



Using predictions from multiple anthropogenic threats to estimate future population persistence of an imperiled species

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ABSTRACT

Imperiled species face numerous and diverse anthropogenic threats to their persistence, and wildlife managers charged with making conservation decisions benefit from a sound understanding of how populations, species, and ecosystems will respond to future changes in threats to biodiversity. In southeastern North America, the gopher tortoise (*Gopherus polyphemus*) is a keystone species in upland ecosystems; however, tortoise populations have declined strongly over the last century, and the species is a candidate for increased protection by the United States federal government under the Endangered Species Act (ESA). Here, we sought to support conservation decision making for *G. polyphemus* by developing a spatially-explicit predictive population model that linked four anthropogenic threats (climate warming, sea-level rise, urbanization, habitat degradation) to demographic vital rates and used the model to estimate future changes in the number of individuals, populations, and metapopulations across the species' range. Using recent survey data, we projected 457 populations for 80 years into the future under scenarios varying in threat magnitude, management magnitude, and demographic uncertainty. Population projections predicted that the number of individuals, populations, and metapopulations would decline among all simulated scenarios in the next 80 years. Model predictions were more sensitive to variation in adult survival and immigration rates than to variation in threat magnitude. A scenario with decreased habitat management and threat effects from climate warming, sea-level rise, and urbanization predicted geographic variation in persistence probabilities for populations that might result in decreased genetic representation across the species' range. Our results can be used to support conservation listing decisions for the gopher tortoise as part of its federal Species Status Assessment and provide an analytical framework for how to link

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diverse threats to geographically-varying demographic rates during population viability analyses for wide-ranging imperiled species around the world.

1. Introduction

Global biodiversity is currently experiencing a sixth mass-extinction event driven by anthropogenic activities (Ceballos et al., 2020), and a fundamental goal of conservation biology is to sustainably conserve biodiversity and ecosystem function in the face of a changing global environment (Meine et al., 2006). This goal is a challenge because endangered species and ecosystems face a myriad of diverse and interactive threats, including habitat loss, climate change, sea-level rise, emerging infectious disease, invasive species, and human take, among others (Côté et al., 2016; Lacy et al., 2017). To manage and conserve endangered species, for example, in the face of threats, managers and regulatory agencies benefit from having predictions for how populations or systems will respond to future conditions and a mechanistic understanding of how threats influence systems (Beissinger and McCullough, 2002). Predictions can estimate the risk of the species becoming extinct (i.e., extinction risk; e.g., Wiegand et al., 1998); if estimated extinction risk is deemed unacceptably high, resources can then be allocated for management (Lyons, 2020). In turn, a mechanistic understanding of threats can identify which ones have the greatest effect on system dynamics and guide management actions to reduce or manipulate the most influential threats (Lunney et al., 2007). However, mechanistic predictive models inferring how human-made threats influence wildlife can be difficult to build, because hypothesized threats can be numerous (Lacy et al., 2017), threat effects may be unknown or characterized with great uncertainty (Runge et al., 2011), and system dynamics may be unstable (Tucker and Runge, 2021). However, predictive modeling tools that account for uncertainty (Zylstra and Zipkin, 2021) are a useful and often essential component of most decision making processes (Runge et al., 2020).

In efforts to prevent extinctions and halt biodiversity declines, countries worldwide have passed laws that provide legal impetus for and create practical structure to support the conservation of imperiled species. In the United States of America (United States), the Endangered Species Act (ESA) is a federal law passed in 1973 (as amended; 16 U.S.C. 1531–1543) that seeks to first protect species from extinction and then recover the populations of imperiled species listed under the ESA to the point where federal protection is no longer needed. However, a common problem is that agencies must make difficult decisions about which species to protect, given limited budgets (Shogren et al., 1999), which requires identifying species with elevated extinction risk in the face of multiple threats that may not be easy to understand.

To support challenging listing decisions under the ESA in the United States, agencies have recently adopted a consistent and transparent approach to inform conservation listing decisions, the Species Status Assessment (Smith et al., 2018). The Species Status Assessment (SSA) process is a standardized, three-step framework that first compiles comprehensive life-history and ecological information available for the species, next evaluates the current conditions of the species and how anthropogenic threats have contributed to population declines, and last predicts how the species will respond to plausible future scenarios, including threats and management alternatives, while accounting for uncertainty (McGowan et al., 2020; Smith et al., 2018). When estimating the current and future predicted conditions of a species, the SSA framework aims to provide a descriptive scientific document to support listing decisions that accounts for the conservation biology principles of population resiliency (the ability of a species to persist in the face of environmental stochasticity), redundancy (the ability of a species to withstand catastrophic events, by spreading risk among multiple populations), and representation (the ability of a species to adapt to a changing environment, as measured by the breadth of genetic and environmental variation among populations; Smith et al., 2018). However, making accurate predictions for how a species' population resiliency, redundancy, and representation might change in the future can be difficult, because numerous, diverse threats may influence populations, threats may vary in space and time, and life history knowledge for the focal species may be characterized by significant uncertainty (Lacy et al., 2017; Runge et al., 2011; Smith et al., 2018).

Here, we describe a spatially explicit predictive population modeling analysis built as part of the SSA for an imperiled species in southeastern North America, the gopher tortoise (*Gopherus polyphemus*). We reviewed the literature describing gopher tortoise life history and adapted a previously published population model for six gopher tortoise populations in Alabama (Folt et al., 2021) to estimate persistence probability of populations across the species' range while accounting for geographic variation in life history and threats. We expanded the model to link intrinsic factors (demographic vital rates) to four extrinsic anthropogenic factors that are hypothesized to threaten gopher tortoise population persistence (climate warming, sea-level rise, urbanization, and shifts in habitat management) across the species' range and estimated future threats using predictions from published models. We projected gopher tortoise population conditions into the future under multiple future scenarios that represent uncertainty in threat magnitude and presence and estimated (1) the sensitivity of populations to uncertainty in demographic rates and individual threats, and (2) how populations will respond to a future world with multiple, synergistic threats in ways useful for risk assessment during SSAs.

2. Materials and methods

2.1. Study species

The gopher tortoise is an ecologically significant, ecosystem engineering species that occupies sandy habitats in the Coastal Plain ecoregion of southeastern North America, with extant populations ranging from the Florida peninsula north to southern South Carolina and west to eastern Louisiana (Auffenberg and Franz, 1982). Gopher tortoises are frequently associated with the longleaf pine (*Pinus*

palustris) ecosystem (Nussear and Tuberville, 2014), where individuals construct long underground burrows that provide habitat for > 350 commensal species (Jackson and Miltrey, 1989; White and Tuberville, 2017). However, the species can also occupy open pine, sandhill, scrub, xeric hammock, dry prairie, coastal dune, and ruderal (i.e., disturbed) ecosystems. Because the diversity of commensal species in the longleaf pine ecosystem has been linked to the abundance of tortoise burrows, the gopher tortoise has been hypothesized as a keystone species (Mills et al., 1993) that may be important in regulating diversity in the longleaf pine ecosystem (Catano and Stout, 2015; Guyer and Bailey, 1993) – an ecosystem that contributes substantially to a globally significant biodiversity hotspot in south-eastern North America (Noss et al., 2015). However, gopher tortoises have declined precipitously throughout much of their range over the last century (Auffenberg and Franz, 1982), including on protected landscapes for conservation that are relatively buffered from anthropogenic threats (McCoy et al., 2006). Mechanisms driving tortoise population declines in the past, present, and future are numerous and include: habitat degradation and loss due to fire suppression (Landers and Speake, 1980), urbanization and sea-level rise (Mushinsky et al., 2006), road mortality (Smith et al., 2006; Steen et al., 2006), disease (Berish et al., 2010; Ozgul et al., 2009), and human take (Guyer et al., 2015).

Given concerns about population declines, the U.S. Fish and Wildlife Service (hereafter, USFWS) gave federal protection for gopher tortoises in 1987 by listing populations in Louisiana, Mississippi, and Alabama west of the Mobile and Tombigbee rivers as ‘Threatened’ under the ESA (US Fish and Service, 1987). Despite the ESA listing designation, concerns about declining population trends and perceived unviability of populations across the species entire range have continued in recent decades (e.g., McCoy et al., 2006), and in 2006 the USFWS was petitioned to list additional populations as ‘Threatened’ as well. Subsequent review found that conditions experienced by the species in the eastern portion of its range potentially warranted listing as well (US U.S. Fish and Wildlife Service, 2011), which led the USFWS to conduct an SSA during 2019–2021 to summarize the species’ biology, review threats to its persistence, evaluate the species’ current conditions, and make predictions about how the species will respond to future conditions. The USFWS will use information gathered during the SSA to make a listing decision, which will include whether to alter the spatial extent of where the species is protected under the ESA by 2022.

2.2. Analysis overview

We sought to predict population growth and extinction risk for the gopher tortoise in a population viability analysis (PVA) framework. We built a stage-based population model (i.e., Lefkovitch model; Lefkovitch, 1965) and used the model to project population size and structure forward in time with simulations. For the PVA, we conceptualized local population demography of tortoises in a two-stage, female-only model with two discrete life stages: juveniles and adults (Fig. 1); we assumed a pre-breeding census. During a given time-step, both stages had a probability of individuals surviving and remaining within the stage, juveniles had a probability of maturing to become adults, and adults had a probability of reproducing and potentially recruiting individuals into the juvenile stage. Individuals that did not survive during a time-step were assumed to have either died or permanently emigrated from the population. We also modeled recruitment into the adult stage by immigration (see below).

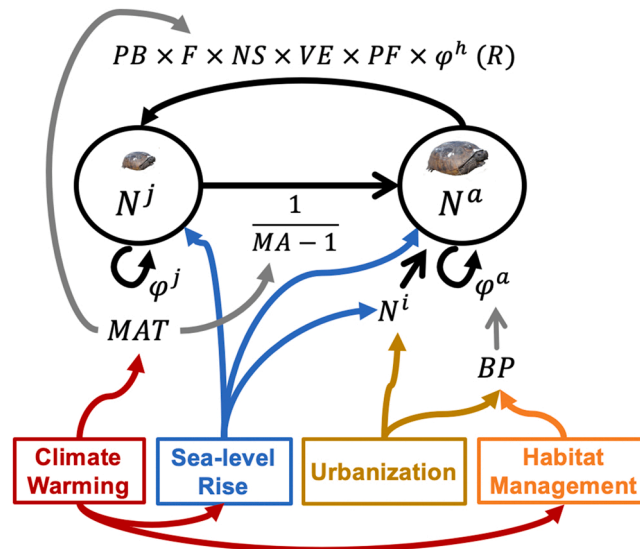


Fig. 1. A conceptual model illustrating a stage-based, female-only, pre-breeding census population model (black text) used to simulate demography and project abundance of gopher tortoise (*Gopherus polyphemus*) populations into the future. Black arrows and circles indicate gopher tortoise demographic parameters (survival, growth, abundance); colored arrows and text indicate predicted threat effects on tortoise demography simulated through scenario analysis. See Table 1 for demographic variable definitions and baseline estimates; MAT is mean annual temperature (°C) and BP is burn probability with prescribed fire (see Methods). For each threat (colored box), we modeled three or four scenarios of future change in threat magnitude (Table 2). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

We aimed to model how predicted future changes to abiotic and biotic features in southeastern North America may threaten future population persistence of gopher tortoises across the species' range. We met with scientists with expert knowledge in both gopher tortoise population biology and habitat management and identified a series of factors that experts considered to have high likelihood of influencing tortoise demographics in the future (hereafter, threats). Using the list of threats, we reviewed the literature to identify research describing quantitative effects of threats (or similar mechanisms) on specific demographic parameters in our stage-based population model for tortoises. Here, we describe hypotheses for how four threats (climate warming, sea-level rise, urbanization, and climate-change effects on habitat management) may influence tortoise demographic rates.

