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Estimating population persistence for at-risk species using citizen science data



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ABSTRACT

Population persistence probability is valuable for characterizing risk to species and informing listing and conservation decisions but is challenging to estimate through traditional methods for rare, data-limited species. Modeling approaches have used citizen science data to mitigate data limitations of focal species and better estimate parameters such as occupancy and detection, but their use to estimate persistence and inform conservation decisions is limited. We developed an approach to estimate persistence using only occurrence records of the target species and citizen science occurrence data of non-target species to account for search effort and imperfect detection. We applied the approach to a highly cryptic and data-limited species, the southern hognose snake (Heterodon simus), as part of its USFWS Species Status Assessment, and estimated current (in 2018) and future persistence under plausible scenarios of varying levels of urbanization, sea level rise, and management. Of 222 known populations, 133 (60%) are likely extirpated currently (persistence probability < 50%), and 165 (74%) populations are likely to be extirpated by 2080 with no additional management. Future management scenarios that included strategies to acquire and improve habitat on currently unprotected lands with existing populations lessened the estimated rate of population declines. These results can directly inform listing decisions and conservation planning for the southern hognose snake by Federal, State, and other partners. Our approach – using occurrence records and auxiliary data from non-target species to estimate population persistence - is applicable across rare and at-risk species for evaluating extinction risk with limited data and prioritizing management actions.

1. Introduction

The designation of species' conservation statuses has become a primary tool for international, national, and local organizations to influence regulatory legislation, inform conservation planning across species' ranges, and prioritize limited funding for management and research (Rodrigues et al., 2006; Miller et al., 2007; Rodríguez et al., 2011; Sutherland and deMaynadier, 2012; Pickens et al., 2017b). Most processes used to designate species' statuses hinge on evaluation methods intended to be repeatable and transparent, the best available scientific information, and standardized criteria that relate status to extinction risk (Miller et al., 2007; Rodríguez et al., 2011; Smith et al., 2018). For example, the U.S. Fish and Wildlife Service (USFWS) uses a standardized approach known as the Species Status Assessment (SSA) to

inform status decisions for each species petitioned for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2016; Smith et al., 2018). SSAs – and often other approaches used to designate species' statuses – require predicting species' risk of extinction under current conditions and potential future scenarios based on available scientific information (Larson et al., 2004; McGowan et al., 2017; Smith et al., 2018). However, data are often limited for many rare or declining species on which these efforts focus, which makes quantitative estimates of extinction risk difficult or impossible to obtain. These limitations can subsequently lead to assessment methods that lack transparency or replicability, vague or highly uncertain predictions about species' statuses, and decisions that are vulnerable to litigation (Regan et al., 2013; Lowell and Kelly, 2016; Murphy and Weiland, 2016; Smith et al., 2018).

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Characterizing species' statuses with rigorous estimates of extinction risk (or its complement, persistence probability) can be hindered by the quality and quantity of data available. One traditional approach is population viability analysis (PVA) that estimates metrics of persistence or abundance over a decision-relevant time frame (Beissinger and Westphal, 1998; Akçakaya and Sjögren-Gulve, 2000; Morris et al., 2002; McGowan et al., 2017), but PVA relies on species' demographic rates (e.g., survival and recruitment) estimated from high quality data from systematic methods, such as capture-mark-recapture or distance sampling (Lebreton et al., 1992; Engler et al., 2004; Marshall et al., 2004). Data sufficient for estimating demographic rates are often unavailable for many species even at local scales. Occupancy modeling is another approach used to estimate population extinction risk with detection-non-detection data from repeated samples when more intensive data (e.g., capture-mark-recapture) or demographic estimates are too challenging or costly to obtain (MacKenzie et al., 2002; Royle and Kéry, 2007; Kéry et al., 2010). However, datasets for many at-risk species are collected opportunistically (Wolf et al., 2015) and lack the sampling design required for occupancy modeling. Collecting high quality data to conduct PVA, occupancy modeling, or additional approaches allows for estimating persistence while also accounting for imperfect detection (i.e., separating variation of underlying demographic processes of interest with observation error in the data: MacKenzie et al., 2002; Kery et al., 2009). Not accounting for imperfect detection can result in biased or imprecise estimates, especially for secretive, data-poor species (MacKenzie et al., 2003; Clark and Bjørnstad, 2004; Kery et al., 2009; Zipkin et al., 2014). An additional challenge for predicting statuses of species is that data should ideally be collected across broad spatial extents (i.e., the species' range) and at multiple points in time. It is inherently difficult and costly to collect demographic data useful for estimating persistence over large spatial scales. Studies for many at-risk species commonly collect data from only a small portion of the species' range, even though demographic rates can vary geographically. This variation in demographic rates should be accounted for when estimating range-wide persistence (e.g., Tuberville et al., 2009; Bonnot et al., 2011). Faced with these challenges, Wolf et al. (2015) contended that estimating persistence was too data-intensive for most at-risk species using approaches such as PVA. Thus, novel approaches are needed that use available datasets to better quantify persistence at a range-wide scale for at-risk species and inform subsequent listing and conservation decisions.

