contribute to red wolf recovery (Hinton et al 2022). The Alligator River refuge is in Manteo, Outer Banks, North Carolina, and contains 152,000 acres of wetland habitat (FWS 2002). Pocosin Lakes National Wildlife Refuge (PL NWR) is located nearby and contains 110,000 acres including pocosin wetland habitat rich in peat soils (FWS 2014). Beyond the refuges, the 5 official red wolf reintroduction counties also support red wolves and comprise an additional 1.5 million acres of habitat (Defenders of Wildlife 2021). Conflict with humans tends to occur primarily outside of the refuge, where wolves attempt to cross roads and pose perceived threats to private landowner property.

In this study, I used GIS data from multiple sources on threats to red wolves, habitat characteristics, and relevant site and connectivity analyses. I collected data by requesting layers that have been used in previous MPs, downloading publicly accessible data, and requesting any additional data from the applicable sources. Because this project was built off previous MPs, I chose to use as much existing data as possible (including results from MPs), giving credit to the applicable parties, so more meaningful work could be done, and my efforts could go to as much new analysis as possible. This method of data collection is limited in that not all layers came from the same source, making it possible that there are small inconsistencies, and that these data are not always automatically up to date, so small or short-term changes may not be captured. Assumptions were that there will not be major, sudden changes to habitat types and availability.

Table A. Data layers used to represent each variable and why they were used.

Variable	**Purpose**
Historic range	The historic range polygon served as the extent on which I based my analyses. Because red wolves occupied this range before disturbance, I inferred that they could and would occupy a similar range today and in the future.
Protected areas	I used federal and state-protected lands to form the origin of potential reintroduction sites. USFWS and state agencies have the authority to manage reintroduction programs in these areas, and they comprise a 'core' area for reintroduction from which wolves can expand outside of the protected area. Protected areas are relatively undisturbed natural areas with little human disturbance, so reintroductions are more likely to be successful here than in non-protected areas.
Age of residents	Previous studies have used age of local residents to represent opinions on red wolf reintroductions. Assumptions are that older residents are less receptive to reintroductions and may pose an increased threat to success of the program.
Amount of livestock owned	The concentration of livestock represents potential conflicts, which may be higher where there are more livestock present, and the abundance of prey (e.g., deer), which may be lower where livestock are present.
Amount of hunting	The amount of hunting represents abundance of prey, which may be lower where there is more hunting, and a risk to red wolf survival from hunters mistaking wolves for coyotes and hunting them.
Prey availability	Red wolves must have enough prey available to satisfy their nutritional requirements to survive, thus this is one of the most important factors for site suitability.

Habitat type	The habitat type represents where red wolves occur, prefer, and are likely to survive. For example, their preferred field habitat is highly suitable, whereas a large body of water is not.
Sea level rise	Sea level rise represents an imminent threat to habitat suitability; leading to diminished and fragmented habitat and fewer resources such as prey. The NEP in coastal North Carolina is extremely susceptible to sea level rise, so this needs to be prioritized accordingly in site suitability models.
Projected urbanization	Urbanization projections also represent a hindrance to suitable habitat. While wolves avoid high density urban areas, they choose low density human landscapes such as agricultural fields. Urban landscapes can also increase habitat fragmentation. The location and density of urban areas is a major factor in site suitability, and is projected to increase drastically in some areas of the southeast, so is imperative to plan for.

Data Analysis

Geospatial analysis was conducted in ArcGIS Pro. I first updated the variables used for O'Neal's prioritization analysis with more recent data when available and prepared the data for analysis, including selecting parameters and assigning suitability scores to attributes. I acquired data for projected sea-level rise and urbanization, and assessed (1) site prioritization with original variables, (2) site prioritization with sea-level rise, and (3) site prioritization with sea-level rise and urbanization.

Model 1: Updated Site Suitability

I recreated the original reintroduction site prioritization method (O'Neal 2018) as the first major analysis step. These methods largely mirrored those of O'Neal, but there were a few differences that I noted.

I used the historic range polygon created by O'Neal to form the extent of my analyses, covering the southeastern United States. I included protected areas at the federal and state level; I retrieved an updated version of these data from the Protected Areas Database of the United States (PAD-US, USGS 2019). I removed sites that were smaller than ARNWR (152 thousand acres), owned/managed by the Department of Defense and Department of Energy, and areas with mostly marine/aquatic habitat. Differing from O'Neal's methods, I also removed submerged waterways, "School trust land", and Tribal lands. I decided to include Everglades and Great Smoky Mountains National Parks. As in O'Neal's method, I also combined areas that overlapped entirely or shared significant amounts of their border into one feature, resulting in 40 protected areas to serve as core sites for potential reintroductions (O'Neal used 21 sites). Similarly, I included the current NEP as the 41st site in the analysis (Fig. 1).