2.2.1. Climate warming

Climate change is predicted to drive warming temperatures and seasonal shifts in precipitation across southeastern North America (Dalton and Jones, 2010). Of these two effects, warming temperatures may have the greater impact on gopher tortoises, because tortoise demography is known to be sensitive to temperature gradients across the species' range. Specifically, maturity age and fecundity vary along a north-south latitudinal gradient, where warmer, southern populations have faster growth rates, younger maturity ages, and increased fecundity relative to cooler, northern populations (Ashton et al., 2007; Meshaka Jr. et al., 2019). As climate warming increases temperatures in the region, individuals in populations may experience more favorable conditions for growth and reproduction across the species' range. Because no studies have linked tortoise growth or fecundity to interannual or interpopulation variation in precipitation, it seems less likely that climate-driven shifts in precipitation will influence tortoise demography.

2.2.2. Habitat management

Through much of its range, gopher tortoises prefer upland habitat with open canopy, sparse midstory, and an understory plant community that provides diverse food sources (Aresco and Guyer, 1999a; Bauder et al., 2014; Birkhead et al., 2005; McCoy et al., 2013; Nussear and Tuberville, 2014). Prescribed fire is the most common management technique to maintain high-quality, open habitat for gopher tortoises (Ashton et al., 2008; Diemer, 1986; Landers and Speake, 1980; Yager et al., 2007); however, when fire is not present in sufficient intervals or intensity to maintain open habitat on the landscape, apparent survival of gopher tortoises decreases (Hunter and Rostal, 2021), potentially to levels that are insufficient for maintaining population viability (Folt et al., 2021). Wildlife managers tasked with maintaining high-quality upland habitat for gopher tortoises and other fire-dependent upland plant and animal species (Guyer and Bailey, 1993) may be challenged because regional climate warming may make habitat management with prescribed fire more difficult to accomplish. Managers require suitable fuel and weather conditions (e.g., relative humidity, temperature, wind speed; i.e., the 'burn window') to facilitate manageable fire behavior that will accomplish intended goals while limiting risk toward human communities. However, climate-change models predict the availability of burn window conditions to shift over future decades, with available conditions for fire management increasing in the winter but decreasing in the spring and summer (Kupfer et al., 2020); summed together, seasonal shifts in the burn window conditions will decrease overall opportunity for management with prescribed fire. If managers become limited in the use of prescribed fire, resulting decreases in habitat quality may drive decreases in gopher tortoise survival (Hunter and Rostal, 2021).

2.2.3. Urbanization

Human development of the landscape (i.e., urbanization) threatens terrestrial wildlife communities in the southeastern United States, including gopher tortoise populations that often rely on upland habitats that are popular sites for urban development or agriculture. While the local tortoise populations we were interested in modeling are largely on conservation lands intended for wildlife conservation, urbanization threatens to surround these conservation lands, disrupt habitat connectivity, and decrease metapopulation dynamics that maintain connectivity and gene flow both within and among metapopulations. Additionally, urbanization can disrupt habitat management by decreasing the ability of managers to use prescribed fire.

2.2.4. Sea-level rise

Warming temperatures across Earth are causing the polar ice caps to shrink, release freshwater into the oceans, and drive substantial increases in oceanic levels worldwide (hereafter, sea-level rise) (IPCC, 2013). In southeastern North America, sea-level rise is predicted to influence low-lying coastal habitats by causing floods, inundation, and shifts in land-cover types (Marcy et al., 2011). Because gopher tortoises are a terrestrial species and not suited to wetland habitats, sea-level rise may negatively affect gopher tortoise populations in low-lying coastal areas, such as coastal sand-dune environments (Blonder et al., 2020).

2.3. Demographic parameters

We used the model to predict future abundance of populations across the range of the gopher tortoise using a first-order Markovian process in which adult abundance at time t was a function of adult and juvenile abundance at time $t-1$ with vital rates stochastically drawn from parameter distributions:

$$N_t^a = N_{t-1}^a \times \varphi_{t-1}^a + N_{t-1}^j \times \varphi_{t-1}^j \times \tau_{t-1} + N_{t-1}^i, \quad (1)$$

where N is abundance, φ is the apparent annual survival rate, and τ is an annual juvenile-adult transition rate (i.e., maturation) during each time step t (year); superscripts a , j , and i denote adults, juveniles, and immigrants, respectively.

Juvenile abundance at time t was a function of juvenile and hatchling abundance at time $t-1$ with vital rates similarly drawn from parameter distributions:

$$N_t^j = N_{t-1}^j \times \varphi_{t-1}^j \times (1 - \tau_{t-1}) + R_{t-1}, \quad (2)$$

where N is abundance, φ is survival, τ is the juvenile-adult transition rate, and R is recruitment (below) during each time step t (year). We did not include immigration in the juvenile stage, because studies of tortoise movement have mostly described long-distance dispersal events for adults. We modeled initial abundance of adults and juveniles as log-normally distributed random variables.

For individuals to recruit into the juvenile stage, adult females must lay eggs that hatch into offspring and survive until the next survey period (i.e., time step). Therefore, we estimated annual recruitment (R) at time t as the product of:

$$R_t = PB_t \times F_t \times NS_t \times VE_t \times PF \times \varphi_t^h, \quad (3)$$

where PB is the probability of females breeding, F is the mean number of eggs laid per breeding female (fecundity), NS is the probability of nests surviving predation, VE is the proportion of eggs that are viable and hatch, PF is the probability of eggs being female, φ^h is the survival probability of hatchlings through the first year to the next survey period at time t (Noon and Sauer, 1992), and the superscript h denotes hatchling. We modeled probabilities (PB , NS , VE , PF , φ^h) as beta-distributed random variables, and we modeled fecundity as a log-normally distributed random variable.

2.4. Spatial variation in demographic parameters

We first sought to construct a baseline population model that approximated demographic conditions experienced by gopher tortoise populations in recent decades across the species' range. However, populations of gopher tortoises experience geographic variation in abiotic characteristics, and variation in abiotic characteristics influences demographic rates among populations across the species' range. For example, at southern latitudes, populations experience significantly warmer mean annual temperature, which may afford greater overall opportunity for thermoregulation, energy acquisition, and metabolism when compared to northern populations. As a result, southern populations of tortoises experience faster growth rates, younger ages of sexual maturity (hereafter, maturity age), and increased clutch size (Ashton et al., 2007; Meshaka Jr. et al., 2019; Mushinsky et al., 1994). Because our goal was to predict population growth and extinction risk of populations across the species' range and predictive population models are most useful when demographic parameters are modeled specific to populations of interest (Ralls et al., 2002), we extended the model to accommodate geographic variation in demographic rates by estimating parameters specific to the geographic location of populations.

We reviewed the literature for demographic estimates from gopher tortoise populations in the wild (Supplementary Figure 1). We fit linear regression models to estimate relationships between demographic rates (maturity age, clutch size) and mean annual temperature (hereafter, MAT; °C) sourced from the 'WorldClim' database (Hijmans, 2020). After testing whether our data met assumptions of parametric statistics, we evaluated whether regression models estimated statistically significant effects of independent variables on response variables with $\alpha = 0.05$. We used observed statistically significant linear relationships between MAT and demographic rates among populations as a predictive tool to generate mean parameter estimates with error for populations in our predictive modeling framework, given georeferenced data describing MAT for populations. If parameters were not known to vary geographically (e.g., survival), we modeled mean values as invariant among populations.

We modeled the proportion of breeding females (i.e., that lay eggs; PB) in a given year as 0.97 (Hunter et al., 2021). We modeled fecundity (F) by using the regression coefficient describing the relationship between MAT and mean clutch size (above) to simulate mean values of F for populations, given the geographic location and MAT of a population. We modeled the probability of nests that

Table 1

Mean and error values used to estimate stochastic demographic parameters in our population projection model for gopher tortoises (*Gopherus polyphemus*) in conservation lands across the species' range. MAT = mean annual temperature (°C) of a population's locality; adult survival (φ^a) was modeled with a baseline rate of 0.96 and with a negative effect of years since last burn (YSB) of habitat using prescribed fire. See Supplementary Figure 1 for the full list of references used to compile parameter estimates for variables in the table.

Parameter	Abbreviation	Distribution shape	Mean (variance)	Source
Probability of breeding	PB	Beta	0.97 (0.01)	Hunter et al. (2021)
Fecundity	F	Log normal	-3.54 (2.42) + 0.48 (0.12) * MAT	Supplementary Figure 1
Nest survival	NS	Beta	0.35 (0.10)	Smith et al. (2013)
Probability of viable eggs	VE	Beta	0.85 (0.05)	Landers et al. (1980), Rostal and Jones (2002)
Probability of female	PF	Beta	0.50 (0.04)	This study
Hatchling survival	φ^h	Beta	0.13 (0.03)	Perez-Heydrich et al. (2012)
Juvenile survival	φ^j	Beta	0.75 (0.06)	Supplementary Figure 1
Adult survival	φ^a	Beta	0.96 (0.03) – 0.027 (0.003) * YSB	Supplementary Figure 1; Hunter and Rostal (2020)
Maturity age	MA	Log normal	43.52 (11.31) – 1.41 (0.53) * MAT	Supplementary Figure 1; this study
Juvenile abundance	N^j	Log normal	Varying by population	This study
Adult abundance	N^a	Log normal	Varying by population	This study
Immigration rate	γ	Beta	0.01 (0.001)	Ott-Eubanks et al. (2003)

survive predation (NS) as 0.35 using an estimate from unmanipulated nests (Smith et al., 2013). We modeled the probability of eggs being viable and hatching (VE) as 0.85 ($\sigma^2 = 0.05$), an average from a review of field hatching rates (Landers et al., 1980; Rostal and Jones, 2002). To account for males (and remove them) during projections, we assumed that sex ratios of eggs were even within populations and modeled the probability of eggs being female (PF) as 0.5 ($\sigma^2 = 0.04$). We modeled hatchling survival (φ^h) from nest emergence until the following survey period as 0.13 (0.04–0.34, 95% confidence intervals [CI]), given results from a meta-analysis of hatchling survival of gopher tortoises (Perez-Heydrich et al., 2012). For each recruitment parameter, we modeled parameters using appropriate statistical distributions (below) and randomly estimated the parameter in each year using stochastic draws using estimates of variance associated with parameter estimates (Table 1).