Citizen science data have been increasingly collected and applied to ecological and conservation contexts in recent years to mitigate data gaps and improve estimation of metrics of interest (Dickinson et al., 2012). One of the most common forms of citizen science data is georeferenced species occurrence records from opportunistic surveys (also called atlas data), which is collected at large spatial scales, verified by species experts, and stored on web-based platforms, such as iNaturalist (www.inaturalist.org), eBird (https://ebird.org), and HerpMapper (www.herpmapper.org: HerpMapper, 2018). Modeling distributions or habitat suitability for focal species requires a sufficient number of occurrence records distributed across the species' range (Elith and Leathwick, 2009; Franklin, 2010), so citizen science data can supplement those contained in State-maintained or other databases (e.g., natural heritage programs: Groves et al., 1995). Because robust absence information is often unavailable, several species distribution modeling studies have begun using citizen science datasets collected for "nontarget" species (i.e., those observed while in search of a focal species) as "inferred absences" of the focal species, which has improved the accuracy of model estimates of species presence (e.g., Phillips et al., 2009; Stratmann et al., 2016; Bradter et al., 2018). Occupancy modeling studies have also incorporated citizen science data from systematic, repeated surveys to capture search effort, account for imperfect detection, and improve estimates of population extinction and colonization (e.g., Kéry et al., 2010; Peach et al., 2017). Integrated population models can also be used to combine occurrence data from citizen scientists with mark-recapture and productivity data from formal sampling efforts to estimate population trends (Robinson et al., 2018; Zipkin and Saunders, 2018). Still, more opportunities exist for incorporating citizen science data into models estimating persistence for at-risk species in order to overcome common challenges of limited data and imperfect detection and better assess species' statuses.

This study developed a novel approach to estimate persistence and characterize the range-wide status of an at-risk species under current and future conditions using only occurrence records of the target species and citizen science data of non-target species. Current conditions reflect those at the time of the study (in 2018). Specifically, we developed and applied the approach to a small, highly cryptic, and datalimited species in the southeastern U.S., the southern hognose snake (Heterodon simus), as part of its SSA (U.S. Fish and Wildlife Service, 2019). Our objectives were (i) to estimate the probability of persistence for each of 222 populations under current conditions while accounting for imperfect detection with citizen science observations of non-target snake species, and (ii) to project population persistence into the year 2080 under scenarios representing plausible future conditions of urbanization, sea level rise, and broad management strategies. This analysis builds on previous research predicting habitat suitability across the southern hognose snake's range (Crawford et al., 2020). We used habitat suitability as a predictor of current population persistence in 2018 and linked changes in habitat suitability from stressors and management to future persistence. In alignment with the SSA framework (Smith et al., 2018), we employed the conservation biology principles of resiliency, redundancy, and representation (the "3Rs") when designing the analysis and summarizing results. In short, resiliency describes the condition of populations and their ability to persist over time using attributes such as population growth rate; redundancy describes the number and distribution of populations and is related to the species' ability to withstand large-scale catastrophic events; and representation describes the breadth of genetic diversity or ecological settings occupied by the species (Shaffer and Stein, 2000; Wolf et al., 2015; Smith et al., 2018). We evaluated southern hognose snake resiliency using population persistence probabilities, redundancy using the number and spatial distribution of populations predicted to persist based on a range of probability thresholds, and representation using the number of populations predicted to persist in each of nine representative units (unique ecological settings). The results from this study can directly inform listing decisions and conservation planning for the southern hognose snake by Federal, State, and other partners. Our approach - using occurrence records and auxiliary data from nontarget species to estimate population persistence - is applicable across rare, data-limited species, including many at-risk species in need of conservation status designations in the U.S. or internationally (e.g., for the International Union for Conservation of Nature Red List), for evaluating extinction risk and prioritizing threats and management actions.

