Chapter 6

GENETIC CONSEQUENCES AND MANAGEMENT IMPLICATIONS OF CLIMATE CHANGE FOR THE AMERICAN ALLIGATOR (*ALLIGATOR MISSISSIPPIENSIS*)

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ABSTRACT

The American alligator (*Alligator mississippiensis*) has been found in essentially its present form in the fossil record for 30 million years. This long relatively unchanged evolutionary history gives the impression that alligator habitat has remained so stable over time that there was little evolutionary pressure to change, but evidence from the fossil record, genetics research reviewed here, and models of climate change presented here, suggest otherwise. In particular, the lack of genetic variation range-wide indicated that alligators were forced into a single Pleistocene refugium, which, according to fossil evidence and model projections in this study, was most likely restricted to the paleo coastline of peninsular Florida. The apparent expansion of suitable habitat from the mid-Holocene to modern day resulted in the current distribution of alligator populations, which follow an isolation by distance model of genetic structure. These data support the theory that alligators were fully capable of tracking changes in their distribution in response to past climate change, rather than evolving absolute climate tolerances to persist. Indeed, the amount and location of suitable habitat available to alligators fluctuated greatly during the last 2.5 million years of glacial-interglacial cycles. Under future climate scenarios, models predicted that suitable alligator habitat will expand north, increasing the number and area of habitat patches, but also retract from the southern tips of both Florida and Texas. In the context of the fossil record, these results illustrated that regions without alligators for thousands of years could potentially be recolonized in the near future, and also that regions that contained alligators for millions of years, such as southern Florida, could include populations that may be difficult or potentially impossible to maintain over the next half-

century. Furthermore, if the distributional response of alligators to climate change is constrained by natural and human barriers, then the rate of climate change may outpace the alligator's capacity to adjust in those areas, leading to rapid localized changes in the size and distribution of alligator populations. These results warn that the alligator could be highly vulnerable to future changes in climate in specific regions throughout its current distribution. Thus, while alligators have shown a remarkable capacity to adjust to long-term climate changes, the potential for alligators to respond to climate change over much shorter timescales (i.e., decades vs. millennia), as depicted here, may be dependent on human intervention. Several landscape conservation perspectives and active management strategies are discussed that could help preserve the adaptive potential of populations and maintain species resilience to climate change.

INTRODUCTION

Crocodilians represent an ecologically successful group of reptiles that originated in the mid- to upper-Cretaceous period (Brochu et al. 2009) with extant members that have existed for approximately 100 million years (Roos et al. 2007, Brochu et al. 2009). These extant crocodilian species have survived the dramatic changes in global climate associated with the Cretaceous–Tertiary (K–T) extinction, 65 million years ago, that caused the eradication of many terrestrial and marine species (Sues 1989), as well as periods of major glaciation during both the late Oligocene and the Pleistocene (Markwick 1994). However, with each major climatic event, the fossil record points to major changes in the distribution and composition of the crocodilian fauna. In North America for example, the warming period of the intervening Miocene was characterized by a return of crocodilians to the continental interior, but the faunal composition shifted from members of the Crocodylidae to the family Alligatoridae, which remains the dominant group today (Markwick 1994). The American alligator (*Alligator mississippiensis*) has been found in essentially its present form in the fossil record for 30 million years since this warming period (Figure 6.1), although alligator-like creatures existed as long as 180 million years ago (Gartside et al. 1977). This long, relatively unchanged evolutionary history gives the impression that habitat of the American alligator and other crocodilians has remained so stable over time that there was little evolutionary pressure to change, but the observed climate-driven turnover in crocodilian composition and extinctions within this once varied and diverse lineage suggest otherwise (Markwick 1994).

Today, the American alligator (hereafter alligator) is distributed across the southeastern United States (Figures 6.2A and B) and typically occupies coastal freshwater habitats characterized by the slow moving waters of marshes and swamps and inland forested habitats composed of streams and creeks interspersed with ponds and lakes (Ryberg and Cathey 2004). While the role of climate in shaping the alligator's current distribution is undeniable, especially along its northern boundary (Gardner et al. 2016), the current distribution also was shaped by years of excessive hunting pressure and over exploitation, followed by successful range-wide conservation efforts (McIlhenny 1935, Ross and Roberts 1979, Joanen and McNease 1987). In particular, over the last century, alligator populations in Texas, Louisiana, and Florida remained relatively large, while populations in other areas suffered dramatic declines and even localized

extirpations (Chabreck 1967, Davis et al. 2000). Almost as quickly, these declines began to reverse over the last four decades with protective legislation, sustained management programs, and the restocking of many thousands of alligators into depleted habitats (Ross and Roberts 1979). The recovery of this species was so remarkable that population management programs were developed at state and federal levels to organize public and private harvests, regulate trade in alligator meat and hides, and address the demand for removal of nuisance animals (Thorbjarnarson et al. 1992).

Figure 6.1. American alligator in habitat (Photo Credit: W. A. Ryberg)
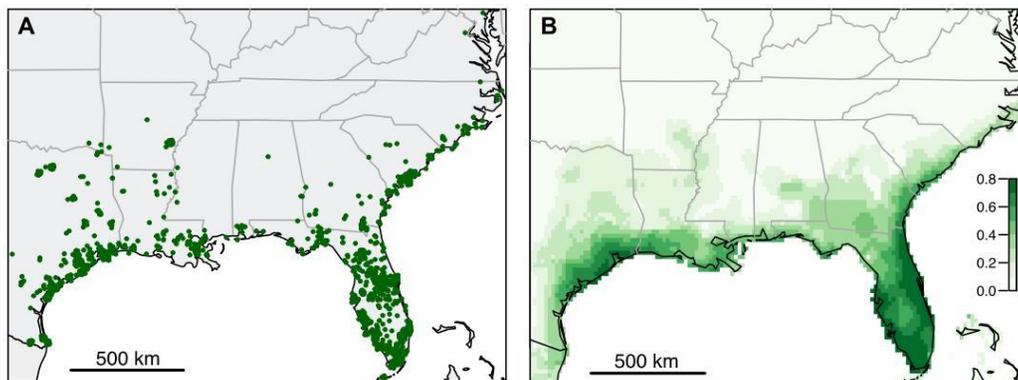

Figure 6.2. A) Distribution of species localities compiled from VertNet and iNaturalist databases. B) Maxent species distribution model showing the probability of occurrence of alligator populations in a modern climate (the legend shows a gradation of light to dark green over a range of 0.0 to 0.8 and these colors, projected on the map, represent the probability of occurrence of alligator populations).

Placing these observations in perspective, humans have been absent from a 30 million-year-old, climate-driven, alligator narrative until the last century, when alligators began playing a continuously expanding economic and sociological role in the human narrative following European colonization of North America. The capacity of humans to orchestrate, in less than a century, both the rapid destruction and prompt recovery of this species through management at

a spatial scale comparable to major glaciation events lasting thousands of years suggests that the alligator's future narrative will be shared with humans, or more likely, completely written by humans. In this study, we characterize what this future narrative might look like in the Anthropocene as humans continue to shape the distribution and abundance of alligator populations through management.

POPULATION GENETICS AND ALLIGATOR MANAGEMENT

Current alligator management is still concerned with controlled harvests, regulation of trade in meat and hides, and issues of nuisance animals with the goal of achieving a balance between maintaining alligators as a sustainable resource and the preservation of healthy wild alligator populations (Davis et al. 2000). The World Conservation Strategy of the IUCN/SSC Crocodile Specialist Group recognized the maintenance of genetic variation of healthy wild alligator populations as the most critical component of this management goal (Thorbjarnarson et al. 1992). In general, to manage a species with that goal in mind, genetic markers must be developed that allow insight into the genetic diversity and structure of the populations of interest, provide important clues about the evolutionary history of species such as recent or ancient bottlenecks, characterize patterns of gene flow and relationships between sub-populations, and trace the reproductive dynamics of local populations (Menotti-Raymond and O'Brien 1995, Paetkau et al. 1995, Ramey 1995, Sugg et al. 1996, Wenburg et al. 1998). For alligators, the genetic marker of interest has changed with advances in molecular techniques over the last half-century to allow for a finer and more precise characterization of the population genetic attributes of this species (reviewed in Dessauer et al. 2002). Below, we briefly summarize the results of this long history of research with a particular focus on those results most relevant for population management.