We modeled maturity age by using the regression coefficient describing the relationship between MAT and maturity age (above) to simulate mean values of maturity age for populations, given the geographic location and MAT of a population. Given a predicted maturity age for a population, we then calculated the proportion of juveniles that transition to become adults, τ , during a given year with:

$$\tau = \frac{1}{\text{Maturity age} - 1} \quad (4)$$

This formula assumes that the transition probability applies to the subset of juveniles that have been in the juvenile population long enough to mature out in year t and that transition probability is the inverse of the age of sexual maturity minus one, to account for one year spent as a hatchling.

Survival rates are difficult to measure for gopher tortoises because individuals are long-lived, challenging to recapture, or may become unavailable for resurvey by emigrating away from study populations (e.g., Folt et al., 2021). When individuals disappear from a study population, mark-recapture analyses are often unable to estimate whether individuals died or emigrated away (Williams et al., 2002). To this end, most mark-recapture studies of gopher tortoise seeking to understand survival have estimated apparent annual survival (φ), which is the probability that individuals survived and stayed within a study area. Studies have found φ to vary between adults and juveniles, with adults having higher survival than juveniles, and with more open habitats to support higher survival than closed habitats (Folt et al., 2021; Howell et al., 2020; Tuberville et al., 2014). We modeled apparent survival of adults (φ^a) as 0.96 and apparent survival of juveniles (φ^j) as 0.75, given demographic rates reported from relatively stable populations in Alabama (Folt et al., 2021) and assuming that populations being modeled here had the potential to be stable.

We modeled a density-dependent limit on population growth where for each time-step when density increased above 2 adult females/ha, we prevented recruitment into the adult age class. This was meant to simulate population conditions where young adults may elect to disperse away from high-density conditions to other populations with lower density, while also enforcing a limit on maximum population size (i.e., carrying capacity). Field studies have estimated tortoise density to range from 0.02 to 1.50 individuals/ha among northern populations (Guyer et al., 2012) and from 4.2 to 24.9 individuals/ha in southern Florida (Meshaka Jr. et al., 2019). We selected a threshold of 2 adult females/ha (i.e., >5 tortoises/ha, assuming even sex ratios and a 3:1 adult to juvenile ratio) as a limit for density dependence because there is much uncertainty when estimating tortoise density and 2 adult females/ha was a conservative intermediate estimate of maximum density among populations across the species' range.

Gopher tortoises infrequently move long distances from established core home range areas; such movements can result in permanent emigration and immigration into other populations. We implicitly modeled losses to local populations due to emigration because our estimates of apparent annual survival (φ) account for mortality and permanent emigration away from local populations. Given ongoing emigration, local populations that are spatially proximate to other local populations might receive immigrants that bolster population size. While little quantitative information is available describing the frequency or success of immigration, one study found that 2% of adults emigrated from local populations each year (Ott-Eubanks et al., 2003). Given it is unlikely that all emigrants successfully immigrate into another population, we modeled the number of immigrants into local populations as a random draw from a binomial distribution, where the immigrants to a local population were selected from a pool of migrants across all nearby populations with a probability equal to a randomly-drawn, beta-distributed, time-varying annual immigration rate (γ ; mean = 0.01). The immigrant pool was calculated by dividing the total number of adult tortoises in adjacent populations (i.e., metapopulation size, N^m ; see below) by the number of nearby local populations and multiplying the dividend by 0.75, because we assumed a 3:1 adult to juvenile ratio and that juveniles do not migrate between local populations. We constrained γ during each time step such that its randomly-drawn value could never exceed $1 - \varphi^a$, so that the proportion of individuals that survive, emigrate, and/or die could not exceed 1. Demographic parameters were modeled as random variables that accounted for both parametric uncertainty and temporal variability (see below).

2.5. Population estimates

We initialized the model with estimates of gopher tortoise population size from populations on protected, conservation lands and nature preserves (e.g., national forests, state forests, state wildlife management areas), military installations, and some private lands across the species' range during the last ten years. Population estimates were collected by a diverse partnership of cooperating state agencies, private organizations, and academic institutions (see Acknowledgements) using standardized survey methods. Population estimates do not represent an assessment of all local populations of tortoises that exist in southeastern North America, but rather represent information that was provided by partners throughout much of the species' range.

We initialized starting population size using population estimates derived from data collected using standardized surveys,

including burrow surveys (comprehensive and area-constrained; both with and without burrow scoping incorporated) and line-transect distance sampling (LTDS; Buckland and Turnock, 1992; Thomas et al., 2010); some burrow data were submitted with unknown methodology. Comprehensive burrow surveys, sometimes called ‘100% surveys’, involve a team of researchers searching a site to count the total number of gopher tortoise burrows present. Area-constrained surveys, also referred to as belt transect surveys, use a similar methodology as comprehensive surveys. However, these surveys are restricted to a transect of pre-delineated length and width, and population estimates are extrapolated site-wide based on the proportion of the site that was surveyed (Auffenberg and Franz, 1982; Cox et al., 1987). Because gopher tortoises often construct and/or use more than one burrow per individual, we used a published estimate of the relationship between the number of tortoises and burrows among six populations (0.4 tortoises/burrow; Guyer et al., 2012) to estimate the number of tortoises at sites from burrow count data. This burrow survey method assumes the tortoise-per-burrow estimate from Guyer et al. 2012 is generalizable to tortoise populations range-wide and that no burrows are missed during surveys. However, other studies suggest higher gopher tortoise conversion rates, indicating our estimate may be conservative in some parts of the tortoise’s range (0.614, Auffenberg and Franz, 1982; 0.5, Ashton and Ashton, 2008). Biologists also sometimes use burrow-scope cameras in conjunction with burrow surveys to directly estimate abundance of local populations by counting individuals within burrows; this method assumes that all potentially occupied gopher tortoise burrows were detected at sites and that only a single gopher tortoise is present in a burrow. LTDS surveys are a population estimation method where a research team walks transects through habitat, observes tortoise burrows, searches the burrow for a tortoise with a burrow scope, records the spatial location of occupied tortoise burrows, and measures the perpendicular distance of each occupied burrow to the transect line (Smith et al., 2009). Invariably, burrows and individuals are imperfectly sampled because detection probability of burrows is less than one. However, analysis of the LTDS survey data generates functions estimating the decay of the detection rate with increasing distance from the transect line, and this detection function can then be used to account for undetected burrows and therefore estimate the total number of occupied

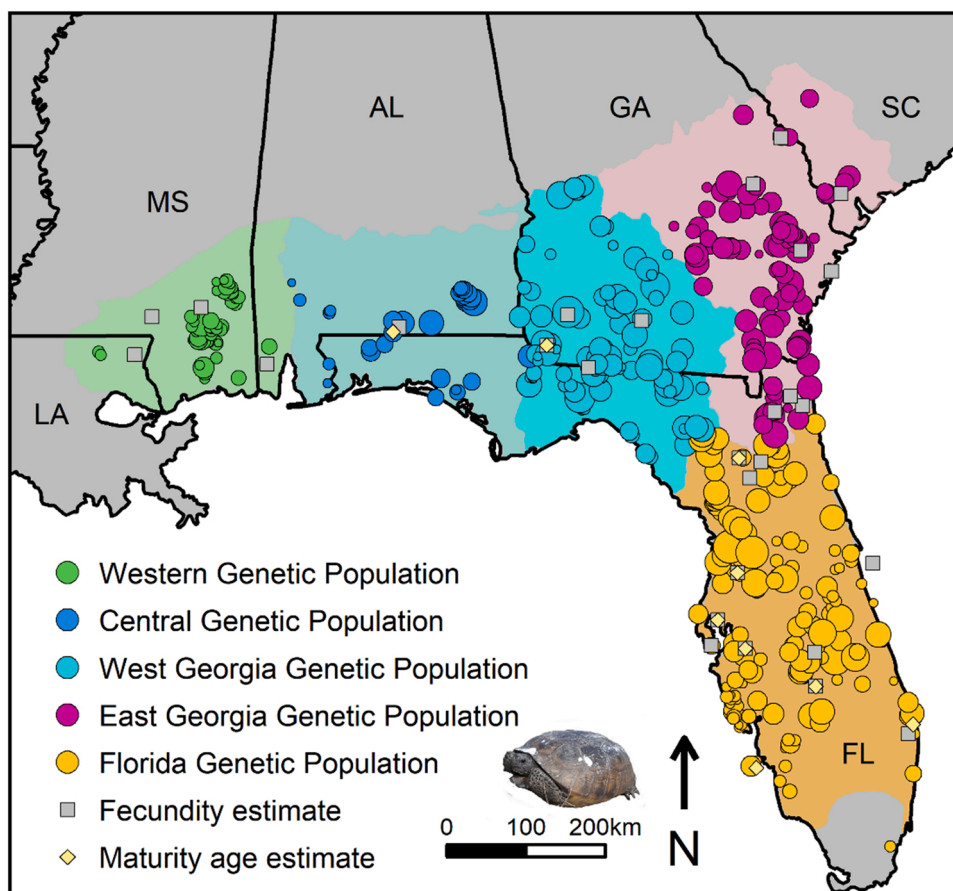


Fig. 2. Current population size of 457 populations of the gopher tortoise (*Gopherus polyphemus*; inset) in the southeastern United States that were modeled to predict future population growth and persistence probability for the species under scenarios of global change. Each circle represents a local population and circles are colored by regional genetic populations (Gaillard et al., 2017), which we used as genetic analysis units. Symbol size reflects a log-transformed scale of population size; population size was estimated from analysis of standardized burrow surveys or line-transect distance sampling (LTDS) at each site within the last ten years. Grey squares and yellow diamonds represent populations from which estimates of fecundity or maturity age, respectively, were used to model geographic variation in demographic rates. Gopher tortoise photograph courtesy of T. W. Pierson. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

burrows in the search area (i.e., total population size). We note that because juvenile tortoises have small burrows that are difficult to observe, detection of juveniles during all burrow survey types (comprehensive, belt transect, LTDS) is lower than adults; thus, surveys may underrepresent smaller size classes in the population estimates (Gaya, 2019; Smith et al., 2009).