2. Methods

We went through the following steps when conducting this analysis and describe each step in more detail in the sections below. First, we gathered a comprehensive dataset of southern hognose snake occurrence records and delineated population boundaries and representative units based on clusters of these records (Section 2.1). We also extracted spatial metrics of current conditions (e.g., mean habitat suitability) for each population in this step to use later as predictors of persistence. Second, we gathered occurrence records for other snake species (nontarget species) commonly observed in southern hognose snake habitats that were found within population boundaries to represent search effort (Section 2.2). Third, we constructed a persistence model to estimate current population persistence that leveraged southern hognose snake detection histories and search effort histories of non-target species to account for imperfect detection (Section 2.3). Fourth, we created seven scenarios of stressors and management representing a range of plausible

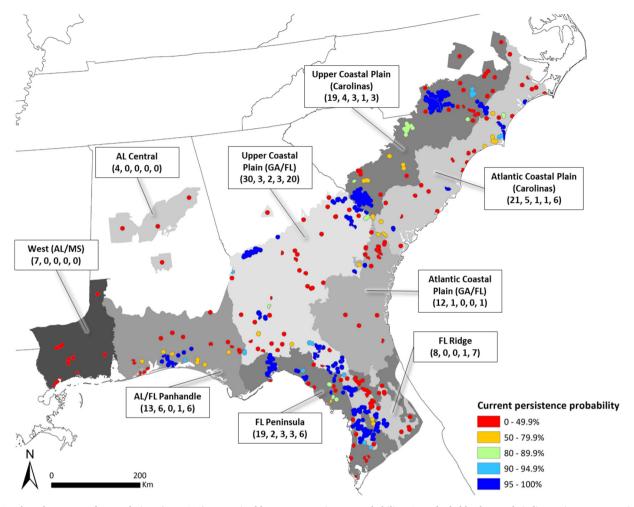


Fig. 1. Southern hognose snake populations (N = 222) categorized by current persistence probability. Grey shaded backgrounds indicate nine representative units across the species' range. Boxes indicate the unit name and number of populations in the unit in each of the five persistence categories (from 0–49% [left] to 95–100% [right]) shown in the legend.

future conditions for the species; we then constructed a projection model to forecast population persistence through 2080 under each scenario, given current population persistence and predicted changes in habitat (Section 2.4). Lastly, we summarized results by representative unit and range-wide currently (in 2018) and in 2080 to characterize the species' status using resiliency, redundancy, and representation (see Section 3. Results). We performed all spatial analyses in ArcGIS version 10.4 (ESRI, Redlands, CA) and statistical analyses in R version 3.5.3 (R Core Team, 2019).

2.1. Target species, populations, and representative units

The southern hognose snake is a small terrestrial species found in the Coastal Plain region of the southeastern U.S. in portions of North Carolina, South Carolina, Georgia, Florida, and west to Alabama and Mississippi (Fig. 1: Tuberville et al., 2000; U.S. Fish and Wildlife Service, 2019). In addition to substantial habitat loss, fragmentation, and degradation caused by infrequent fire of longleaf pine (*Pinus palustris*) systems (Outcalt and Sheffield, 1996), threats to the species include spread of invasive species such as the red imported fire ant (*Solenopsis invicta*), road mortality, and other factors (Gibbons et al., 2000; Tuberville et al., 2000; Beane et al., 2014). The southern hognose snake is highly cryptic with low rates of detection (Steen et al., 2012), which has made it challenging to explicitly estimate demographic rates, population trends, or effects of threats (Beane et al., 2014; Willson et al., 2018). Only a few, localized studies have been able to estimate

certain demographic rates and population densities for this species using road surveys and radio-tracking of a few individuals (Enge and Wood, 2002; Beane et al., 2014; Willson et al., 2018). Tuberville et al. (2000) conducted a range-wide review of published information and species occurrence records to identify qualitative trends in distribution of occupied areas, and evidence suggested population extirpations are likely to have occurred across a large portion of the species' range while other populations appeared stable at the time. The USFWS was petitioned to list the southern hognose snake in July 2012 and subsequently published a 90-day finding indicating that listing may be warranted for the species (80 FR 37568, July 1, 2015). In 2019, the USFWS conducted an SSA to formally assess the species' viability using the best available scientific data despite the limited data available for the species.