Early research quantifying genetic variation in alligator populations focused on protein polymorphisms (Gartside et al. 1977, Menzies et al. 1979, Adams et al. 1980). Proteins of similar function can have dissimilar amino acid sequences (i.e., polymorphisms, allozymes), which can be detected using electrophoresis (e.g., migration of proteins through a gel exposed to an electrical field). Variation in the migration patterns of inherited polymorphic proteins can reveal differences (and similarities) in individuals of the same species and allow estimation of the frequencies of such genetic variants in populations (Coulson and Hernandez 1983). In a survey of alligators from a population in Rockefeller Refuge in southwestern Louisiana (n = 80), only two of the 49 loci examined (i.e., amino acid sequences determining enzymes and other proteins) were polymorphic, and average heterozygosity (i.e., average proportion of individuals that are heterozygous for a set of loci; 0.021) was lower than most vertebrate species (range 0.05-0.18; Gartside et al. 1977, Nevo et al. 1984, Davis et al. 2000). Similarly low levels of protein polymorphisms also were observed from populations of alligators in the Everglades (Menzies el al. 1979) and South Carolina (Adams et al. 1980), making the alligator one of the most genetically homogenous vertebrate species (Coulson and Hernandez 1983; see also subsequent tests in Glenn et al. 1998 using randomly amplified polymorphic DNA (RAPD), M-13, and other DNA probes).

More recently, the alligator's mitochondrial genome (mtDNA) was sequenced to quantify levels of genetic variation (Janke and Arnason 1997, Mindell et al. 1999). The entire genome

of the alligator (and most reptiles) mitochondrion is a closed double-stranded loop typically about 16,000 to 18,000 base pairs long that appears to evolve 5-10 times faster than the average nuclear gene (Wayne 1992). This faster rate of evolution makes it possible to more effectively discriminate closely related species and populations than protein electrophoresis methods. However, because mtDNA is maternally inherited, analysis of its sequence provides data on maternal lineages only and may not precisely reflect nuclear DNA evolution (Wayne 1992). A study comparing sequences of the cytochrome b (cyt b) and control region or D-loop, two regions of mtDNA shown to be variable in a variety of organisms and easy to amplify (Kocher et al. 1989), revealed a complete lack of genetic subdivision in 25 individuals sampled across the alligator's entire geographic range (Glenn et al. 2002). Specifically, only one polymorphism was detected at the cyt b locus and only two polymorphisms were detected in the control region. These observations suggest that the alligator experienced a severe population bottleneck, probably during the late Pleistocene, resulting in nearly homogeneous mtDNA among alligator populations, which provides little information for management.

Finally in the late 1990's, microsatellites were developed that provided the highly polymorphic loci needed for addressing fine-scale management questions regarding the population genetics of alligators and other crocodilians (Glenn et al. 1996, 1998; Dessauer et al. 2002). Microsatellites are arrays of tandem repeat sequences of DNA (e.g., 2 base pair or dinucleotide repeats) commonly found in the nuclear genome of eukaryotes. The number of repeats in an array can vary among alleles at the same or different loci, and the variation in length can be quantified using restriction enzymes that excise array fragments of different lengths producing what has widely become known as a DNA fingerprint (Wayne 1992). The sharing of diagnostic fragments between related individuals in a population, or even parents and offspring, has allowed the distinction of close and unrelated classes of individuals and even accurate assessment of paternity, as well as overall genetic variability of alligator populations (Glenn et al. 1996, 1998; Davis et al. 2001). In the original microsatellite study, 11 of 15 microsatellites developed were polymorphic in alligators from the Rockefeller Refuge in Louisiana and Florida Everglades, with an average heterozygosity across sites nearly 20 times higher than those reported for protein polymorphisms (Glenn et al. 1996, 1998). The level of variability demonstrated by these loci was extensive enough to distinguish between alligator populations and even related individuals sampled within populations (Glenn et al. 1996, 1998; Davis et al. 2001).

Shortly after their development, these microsatellites were used to characterize the genetic structure of alligator populations at different geographic and ecological scales (Davis et al. 2000, Ryberg et al. 2002, Davis et al. 2002). In the first range-wide analysis of genetic structure using microsatellites, 178 individuals were analyzed from 6 populations spanning from southwest Louisiana to South Carolina and down to Everglades National Park in Florida (Davis et al. 2000). The amount of genetic variation observed was higher than any other previous study of the species. Observed mean heterozygosity ranged from 0.52 to 0.76 across all loci for all populations, and measures of genetic distance revealed significant genetic differentiation among populations that appeared to support an isolation by distance model (i.e., geographic and genetic distance were positively correlated; Figure 3). Although no large-scale pattern of genetic structure was apparent, each population contained unique genetic characteristics that could be used as location-specific genetic markers to address wildlife forensic management issues. The Savannah River Site population in particular, which was the only inland population in this study, contained genetic characteristics distinct from the other coastal populations,

leading to the hypothesis that inland alligator populations might exhibit more restricted gene flow than coastal populations and therefore contain different levels of genetic variation and a unique genetic structure.
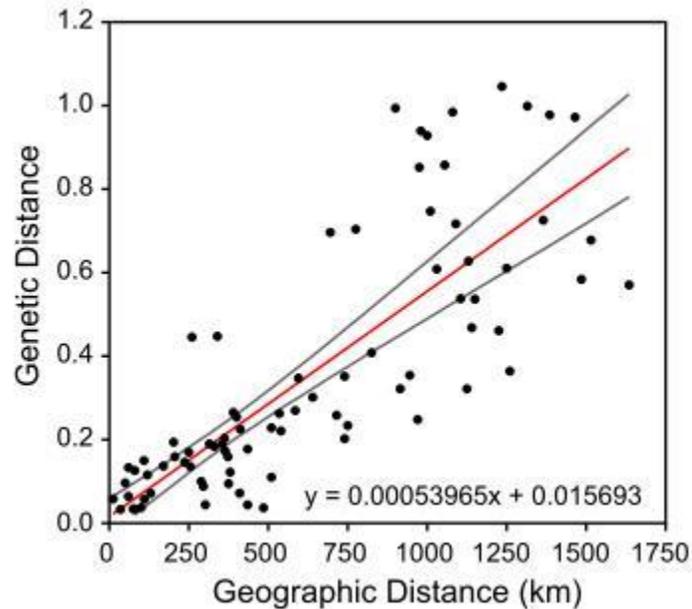

Figure 6.3. Isolation by distance meta-analysis from a literature review showing a positive relationship between genetic distance and geographic distance between populations.

This hypothesis was explored using the same microsatellites in a study of alligator populations from both coastal and inland localities in Texas (Ryberg et al. 2002). These populations demonstrated varying scales of geographic and ecological separation along the Texas Gulf Coast and among several river drainages. The coastal alligator populations occupied expansive swamps and marshes and maintained large population sizes, while the inland alligator populations occupied smaller, fragmented, aquatic ecosystems and maintained smaller population sizes. Similar to the previous study, observed mean heterozygosity across all loci for both coastal and inland populations ranged from 0.50–0.61. Additionally, both inland and coastal populations revealed similar levels of genetic variation, thus refuting the hypothesis of ecological distinction. Measures of genetic distance revealed significant genetic differentiation among populations with geographic distance, even at very small scales (~15 km; Figure 6.3). The fine-scale genetic distinctiveness of populations observed in this study, regardless of habitat type, suggested that alligators can exhibit localized demography, life history, and population dynamics with clear implications for management. Rather than managing alligators in Texas as a single panmictic population, translocation programs and harvest quotas should consider the ecological and genetic distinctiveness of local alligator populations.

The development of two additional microsatellites with tetranucleotide repeats (i.e., 4 base pair) motivated the most comprehensive study, both in geographic scope and molecular information, of alligator genetic variation to date (Davis et al. 2002). The new microsatellites were paired with the original set to characterize genetic variation among 12 populations of alligators distributed throughout the species range and separated by geographic

distances ranging from 35 to 1,635 km (Davis et al. 2002). Observed levels of genetic variation were similar to those of previous studies; however, for the first time a pattern of large-scale genetic structure emerged providing a genetic framework for the establishment of conservation units. Four genetic groups were identified: 1) a peninsular Florida and south Georgia group, 2) a north Atlantic coast group extending through South Carolina, 3) an intermediate group in Alabama, and 4) a western group including alligator populations from Texas and Louisiana. Additional analyses of genetic distances and allele frequency distributions indicated that variation among groups appeared to be gradual following an isolation by distance model with Alabama alligators grouping closer to Texas and Louisiana populations (Figure 6.3). This phylogeographic pattern of genetic structure (i.e., using genetic relationships among populations to deduce historic patterns of movement and gene flow) suggested an east-west split in alligator populations centered around the Apalachicola River, which forms a partial boundary between Alabama and Georgia. A similar east-west split forming two large-scale phylogeographic regions following an isolation by distance model has been described for freshwater fish and aquatic and terrestrial turtles distributed throughout the same geographic region (Swift et al. 1986, Walker et al. 1997, Walker and Avise 1998, Soltis et al. 2006).