Using spatial survey data associated with population estimates, we sought to operationally identify populations at two spatial scales: local populations and metapopulations. Population estimates from surveys (number of tortoises in a population) allowed us to parameterize initial population size during simulated projections of populations. However, many population estimates were based on large areas that may functionally represent more than one local population. We defined local populations as geographic aggregations of individuals that interact significantly with one another in social contexts that make reproduction significantly greater between individuals within the aggregation than with individuals outside of the aggregation (*sensu* Smallwood, 1999). We operationally delimited local populations by identifying aggregations of individuals or burrows where individuals were clustered together within a 600 m buffer to the exclusion of other adjacent individuals or burrows. Analysis of gopher tortoise movement data from Alabama, Georgia, and Florida suggested that > 80% of gopher tortoise movements within and among years were less than 500 m (Hunter and Rostal, 2021). We selected a 600 m distance to buffer populations to encompass typical movement distances and adjacent habitat around surveyed populations that might include tortoises. We assumed that unsuitable habitat for tortoises (i.e., interstates, freeways, and expressways; U.S. Department of Transportation Office of Highway Policy Information, 2016; major rivers and lakes [Sciencebase.org]; wetlands; and highly urbanized areas [as determined by visual inspection with ESRI imagery]) were unsuitable for tortoise movement or survival and considered those as strict barriers when delimiting local populations. Adjacent local populations connected to each other by suitable habitat through which dispersal might occur formed a metapopulation. We operationally delimited a metapopulation by identifying local populations connected by suitable habitat within a 2.5 km buffer around each local population, because > 95% of individual movements were less than 2.5 km in southeastern Georgia (Hunter and Rostal, 2021). We received some population estimates from properties that were delimited to have two or more local populations of tortoises; in these instances, we assumed equal densities and distributed the population size (and confidence limits) proportionally to the areas of each local population.

We restricted the dataset to only consider populations with ≥ 8 individuals (or ≥ 3 females, assuming 1:1 sex ratio and a 3:1 adult to juvenile ratio), because populations with 7 or fewer tortoises likely lack sufficient genetic diversity for long-term persistence. Our process of delimiting local populations and metapopulations resulted in a dataset of 457 local populations (Fig. 2) that formed 202 metapopulations and comprised ca. 70,500 female tortoises. Populations with abundance estimates were distributed across each of five regional population genetic units delimited within the species (Gaillard et al., 2017): Western (51 populations), Central (41 populations), West Georgia (97 populations), East Georgia (110 populations), and Florida (158 populations; Fig. 2). We refer to these regional genetic units as ‘genetic populations’ hereafter. We used population estimates from local populations to parameterize initial population size of adults (N^a) and juveniles (N^j) during simulated population projections. We assumed a 1:1 sex ratio and a 3:1 adult:juvenile ratio in populations, given observations from stable local populations in Alabama (Folt et al., 2021), and used these ratios to quantify the population sizes of juvenile and adult females.

2.6. Modeling threats

2.6.1. Climate warming

We modeled how climate warming may influence gopher tortoise demography. We considered demographic rates that are currently known to be influenced by variation in temperature (maturity age, F ; above). We then used the estimated linear relationships of MAT with maturity age and F (above) to predict how future warming temperatures experienced by populations will drive concurrent changes in demography. For each population, we extracted historic estimates of MAT using the ‘WorldClim’ database (Hijmans, 2020) and then simulated annual, step-wise climate-warming effects on MAT each year in the future where warming rates were parameterized by three treatments of climate warming: (1) a 1.0 °C increase in MAT over the next 80 years, (2) a 1.5 °C increase in MAT over the next 80 years, and (3) a 2.0 °C increase in MAT over the next 80 years. Each year in the future, we used simulated changes in MAT – assumed to increase at a constant rate within each treatment – to calculate mean maturity age and F at sites. This analysis assumes that: (i) warming is homogeneous in space and occurs linearly in time, (ii) all local populations will respond homogeneously to warming temperatures, and (iii) there are no potential climatic ceilings that would limit growth and reproduction.

2.6.2. Habitat management

We modeled effects of habitat management on gopher tortoise populations by linking the frequency of management with prescribed fire to adult survival. We assumed that a baseline fire-return interval (FRI) of 1–4 years (mean = 2.5 years) maintains high-quality habitat for gopher tortoises (Crawford et al., 2020b; Guyette et al., 2012) and then modeled the probability that a population is burned during a given year (burn probability; BP) as the inverse of the fire-return interval:

$$BP_i = \frac{1}{FRI} \quad (5)$$

For example, an intended two-year FRI for a population would yield a BP of 0.5. Next, using historic baseline data describing average seasonal burn opportunity across southeastern North America (Kupfer et al., 2020), we modeled the number of available burn days (i.e., days within the burn window) in winter (January–February; W), spring (March–May; Sp), and summer (June–July; Su) as a product of the total days per season (59, 92, and 61 days, respectively) and the stochastically-drawn percentage of days historically available for burning (0.766, 0.800, and 0.645, respectively). We modeled four treatments for how the number of days available for

prescribed fire may change in the future (Kupfer et al., 2020): (1) prescribed fire use will decrease consistent with climate shifts predicted by RCP4.5 ('less management'), (2) prescribed fire use will decrease with climate shifts predicted by RCP8.5 ('much less management'), (3) prescribed fire use will increase opposite of the effect predicted by RCP4.5 ('more management'), and (4) prescribed fire use will remain at current levels ('status quo'). For each treatment, we modeled effects of climate change on the percentage of available burn days over the next 80 years using average effects from across southeastern North America extracted from Kupfer et al. (2020): 0.016 increase in winter, 0.040 decrease in spring, and 0.239 decrease in summer ('less management' treatment); 0.030 increase in winter, 0.105 decrease in spring, and 0.436 decrease in summer ('much less management' treatment); 0.016 decrease in winter, 0.040 increase in spring, and 0.239 increase in summer ('more management' treatment), and no effects on burn days ('status quo' treatment). The 'more management' and 'status quo' scenarios could result if habitat managers can offset effects of climate change by benefiting from methodological advances in fire management or by using alternative methods rather than prescribed fire, such as mechanical or chemical treatments, to achieve similar management goals.

For the 'less management', 'much less management', and 'more management' treatments, we used the predicted effects to model annual incremental changes in the percentage of available burn days per season in each year. Assuming that changes in total burn opportunity result in changes in total burn frequency, we modeled BP in each year t as a product of the function of the inverse of FRI and predicted changes in the total number of burn days available due to climate change:

$$BP_t = \frac{1}{FRI} * \frac{W_t + Sp_t + Su_t}{W_1 + Sp_1 + Su_1} \quad (6)$$

where subscript 1 is the first year of the projection and t is each year ranging from 1 to the last year in the projection. For the 'status quo' treatment, we modeled no effects of climate on the number of available burn days per year in an attempt to simulate unvarying management ability in the future.

We used estimates of BP to simulate whether a population was burned in each year. Apparent annual survival probability of female gopher tortoises is highest in the first year after a site is burned, but declines by 0.027 each year without fire (Hunter and Rostal, 2021). During each year of projections, we simulated adult survival as a stochastic effect of the number of years since last burn (YSB):

$$\varphi_t^a = 0.96 - 0.027 \times YSB. \quad (7)$$

Because Hunter and Rostal (2021) only estimated the effect of year-since-burn on survival of adults up to three years since burn, we did not extrapolate this effect beyond three years or to juveniles. This formulation assumes that: (i) changes in the number of days available to burn result in changes in burn frequency (i.e., management is limited by available burn days), (ii) the season that a burn is performed does not influence habitat quality (but see: Aresco and Guyer, 1999b; Yager et al., 2007) and (iii) the effect of YSB on survival from Georgia (Hunter and Rostal, 2021) is generalizable to all populations of gopher tortoises.

2.6.3. Urbanization

We sought to model effects of urbanization pressure on tortoise populations by linking urbanization predictions from the SLEUTH urban growth model (Clarke, 2000) to habitat management of local populations with prescribed fire and to baseline immigration rates (γ) of tortoises across metapopulations. First, we modeled an effect of urbanization on habitat management by making BP a function of each population's distance to the nearest urban area ($dNUA$). We did this to account for fire suppression and/or exclusion that occurs in habitat near urban areas, due to concerns about fire safety and smoke management restrictions (i.e., the wildland-urban interface; Theobald and Romme, 2007). Because studies have found evidence for fire exclusion at distances from 1 to 5 km from urban areas (Theobald and Romme, 2007), we followed (Crawford et al., 2020a) and assumed a moderate distance (3.2 km) within which to model effects between urbanization and fire frequency. Specifically, we assumed that local populations immediately adjacent to urban areas (distance < 0.1 km) are unable to be managed with prescribed fire and forced BP to 0, management is uninfluenced for populations far from urban areas (> 3.2 km; no effect on BP), and management of populations between 0.1 and 3.2 km from an urban area experience a negative effect on fire management with BP declining as a linear function of the population's proximity to the urban area (i.e., populations closer to urban areas experience less prescribed fire). For populations between 0.1 and 3.2 km of an urbanized area, we added an additional term to Eq. 6 to estimate BP as a consequence of $dNUA$ at time t :

$$BP_t = \frac{1}{FRI} * \frac{W_t + Sp_t + Su_t}{W_1 + Sp_1 + Su_1} * \frac{dNUA_t}{3.2}. \quad (8)$$

To calculate $dNUA_t$, we first used the SLEUTH model to estimate $dNUA$ from the geometric center of local populations to the edge of the nearest neighbor urban area in the current conditions ($dNUA_i$) and at the end of the projection interval ($dNUA_f$). We then calculated $dNUA_t$ using:

$$dNUA_t = dNUA_i + \left[(dNUA_f - dNUA_i) * \frac{t}{total} \right], \quad (9)$$

where $total$ is the total number of years in the projection interval.

To model effects of urbanization on migration dynamics among local populations within metapopulations, we first estimated the total area (A ; ha) and urbanized area (UA ; ha) within metapopulations in year 2020 using the SLEUTH model. Assuming that tortoises cannot survive and/or move through urbanized areas but can survive and move in unurbanized areas, we estimated the initial proportion of suitable dispersal habitat (PDH_i) in metapopulations at the start of population projections as:

$$PDH_i = \frac{A_i - UA_i}{A_i}. \quad (10)$$

We next estimated future urbanization and its effect on dispersal habitat for tortoises using the SLEUTH model predictions for 80 years in the future. We estimated predicted urbanized area in the future (UA_f ; ha). Similar to Eq. 10, we estimated the future proportion of suitable dispersal habitat (PDH_f) around populations in the future:

$$PDH_f = \frac{A_i - UA_f}{A_i}. \quad (11)$$

We calculated the predicted change in proportion of dispersal habitat (ΔPDH) due to future urbanization for metapopulations by taking the difference between PDH_f and PDH_i . For each year $t \geq 3$ during population projections, we modeled the number of adult immigrants (N_t^i) into local populations in each year as a function of the number of individuals in the metapopulation available for immigration to the local population during the previous year (N_{t-1}^m), the total number of local populations in the metapopulation (N^p), γ_t , PDH_i , ΔPDH , and the time-step in the future:

$$N_t^i = \frac{N_{t-1}^m}{N^p - 1} * \gamma_t * \left[PDH_i + \Delta PDH * \frac{t_i}{total} \right], \quad (12)$$

where t_i is the year in the population projection, ranging from $t_i = 3$ to the total projection interval (*total*). We estimated N^m at $t = 1$ by summing the starting population size of all local populations in the metapopulation and subtracting the abundance of the focal population, because individuals from the focal population would be unavailable for immigration into their own population. We assumed that population growth of the metapopulation term would change through time similarly to that of the local population being modeled in any instance; therefore, we modeled changes in N^m through time as a function of changes in abundance of the local adult population size during the previous time step, $\frac{N_t^p}{N_{t-1}^p}$, during year 3 and beyond. We assumed N^m would not change in years 1 and 2 due to constraints related to calculating population growth of the local population.