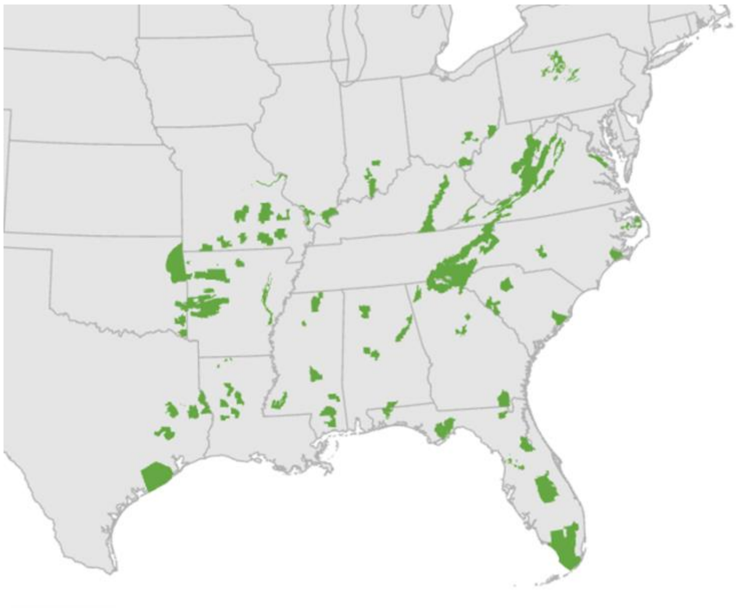

Fig. 1. Protected areas used as core habitat sites for potential reintroductions.

I used O'Neal's five variables: Age of residents, the amount of livestock owned by people in the area, the amount of hunting that takes place around the site, the amount of prey available for red wolves to consume, and the type of land cover and habitat available to them. I used the reclassification values for each attribute within each variable representing their suitability scores (1-10, with 10 representing the most suitable attribute), and a weight for each variable to represent its relative importance for red wolf survival (O'Neal 2018). Data were put into WGS84 Datum and Albers Conical Equal Area Projection, and raster format with 30-by-30 m cell size.

I used the Raster Calculator as a substitute for the Weighted Sum tool, and input the five reclassified variables into this tool with their weight values using the equation:

0.789*(Hunting reclassification) + 0.676*(Deer reclassification) + 0.62*(Land Cover reclassification) + 0.448*(Age reclassification) + 0.394*(Cattle reclassification).

The result was a "Suitability Landscape", a raster image with suitability scores calculated for all pixels in the historic range (Fig. 2).

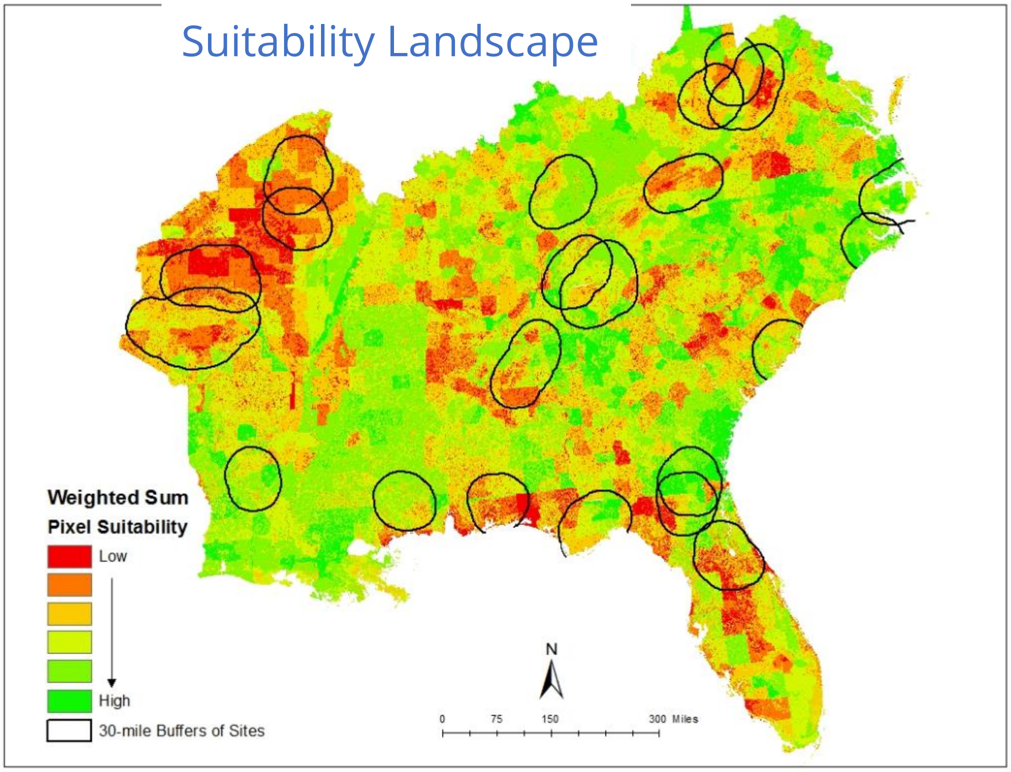

Fig. 2. Suitability Landscape (O'Neal 2018).

To score the potential reintroduction sites, I first placed a 30-mile buffer around each site (Fig. 3). Then, I used Zonal Statistics to analyze the mean suitability score and other values for each buffered site and ranked each buffered site according to their mean suitability score.