Development and screening of additional microsatellite markers to allow for even more fine-scale resolution of population genetic structure in alligators essentially stalled following the Davis et al. (2002) study (but see Subalusky et al. 2012). This is most likely due to the belief that patterns of genetic variation among alligator populations cannot be resolved further with this molecular marker even with greater sampling in geographically intermediate areas (Davis et al. 2000, Ryberg et al. 2002, Davis et al. 2002). While this may be true, microsatellite markers still maintain value, because their data come in the form of individual genotypes allowing estimates of the effective population size, breeding structure and other relevant measures of local populations that can assist in determining harvest quotas and addressing other management issues (Glenn et al. 1996, 1998; Davis et al. 2000). Many of these applied genetics questions remain unanswered for alligator populations. Indeed, it is surprising that far less is known about the detailed reproductive and social dynamics of locally managed alligator populations compared to other game species (e.g., deer, quail) with similar molecular tools available (but see Davis et al. 2001). Perhaps the recent completion of the alligator genome (St. John et al. 2012, Putnam et al. 2016) and advances in genomic analyses (Wayne and Morin 2004, Avise 2010, Funk et al. 2012) will stimulate the next round of population genetics research on alligators. In addition to answering questions regarding the reproductive and social dynamics of alligators, genomic approaches may increase the power to detect variable gene flow among adjacent populations, or even inform more fundamental conservation and management questions concerning the relationship between genetic diversity and the adaptive or evolutionary potential of threatened and endangered species' populations.

THE ROLE OF CLIMATE CHANGE

The last half-century of genetics research on alligators consistently revealed two major phylogeographic patterns that help characterize the recent evolutionary history of the species. First, alligators went through a pre-historic, but evolutionarily significant, population bottleneck during or following the late Pleistocene, which stripped nearly all genetic variation

from the species on a range-wide scale. Second, after an apparent range expansion, current alligator populations are continuously distributed range-wide following an isolation by distance model of population structure, although there is some support for an east-west split around the Apalachicola River. Changes in climate have been proposed to explain each of these phylogeographic patterns.

Evidence of climate change effects on the first pattern are provided in the fossil record, which indicates that alligator populations extended into more northern regions prior to the Last Glacial Maximum (LGM; 25 - 21 kya; Sues 1989), but then were restricted to more maritime localities as glaciation ensued (Markwick 1994). Indeed, evidence of shifting species distributions in response to climate change is far more common in the Pleistocene fossil record than evidence supporting the major evolution of stationary species through adaptation (Parmesan 2006). This trend suggests that evolutionary changes in species' absolute climate tolerances are rare and probably insufficient to prevent extinctions when shifts in species' distributions are not possible (Parmesan 2006).

The second pattern is consistent with a gradual range expansion due to warming trends following the last glaciation. Many other species from this region experienced extreme bottlenecks during Pleistocene glaciation and then congruent patterns of recolonization during subsequent climate warming (Swift et al. 1986, Walker et al. 1997, Walker and Avise 1998). Indeed, the Apalachicola River is considered a primary geographic marker that coincides with phylogeographic breaks for several aquatic (e.g., Atlantic sturgeon; Wirgin et al. 2002) and terrestrial (e.g., pocket gopher, Avise et al. 1979; white-tailed deer (*Odocoileus virginianus*) Ellsworth et al. 1994) species, reflecting similar east-west genetic structure. For some of these species, the phylogeographic structure was supported by large genetic differences worthy of subspecific or putative species designations that originated in populations emerging from glacial refugia on either side of the Apalachicola River and coming into secondary contact (Soltis et al. 2006). However, for other species like the alligator, genetic distinctions were more subtle, as samples from one or more western localities possessed genetic attributes of eastern localities and vice-versa (Davis et al. 2002).

Several climate-driven phylogeographic scenarios have been proposed for this region that could account for the weak genetic structure observed in alligators. They all propose that genetic structure observed in species of this region resulted from fluctuating sea levels throughout the Pleistocene that repeatedly fragmented populations at alluvial valleys along the Gulf Coast (Scott and Upchurch 1982, Riggs 1983, Hayes and Harrison 1992, Ellsworth et al. 1994). During the LGM, sea level was 35 to 45 m lower and the shoreline was, on average, more than 80 km further into the Gulf of Mexico than present day. Under these conditions, glacial outwash flowed from retreating ice sheets through most coastal rivers cutting deep valleys into coastal plain sediments. Thus, there were many alternative drainages capable of isolating populations of species along the Gulf Coast. For example, sunfish (*Lepomis gulosus*; Bermingham and Avise 1986) and water snakes (*Nerodia rhombifera* and *N. taxispilota*; Lawson 1987) exhibit a phylogeographic split that corresponds with the Tombigbee River in Alabama, instead of the Apalachicola River. Freshwater turtles demonstrate support for several phylogeographic breaks along the Gulf Coast due to the physical isolation of drainages (Walker and Avise 1998). Finally, eastern, central, and western forms of the rat snake (*Elaphe obsoleta*; Burbrink et al. 2000) are separated by the Apalachicola River and Appalachian Mountains and then again by the Mississippi River (respectively) showing support for phylogeographic breaks including different types of isolating features. This phylogeographic pattern suggests glacial

refugia persisted in peninsular Florida, south Texas or Mexico, and a locality west of the Apalachicola River (see also the eastern fence lizard (*Sceloporus undulatus*; Leache and Reeder 2002). These examples illustrate that many different and overlapping phylogeographic patterns are possible depending on the location and number of refugia and the timing or frequency of separation caused by fluctuating sea levels throughout the Pleistocene.

In the case of the alligator, one of these climate-driven variations on the general east–west phylogeographic theme might explain the weaker genetic structure observed around the Apalachicola River. Here, we make an effort to distinguish among these variants with species distribution modeling, which uses statistical methods to correlate species occurrences with environmental predictor variables in an attempt to quantify the environmental niche, the environmental requirements a species needs to survive and reproduce (Pearson and Dawson 2003, Kozak et al. 2008). The model of a species' environmental niche can be projected across a landscape in the past, present, or future (Pearson and Dawson 2003, Elith et al. 2010). Although the environmental niche may evolve in some cases (Knouft et al. 2006, Evans et al. 2008, Warren et al. 2008, Lawing et al. 2016), it is reasonable to assume niche conservatism over shorter time scales (Wiens and Graham 2005, Peterson 2011). Specifically, by projecting a model of the alligator's environmental niche into the Pleistocene (i.e., hindcasting), we hope to better understand how climate change shaped the distribution and abundance of this species in the past and help explain the observed current patterns of genetic variation. We then reverse perspectives and project the alligator's environmental niche through the immediate Anthropocene (i.e., forecasting) to estimate the extent and direction of climate-change effects on the alligator's future distribution.

Most hypotheses for the shifting distribution of species in the southeastern United States predict poleward expansion with a warming climate, but the disappearance of well-known habitats and emergence of non-analogous ones also is possible where established environmental gradients might be shifting with climate change (Debinski and Cross 2009). To date, there are very few studies exploring the effects of future climate change scenarios on alligators, and the ones that do exist are specific to the Florida Everglades (Pearlstine et al. 2010, Catano et al. 2015). Alligators in the Everglades are at the southern end of their climate tolerance and display higher metabolic costs than alligators in other areas, leading to slower growth and maturation rates (Mazzotti and Brandt 1997). Forecasts for climate change in this region predict warmer temperatures overall and earlier in the season and more intense precipitation events separated by longer, more extreme droughts that decrease the availability of freshwater wetlands (Craft et al. 2009, Li et al. 2011, Selman et al. 2013). Such temperature increases might decrease the alligator's overall physiological well-being and more importantly skew population sex ratios toward females (i.e., alligators have temperature-dependent sex determination; Ferguson and Joanen 1982, Rhen and Lang 1998). Changes in hydrology may affect a suite of alligator behaviors related to breeding, nesting, foraging, and dispersal (Fryxell et al. 2014, Urban et al. 2014) that, when combined with the potential effects of increased temperatures, might further exaggerate the low growth and reproductive rates of Everglades alligator populations (Pearlstine et al. 2010, Catano et al. 2015).