We estimated predicted effects of urbanization on the burn probability of local populations and dispersal within metapopulations (i.e., with the above equations) using three treatments from the SLEUTH urbanization model that corresponded to uncertainty in future urbanization magnitude: (1) a low urbanization treatment where future urbanization was limited to areas with extremely high urbanization probability (≥ 0.95), (2) a moderate urbanization treatment where areas were considered urbanized if urbanization probabilities were ≥ 0.50 , and (3) a high urbanization treatment where areas were considered urbanized if urbanization probabilities were ≥ 0.20 . We assumed that: (i) immigration was limited to adults and that no juveniles successfully migrate among populations, and (ii) immigrants cannot survive or move through urbanized areas (e.g., due to road mortality) but survive perfectly while moving through unurbanized areas.

2.6.4. Sea-level rise

Projected sea-level rise scenarios provide a range of coastal inundation scenarios that vary in severity. We modeled effects of sea-level rise on tortoises using three scenarios of sea-level rise predicted by NOAA, the ‘intermediate-high’, ‘high’, and ‘extreme’ scenarios, which correspond to predictions from two of the most likely global emission scenarios, RCP6.0 and RCP8.5 (IPCC, 2013; NOAA, 2020). Local predictions for the two scenarios are available from USGS sea-level monitoring stations across the southeastern United States, providing estimates of sea-level rise for stations at decadal time steps in the future to year 2100. We modeled three treatments of sea-level rise using predictions from NOAA: (1) the ‘intermediate-high’ scenario derived from RCP6.0, which predicts ca. 1.83 m of sea-level rise over the next 80 years, (2) the ‘high’ scenario which predicts 2.55 m of sea-level rise over the next 80 years (an intermediate prediction between RCP6.0 and RCP8.5), and (3) the ‘extreme’ scenario derived from RCP8.5, which predicts 3.16 m of sea-level rise over the next 80 years (NOAA, 2020). We modeled sea-level rise effects on populations in two ways. First, assuming that gopher tortoise populations cannot persist when oceanic levels encroach too close upon their habitat, we simulated decreasing elevation of tortoise populations due to sea-level rise. We extracted historic estimates of elevation above sea level (asl; in m) using the centroid geographic coordinates of each local population using the ‘WorldClim’ database (Hijmans, 2020). Given the total predicted sea-level rise of each treatment over the next 80 years, we simulated incremental sea-level rise at each population in each year in the future and subtracted this incremental oceanic rise from the site’s elevation through time. When the site elevation of populations decreased to less than 0 m asl, we considered the populations functionally extirpated and forced the population size vectors, N^j and N^a , to zero. Second, we assumed that habitat inundated by sea-level rise adjacent to local populations would decrease connectivity and dispersal dynamics of individuals among populations within metapopulations. We used spatial predictions from NOAA to estimate future inundation area due to sea-level rise for each metapopulation, and then we modeled γ to decline as a function of decreasing habitat available for dispersal at the landscape scale. Assuming that tortoises cannot survive and/or move through inundated areas but can survive and move in un-inundated areas, we extended Eq. (12) to subtract the proportion of area lost to sea-level rise (SLR) from the proportion of dispersal habitat (PDH_i) in each year:

$$N_t^i = \frac{N_{t-1}^m}{N^p - 1} * \gamma_t * \left[PDH_i + \Delta PDH * \frac{t}{total} - SLR * \frac{t}{total} \right], \quad (13)$$

The analysis of sea-level rise effects assumes that: (i) sea-level rise throughout southeastern North America will be homogeneous and characterized by NOAA predictions derived from data from Ft. Myers, Florida, (ii) populations less than 0 m asl are unable to

persist, and (iii) populations are unable to migrate away from sites to form populations outside of the study areas.

2.7. Scenarios

We created 32 scenarios varying in estimates of demographic rates and future threats for projection to understand how demographic rates and threats, individually or synergistically, may influence future population conditions of tortoises over the next 80 years (Table 2). The first model was a ‘status quo’ scenario that assumed $\varphi^a = 0.96$, a density-dependent limit on recruitment to the adult age class of 2.0 females/ha, $\gamma = 0.01$, no future climate warming, sea-level rise, and urbanization, and future management consistent with status quo efforts. The next 20 models were single-factor alterations of the ‘status quo’ scenario that varied in φ^a (0.98,

Table 2

Simulation scenarios used to understand how demographic variation, climate warming, sea-level rise, urbanization, and habitat management might influence persistence of gopher tortoise (*Gopherus polyphemus*) populations into the future. The first 21 scenarios (‘sensitivity scenarios’) were used to explore the sensitivity of populations to perturbations in demographic rates (adult survival, density-dependent limit, immigration rate) and threats (climate warming, sea-level rise, urbanization, and habitat management) relative to a ‘status quo’ model with no additional future threats and status-quo management. The final 11 scenarios (‘future conditions scenarios’) were used to predict how populations might respond to potential future conditions that involve multiple threats and uncertainty in key demographic rates. Threat levels included three levels of climate warming (1.0, 1.5, and 2.0 °C increase), three levels of sea-level rise (intermediate-high [1.83 m], high [2.55 m], and extreme [3.16 m] scenarios), three levels of urbanization scenarios predicted by the SLEUTH model (Clarke, 2000) at probability thresholds of 0.95 (‘low’ prediction), 0.50 (‘medium’ prediction), and 0.20 (‘high’ prediction), and four levels of changes in habitat management (no change from status quo, ‘less management’ predicted by RCP4.5 (Kupfer et al., 2020) [‘low’], ‘much less management’ predicted by RCP8.5 (Kupfer et al., 2020) [‘very low’], and ‘more management’ [the opposite of the effect predicted by RCP4.5 in (Kupfer et al., 2020); ‘high’]).

Scenarios	Adult apparent survival	Density-dependent limit (females/ha)	Immigration rate	Climate warming (deg C)	Sea-level rise (m)	Urbanization	Management
Sensitivity scenarios							
Status quo	0.96	2	0.01	0	0	None	Status quo
Survival (high)	0.98	2	0.01	0	0	None	Status quo
Survival (low)	0.94	2	0.01	0	0	None	Status quo
Survival (very low)	0.92	2	0.01	0	0	None	Status quo
Max density (high)	0.96	4	0.01	0	0	None	Status quo
Max density (low)	0.96	1	0.01	0	0	None	Status quo
Immigration (very high)	0.96	2	0.04	0	0	None	Status quo
Immigration (high)	0.96	2	0.02	0	0	None	Status quo
Immigration (zero)	0.96	2	0.00	0	0	None	Status quo
Climate warming (low)	0.96	2	0.01	1.0	0	None	Status quo
Climate warming (medium)	0.96	2	0.01	1.5	0	None	Status quo
Climate warming (high)	0.96	2	0.01	2.0	0	None	Status quo
Sea-level rise (low)	0.96	2	0.01	0	1.83	None	Status quo
Sea-level rise (medium)	0.96	2	0.01	0	2.55	None	Status quo
Sea-level rise (high)	0.96	2	0.01	0	3.16	None	Status quo
Urbanization (low)	0.96	2	0.01	0	0	P = 0.95	Status quo
Urbanization (medium)	0.96	2	0.01	0	0	P = 0.50	Status quo
Urbanization (high)	0.96	2	0.01	0	0	P = 0.20	Status quo
Management (more)	0.96	2	0.01	0	0	None	More
Management (less)	0.96	2	0.01	0	0	None	Less
Management (much less)	0.96	2	0.01	0	0	None	Much less
Future condition scenarios							
Low threats	0.96	2	0.01	1.0	1.83	P = 0.95	Status quo
Medium threats	0.96	2	0.01	1.5	2.55	P = 0.50	Status quo
High threats	0.96	2	0.01	2.0	3.16	P = 0.20	Status quo
Management (more) + medium threats	0.96	2	0.01	1.5	2.55	P = 0.50	More
Management (less) + medium threats	0.96	2	0.01	1.5	2.55	P = 0.50	Less
Management (much less) + medium threats	0.96	2	0.01	1.5	2.55	P = 0.50	Much less
Survival (high) + medium threats	0.98	2	0.00	1.5	2.55	P = 0.50	Status quo
Survival (low) + medium threats	0.94	2	0.02	1.5	2.55	P = 0.50	Status quo
Immigration (very high) + medium threats	0.96	2	0.04	1.5	2.55	P = 0.50	Status quo
Immigration (high) + medium threats	0.96	2	0.02	1.5	2.55	P = 0.50	Status quo
Immigration (zero) + medium threats	0.96	2	0.00	1.5	2.55	P = 0.50	Status quo

0.94, or 0.92), density-dependent limit on recruitment (4, 1), γ (0, 0.02, 0.04), climate warming (1 °C, 1.5 °C, 2 °C), sea-level rise (1.83 m, 2.55 m, 3.16 m), urbanization (low, medium, high), and habitat management ('less', 'much less', and 'more' management). Simulation of the 20 models allowed us to evaluate how tortoise populations would respond to changes in a single demographic parameter or threat estimate, relative to the 'status quo' scenario, similar to a sensitivity analysis (i.e. 'sensitivity scenarios'). However, future threats to tortoise populations are not independent and most threats are interrelated (e.g., sea-level rise is a consequence of climate warming). To understand how tortoise populations will respond to future conditions with multiple concurrent threats, we created a set of 11 scenarios with varying levels of threat magnitude and combination as well as uncertainty in important demographic rates (i.e., 'future conditions scenarios'; Table 2). Specifically, we created three scenarios with different levels of threats ('low threats', 'medium threats', and 'high threats') that experienced habitat management consistent with contemporary target management goals. We then used the values from the medium threat scenario and built three scenarios that varied in habitat management treatments ('less', 'much less', and 'more' management conditions, each with $\gamma = 0.01$) which reflect uncertainty in future management practices with a medium level of threats. Our preliminary analyses indicated that populations are sensitive to two demographic parameters: φ^a and γ . To this end, we created five more scenarios that varied in survival ('high survival', 'low survival') and γ ('very high immigration', 'high immigration', 'zero immigration'), each with medium threats and status quo habitat management (Table 2). The 11 future condition scenarios were meant to estimate the effects of uncertainty in future threats (climate warming, sea-level rise, urbanization; 3 scenarios), actionable management practices (habitat management; 3 scenarios), and demographic rates (survival, immigration; 5 scenarios) on future population persistence.