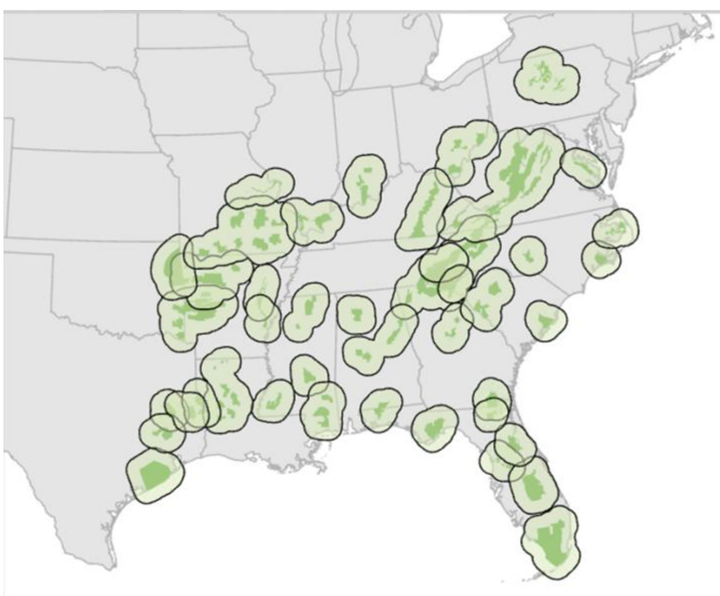

Fig. 3. Potential sites with a 30-mile buffer around each site.

Sea Level Rise Model

To use sea-level rise projections in the suitability analysis, I retrieved projections from NOAA's Office for Coastal Management (NOAA 2022, Fig. 4). This consisted of several shapefiles for each state containing sea level rise projections at various inundation levels. I chose the 1m projection because it was fairly close to the predicted value (for 2050, sea level was projected to be 0.38 m above the 'current level') from a Nature Conservancy (TNC) model (Pearsall 2011) and other models used in the region (Desmul 2013, Poulter & Halpin 2008).

Fig. 4. Sea-level rise projection data retrieved from NOAA, 1 meter (NOAA).

Model 2: Site suitability with sea-level rise

To incorporate sea-level rise into the site prioritization, I calculated the area of overlap between each site and projected sea-level rise using Pairwise Clip and Calculate Geometry. I then determined which sites are projected to have 10% or more of their buffered area covered by sea-level rise (calculated in MS Excel); these sites were separated and the remaining sites that were less susceptible to sea level inundation were ranked.

Urban Development Model

To use projected urbanization in the suitability analysis, I used the SLEUTH Urban Growth Model (Terando et al 2014, Fig. 5). SLEUTH stands for the inputs to the model: Slope, Land use, Excluded, Urban, Transportation, and Hillshade. It was created by Dr. Keith Clarke at UC Santa Barbara and has been further developed by David Donato of USGS and Terando et al of NCSU (ScienceBase-Catalog 2019). It predicts the extent and probability of urbanization in the southeast at 10-year increments through 2100 (Terando et al 2014).

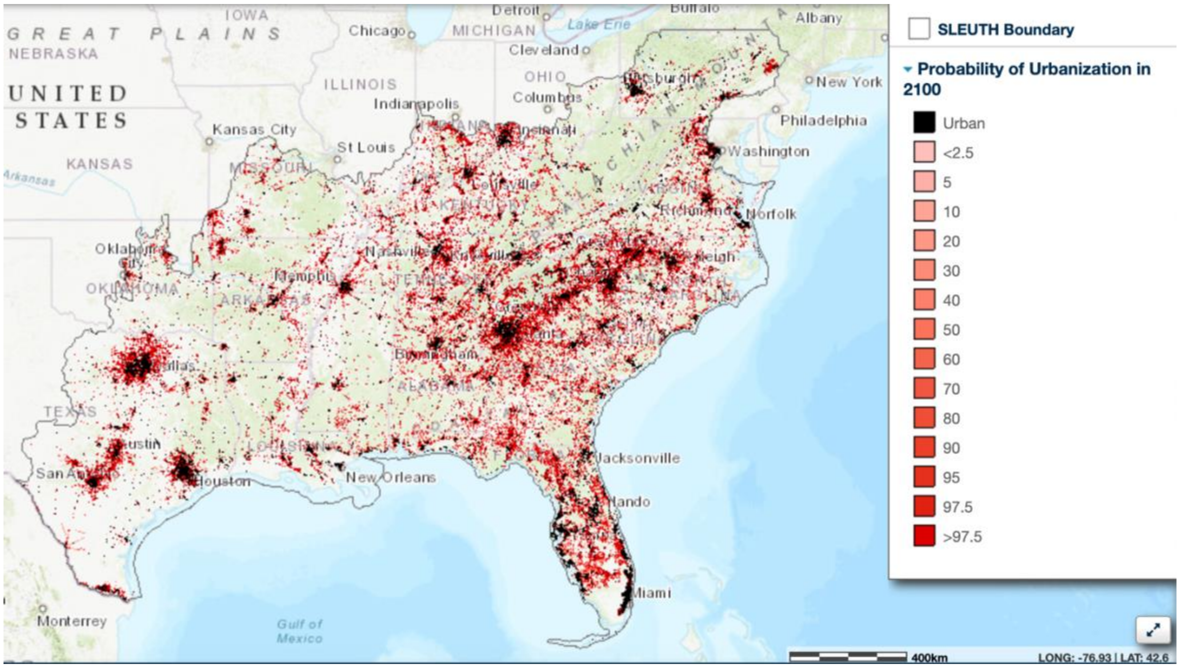

Fig. 5. Urbanization projection data retrieved from the SLEUTH model, 50% or greater probability of urbanization in 2100 (Terrando).