The results of these studies suggest that the alligator will be highly vulnerable to future changes in climate (Staudinger et al. 2013). Climate-change vulnerability is typically defined according to a species' exposure to climatic changes, its adaptive capacity, and its ability to cope with and adjust to those changes (IPCC 2007, Glick et al. 2011). Using this vulnerability framework, in this study we characterize the potential for alligators to respond to climate

change over the short-term (decadal time scale) and outline management options for long-term species resilience that maintain genetic diversity and the capacity for adaptive change.

METHODS

Response and Predictor Variables

To model the climatic drivers of occurrence for alligator species distribution, we collected occurrence data from two online databases, VertNet (n = 257) and iNaturalist (n = 1409). VertNet is an online database that combines data from the collections of museums across the country. VertNet records are a reference to physical specimens collected, documented, and deposited by researchers to museums, which are then persevered in perpetuity. iNaturalist is an application, online community and database that stores and preserves records of observations of species contributed by scientists and citizen scientists. iNaturalist species identifications are confirmed through photograph observations. Participants in iNaturalist upload photographs of specimens along with their geographic coordinates and species identification. At least two taxonomic curators must confirm the species identification from the photograph for the occurrence to be cataloged as research grade. We only incorporated research grade occurrence data into our dataset. These iNaturalist occurrences became abundant after 2008. The combined occurrence data from VertNet and iNaturalist make up the basis of our occurrence records that we used in developing our species distribution models.

Variable selection is subjective, but it is important to evaluate the correlation structure between predictor variables to avoid misinterpretation of a species distribution model. We evaluated the correlation structure of 19 bioclim variables from the Worldclim database (Hijmans et al. 2005). Bioclim variables are derived variables from daily climate records and are considered biologically meaningful descriptors of climate (Nix and Busby 1986). Bioclim variables describe the means and extremes of temperature and precipitation at monthly, quarterly, and annual scales (Table 6.1 or see Nix and Busby 1986 for variable definitions). To avoid correlated predictor variables, we used a principal components ordination to identify uncorrelated variables that contribute to the first few axes of greatest variation. We obtained values for the 19 bioclim variables by extracting values on a 2.5 arc minute resolution raster at each occurrence record from our occurrence dataset. We used the function 'prcomp' for the principal components ordination from the stats package in the R Statistical Programming Language (Mardia et al. 1979, Becker et al. 1988, Venables and Ripley 2002, R Core Team 2016). We identified four variables that are relatively uncorrelated and that contribute to the most variation between species occurrences, namely Mean Annual Temperature, Diurnal Range, Mean Temperature of the Driest Quarter and Annual Precipitation (see Results). We used these four variables as predictors in the species distribution model.

Table 6.1. Bioclimate variables describing the means and extremes of monthly temperature and precipitation at monthly, quarterly, and annual temporal scales. These variables were evaluated for inclusion in the species distribution model to identify which variables contain the most variation related to the occurrences of alligators. They were originally described by Nix and Busby (1986) to characterize potentially biologically meaningful descriptors of climate data.

	Variable	Description
1	Mean annual temperature	Mean of monthly mean temperature
2	Diurnal Range	Mean of monthly (maximum temperature - minimum temperature)
3	Isothermality	Mean diurnal range/ temperature annual range
4	Temperature seasonality	Standard deviation monthly mean temperature
5	Maximum temperature warmest month	Maximum of monthly temperature
6	Minimum temperature coldest month	Minimum of monthly temperature
7	Temperature annual range	Maximum temperature warmest month – minimum temperature coldest month
8	Mean temperature wettest quarter	Mean temperature of the wettest quarter of the year
9	Mean temperature driest quarter	Mean temperature of the driest quarter of the year
10	Mean temperature warmest quarter	Mean temperature of the warmest quarter of the year
11	Mean temperature coldest quarter	Mean temperature of the coldest quarter of the year
12	Annual precipitation	Sum monthly precipitation
13	Precipitation wettest month	Maximum monthly precipitation
14	Precipitation driest month	Minimum monthly precipitation
15	Precipitation seasonality	Coefficient of variation of monthly precipitation
16	Precipitation wettest quarter	Sum precipitation of wettest quarter
17	Precipitation driest quarter	Sum precipitation of driest quarter
18	Precipitation warmest quarter	Sum precipitation of warmest quarter
19	Precipitation coldest quarter	Sum precipitation of coldest quarter

Modeling the Probability of Occurrence

To model the probability of occurrence, we first down-sampled occurrence data to account for collection and environmental bias. We used the extracted predictor variables to plot occurrences in climate space. We gridded the four dimensional climate space into 5 degree C and 20 mm precipitation grid cells and randomly sampled one occurrence from within each cell resulting in 444 occurrence points. This method was shown to reduce bias and

improve predictions of species distribution models (Varela et al. 2014). In our study, the bias reduction method did not produce qualitatively different results from a model using no binning in climate space, but the binning model had a slightly better model performance, so we use the binned model in the following analyses.

We split our occurrence dataset into training and test data and we sampled pseudo-absence points from a defined background for model fitting and cross-validation. We split the occurrence data (presence data) into training and test datasets by randomly assigning 80% of the data to the training set and assigning the remaining 20% to the test set. We created pseudo absence data by randomly sampling 1000 points across the extent of all occurrences, which is the boundary of occurrences delimited by minimum and maximum occurrence longitude and latitude. We split the pseudo-absence data into training and test sets by randomly assigning 80% of the pseudo-absence data to the training set and assigning the remaining 20% to the test set.

We fit the presence and pseudo-absence training occurrence data to the predictor variables with a maximum entropy species distribution model, Maxent 3.3.3 (Phillips et al. 2006, Phillips and Dudik 2008). Maxent has been shown to consistently work well compared to profile and regression type models (Elith et al. 2006). We fit the Maxent model with the presence training data to four predictor variables, estimated the amount of variance explained by each predictor variable for the fitted Maxent model, and estimated the amount of explained variance lost by dropping out each predictor variable in a jackknife analysis. The jackknife analysis quantified the relative contribution of each variable based on the performance of the overall model without the variable of interest, and then compared it to a univariate model with only the variable of interest. Model performance was assessed using the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997, Liu et al. 2006). The AUC is a rank-based statistic and represents the probability that a randomly selected presence point will have a higher probability of occurrence than a randomly selected pseudo-absence point. If all of the points are randomly distributed, then the AUC is expected to be 0.5 and a perfectly fit model yields an AUC of 1. In species distribution modeling, AUC is considered a reasonable and informative model if it is above 0.75 (Elith 2002, Phillips and Dudík 2008). We also evaluated the model with the correlation coefficient for the cross-validation (r) and true skill statistic (TSS). The correlation coefficient is Pearson correlation between the probability of occurrence of the training and testing datasets and ranges between -1 and 1. TSS is the maximum value of the true positive rate, sensitivity, plus the true negative rate, specificity (max TPR + TNR). TSS normalizes the accuracy by the accuracy that could have randomly occurred through chance and is robust to changes in prevalence (Allouche et al. 2006).

Projection of Species Distribution Model (SDM) on Past and Future Climate Scenarios

We projected the species distribution model onto past and future climate models. We chose two general circulation models from the CMIP5 models (Taylor et al. 2012) that have both hindcasts and forecasts of the climate: CCSM4, Community Climate System Model (Gent et al. 2011), and MIROC-ESM, Model for Interdisciplinary Research on Climate - Earth System Model (Watanabe et al. 2011).