We compiled a geospatial database of southern hognose snake occurrence records from datasets maintained by natural heritage programs, USFWS, U.S. Forest Service (USFS), U.S. Department of Defense (DoD), State agencies, academic researchers, and HerpMapper (HerpMapper, 2018). We note that all species records submitted to HerpMapper were validated by professional herpetologists. Records included opportunistic sightings, as well as observations from systematic studies from trained researchers (e.g., Enge et al., 2014).

Next, we created population boundaries around occurrence records. Delineating populations ideally relies on information about genetics, home ranges, or dispersal distances, but this does not exist for the southern hognose snake. Therefore, we buffered all records by 5 km, joined overlapping buffers to represent the same population, and

Table 1
List of predictors used to model southern hognose snake population persistence, the hypothesized relationships to population resilience, and the average and range of predictors across 204 populations modeled.

Site condition predictor	Biological justification	Mean (range)
Habitat suitability index (HSI)	Higher habitat suitability represents areas of higher quality (well-drained, sandy soils, compatible forest/grassland landcover, frequent fires) that should increase southern hognose snake survival, recruitment, and persistence. The average HSI within a population boundary is highly correlated to the amount of suitable habitat. See Crawford et al. (2020).	22% (0-83.2%)
Percentage protected	Higher percentages of area within a population's boundary in protected status should increase habitat quality through regular management practices and may limit direct threats such as road mortality and collection.	21.1% (0–100%)
No. of populations within 10 km	Populations close to (within 10 km) other populations may have a higher chance of long-term persistence. Nearby populations may provide opportunities for "rescue" where recolonization can occur after a catastrophe; alternatively, nearby populations could provide a signal that there are localized conditions (e.g., geological, climatic) that promote population persistence that have not been otherwise captured in our analyses.	1.8 (0–7)

divided population boundaries by large (6th order or higher) rivers and major highways that likely represent barriers to southern hognose snake movement. We based these methods on species expert input and NatureServe protocols for defining populations for small terrestrial snakes (NatureServe, 2018). Using population boundaries, we conducted spatial analyses and extracted three population-specific metrics to use as predictors in the persistence model: (1) mean Habitat Suitability Index (HSI), that was derived from the work of Crawford et al. (2020), where HSI was positively influenced by the amount of welldrained soil, compatible land cover, and fire frequency in a focal area, (2) percentage of area within the population boundary on protected lands, and (3) the number of additional populations within 10 km (Table 1). We defined all areas as protected if they were found in the U.S. Geological Survey (USGS) Protected Areas Database (http://www. protectedlands.net/), as well as State-maintained conservation lands databases, and these databases included publicly-owned and managed lands as well as private lands registered in State or Federal programs where natural resource conservation is one of the management goals. For further spatial processing details, see U.S. Fish and Wildlife Service (2019, section 4.1.2, Appendix A).

We delineated nine subdivisions of the range (hereafter, representative units: Fig. 1) in collaboration with species experts to represent variation in ecological roles of the species across its range. Units were based on EPA IV ecoregions (U.S. Environmental Protection Agency, 2017) that were grouped by similar ecological characteristics (e.g., soil, geology) and divided by the Savannah, Chattahoochee, and Mobile-Tombigbee Rivers.

Lastly, we assigned the appropriate population ID and representative unit ID for each southern hognose snake record. From these records, we created detection histories (denoted as $y_{i,t}$) describing if at least one individual was observed in a population i in a given year t ($y_{i,t} = 1$, 0 otherwise) to model persistence (see Section 2.3).