Model 3: Site suitability with sea-level rise and urbanization

Using the results from Model 2, I then overlayed projected urbanization from the SLEUTH model in the year 2100. I separated sites that had 10% or more of their buffered area projected to have a 50% or higher probability of urbanization, and ranked the remaining sites.

The differences in site rankings between each model were compared and recommendations were made to management.

Results

Site Suitability Analysis

Model 1: Updated Site suitability

Suitability scores were calculated for each site with its 30m buffer. Scores ranged from 13.6 (least suitable) to 20.1 (most suitable). There were a total of 41 sites evaluated and 23 sites with Moderate to Highly Suitable scores of 16.5 or above. The most suitable reintroduction sites in this model were (1) Croatan NF, (2) Okefenokee NWR, (3) AR/PL NWR (the current NEP), (4) Bienville NF, and (5) Hoosier NF. The top three sites were the same as O'Neal's analysis, however, in my analysis, Croatan NF replaced Okefenokee NWR as rank 1. Note that my methods included Great Smoky Mountains (rank 17) and Everglades (combined with surrounding areas) National Parks, while O'Neal (2018) did not (Fig. 6).

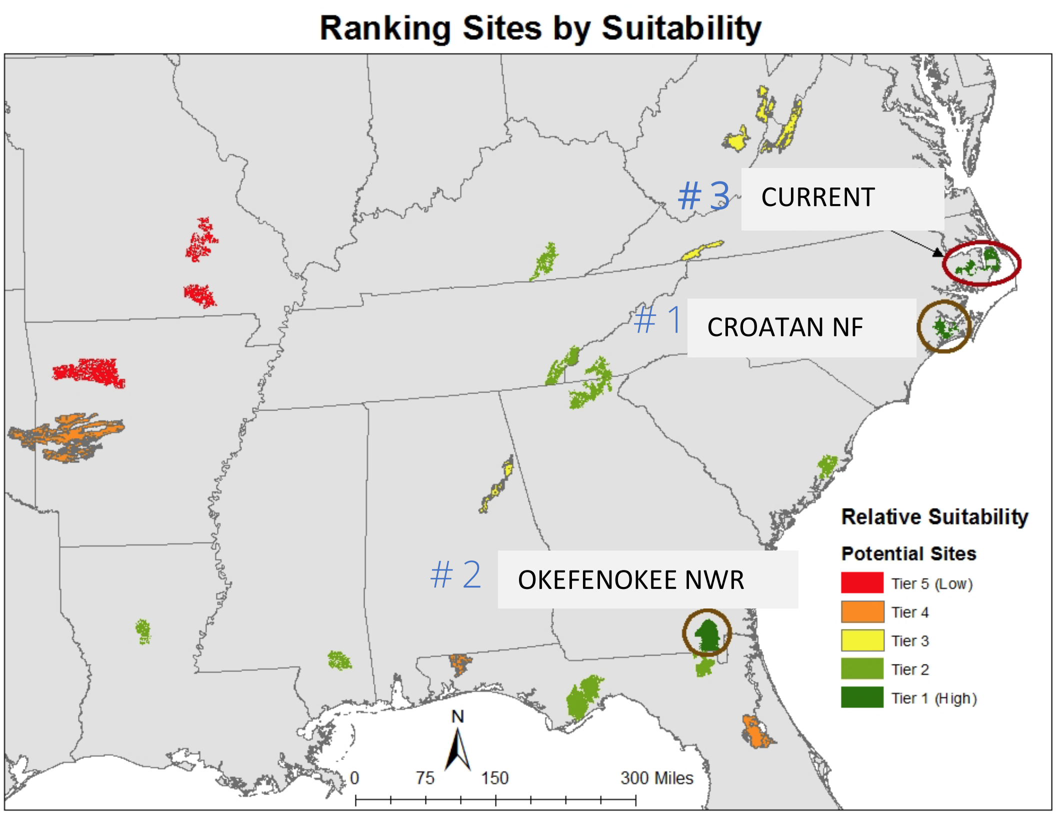

Fig. 6. Map of potential reintroduction sites ranked by suitability scores (modified from O'Neal).

Model 2: Site suitability with sea-level rise

Projected sea-level rise of 1m is expected to impact all 12 coastal states in the study area and Washington D.C. There were 8 sites projected to have at least 10% or more of their area (including their 30m buffer) covered by projected sea-level rise and were thus removed from this ranking. Some of these removed sites included several that would have been highly suitable if sea level rise was not considered: Croatan NF and AR/PL NWR (the current NEP). The most suitable sites after incorporating sea-level rise were (1) Okefenokee NWR, (2) Bienville NF, and (3) Hoosier NF (Fig. 7, Table B).