We chose to project the SDM onto past climate models representing the mid-Holocene, the last glacial maximum, and the last interglacial. The mid-Holocene is a climate period of particularly profound changes in our climate system and lasted from 7,000 to 5,000 years ago (reviewed in Steig 1999). During the mid-Holocene, the summers were warmer and the winters were colder than in our modern climate, except in monsoon regions, where the summers were also colder than today (Bartlein et al. 2011). The last glacial maximum was the most recent period in Earth's history when the ice sheets were at their maximum extent and occurred before 20,000 years ago (Clark et al. 2009). The mid-Holocene and last glacial maximum time periods have been modeled with CCSM4 and MIROC-ESM general circulation models. The last interglacial has not been modeled by CCSM4 or MIROC-ESM to our knowledge, so we used a third general circulation model for another warm period comparison (Otto-Bliesner et al. 2006). The last interglacial is the interglacial period just before the last glacial maximum, it was warmer than modern climate, probably had more seasonal temperatures, and lasted between about 140,000 and 120,000 years ago (Dahl-Jensen et al. 2013). We chose to project species distribution models onto future climate scenarios derived from two representative concentration pathways (RCP +2.6 and +8.5 W/m^2) for two time periods (2050 and 2070). RCP +2.6 W/m^2 assumes that global greenhouse gas emissions peak between 2010 and 2020 and then substantially decline thereafter (Meinshausen et al. 2011). RCP +8.5 W/m^2 assumes that greenhouse gas emissions continue to increase through the 21st century (Meinshausen et al. 2011). Climate change scenarios were averaged for two 20-year periods: 2041–2060 (2050s) and 2061–2080 (2070s). For all climatic projections, the same set of four climate variables were bias-corrected and downscaled to 2.5 arc minutes resolution.

Simple Fragmentation Statistics

Past research on climate change in other species highlights the importance of habitat patch size, number, and location in determining persistence (e.g., Tejo et al. 2017). As such, in addition to exploring uncertainties regarding the extent of past and future climate change effects on the distribution of alligator habitat, we quantify the size and number of highly suitable habitat patches and identify locations of habitat patches most at risk of potential ecological changes under past and future climate scenarios.

We used the functions ConnCompLabel (Chang et al. 2004) and PatchStat (McGarigal et al. 2002) from SDMTools (VanDerWal et al. 2014) in the R Statistical Programing Language (R Core Team 2016) to identify patches and calculate simple fragmentation statistics at three threshold values (0.3, 0.4, and 0.5) of the probability of occurrence. These values are interpreted as somewhat suitable, suitable, and core habitat, respectively. For each projection, we divided the number of contiguous pixels into patches, counted the resulting patches, and calculated the average area of the patches. For the time periods with more than one projection, we calculated the mean and standard error for patch number and size across models.

RESULTS

Selection of Predictor Variables

The principal components ordination of the 19 bioclim variables showed that the first four axes representing independent orthogonal variation in the climate dataset accounted for more than 90% of the variation in the data (Table 2), and also had a standard deviation greater than one. The first axis, principal component 1 (PC1), explained 51% of the variation in the climate dataset. Many of the variables had both strongly positive and strongly negative influences on this axis of variation. PC1 had particularly high positive loadings from Mean Annual Temperature (0.30), Isothermality (0.25), Minimum Temperature of the Coldest Month (0.31), Mean Temperature of the Coldest Quarter (0.31), Precipitation of the Wettest Quarter (0.26), and Precipitation Seasonality (0.30). PC1 also had particularly high negative loadings from Temperature Seasonality (-0.31), Temperature Annual Range (-0.30), Precipitation of the Driest Month (-0.22), and Precipitation of the Driest Quarter (-0.23). We chose to use Mean Annual Temperature as a representative of this axis of independent variation, because it is commonly used in ecological studies. The next three principal components axes (PC2, PC3 and PC4) all had one bioclim variable that was the most important influence on its axis. The loading of Annual Precipitation on PC2 was 0.44, the loading of Diurnal Range on PC3 was 0.60, and the loading of Mean Temperature of the Driest Quarter on PC4 was 0.78. Therefore, we used Mean Annual Temperature, Annual Precipitation, Diurnal Range, and Mean Temperature of the Driest Quarter in the remaining analyses.

Model Evaluation

The MaxEnt model adequately discriminated between the test presence and pseudo-absence data. After splitting the presence points into training and test sets, we had a training set of 329 points and a test set of 115 points. The AUC was particularly high at 0.91, the correlation coefficient between the predicted and the observed test sets was strong at 0.74, and the max TPR + TNR was 0.303. Mean Annual Temperature was the most important variable to the species distribution model, accounting for 74.7% of the variation in the model prediction and with a permutation importance of 85.7%, which calculated from the jackknife procedure (Table 6.3).

The model suggests that this species should find suitable habitats along the Texas, Louisiana, Mississippi, Alabama and Georgia coast and throughout most of Florida (Figure 6.2B). The model also indicates there is relatively suitable habitat inland from the coastal regions, but decreases in suitability with distance from the coastline (Figure 6.2B).

Table 6.2. Principal component axes standard deviation, proportion of variation, and cumulative proportion of variation. The principal component ordination of the 19 bioclim variables described in Table 1 shows that the first four axes of variation represent more than 90% of the variation in the occurrence dataset. The remaining orthogonal axes contribute little variation to the occurrence dataset.

	Standard Deviation	Proportion of Variation	Cumulative Proportion of Variation
PC1	3.12	0.51	0.51
PC2	2.14	0.24	0.75
PC3	1.34	0.10	0.85
PC4	1.09	0.06	0.91
PC5	0.93	0.05	0.96
PC6	0.62	0.02	0.98
PC7	0.47	0.01	0.99
PC8	0.31	0.00	0.99
PC9	0.23	0.00	1.00
PC10	0.17	0.00	1.00
PC11	0.16	0.00	1.00
PC12	0.12	0.00	1.00
PC13	0.10	0.00	1.00
PC14	0.07	0.00	1.00
PC15	0.06	0.00	1.00
PC16	0.03	0.00	1.00
PC17	0.02	0.00	1.00
PC18	0.01	0.00	1.00
PC19	0.00	0.00	1.00

Table 6.3. Percent variable contribution and permutation importance to the fitted Maxent model for the four bioclim variables included. The percent contribution is a measure of how much variation each variable actually contributed to the Maxent model and permutation importance is calculated by a jackknife procedure. The jackknife quantifies the relative contribution of each variable independently based on the performance of the overall model without the variable of interest. The procedure then compares the performance of that model to a univariate model with only the variable of interest. The results of this procedure can be interpreted as the amount of independent variation each variable contributes to model performance. Percent contribution and permutation importance are measures that allow for the comparison of the importance of each predictor variable to the overall fitting of the model.

	Percent Contribution	Permutation Importance
Mean Annual Temperature	74.7	85.7
Diurnal Range	12.4	6.7
Annual Precipitation	9.2	6.2
Mean Temperature Driest Quarter	3.7	1.4

Projections on Past and Future Climate Scenarios

The projections of the species distribution model onto the mid-Holocene general circulation models shows a similar distribution as the modern projection, but the habitat suitability has a much greater decrease in suitability with distance away from the coastline (Figures 6.4A and B). The projection of the species distribution model onto the last glacial maximum general circulation model demonstrated a greatly reduced area of suitable habitat, which was mostly distributed around the continental shelf of Florida that was exposed with lower sea levels during that ice age (Figures 6.4C and D). The distribution occurred along the paleo coastline and suitability decreased with distance from the coastline. In both general circulation models, there also was a very small area of suitable habitat identified along the paleo coastline of Louisiana (Figures 6.4C and D). The projection of the species distribution model onto the last interglacial general circulation model exhibited a distribution similar to the other warm periods, with a potential fragmentation in the distribution just south of the Florida panhandle (Figure 6.4E).

The projections of the species distribution models onto future climate scenarios show that, in general, the suitable habitat is expanding north and increasing in overall area (Figure 6.5). However, the northward expansion is accompanied by a southward retraction. The lowest representative concentration pathway scenario shows that suitable habitat will slightly expand northward accompanied with a slight southward retraction (i.e., the southern tip of Florida and the southern coastline in Texas; Figures 6.5A, B, E, and F). The highest representative concentration pathway scenarios show that suitable habitat will expand northward with an even greater and more complex southward retraction (Figures 6.5C, D, G, and H).

Fragmentation Statistics

Our models indicate that there was generally more fragmentation and larger areas of suitable habitat in the past and this pattern is likely to hold in the future (Figure 6.6). However, the magnitude of fragmentation is greater in future projections (about 6X), than in past projections (about 3X).