2.8. Population projections

We projected population growth for each local population under each of the 32 scenarios using a stochastic projection structure that accounted for scenario uncertainty, geographic variation among populations, parametric uncertainty, and temporal stochasticity (Fig. 3). For each scenario, we parameterized certain stochastic variables specific to the scenario and then projected gopher tortoise populations across the species' range into the future. For each population, we specified mean demographic rates specific to the MAT of the population's geographic location (Table 1) and then simulated future population trajectories with 50 replicates each projected 80 years into the future. During simulations, we applied an uncertainty structure that accounted for both parametric uncertainty (among replicates) and temporal stochasticity (within replicates; McGowan et al., 2011). For each replicate, we drew mean values (and an associated error term) to model parametric uncertainty; we then modeled temporal stochasticity by drawing stochastically from the mean (given its error) during each time step within the replicate. We simulated parameters by drawing replicate-level means stochastically from either beta distributions (e.g., probabilities) with shape parameters calculated from mean and standard deviation estimates (Morris and Doak, 2002), log-normal distributions (e.g., fecundity), or binomial distributions (e.g., probabilities simulating discrete events). We projected populations 80 years into the future because this interval overlapped with the maximum duration of future predictions of the climate, urbanization, and sea-level rise models that we used and the interval also encompassed ca. two generations for stable populations of gopher tortoises (Folt et al., 2021).

We used our population projections to estimate future changes in tortoise populations under each scenario (Table 2) in ways that could assess future population resiliency, redundancy, and representation. We defined resiliency as the ability of populations to withstand stochastic environmental variation that might influence population persistence. We operationally assessed resiliency in two

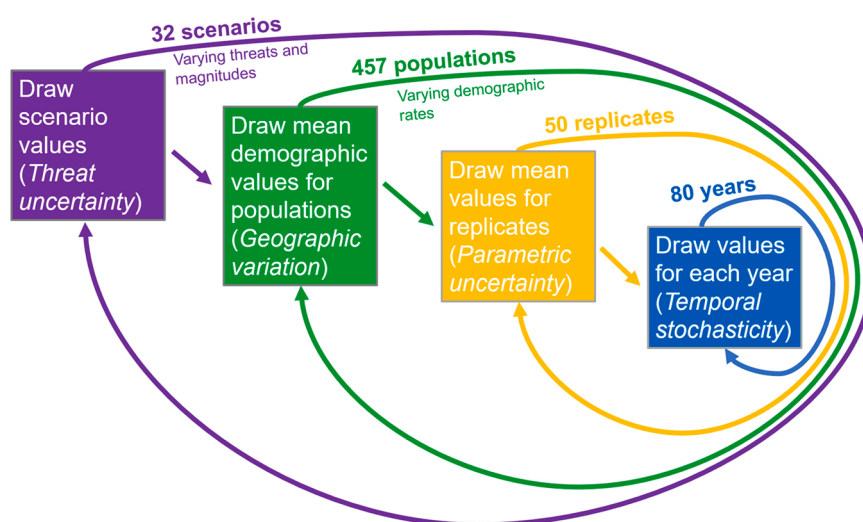


Fig. 3. We used a four-loop uncertainty structure to simulate demographic variation and uncertainty in threats, populations, parameter estimates, and temporal stochasticity of stochastic variables during population projections for gopher tortoises. For each scenario, we simulated each population using 50 replicates and projected each replicate into the future for 80 years.

ways. First, we measured the predicted percent change (% Δ) in the total number of individuals, local populations, and metapopulations in the future relative to current conditions:

$$\% \Delta = \frac{N_{\text{future}} - N_{\text{current}}}{N_{\text{current}}} * 100\%, \quad (14)$$

where % Δ values summarize population size as increasing (positive), stable (near zero), or decreasing (negative) over a projection interval; we measured predicted % Δ across the species' range and by genetic population over the entire projection interval. We assumed that more resilient populations would be characterized by larger % Δ values than less resilient populations. Second, we also assessed the resiliency of future populations to changing environments by estimating extinction risk of populations. For each population, we estimated the probability that the population was extant during any given year (i.e., persistence probability; P_p) by dividing the number of replicates with ≥ 3 females alive by the total number of replicates. We chose < 3 females as a threshold to approximate functional extinction because populations with fewer than three females are extremely likely to be inbred (Chesser et al., 1980; Frankham et al., 2011). We then used P_p to categorize populations as 'Extremely Likely to Persist' ($P_p \geq 0.95$), 'Very Likely to Persist' ($0.80 \leq P_p < 0.95$), 'More Likely Than Not to Persist' ($0.50 \leq P_p < 0.80$), and 'Unlikely to Persist' (i.e., extirpated; $P_p < 0.50$). To assess resiliency of metapopulations at the end of the projection interval, we selected the constituent focal population with the greatest P_p and used that value to categorize metapopulation persistence.

We defined redundancy as the number of populations predicted to persist in an area in the future. We operationally assessed redundancy by predicting the total number of populations and metapopulations likely to persist in the future through simulation with P_p for each population. To do so, we took random draws from a Bernoulli distribution with $p = P_p$ for each population and summed the number of populations that persisted. We performed 100 replicates and summarized the simulation with the median (95% CI).

We defined representation as the breadth of genetic diversity across the species' range. We viewed regional genetic populations across the species' range (Gaillard et al., 2017) as surrogates for genetic representation and operationally evaluated how representation is predicted to change in the future by examining how the number of individuals, local populations, and metapopulations was predicted to change for each genetic population. For each scenario, we summarized the results among all populations across the species' range, but also by genetic populations ('West', 'Central', 'West Georgia', 'East Georgia', and 'Florida'; Gaillard et al., 2017).

We performed all analyses in the statistical program R (R Core Team, 2018). The general conceptual and predictive population modeling structure was adapted from a recently-published population viability analysis for gopher tortoises (Folt et al., 2021). The R code and associated files are provided in a USGS software release (Folt and McGowan, 2022). Requests to access the data used to perform the analyses should be directed towards the U.S. Fish and Wildlife Service's Jacksonville Field Office.

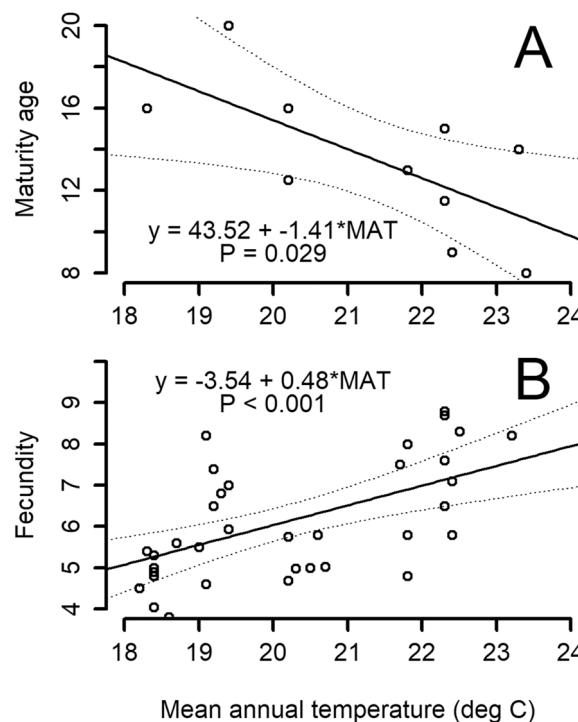


Fig. 4. Effect of mean annual temperature (MAT; °C) on (A) maturity age and (B) fecundity of female gopher tortoises (*Gopherus polyphemus*) among populations across the species' range.

Table 3

Simulated population projections for gopher tortoise (*Gopherus polyphemus*) populations under scenarios of varying demographic rates and anthropogenic threats in the future. Columns summarize the initial number (in 2020), future predicted number in 2100, and percent change (%Δ with 95% confidence intervals [CI]) for the total population size, number of local populations, and number of metapopulations for 32 scenarios projected 80 years into the future. See Table 2 for descriptions of scenarios and parameters for each model.

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	%Δ	Initial	Future	%Δ	Initial	Future	%Δ
Sensitivity scenarios									
Status quo	70122	21689	-69 (-85, -17)	457	192	-58 (-61, -56)	202	92	-55 (-73, -30)
Survival (high)	69658	26344	-62 (-80, 26)	457	279	-39 (-43, -36)	202	132	-35 (-52, -14)
Survival (low)	69759	18235	-74 (-91, -38)	457	130	-72 (-74, -69)	202	54	-73 (-81, -50)
Survival (very low)	70150	14886	-79 (-93, -50)	457	84	-82 (-84, -79)	202	40	-80 (-85, -71)
Max density (high)	70186	50740	-28 (-75, 3669)	457	194	-58 (-60, -54)	202	90	-55 (-73, -33)
Max density (low)	69929	12204	-83 (-91, -47)	457	193	-58 (-61, -55)	202	93	-54 (-73, -34)
Immigration (very high)	69948	77915	11 (-44, 25748)	457	309	-32 (-36, -30)	202	148	-27 (-49, -8)
Immigration (high)	69461	39149	-44 (-71, 48)	457	245	-46 (-49, -44)	202	112	-45 (-67, -19)
Immigration (zero)	69685	1423	-98 (-99, -84)	457	83	-82 (-84, -80)	202	56	-73 (-88, -49)
Climate warming (low)	69594	21680	-69 (-86, -14)	457	200	-56 (-60, -54)	202	90	-55 (-72, -33)
Climate warming (medium)	69824	22034	-68 (-85, -6)	457	200	-56 (-58, -54)	202	102	-50 (-71, -30)
Climate warming (high)	69838	22091	-68 (-86, -2)	457	203	-56 (-58, -52)	202	93	-54 (-73, -31)
Sea-level rise (low)	69905	21482	-69 (-85, -19)	457	192	-58 (-60, -55)	202	91	-55 (-74, -33)
Sea-level rise (medium)	70101	21146	-70 (-88, -18)	457	194	-58 (-60, -54)	202	91	-55 (-73, -35)
Sea-level rise (high)	69879	21302	-70 (-87, -22)	457	193	-58 (-61, -55)	202	93	-54 (-71, -35)
Urbanization (low)	69942	19320	-72 (-90, -27)	457	183	-60 (-63, -57)	202	81	-60 (-74, -35)
Urbanization (medium)	70049	18872	-73 (-88, -36)	457	177	-61 (-64, -59)	202	77	-62 (-77, -39)
Urbanization (high)	69983	17913	-74 (-91, -35)	457	174	-62 (-65, -59)	202	76	-62 (-76, -42)
Management (high)	70194	21470	-69 (-85, -16)	457	195	-57 (-60, -55)	202	94	-54 (-73, -32)
Management (low)	69894	21280	-70 (-85, -17)	457	192	-58 (-61, -55)	202	89	-56 (-74, -33)
Management (very low)	69993	21238	-70 (-86, -22)	457	186	-59 (-62, -56)	202	82	-59 (-74, -36)
Future condition scenarios									
Low threats	70140	19497	-72 (-89, -16)	457	186	-59 (-62, -57)	202	85	-58 (-74, -37)
Medium threats	69744	18768	-73 (-90, -29)	457	180	-61 (-63, -58)	202	79	-61 (-77, -38)
High threats	69990	19043	-73 (-90, -23)	457	181	-61 (-63, -58)	202	83	-59 (-75, -40)
Management (high) + medium threats	70187	19634	-72 (-89, -13)	457	183	-60 (-62, -57)	202	86	-57 (-74, -38)
Management (low) + medium threats	69976	19463	-72 (-88, -14)	457	178	-61 (-63, -58)	202	77	-62 (-76, -40)
Management (very low) + medium threats	69918	19054	-73 (-90, -21)	457	178	-61 (-64, -58)	202	83	-59 (-75, -39)
Survival (high) + medium threats	69867	23806	-66 (-85, 16)	457	263	-42 (-45, -39)	202	121	-40 (-59, -20)
Survival (low) + medium threats	69688	15545	-78 (-91, -45)	457	116	-75 (-77, -72)	202	52	-75 (-83, -57)
Immigration (very high) + medium threats	69854	70632	1 (-52, 1396)	457	286	-37 (-40, -35)	202	134	-34 (-57, -13)
Immigration (high) + medium threats	70070	33976	-52 (-75, 29)	457	228		202	100	

(continued on next page)

Table 3 (continued)

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	%Δ	Initial	Future	%Δ	Initial	Future	%Δ
Immigration (zero) + medium threats	69866	1573	-98 (-99, -68)	457	80	-50 (-52, -47)	202	50	-50 (-69, -28)
						-82 (-85, -80)			-75 (-88, -52)

3. Results

Linear regression analysis found that fecundity and maturity age vary significantly by MAT across the species' range (Fig. 4). For each 1 °C increase in MAT, we found that maturity age decreased by 1.41 years (0.18–2.62, 95% CI; $P = 0.029$). For each 1 °C increase in MAT, we found that fecundity increased by 0.48 eggs per clutch (0.24–0.72, 95% CI; $P < 0.001$).