2.2. Non-target species data collection

Models estimating persistence or other demographic parameters typically rely on non-detection information - i.e., when searches occurred but the target species was not observed - to account for imperfect detection (MacKenzie et al., 2002; Kery et al., 2009; Kery and Schaub, 2012). However, robust absence or search effort data do not exist for the southern hognose snake. Therefore, we developed a search effort index to estimate detection from citizen-collected occurrence records of southern hognose snakes and other non-target snake species commonly observed in southern hognose snake habitats obtained from HerpMapper and other partners (hereafter search effort dataset). We developed a list of 13 non-target species most commonly observed while surveying for southern hognose snakes that are active during the same months of peak activity (May, June, September, and October): Agkistrodon contortrix subspp., Agkistrodon piscivorus subspp., Cemophora coccinea subspp., Coluber constrictor subspp., Crotalus adamanteus, Crotalus horridus, Lampropeltis getula subspp., Masticophis flagellum subspp.,

Opheodrys aestivus subspp., Pantherophis guttatus, Pantherophis obsoletus subspp., Pituophis melanoleucus subspp., and Thamnophis sirtalis subspp. (multiple experts, pers. comm.). We queried HerpMapper and accessed 11,631 records of these snake species within the study extent. These records included data on observer name and date of observation. We added 1522 Florida pine snake (Pituophis melanoleucus mugitus) records collected during a previous study (Crawford et al., 2020) and all southern hognose snake records, since these also indicated search events, to the search effort dataset. Snake datasets included records collected between 1880 and 2018 that we used to create a search effort index

We assigned the appropriate population ID to each record in the search effort dataset and removed any record falling outside of any population boundary, which left 5473 records. We noticed occasions in the HerpMapper data where the same observer would submit multiple records from the same date. In order to better capture the number of search events and create an index of search effort, we filtered the search effort dataset to remove duplicate records coming from the same observer on the same date. Thus, the final dataset represented unique searches by individuals, which we refer to as observer-days, and included 3825 observer-days in total. We then followed the same process used to create detection histories of southern hognose snakes to create search effort histories for each population. Search effort histories ($s_{i,t}$) described the number of observer-days for population i in year t. Lastly, we scaled all search effort values so they were centered on 0 for use in the persistence model.

Records of non-target snake species that fell within a given population boundary indicate that the area was searched by an individual in a given year and informed the likelihood a population is still persisting. In using non-target species data, we made the following assumptions: (i) non-target records indicated an event when an area known to have southern hognose snakes at some time was searched, (ii) the search was performed in a way that southern hognose snakes could be observed (e.g., road surveys), and (iii) when a person submitted non-target records but not southern hognose snake records to HerpMapper after a search, this indicated the area was searched but no southern hognose snake was found (i.e., we assumed southern hognose snakes would be reported if found).

2.3. Current persistence model

We developed a model (hereafter, persistence model) to estimate trends in southern hognose snake populations and derive probabilities that each population in the species' range persists currently in 2018. We adapted the Cormack-Jolly-Seber model (Lebreton et al., 1992; Brooks et al., 2000), designed to estimate survival of individual animals based on mark-recapture data, to analogously estimate persistence ("survival") of populations based on their detection histories. We applied a state-space formulation fitted in a Bayesian framework (Kery and Schaub, 2012) to estimate the annual population persistence probability ($\varphi_{i,t}$) and detection probability ($p_{i,t}$), given the population was

still persisting in year t.

We modeled the persistence state history $(z_{i,t})$ of a population over the period from 1950 to 2018. Although 55 southern hognose snake records (2.5% of total records in dataset) were found between 1880 and 1950, fitting the model to this full time period would have been computationally difficult. We modeled state histories of populations using a Bernoulli trial with an annual population-specific persistence probability $\varphi_{i,t}$, where a population could either persist $(z_{i,t} = 1)$ or become extirpated $(z_{i,t} = 0)$, given that it persisted the year before $(z_{i,t-1} = 1)$. We assigned each population a state of $z_{i,1} = 1$ (representing the first year [1950] in the model time frame) and assumed that any area where southern hognose snakes have ever been observed had a population persisting at that location in 1950. We also assumed each population had persisted each year $(z_{i,t} = 1)$ between 1950 and the year of last observation and supplied these known states as data in the model. The model then predicted z states each year after the year of last observation. The prediction of a z state in any year following a final sighting is a random outcome of the model (0 or 1) and is a deterministic outcome (1) for years prior to and including the final year when snakes were observed. We modeled the observation process of detecting at least one southern hognose snake in a population in a given year $(y_{i,t} = 1, 0)$ otherwise), conditional on the population still persisting as a Bernoulli trial with probability $p_{i,t}$.