DISCUSSION

Both major phylogeographic patterns of genetic variation in alligator populations were consistent with predicted historical shifts in the distribution of habitat due to changing climate, especially temperature. The hypothesized Pleistocene population bottleneck, apparent in multiple genetic studies (Gartside et al. 1977; Menzies et al. 1979; Adams et al. 1980; Glenn et al. 1996, 1998, 2002) and supported by the fossil record (Sues 1989, Markwick 1994), coincided well with the predicted reduction and restriction of suitable alligator habitat to the continental shelf of Florida during the last ice age (Figures 6.4C and D). In particular, the lack of observed mtDNA variation range-wide (Glenn et al. 2002) suggested that the species was forced into a single Pleistocene refugium, which, according to model projections in this study, was most likely restricted to the paleo coastline of peninsular Florida, more than 80 km further into the Gulf of Mexico.
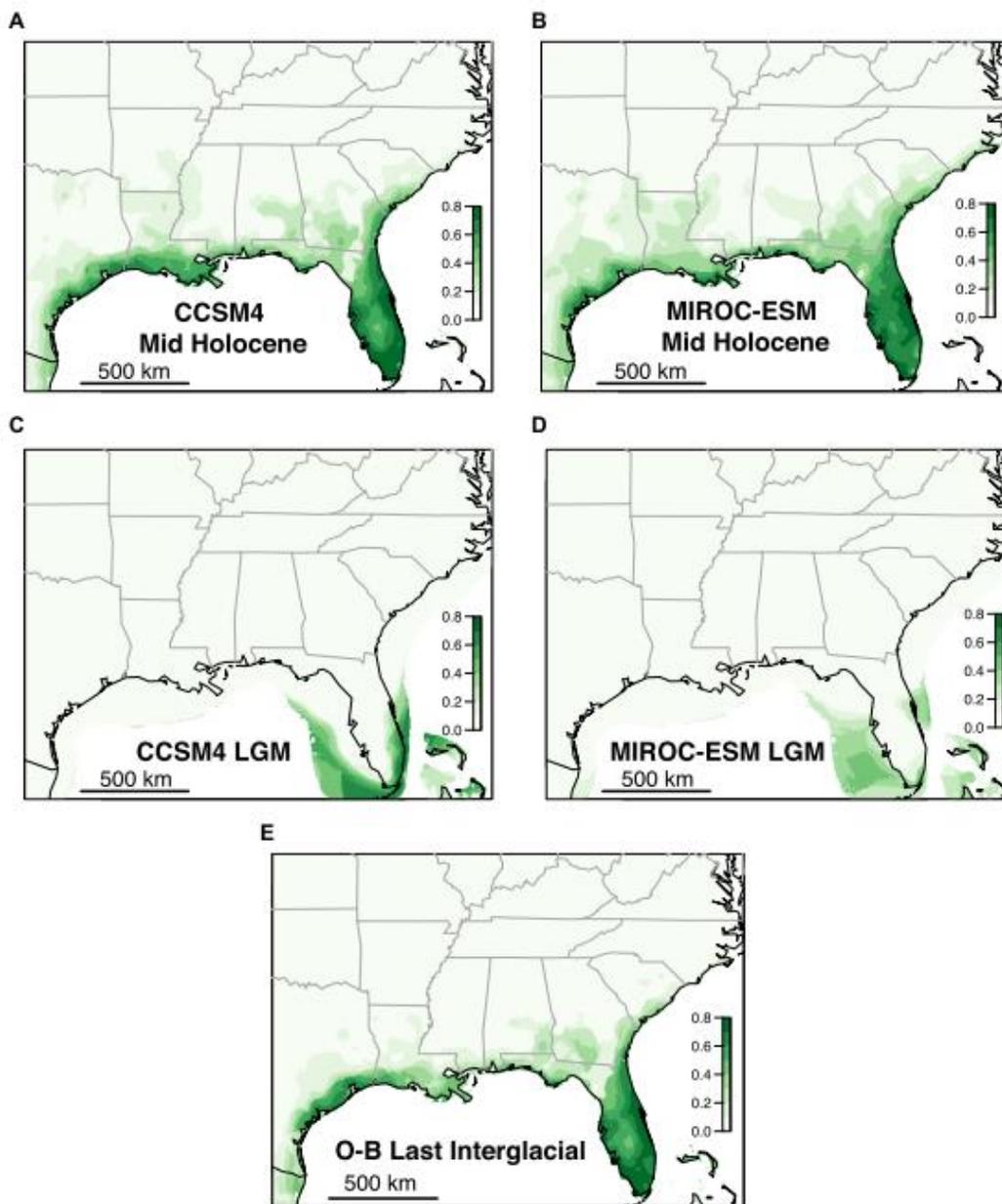
Figure 6.4. Maxent species distribution models projected (hindcast) onto general circulation models of the mid-Holocene (A,B), last glacial maximum (C,D), and last interglacial (E). Two of the three general circulation models shown here are from the CMIP5 models (Taylor et al. 2012): CCSM4, Community Climate System Model (A,C; Gent et al. 2011) and MIROC-ESM, Model for Interdisciplinary Research on Climate - Earth System Model (B,D; Watanabe et al. 2011). The third general circulation model represents a previous warm period comparison (E; Otto-Bliesner et al. 2006). The legend in each panel shows a gradation of light to dark green over a range of 0.0 to 0.8 and these colors, projected on the maps, represent the probability of occurrence of alligator populations for each given climate scenario.
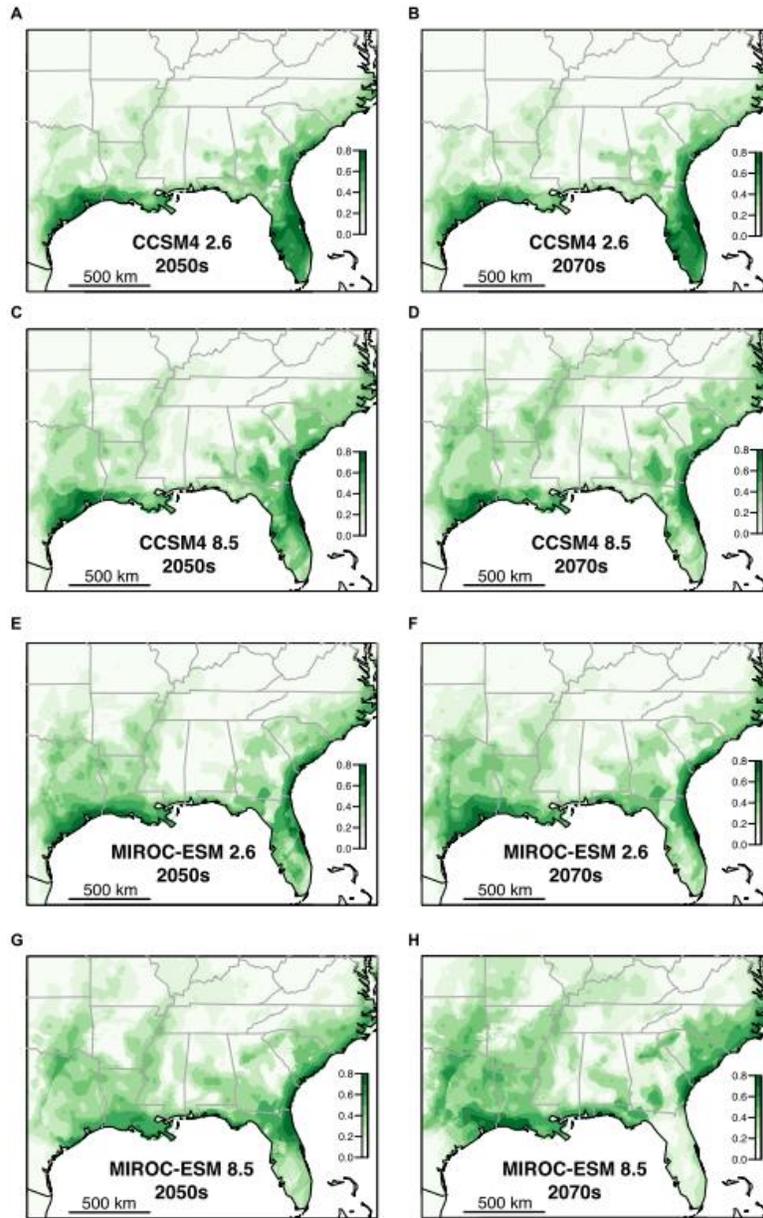
Figure 6.5. Maxent species distribution models projected (forecast) onto two general circulation models from the CMIP5 models (Taylor et al. 2012): CCSM4, Community Climate System Model (A-D; Gent et al. 2011) and MIROC-ESM, Model for Interdisciplinary Research on Climate - Earth System Model (E-H; Watanabe et al. 2011). Within each general circulation model, there are two future climate scenarios derived from two representative concentration pathways (RCP) for two time periods. RCP +2.6 W/m^2 is the more conservative scenario, where global greenhouse gas emissions are presently at their peak and will substantially decline in the future (A,B,E,F; Meinshausen et al. 2011). RCP +8.5 W/m^2 is the worst case scenario modeled, where greenhouse gas emissions continue to increase through the 21st century (C,D,G,H; Meinshausen et al. 2011). Two 20-year periods are represented, 2041–2060 (A,C,E,G; 2050s) and 2061–2080 (B,D,F,H; 2070s). The legend in each panel shows a gradation of light to dark green over a range of 0.0 to 0.8 and these colors, projected on the maps, represent the probability of occurrence of alligator populations for each given climate scenario.