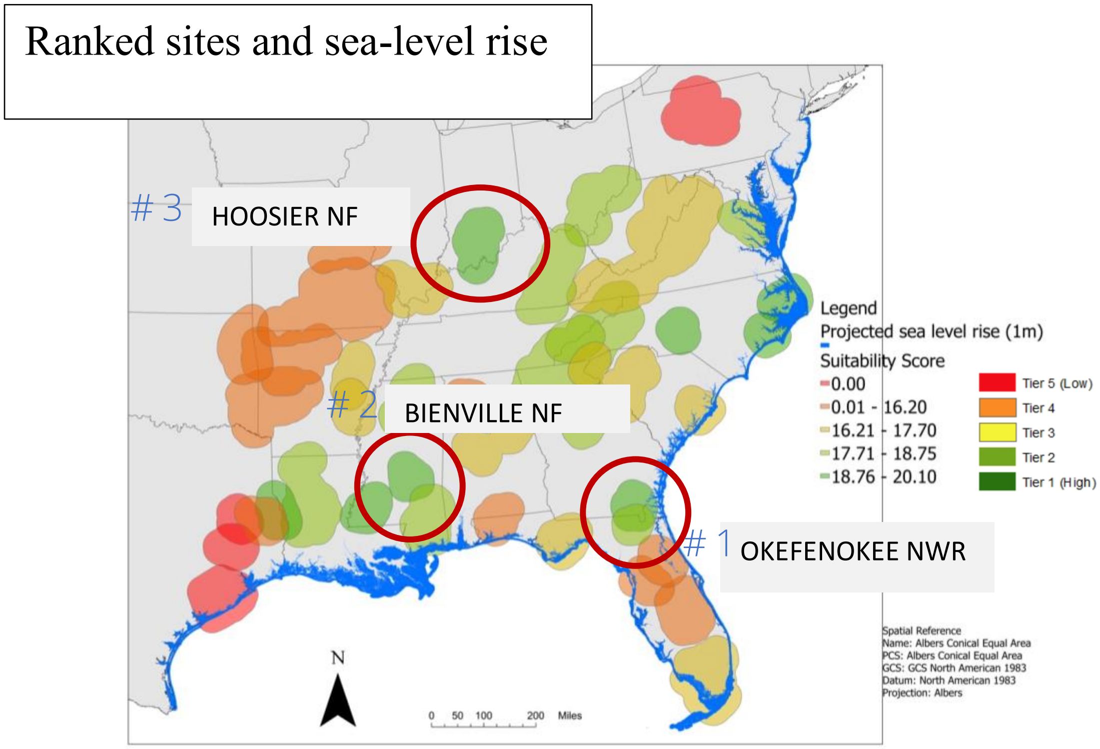

Fig. 7. Map of potential reintroduction sites ranked by suitability scores overlaid with projected sea-level rise of 1m.

Table B. Mean suitability scores, ordered from most (top) to least (bottom) suitable, for each potential reintroduction area after those with 10% or greater area projected to be impacted by sea-level rise were removed.

Site Name	**Suitability Score**
Okefenokee National Wildlife Refuge and Wilderness Area	20.08
Bienville National Forest	19.49
Hoosier National Forest	19.23
Uwharrie National Forest	19.20
Homochitto National Forest	19.19
Sabine National Forest	19.09

Kisatchie National Forest	18.75
Oconee National Forest	18.70
Daniel Boone National Forest	18.65
Wayne National Forest	18.63
Osceola National Forest	18.34
Holly Springs National Forest	18.29
De Soto National Forest	18.22
Great Smoky Mountains National Park	18.05
Piscah, Cherokee, Nantahalla, Chatahoochee National and State Forests	17.83
Apalachiacola and Tate's Hell National Forests	17.70
Shawnee National Forest	17.25
Sumter and Francis Marion National Forests	17.14
West Virginia and Virginia Protected Areas	17.14
Talladega National Forest	17.07
Cache River National Wildlife Refuge	16.55
Dale Bumpers White River National Wildlife Refuge	16.54
Angelina National Forest	16.20
Everglades Headwaters National Wildlife Refuge and Conservation Area	16.15
Ouachita National Forest	15.89
Florida Panhandle and Alabama National Forests	15.86
William B. Bankhead National Forest	15.73
Big Muddy National Fish and Wildlife Refuge	15.51
Ozark Plateau National Wildlife Refuge	14.95

Mark Twain National Forest	14.65
Ozark and St. Francis National Forests	14.13

Model 3: Site suitability with sea-level rise and urbanization

Projected urbanization in 2100 within the study area is expected to show an increase of 18.3 million hectares of at least 50% probability of urbanization compared to 2020. 16 buffered sites are predicted to have at least 10% of their area urbanized (50% or greater probability of urbanization) in 2100. I had to remove an additional 12 sites from further analysis because the SLEUTH model did not provide adequate data for those sites. These were sites near the edge of the extent of the latest SLEUTH update. Based on an earlier version of the SLEUTH model that did include the areas toward the west of the range, I don't expect urbanization to cover over 10% of any of those sites, so some of them, including those in northern Louisiana, should be prioritized as well. Several areas, such as the Greater Everglades site in south Florida, are projected to be impacted heavily by both sea-level rise and urbanization (Fig. 8, Table C).