This framework required a few key assumptions. Importantly, our model lacked a recolonization mechanism typical of occupancy models (MacKenzie et al., 2003; Kéry et al., 2010), as preliminary models that included a recolonization parameter showed poor convergence and produced unreliable estimates. Although not including recolonization could lead to underestimates of persistence, our study focused on a small, terrestrial snake and defined population boundaries relatively larger than the small home ranges and movement distances suspected for the species (SSA experts, pers. comm.; Beane et al., 2014; Willson et al., 2018). In this context, it is reasonable to assume colonization rates are negligible. It is also reasonable to assume populations persisted between 1950 and the year of last observation. The species has relatively low dispersal distances and is very difficult to detect (Beane et al., 2014; Willson et al., 2018), so it seems more likely that populations not discovered until after 1950 had simply persisted undetected in 1950 rather than had colonized the area more recently through immigration.

We modeled persistence as a logit-linear function of a population's representative unit and spatial conditions using the relationship

$$logit(\varphi_{i,t}) = \mu_{rep} + \beta_{HSI} X 1_{i,t} + \beta_{protect} X 2_{i,t} + \beta_{near} X 3_{i,t}$$
(1)

where estimated parameters were μ_{rep} (representative unit-specific intercept), β_{HSI} (fixed effect for mean HSI), $\beta_{protect}$ (fixed effect for percentage of a population boundary on protected lands), and β_{near} (fixed effect for number of nearby populations), and $X1-3_{i,t}$ were spatial condition data. We note that spatial condition data did not vary by time in the current persistence model but were allowed to vary annually when projecting future conditions (see Section 2.4). We assumed that spatial conditions, which were derived from relatively recent datasets (see Crawford et al., 2020), are representative of conditions that have influenced persistence since 1950. We modeled detection as a logit-linear function of a long-term trend and search effort using the relationship

$$logit(p_{i,t}) = \mu_{mean} + \beta_{trend}t + \beta_{effort}s_{i,t}$$
(2)

where estimated parameters were μ_{mean} (intercept), β_{trend} (fixed effect for a linear temporal trend in detection), and β_{effort} (fixed effect for search effort). Predictors were year, t, and search effort history, $s_{i,t}$ (scaled number of observer-days), specific to that population and year. We included the trend effect to allow mean detection to change over time, given that the quality of search effort may be higher in recent years due to more easily accessible information on where and how to

search for snake species.

We used standard practices for fitting Bayesian models following Kery and Schaub (2012). We fit the persistence model with Markov chain Monte Carlo (MCMC) methods in Jags called from R via the R2jags package (Su and Yajima, 2012). We assigned diffuse prior distributions for all parameters, and we generated three MCMC chains using 100,000 iterations where we retained every third iteration from the last 50,000 iterations, yielding a final set of 50,001 samples from posterior distributions of the parameters. We assessed convergence for all models by visually inspecting chain mixing in MCMC trace plots, confirming unimodality in posterior distribution plots, and assessing if Brooks-Gelman-Rubin statistics < 1.1 for all parameters. We assessed model fit by conducting posterior predictive checks (Gelman et al., 2000). For the latter technique, we simulated datasets using parameters estimated in the model, calculated the mean number of populations with simulated detections of southern hognose snakes in three time periods (1970-1974, 2000-2004, and 2014-2018), and compared mean observations in these periods from the real dataset with values from simulated datasets. We based parameter inferences on posterior means and 95% Bayesian credible intervals (BCIs; 2.5th-97.5th percentile of the distribution) and interpreted parameters as having ecologically important impacts when BCIs did not overlap 0.

We used model outputs to characterize range-wide resiliency, redundancy, and representation for the southern hognose snake. We estimated population-specific resiliency as the probability that each population persisted in 2018 (t = 69) by calculating the percentage of model iterations where $z_{i,69} = 1$. We interpret this value as the probability a population has persisted through the entire time period modeled (hereafter, current persistence), and we note that this value differs from $\varphi_{i,t}$ (annual persistence) estimated in the model that reflects the probability a population will persist into the next year. We further assessed redundancy and representation by summing the number of populations predicted to persist in 2018 within each representative unit and range-wide in each iteration of the model and then used all model iterations to calculate the mean (the most likely prediction) and 95% BCIs for the predicted number of persisting populations in 2018. Because status assessments and conservation planning involve making value judgments related to risk tolerance, we summarized results using a range of persistence probability thresholds that may aid users in evaluating species conditions. We grouped populations based on current persistence probabilities into the following five categories: unlikely to persist or "extirpated" (persistence < 50%), more likely than not on landscape (50-79%), very likely on landscape (80-89%), highly likely on landscape (90-95%), and extremely likely on landscape or "extant" (95-100%). We characterized redundancy using the number of populations above a certain persistence threshold range-wide. We characterized representation using the number of populations above a certain persistence threshold in each representative unit, as well as the spatial distribution of extant populations relative to the historical species range. We also note that the laws of probability make it so this mean number of persisting populations (calculated using all model iterations) approximately equals the number of populations with a 50% or greater persistence probability.