Model projections of suitable habitat prior to and after glaciation (i.e., last interglacial and mid-Holocene, respectively) were comparable to the alligator's modern distribution with similar decreases in habitat suitability moving inland away from the coastline (Figures 6.2B, 6.4A, B, and E). One notable exception in this comparison was the fragmentation in the distribution just south of the Florida panhandle seen both prior to and after glaciation (Figures 6.4A and E, but not 6.4B), but not in the modern distribution (Figure 6.2B). This potential break in suitable habitat coincided with the observed, albeit weak, east-west genetic split in alligator populations around the Apalachicola River. While the ultimate drivers and frequency of this potential break in suitable habitat are not known, microsatellite data suggest it is possible that a cyclical, or at least recurring, climate-driven fragmentation event at this location could account for the weak differentiation observed in alligator populations (Davis et al. 2002). Unfortunately, this correspondence between the predicted historical fragmentation of suitable habitat and weak east–west genetic structure does not eliminate other phylogeographic hypotheses linking the genetic isolation of populations to repeated glacial outwash within drainages along the Gulf Coast under fluctuating sea levels (Scott and Upchurch 1982, Riggs 1983, Hayes and Harrison 1992, Ellsworth et al. 1994). Indeed, many different and overlapping phylogeographic scenarios are still conceivable for the weak east–west genetic structure observed, depending on the location, timing, and frequency of separation caused by fluctuating sea levels throughout the Pleistocene.

Alternatively, the weak east–west genetic structure observed could have been eroded by increasing gene flow among regions since the mid-Holocene (Figures 6.2B, 6.4A). Dispersal appears to be restricted in space by the limits of individual lifetime movements such that an isolation by distance model best explains the observed genetic differentiation among populations (Figure 6.3). The apparent expansion of suitable habitat from the mid-Holocene to modern day could have ensured the continuous distribution of alligator populations range-wide, thus eroding any genetic structure reflecting past divergences. There is also a possibility that the east–west genetic structure observed has been diluted by the history of human-assisted migration during species conservation efforts in the 1960s - 1980s (Ross and Roberts 1979, Davis et al. 2002). For example, thousands of alligators from Louisiana were released in Mississippi and Arkansas resulting in substantial increases in recruitment for those populations in the years that followed translocation. Thus, it is possible that a stronger separation between eastern and western populations of alligators has been masked by human translocation of animals across regions. This genetic homogenization among distant populations can be seen in the pattern of isolation by distance described using microsatellite data (Davis et al. 2000, Ryberg et al. 2002, Davis et al. 2002), which is strong at small spatial scales and then erodes at larger spatial scales (Figure 6.3). This increased variance most likely reflects the poorly documented translocation of individuals between geographically distant populations.

Under future climate scenarios, forecasted projections of the species distribution models suggested that suitable habitat will expand north, increasing the number and area of habitat patches, but also retract from the southern tips of both Florida and Texas (Figures 6.5 and 6.6). Suitable habitat was still predicted to occur along the Louisiana, Mississippi, Alabama, Georgia, and South Carolina coasts, as well as the northern coasts of Texas and Florida. However, it also was predicted to occur along the coasts of North Carolina, Virginia, Maryland, and Delaware, through the southern states of Oklahoma, Arkansas, Tennessee, and Kentucky, and into the interior of midwestern states like Kansas, Missouri, Illinois, Indiana, and Ohio (Figure 6.5). Thus, this forecast illustrated that, in the near future, regions without alligators for

thousands of years could potentially have them back, and also that regions with alligators for millions of years, such as southern Florida, might be without them.
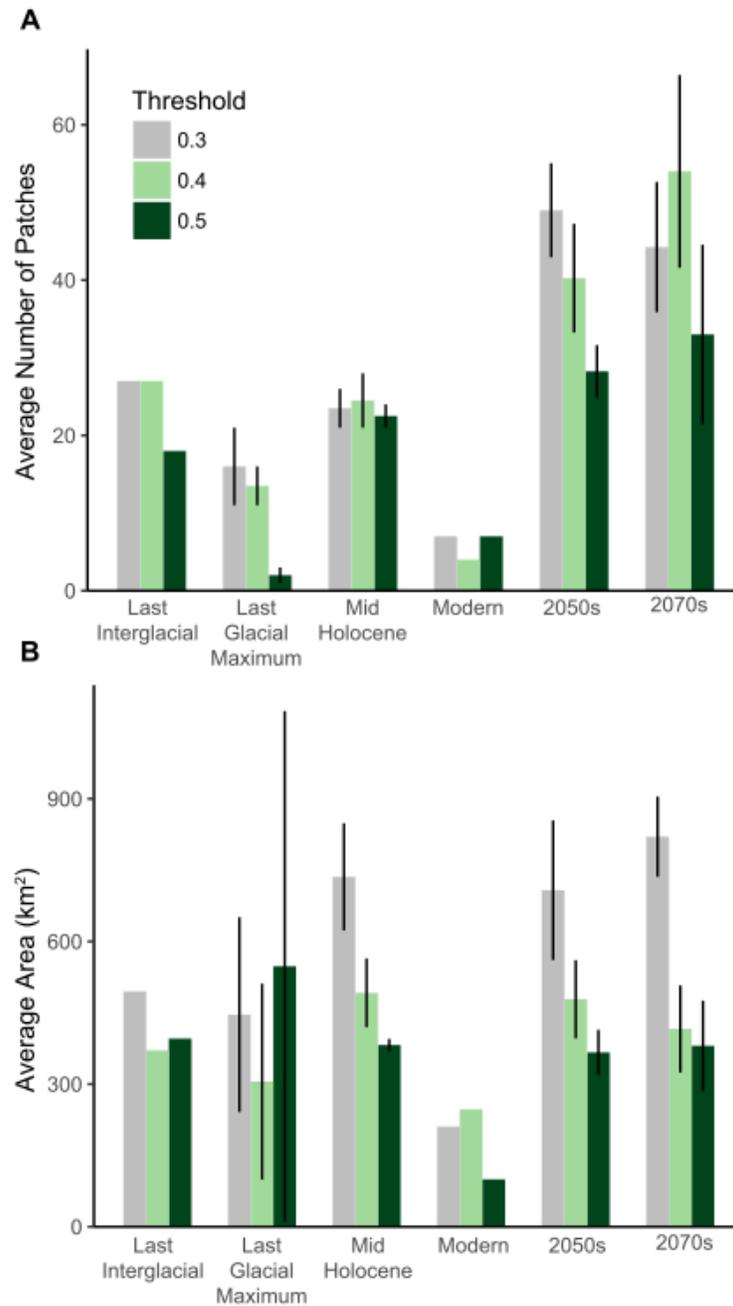

Figure 6.6. Simple fragmentation statistics for hindcast, modern and forecast species distribution models showing average number of patches (A) and average area (B) of modeled suitable habitat. Error bars show the standard error of the statistic, if more than one model was generated for time period. Threshold values for the probability of occurrence were set to 0.3, 0.4, and 0.5 for both analyses.

Past research has been important in highlighting the impact of patch size and climate change velocity, as well as the role of dispersal in determining species persistence or vulnerability to future climate change scenarios (Tejo et al. 2017). Indeed, evidence from the Pleistocene fossil record (Sues 1989, Markwick 1994), studies of genetic variation (Davis et al. 2002, Glenn et al. 2002, Ryberg et al. 2002), and now this study, all support the theory that alligators were fully capable of tracking changes in their distribution in response to past climate change rather than evolving absolute climate tolerances to persist (Parmesan 2006). Nevertheless, while alligators have shown a remarkable capacity to adjust to long-term climate changes, the potential for alligators to respond to climate change over much shorter timescales (i.e., decades vs. millennia), as depicted here, is unknown. Alligator traits seemingly favored by climate change, such as high phenotypic plasticity and dispersal capacity and being habitat and dietary generalists (Lurgi et al. 2012), could be proven ineffective if dispersal limitation and/or barriers created by human activities dominate future landscapes (Tejo et al. 2017). If the distributional response of alligators to climate change is constrained by natural ecotone boundaries, existing protected and management areas, or simply anthropogenic habitat loss and fragmentation, then the rate of climate change may actually outpace the alligator's capacity to adjust in those areas, leading to rapid localized changes in the size and distribution of alligator populations. Thus, there is not a single climate change but many (Tejo et al. 2017), and they depend on the interactions between changes in climate, variation in a species' life history and perceptual range, and regional landscape connectivity.