Population projection under a 'status quo' scenario predicted that populations would experience a -69% (-85%, -17%; 95% CI) change in total population size, a -58% (-61%, -56%; 95% CI) change in number of populations, and a -55% (-73%, -30%; 95% CI) change in the number of metapopulations (Table 3) over 80 years. Relative to the 'status quo' scenario, populations were most sensitive to perturbation of γ and φ^a the 'very high immigration' and 'high survival' scenarios predicted the highest future numbers of individuals, populations, and metapopulations, while the 'no immigration' and 'very low survival' scenarios drove the greatest reductions in all population metrics. Across the sea-level rise and urbanization scenarios, increasing threat magnitude drove small increases in predicted population declines, while increased climate warming and increased habitat management slightly alleviated population declines. However, the model was not particularly sensitive to variation in climate warming, sea-level rise, urbanization, and habitat management threats relative to scenarios varying in γ and φ^a (Table 3, Fig. 5). Variation in the density-dependent limit on recruitment to the adult age class caused strong effects on the predicted number of individuals but not the number of local populations or metapopulations; increased density-dependent limits allowed greater population size in a few, large populations, but did not influence the persistence of most local populations or metapopulations (Table 3).

Future condition scenarios predicted populations to experience slightly increased declines in the number of individuals, populations, and metapopulations over the next 80 years relative to the 'status quo' scenario (Table 3, Table 4). Among the three scenarios varying in threat magnitude, scenarios predicted between 72% and 73% declines in the number of individuals (range of 95% CI among scenarios [95% CI range]: -90%, -16%), 59–61% declines in number of populations (95% CI range: -63%, -57%), and 58–61% declines in the number of metapopulations (95% CI range: -77%, -37%). Increased habitat management erased a small percentage (ca. 1%) of predicted declines in individuals, populations, and metapopulations relative to the 'medium threat' scenario, while decreased management scenarios contributed to additional predicted declines (Table 3). Scenarios of future change varied in their effect on populations across a regional scale, with greater declines in the number of individuals and the number of local populations predicted for the Western and Central genetic populations relative to the West Georgia, East Georgia, and Florida genetic populations (Supplementary Figure 2).

Categorization of populations by four levels of persistence probability revealed patterns of how varying magnitude of threats and demographic rates influenced persistence probability (Table 4). Variation in future threats and management had little influence on the number of Extremely Likely to Persist populations, while increases in uncertain demographic rates (γ , φ^a) caused increases in the number of Extremely Likely to Persist populations and decreases in Unlikely to Persist populations relative to the 'medium threat' scenario. Spatial visualization of population persistence categories from the 'medium threat with less management' scenario (perhaps the most likely future scenario) illustrated importance of metapopulation structure for persistence probabilities. We observed spatial variation in persistence probabilities where Extremely Likely to Persist or Very Likely to Persist populations tended to occur in metapopulations composed of a relatively large number of local populations (Fig. 6). We also observed geographic variation in persistence probabilities among genetic populations. Specifically, the West Georgia, East Georgia, and Florida genetic populations all possessed local populations and metapopulations that were Extremely Likely to Persist and Very Likely to Persist at 80 years in the future under the 'low management + medium threat' scenario (15 of 97, 11 of 110, and 20 of 158 local populations, respectively), but the Western and Central genetic populations lacked any populations from the top two persistence categories (0 of 51 and 0 of 41 local populations, respectively; Fig. 6).

4. Discussion

We built a multi-site predictive population model for gopher tortoises that accounted for geographic variation and uncertainty in both life history and threats and used a scenario analysis to understand the relative influence of demographic rates and threats for influencing future population redundancy, resiliency, and representation under uncertain future conditions. Using this integrative framework, we observed small, negative effects on future tortoise population conditions due to three threats (sea-level rise, urbanization, decreased habitat management) and small, positive effects from climate warming and increased habitat management. Climate warming exerted a positive effect due to increased reproduction in populations, a hypothesis that was recently supported by an empirical field study (Hunter et al., 2021). However, scenarios with one or more threats did not differ strongly in their predicted effect on population metrics relative to a 'status quo' scenario with no change in future threats. The minimal predicted effects of threats and management on populations may have occurred for a few reasons. For one, the future changes modeled by scenarios may be relatively

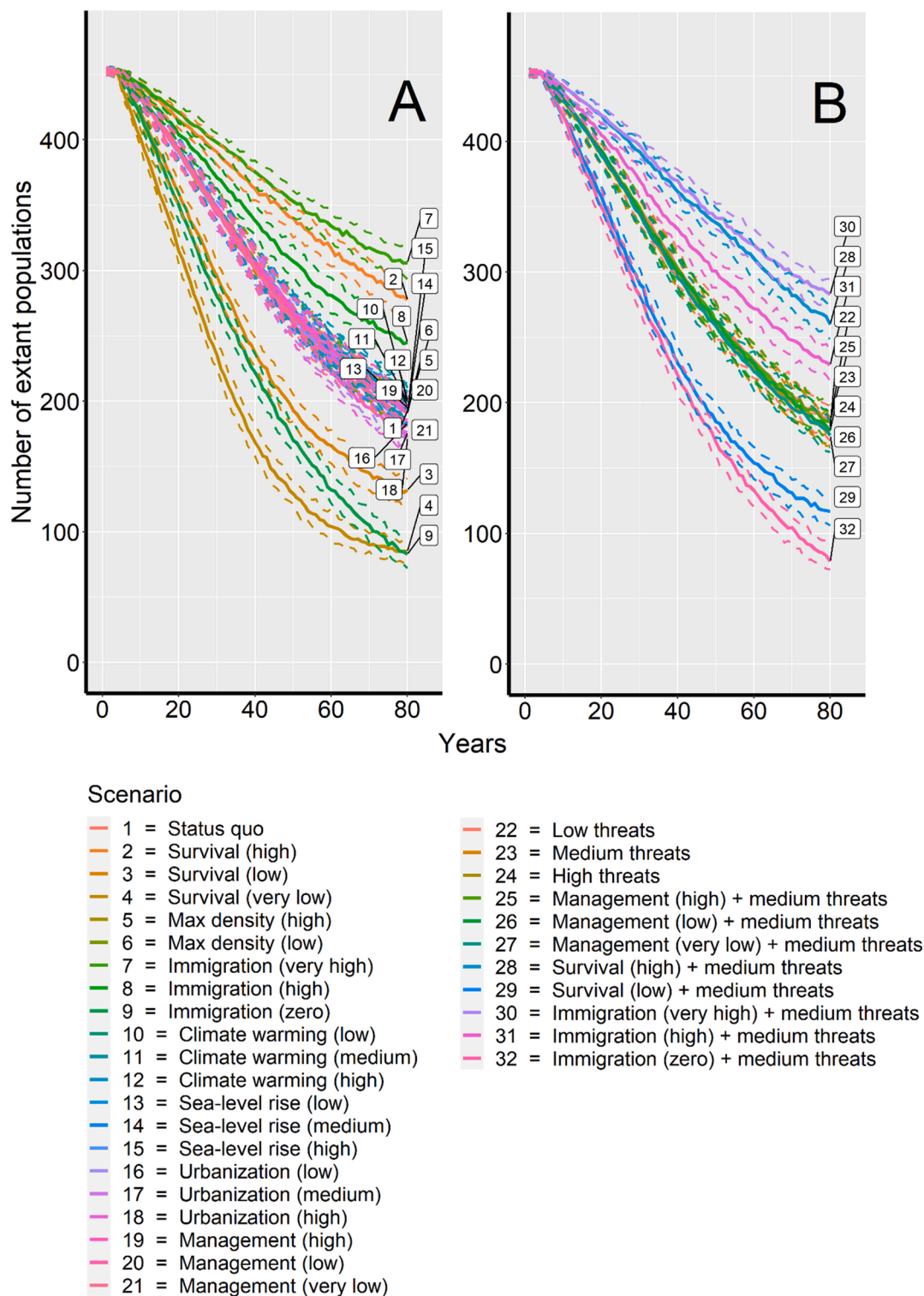


Fig. 5. The number of extant populations through time during simulated projection of 457 populations of gopher tortoises (*Gopherus polyphemus*) over 80 years. Bold lines are mean predictions, dashed lines are 95% confidence intervals, and white labels indicate scenario numbers from the legends. (A) Results from simulations of 21 scenarios, including a ‘status quo’ scenario of current demographic and threat conditions and 20 scenarios varying in single demographic or threat factors relative to the ‘status quo’ scenario (i.e., ‘sensitivity scenarios’). (B) Results from simulations of 11 scenarios that vary in threat levels and two demographic parameters: adult apparent survival and immigration (i.e., ‘future condition scenarios’).

Table 4

Predicted population persistence probabilities (P_p) categories for 457 populations of gopher tortoises (*Gopherus polyphemus*) in year 2100 under future 11 scenarios varying in demographic rates and threats (i.e., ‘future condition scenarios’). Persistence categories are Extremely Likely to Persist ($P_p > 95.0\%$), Very Likely to Persist ($P_p = 80.0\text{--}94.9\%$), More Likely Than Not to Persist ($P_p = 50.0\text{--}79.9\%$), and Unlikely to Persist ($P_p < 50.0\%$; i.e., extirpated). See Table 2 for scenario descriptions.