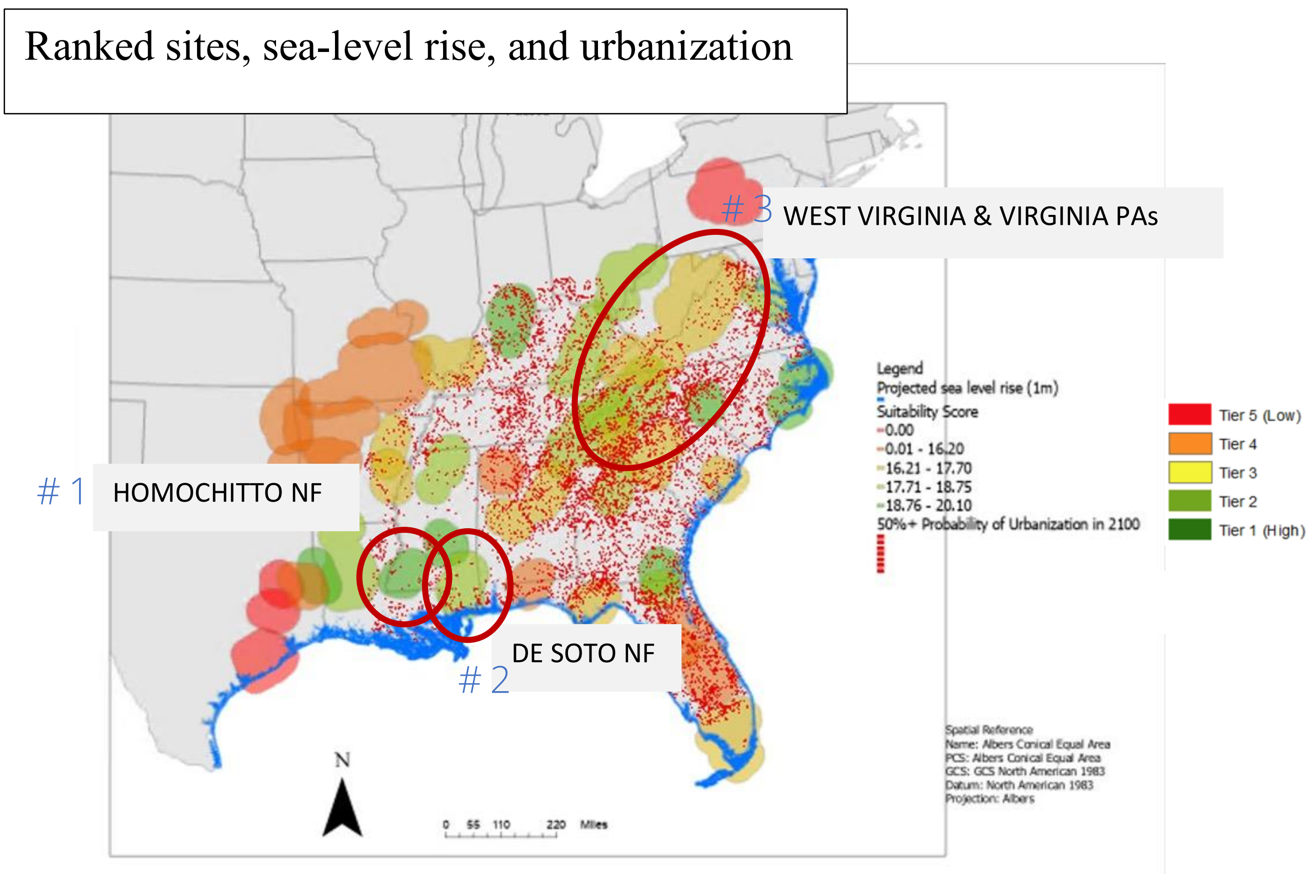

Fig. 8. Map of potential reintroduction sites ranked by suitability scores overlaid with a projected sea-level rise of 1m and urbanization probability of 50% or greater in 2100.

Table C. Mean suitability scores, ordered from most (top) to least (bottom) suitable, for each potential reintroduction area after those with 10% or greater area projected to be impacted by sea-level rise and 10% or greater area of 50% and above likelihood of urbanization in 2100 were removed.

Site Name	**Suitability Score**
Homochitto NF	19.19
De Soto NF	18.22
West Virginia and Virginia Protected Areas	17.14
Cache River NWR	16.55
Dale Bumpers White River NWR	16.54

Model Comparisons

Model 1 (Updated Site Suitability), Model 2 (Site Suitability and Sea Level Rise), and Model 3 (Site Suitability with Sea Level Rise and Urbanization) resulted in very different site suitability rankings. Model 2 assessed 31 sites, of which Model 3 only assessed 5. The top 3 sites from Model 3 (Homochitto NF, De Soto NF, West Virginia and Virginia Protected Areas) ranked 5th, 13th, and 19th, respectively, in Model 2. All five ranked sites in Model 3 were above the Moderate to Highly Suitable score of 16.5.

The most suitable site overall (using Model 3) is Homochitto National Forest in Mississippi, with a suitability score of 19.19.

Management recommendations

Management priorities going forward should be to focus reintroduction efforts on sites with Moderate to Highly Suitable scores of 16.5 or above in the Model 1, Model 2 (sea level), and Model 3 (sea level and urbanization) scenarios. This will allow for the most efficient use of agency funds and time, and lead to the likely success of reintroductions and recovery efforts going forward. Management should also plan to eventually transition out of the current NEP to avoid harm from sea level rise. Future reintroductions in multiple places to stronghold the wild population should also be strongly considered. I recommend that management incorporate adaptive management strategies and new research findings into the program to strengthen it and make it more effective, implement better strategies to avoid red wolf mortality from guns and vehicle collisions, and continue to involve people through public engagement and landowner incentives programs.