2.4. Future projection model

We developed a projection model that used a Markovian process to predict the probability of persistence for each population through 2080 based on the current probability of persistence and future predicted changes in habitat suitability and land protection, given conditions specified in seven plausible scenarios of stressors and management strategies (Table 2). The first three scenarios projected persistence under varying levels of future stressors (threats) with current management conditions continuing; the last four scenarios used the most likely level of future stressors and varying levels of management effort.

Across scenarios, we considered several processes that may

Table 2
List of seven scenarios used to project future habitat suitability and population persistence for the southern hognose snake. The last four scenarios are ordered from lowest to highest relative effort. Note: sea level rise represents inundation levels at 2080.

Scenario name	Urbanization	Sea level rise	Management level
Low stressors	Low (90%)	Low (1 ft. [0.3 m])	Status quo
Medium stressors	Medium (50%) (most	Medium (3 ft. [0.9 m])	Status quo
	likely)	(most likely)	
High stressors	High (10%)	High (6 ft. [1.8 m])	Status Quo
Decreased management	Medium (50%) (most	Medium (3 ft) (most	Decreased management effort on protected lands by decreasing fire frequency by 20%
	likely)	likely)	(one fewer burn every 5 years).
Improved management	Medium (50%) (most	Medium (3 ft) (most	Increased management effort on protected lands by increasing fire frequency by 20% (one
	likely)	likely)	extra burn every 5 years).
Protect more populations	Medium (50%) (most	Medium (3 ft) (most	Acquire, protect, and improve additional land within population boundaries for those
	likely)	likely)	populations that are very likely to currently persist (> 80% current persistence
			probability) but are not currently protected, and improve mgmt. on all protected lands by
			increasing fire frequency by one extra burn every 5 years.
Protect even more populations	Medium (50%) (most	Medium (3 ft) (most	Acquire, protect, and improve additional land within population boundaries for those
	likely)	likely)	populations that are more likely than not to persist (> 50% current persistence
			probability) but are not currently protected, and improve mgmt. on all protected lands by
			increasing fire frequency by one extra burn every 5 years.

influence future habitat suitability and population persistence of the southern hognose snake and used spatial analyses to capture changes in land cover and fire frequency rasters (developed in Crawford et al., 2020). Specifically, we captured the effects of future urbanization and sea level rise on compatible land cover within population boundaries. We represented low, medium, and high levels of urbanization using areas predicted to have a 0.9, 0.5, and 0.1 probability of being developed by 2080, respectively, in the Slope, Land cover, Exclusion, Urbanization, Transportation, and Hillshade (SLEUTH) model (Chaudhuri and Clarke, 2013; Terando et al., 2014). Thus, the scenario using a low level of urbanization only considered areas to be urbanized in the future if the SLEUTH model predicted this with a 90% or greater probability; the scenario using a high level of urbanization included additional areas predicted to be developed with a lower (10% or greater) probability. We represented low, medium, and high levels of sea level rise using coastal areas in NOAA's spatial datasets (https://coast.noaa.gov/slr/; accessed 15 Nov 2018) predicted to be lost by 2080 to inundation heights of 1, 3, and 6 ft. (0.3, 0.9, 1.8 m), respectively. We removed any areas currently classified as compatible land that overlapped future areas of urbanization and sea level rise by 2080 and interpolated annual habitat loss each year between 2018 and then. We also captured the effects of urbanization on fire frequency. This was done to account for fire exclusion/suppression that often occurs in habitat adjacent to urban areas, known as the wildland-urban interface, due to safety and smoke management restrictions (Theobald and Romme, 2007). Studies have found evidence of fire exclusion/suppression in habitats within 600 m to 5 km of urban areas (Theobald and Romme, 2007; Pickens et al., 2017a). Therefore, we chose a moderate value of 3.2 km (2 mi) to capture the interaction between urbanization and fire frequency. Using the areas predicted to be urbanized under low, medium, and high scenarios, we applied a distance-weighted reduction in fire frequency to the current fire raster where the value of any cell in a future urban area was reduced by 100%, the value of any cell between 0 and 3.2 km away from an urban area was reduced proportionally to its distance, and the value of any cell further than 3.2 km away from an urban area was unchanged.