Scenarios	Extremely Likely to Persist	Very Likely Extant to Persist	More Likely Than Not to Persist	Unlikely to Persist (i.e., Extirpated)
Status quo	28 (6.1%)	28 (6.1%)	102 (22.3%)	299 (65.4%)
Low threats	26 (5.7%)	22 (4.8%)	103 (22.5%)	306 (67%)
Medium threats	24 (5.3%)	22 (4.8%)	102 (22.3%)	309 (67.6%)
High threats	27 (5.9%)	21 (4.6%)	104 (22.8%)	305 (66.7%)
Management (high) + medium threats	25 (5.5%)	24 (5.3%)	110 (24.1%)	298 (65.2%)
Management (low) + medium threats	22 (4.8%)	24 (5.3%)	99 (21.7%)	312 (68.3%)
Management (very low) + medium threats	24 (5.3%)	25 (5.5%)	91 (19.9%)	317 (69.4%)
Survival (high) + medium threats	34 (7.4%)	84 (18.4%)	169 (37%)	170 (37.2%)
Survival (low) + medium threats	20 (4.4%)	12 (2.6%)	39 (8.5%)	386 (84.5%)
Immigration (very high) + medium threats	82 (17.9%)	74 (16.2%)	141 (30.9%)	160 (35%)
Immigration (high) + medium threats	44 (9.6%)	46 (10.1%)	132 (28.9%)	235 (51.4%)
Immigration (zero) + medium threats	0 (0%)	2 (0.4%)	37 (8.1%)	418 (91.5%)

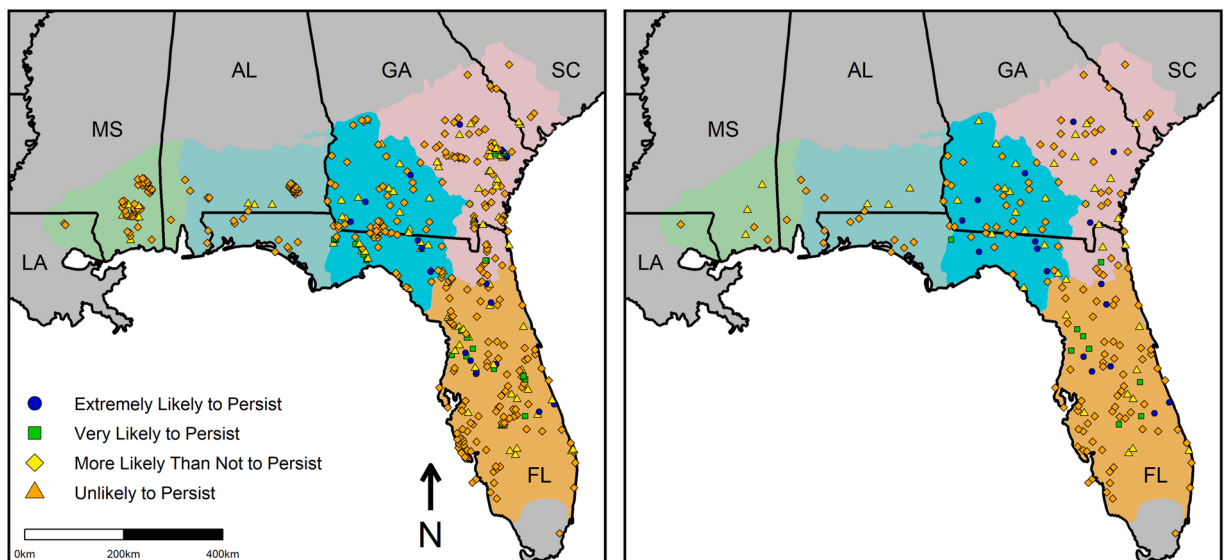


Fig. 6. Persistence probabilities (P_p) of gopher tortoise (*Gopherus polyphemus*) local populations (left) and metapopulations (right) predicted by a future scenario of less habitat management with medium levels of climate warming, sea-level rise, and urbanization (Table 2) projected 80 years into the future. Symbols are colored by persistence probability categories: Extremely Likely to Persist ($P_p \geq 95.0\%$), Very Likely to Persist ($P_p = 80.0\text{--}94.9\%$), More Likely Than Not to Persist ($P_p = 50.0\text{--}79.9\%$), and Unlikely to Persist ($P_p < 50.0\%$; i.e., extirpated); map background colors correspond to five regional genetic populations.

unimportant compared to the current ‘status quo’ conditions of habitat management and connectivity already present at populations, which are predicted to cause considerable population declines over the next 80 years. Alternatively, the predicted effects of threats may have been small if we underestimated their effect size or did not appropriately link the threats to demographic rates in realistic ways to populations.

Rather, population outcomes were more strongly influenced by variation in two demographic rates currently characterized with substantial uncertainty (survival and immigration), which suggests that predictions about tortoise future conditions could benefit most from increased accuracy and reduced uncertainty in estimates of survival and immigration rates. While recent studies have estimated habitat and management effects on gopher tortoise survival (e.g., Howell et al., 2020; Folt et al., 2021; Hunter and Rostal, 2021), modeling site-specific variation in survival across the gopher tortoise’s entire range is a challenging task. We assumed all populations have the potential to be stable and modeled all populations with a baseline survival rate expected under high-quality habitat maintained with prescribed fire management at a regular management return interval. However, future studies may devise stronger ways to model survival and how it varies by habitat type, management frequency, or geographic region (e.g., populations in some southern

areas or habitats may be less reliant on prescribed fire), such that survival estimates more accurately reflect habitat heterogeneity and/or are less uncertain. With respect to immigration, previous demographic models for gopher tortoises have largely ignored including immigration parameters (e.g., [Tuberville et al., 2009](#), [Folt et al., 2021](#)) and modeled tortoise demography as closed to immigration, perhaps due to the paucity of field estimates of immigration in wild populations. These models often predicted population declines, even though recent evidence at some studied populations was more consistent with population stability ([Goessling et al., 2021](#)). This discrepancy suggests a disconnect between demographic projections that are largely influenced by apparent survival projections and actual trends occurring in populations, a discrepancy that may be resolved by incorporating immigration during projection analyses. To this end, we incorporated an immigration parameter, γ , for local populations and found scenarios of 'no immigration' and 'high immigration' predicted results that strongly deviated from results of the threat and management scenarios predictions. Our results suggest that immigration is an important parameter in tortoise demography that may deserve future attention when studying tortoises in the field and building models of tortoise demography in the laboratory. Reduction of uncertainty related to survival and immigration rates might increase predictive accuracy and provide stronger information to support future decisions.

We observed spatial variation in persistence probabilities where Extremely Likely to Persist or Very Likely to Persist populations tended to occur in metapopulations composed of a relatively large number of local populations. This result suggests that groups seeking to manage for resilient tortoise populations with high future persistence probabilities could aim to conserve tortoise populations on large tracts of land that are connected to other populations and managed for open, high-quality habitat for gopher tortoises ([Howell et al., 2020](#)). Similarly, increased urbanization will decrease connectivity, habitat quality (through decreased management at the urban-wildland interface), and immigration among populations, so conservation planning strategies could emphasize securing connectivity of existing local populations through strategic land acquisitions or partnerships ([Ashrafzadeh et al., 2020](#)).

While the number of individuals, populations, and metapopulations were predicted to decline across most scenarios, overall projections suggest that overall extinction risk for the gopher tortoise is low in the future. Of the populations modeled here (a subset of populations that exist in nature), the 'low management + medium threat' scenario predicted the presence of ca. 19,000 females persisting among 202 local populations and 78 metapopulations in year 2100. The persistence of relatively large numbers of individuals and populations suggests resiliency of the species in the face of global change and redundancy to buffer from future catastrophic events. However, our analysis predicted geographic variation in future population conditions, with the Western and Central genetic populations predicted to experience greater reductions in population redundancy and resiliency relative to the Georgia and Florida genetic populations. For example, the Western and Central genetic populations were predicted to have less than 18 and 12 local populations, respectively, in year 2100 under the 'low management + medium threats' scenario, and none of those populations were predicted to have a high persistence probability ($P_p \geq 0.75$). Such large reductions in the number of populations and low persistence probabilities in the Western and Central genetic populations suggests decreased genetic representation range-wide in the future. Notably, the Western genetic population includes all the gopher tortoise populations that currently receive federal protection as 'Threatened' under the ESA (US Fish and Service, 1987). These results are useful to decision makers that are interested in understanding the risk of losing population redundancy and resiliency among genetic populations across the species' range.

We sought to build a population modeling framework that accounted for important elements of population viability analyses, such as clear objectives, detailed demographic data and knowledge of life history, temporal stochasticity, parametric uncertainty, density dependence, relevant extrinsic factors (i.e., threats), sensitivity analysis, and uncertainty in future conditions ([Chaudhary and Oli, 2020](#)). However, like all models, our framework has limitations and opportunities for improvement. Our model was sensitive to immigration, a parameter that we estimated from a single study of tortoise movement in which 2 of 123 individuals emigrated from a study area ([Ott-Eubanks et al., 2003](#)). We modeled demography as an effect of predicted values of climate warming and fire management at broad spatial scales and made broad assumptions about baseline survival rates being constant across the species' range. Future models could evaluate regional variation in effects of warming and fire management for more realistic predictions of threat effects at more detailed spatial scales and seek to model survival as varying among local populations due to covariates, such as habitat quality. Our model also focused on simulating the fate of known populations and did not estimate the formation of new populations or project the abundance of existing populations not included in the data provided by our partners. Therefore, future predictions for persistence of local populations and metapopulations described here were constrained by an upper limit of initial inputs (457 local populations, 202 metapopulations) and therefore were unable to exceed these limits.

While our model cannot provide perfect predictions of future population persistence of gopher tortoises, we do believe the predictions will be useful in supporting decisions ([Lawson et al., 2021](#)) for how to conserve and manage gopher tortoises and is specifically useful for the impending listing decision for the species under the ESA. Our analysis provides a transparent and repeatable assessment of how threats and management actions may influence future population growth, overall extinction risk of both local and regional genetic populations, and how uncertainty in important input parameters (e.g., immigration, survival) influences predictions. Our paper illustrates a framework for how future conditions analyses that evaluate predicted population trends for Species Status Assessments and other endangered species risk assessments can incorporate multiple extrinsic threats during projection analyses to estimate resiliency, redundancy, and representation of populations in the future.

5. Conclusions

Imperiled species face numerous and diverse anthropogenic threats to their persistence, and conservation decisions benefit from a sound understanding of how populations, species, and ecosystems will respond to future changes in threats. Our analytical framework demonstrates an approach to link predictions from multiple, diverse, spatially-explicit threats to demographic vital rates of imperiled species, which permits predictions for how population conditions will be influenced under plausible scenarios of future change.

Plausible future scenarios of global change for the gopher tortoise suggest that the species will decline in number and size of populations and that populations are less likely to persist in two of the regional population genetic units across the species' range. Predictions were sensitive to variation in survival and immigration, and increased accuracy and reduced uncertainty of these variables could increase the usefulness of future predictions. Our approach provides a useful framework for risk assessments for other widely distributed, imperiled species with geographic variation in demographic rates and threats that require predictions about future populations conditions to support conservation and management decisions.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02143](https://doi.org/10.1016/j.gecco.2022.e02143).

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