Discussion

The major findings of this study are the resulting prioritized sites for red wolf reintroduction, and how rankings change when different threats are accounted for. The highest priority sites changed drastically from eastern coastal plain to more inland, north, and west areas when sea-level rise and urbanization are used as factors in the model.

Therefore, the threats of sea-level rise and urbanization are important factors in determining site suitability for the red wolf and are important to incorporate into conservation planning. Accounting for these factors will provide better chances for the future survival of the species, ecosystem health, and importantly, cost-effectiveness of the management program.

My initial findings of the most suitable sites (Model 1) are similar to those of O'Neal 2018, with the same top three sites of Croatan NF, Okefenokee NWR, AR/PL NWR (the current NEP). However, I found Croatan NF to be rank 1 and Okefenokee NWR to be rank 2, while O'Neal found those two sites' rankings switched (O'Neal 2018). My identification of Croatan NF as a suitable habitat site was also identified by Desmul 2018; however, other sites in North Carolina identified in that study were mostly smaller patches of land, except for larger areas near the Smoky Mountains. My interpretations of future sea-level rise and urbanization pressures on the red wolf were similar to Desmul, with the Abermarle Peninsula facing extreme inundation by 2100 and high urbanization around the middle of North Carolina, especially the Triangle region (Desmul 2013).

In Model 1, the top sites have average to very good deer abundance, and habitat types include cultivated crop areas, woody wetlands, shrubs and herbaceous wetlands. Croatan NF and AR/PL NWR are surrounded by water and contain rare pocosin wetland habitat (USFS and USFWS). Both of these sites host large populations of black bear. Okefenokee NWR is an important swamp and serves as headwaters for two rivers (USFWS). Okefenokee and AR/PL NWR are refuge areas for migratory waterfowl. Croatan NF is more coastal and hosts estuarine birds; it also contains pine forests. The buffered area for Okefenokee NWR is the largest usable area of these three because Croatan NF and AR/PL NWR are so close to the coast.

In Model 2, the top sites begin to shift farther inland. Bienville NF has excellent deer abundance and a variety of habitat types, most of which are fairly suitable, such as mixed forest (oak-hickory and pine) and cultivated cropland; but it also has some low intensity development (less suitable). Hoosier NF has average deer abundance and very suitable habitat with a mixture of deciduous forests, pasture, and croplands. It also has karst systems and hills, and is nearby rural communities (USFS). All three of these top sites have wetlands (USFS, USFWS) and are of comparable size, around 200 thousand acres.

In Model 3, the top sites have either excellent deer abundance and moderate-highly suitable habitat (i.e., Homochitto NF), or average deer abundance and highly suitable habitat (i.e., De Soto NF and WV and VA PAs). Homochitto NF has a diversity of habitat types seen in a gradient from cultivated crops and woody wetlands near the Mississippi River Delta to deciduous and mixed forest, shrubs, and evergreen forest and grassland moving east. De Soto NF also has a diversity of ecosystems, including pine and hardwood forests, vast grasslands, and frequently flooded swamps; it has a rolling terrain (USFS). VA and WV PAs are much more mountainous, and I note that elevation/elevation gradients were not explicitly included in the site suitability analysis. This site has much more deciduous forest/pasture areas, with some mixed forest and cultivated crops. It is also much larger, about three times the size of the other top sites from this model, made up of many smaller protected areas.

Sites in Mississippi (i.e., Bienville, Homochitto, and De Soto NFs) had unfavorable hunting suitability scores, because the concentration of hunting for the entire state was fairly high. However, hunting data for this state was very course. All other top sites in other states had similar average hunting scores.

The current NEP (AR/PL NWR) is unsustainable because of the major threat from sea-level rise. A significant portion of the site will become below sea-level, functionally erasing the available red wolf habitat. Moreover, the site is expected to become disconnected from the mainland due to sea-level rise, severely limiting the wolf's ability to migrate inland. The site will also face more frequent flooding, temporarily reducing habitat, and decreasing prey availability. Even if the wolves were able to migrate inland as sea level rises, the threats from vehicle collisions, hunting, and coyote hybridization make their chances of survival extremely grim.

Table D. Summary table showing an examination of strengths and weaknesses for a subset of alternative reintroduction sites.

Alternative Reintroduction Site	**Strengths**	**Weaknesses**
Croatan NF	Close to current NEP, high deer abundance, high habitat suitability	Surrounded by water, high sea-level rise vulnerability, lower usable area
Okefenokee NWR	High habitat suitability, resilient to sea-level rise, average deer abundance	Vulnerable to urbanization
Homochitto NF	High habitat suitability, high deer abundance, resilient to sea-level rise, resilient to urbanization, close to other top sites (connectivity potential)	Medium-high hunting (course data)
Hoosier NF	High habitat suitability, average deer abundance, resilient to sea-level rise	Vulnerable to urbanization, far from other top sites
WV/VA PAs	High habitat suitability, average deer abundance, large area, resilient to sea-level rise, resilient to urbanization	Mountainous, far from other top sites

Site prioritizations for other wildlife species generally consider habitat requirements for the species, geographical areas where habitat requirements are met, and threats to the species (Tack & Fedy 2015, Fedy et al 2014, Kornse 2020, Anoop et al 2020). While there are many types of models used, such as niche models, predictive models, quantitative models, and species-specific restoration assessment models; there does not seem to be a generally agreed-upon procedure for identifying and prioritizing wildlife reintroduction sites. This increases flexibility for scientists to be able to design their methods, but it is more difficult to compare and interpret findings when methods vary.