The most striking example of this phenomenon is the Florida Everglades, where many species are tightly tied to the hydrologic cycle, and are therefore vulnerable to changes in climate that affect availability of water. Several different future climate scenarios in this and other studies (Pearlstine et al. 2010, Catano et al. 2015) predict a large reduction in the total area of suitable alligator habitat for southern Florida due to warming temperatures and more intense precipitation events separated by longer, more extreme droughts (Li et al. 2011, Selman et al. 2013). Additional losses of tidal fresh water marshes were predicted as sea level rises, saltwater intrudes, and brackish marshes migrate inland (Craft et al. 2009). However, in areas with high canal density, water depth, and temperatures were predicted to remain within a tolerable range for alligators offering a potential refuge from drier, warmer conditions in more natural environments (Catano et al. 2015). This kind of spatial complexity in potential species' responses to climate change creates uncertainty in model predictions and also conservation and management responses.

In the Everglades, scenario planning has been used to develop adaptive conservation and management strategies for species resilience that can incorporate significant uncertainties about the extent, distribution, and direction of climate-change effects for most natural communities (Pearlstine et al. 2010). In general, landscape conservation perspectives that focus on corridors and habitat linkages, rather than fixed boundary-protected areas, have been developed to preserve the adaptive potential of populations in this ecosystem. More specifically, a number of active management strategies with the goal of maintaining genetic diversity of focal species in this ecosystem also were considered within this framework of scenario development and modeling with uncertainty (e.g., Mawdsley et al. 2009, Running and Mills 2009, West et al. 2009). These strategies are examined for alligators below through the broader lens of range-wide climate change.

Management Implications

With the goal of maximizing alligator resilience to the effects of future climate change, restoration efforts should focus on improving the quality of projected habitat refugia, even if they are likely to be unsustainable in the face of long-term climate change. Maintaining habitats that might otherwise be displaced by climate change, especially in southern Florida, could increase the likelihood and duration of alligator persistence in a region that has been home to the species for millions of years (Hannah and Hansen 2005). A key component of restoring projected habitat refugia is the reduction of human barriers to dispersal that could reduce the alligator's ability to cope with climate change. Although locally driven, the culmination of these restoration goals could lead to a regional pathway for alligator movements between projected refugial stepping stones. Plans for such corridors are already being discussed for wildlife in southern Florida that would allow migration from southern habitats northward along the peninsula (e.g., Kautz et al. 2006).

If habitat restoration via removal of human barriers to dispersal is not possible, assisted migration and translocation are artificial ways of increasing landscape connectivity for wildlife populations responding to climate change (e.g., Hunter 2007, McLachlan et al. 2005). Although typically options of last resort for most species conservation scenarios, assisted migration and translocation strategies were already implemented to rescue alligator populations from localized extirpations after historical over-utilization (Thorbjarnarson et al. 1992). As such, these strategies should be viewed as effective forms of intervention and applied according to regionally-integrated, research and management plans for the species. For populations occupying extremely isolated habitats predicted to become more isolated in the future (e.g., southern Texas and Florida), assisted migration and translocation could lead to the swamping of unique genetic diversity. Such populations may be better conserved through assisted propagation via captive breeding, artificial fertilization, or even directed evolution, which preserves traits favorable for adapting to climate change by manipulating reproductive success in captive populations (Running and Mills 2009). These captive maintenance strategies are usually considered the final conservation option, because they remove species from the wild, are resource intensive (Kleiman et al. 1997), and only may be viable for a few populations (Mawdsley et al. 2009). However, for the alligator, captive breeding efforts in zoo populations and alligator farms are extremely efficient, large-scale operations that contributed to the quick recovery of wild populations following localized extirpations from past over-utilization (Thorbjarnarson et al. 1992). Thus, these strategies also should be viewed as effective forms of intervention and applied according to regionally-integrated, research and management plans for the species.

Of course, climate change imposes long-term, continuous change on systems, which makes conservation and management goals moving targets (Barnosky et al. 2017). Some of these targets will be missed resulting in permanent changes. Thus, an adaptive management strategy must include preparation for gradual changes as well as large abrupt changes. In the Everglades, for example, climate-change projections paired with human landscape fragmentation suggest that restoration efforts cannot return the system to its past condition. Indeed, the Department of Interior Task Force on Climate Change (DOI 2009) and the National Research Council (NRC 2008) concluded that historic conditions in this ecosystem should not be the only basis for decisions regarding future resource management, because historic climate regimes of the Everglades are predicted to disappear even if human interventions stabilize climate in other

regions (Ruhl 2008). In the face of such uncertainty, continued monitoring of alligator populations to support ecological modeling and decision making that promotes species' resilience is still the best practice (Pearlstine et al. 2010).

Climate Change Vulnerability and Research Needs

Our results suggest that the alligator will be highly vulnerable to future changes in climate in specific regions throughout its current distribution. In particular, alligator populations in both southern Texas and Florida are predicted to potentially experience all three sources of climate change vulnerability: exposure to climatic change, limits in adaptive capacity, and limits in ability to adjust to change (IPCC 2007, Glick et al. 2011). Suitable habitat in both regions is expected to retreat northward over the next 50 years, leaving behind increasingly patchy populations of one of the most genetically homogenous vertebrate species (Coulson and Hernandez 1983). In addition to high exposure and potentially limited adaptive capacity, alligator populations in both regions will be limited by human barriers to dispersal and natural ecotone structure, the latter being especially prevalent in south Texas where suitable alligator habitat is embedded within inhospitable scrub land. Alligator populations along the northern edge of the current distribution also are predicted to experience all three sources of climate change vulnerability, but in a compensatory manner. Suitable habitats are expected to expand northward as a patchy network, creating a series of small populations with even less genetic diversity due to independent founder events, and possibly limited opportunities to maintain that genetic diversity regionally due to restricted gene flow from human or natural barriers, or both.

The apparent vulnerability of alligator populations to climate change at the northern and southern extremes of the species range motivates numerous research topics that exploit the area and distributional shifts of alligator populations and their estuarine and freshwater wetland habitats. Future ecological and evolutionary research topics for those regions could include the: 1) characterization of shifts in phenology, reproductive biology, and sex-ratios, 2) delineation of future core alligator populations based on past locations from fossil record, 3) estimation of population diffusion rates through different human barriers to dispersal, 4) depiction of short- and long-term adaptive capacity (e.g., genomic diversity) of northern and southern populations or identified conservation units, 5) description of changes in habitat, trophic linkages, and species interactions, and 6) understanding the combined effects of sea level rise, climate change, and anthropogenic stressors on alligator resilience over short and long timescales. Addressing these research topics will require continued range-wide survey and monitoring efforts to provide data on alligator populations that can be analyzed using traditional genetic and advancing genomic approaches, expanding climate change models, and spatially explicit models of ecosystem function.

CONCLUSION

The results of this study suggest that alligators could continue to play an expanding role in the human narrative in the future, but only where humans choose to be responsible for the species' continued persistence. The past has shown we are capable of causing both the rapid

destruction and swift recovery of alligator populations range-wide. However, model predictions for the future indicate that, in certain regions where alligators have persisted for millions of years, such as southern Florida, populations may be difficult and potentially impossible to maintain. Ideally the potential loss of southern alligator populations will be compensated for by the predicted northern expansion of populations into regions that have been without alligators for thousands of years. Granted the success of such a scenario will undoubtedly rely on the kind of human interventions described above, as the capacity and ability of alligator populations to deliver such an expansion northward through modern landscapes is limited by habitat loss and fragmentation. Thus, while humans have been absent from the 30 million-year-old, climate-driven, alligator narrative until the last century, they will largely be responsible for writing the alligator's future narrative over the next century through management decisions promoting species resilience, maintenance of genetic diversity, and the capacity for adaptive change.

ACKNOWLEDGMENTS

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