Analysis of canid habitat suitability under climate change has focused more on changes to the extent of the suitable range rather than site-specific habitat scores. Most of the world's canids, including the red wolf, are expected to experience a decrease in their overall suitable range; a few species are expected to maintain and/or expand their current ranges (Porto et al pre-print). Many of these ranges shift towards the poles and expand into desert areas (Jones et al 2016). Range shifts will also alter species interactions and can have cascading effects.

Species may also adapt to their changing environment, and their ability to do so is dependent on the amount of temperature change and their generation time (Porto et al pre-print). Canid species that are expected to experience habitat reductions also tended to have lower adaptive evolution capacity. An example of this can be seen in South America, where the short-eared dog's habitat is expected to be reduced and fragmented, while the crab-eating fox's range is expected to expand, creating more competition with and increasing pressures on the former, more specialized species.

The coyote has already expanded its range significantly and experienced adaptations. Clearly, it competes with the red wolf. This is problematic because, perhaps the red wolf would have been able to evolve to adapt to the changing climate and shift its range, but because of the high abundance of coyote and low number of red wolves, the two species will mix and red wolf DNA will be 'diluted', potentially to near obliteration.

The sea-level rise and urbanization variables I used did not have expert-determined values representing their relative importance, as the other site prioritization variables did. More precise results may be obtained if more details on values for the threats variables were elicited by experts as well. The purpose of including them here was to show the differences in results depending on whether they are included.

These findings are very relevant to management. The Red Wolf Recovery Program has stated that prioritizing sites for future reintroductions is a high priority, and this study does that. It should be used, along with other similar, available studies, to decide where to reintroduce red wolves in the future. The USFWS' selection of reintroduction sites should depend on the timeframe of introduction. Sea level rise and urbanization will increase pressures on wolves in the future, but it is also important to consider these future scenarios while implementing actions in the near term. For example, reintroducing wolves to a site that is medium to highly-suitable today and will likely remain that way into the future may be better than reintroducing them to a site that is highly suitable today, but in 10 years will be underwater.

I also recommend that USFWS designate critical habitats for the red wolf in some of these key sites and work with land conservationists to ensure connectivity pathways between these sites. This is important for increasing genetic diversity and increasing versatility. A tool that can be used for this is conservation easements. The Prey for the Pack program around the current site is a good start. The suitable sites in

Mississippi that are fairly close to each other could be a place to focus on for connectivity. Another previous master's project (Desmul 2013) analyzed connectivity pathways for the red wolf in North Carolina. This method can be applied to other areas for prioritizing connectivity options.

It is interesting to see highly suitable sites in different states and ecological regions, underscoring the versatility of the red wolf in the natural environments of the southeast. Management should use this to the advantage of the program by diversifying reintroduction sites. Multiple reintroduction sites would allow the wolf to re-establish multiple populations in the wild, increasing genetic diversity and resilience to threats such as natural disasters and disease. This would also create a 'bank' of wild populations in addition to the large captive population. Diversifying reintroduction sites would also allow for more research on habitat use and preferences of red wolves.

Specific plans for reintroduction sites depends on timing. For example, does it make more sense to reintroduce sooner in one of the sites from the first model, and then gradually shift to other sites later; or to reintroduce them in a site that we know is going to be more resilient in the future, but the habitat characteristics may be a little less suitable right now?

The sustainability of a successful red wolf reintroduction program in the face of climate change is of utter importance to the survival of the red wolf, and its ability to keep prey in check and ecosystems healthy. The current NEP is highly threatened by sea-level rise, which will overtake and fragment the wolf's habitat, lowering its chances of survival. The red wolf needs additional reintroduction sites with suitable habitat and other characteristics and a lower risk of habitat loss from sea-level rise and urbanization.

A limitation of this study is that there is a trade-off between assessing the entire historic range and obtaining a high level of detail. These models also do not predict extreme events like major storms or disease outbreaks.

There are many areas of further research that would be helpful to red wolf management, many of which are underway and should continue to build knowledge that should be implemented into management. This includes research on prey, 'ghost' wolf genetics, management strategies, landscape use and detailed preferences, behavior, and preventing human-wolf conflict, especially vehicle collisions and gunshots.

These results will be given to the USFWS to help inform their red wolf management and to Wildlands Network to help guide research and management recommendations for the red wolf going forward. This body of knowledge on priority red wolf reintroduction sites should be used to choose sites and reintroduce wolves there soon in order to create a stronghold of wild red wolves going forward that is resilient to eminent threats and will help improve the landscape for wildlife, natural systems, & humans.

Conclusion

Red wolf reintroduction should occur at a combination of sites identified here as Moderately to Highly Suitable (score of 16.5 and above) in all three models. High priorities for red wolf conservation are continued research and actions related to site suitability and prioritization, reduction of human-related mortality (especially due to vehicle collisions), coyote hybridization, and climate resilience. As natural apex predators, red wolves have a unique ability to help restore health and balance to our ecosystems of the southeast, benefiting wildlife, natural systems, and people. With the right plan in place, we can coexist with America's wolf.

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