We made additional changes to spatial layers to capture the effects of the last four scenarios varying in management practices, which range from lowest to highest relative management effort. In the "Decreased Management" scenario, we decreased future fire frequency by 20% on protected lands to simulate the equivalent of applying one less prescribed burn every five years in these areas, representing cost or other logistical constraints to prescribed burning in the future. In the "Improved Management" scenario, we increased future fire frequency by 20% on protected lands to simulate applying one additional fire every five years in these areas. In the "Protect More Populations"

scenario, we represented conditions where current management efforts, including State-level parcel acquisition and regional longleaf pine restoration facilitated by the Longleaf Alliance (a non-governmental organization), continue and increase in the future. We selected populations that are very likely to currently persist (≥80% current persistence probability) but are not currently protected (< 10% on protected land) and simulated the following changes: (i) we changed the percentage of the population on protected land to 90% to simulate protecting the majority of land within the population boundary, (ii) we increased the percentage of compatible land cover by 10% to simulate restoring habitat in the population area, and (iii) we increased future fire frequency on protected lands to simulate applying one additional fire every five years in these areas. In the "Protect Even More Populations" scenario (the most intensive and costly management scenario), we simulated the same changes as the previous scenario except we selected populations that are more likely than not to persist (> 50% current persistence probability) but are not currently protected (< 10% on protected land). See U.S. Fish and Wildlife Service (2019, Section 5.1.2) for additional information on future scenarios.

We built a multi-loop stochastic simulation model (following McGowan et al., 2014) that allowed us to simulate thousands of replicates of each population under different scenarios and examine the relationship between threats and management with future persistence. This approach accounted for random year-to-year stochasticity as well as uncertainty around rates (i.e., annual persistence probability) estimated from the current persistence model. The model looped through 10,000 iterations for each of the seven scenarios. In each iteration, it simulated persistence states $(z_{i,t})$ of each southern hognose snake population over 62 time steps from the present (2018) to 2080. In each iteration of the model, future population persistence was predicted using a series of four steps (Fig. 2). In step 1, we calculated annual values of land cover, fire frequency, and percentage of protected land for each population using the spatial layers representing stressors and management in each scenario. In step 2, we used inputs of future land cover and fire frequency, along with all other constant predictors used in the habitat suitability model (e.g., soil drainage, local elevation: Crawford et al., 2020), to calculate mean habitat suitability for each population and year using the predict.glm function in R, given conditions of each scenario. In step 3, we randomly selected a single set of posterior estimates of all parameters (e.g., representative unit intercept, effect of HSI) generated from one iteration of the current persistence model to account for parametric uncertainty. In step 4, we used the posterior estimates and scenario-, population-, and year-specific inputs to simulate populations persisting or becoming extirpated each year through 2080 using the current persistence model structure. The probability of persistence of a population in 2019 was predicted by

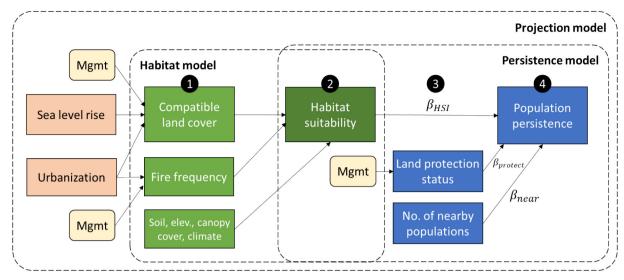


Fig. 2. Conceptual model linking components included in the habitat suitability model (green), current persistence model (blue), and impacts of stressors (orange) and management (yellow) in the projection model for future persistence of southern hognose snake populations. Numbers correspond to projection model steps 1–4 discussed in Section 2.4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

multiplying its mean current persistence probability (in 2018) by its expected annual persistence probability based on scenario inputs in the current persistence model ($\phi_{current}^*\phi_t$). The state of the population (persisting or extirpated) in 2019 was drawn from a Bernoulli trial using that probability. For years 2020 through 2080, the state of a population was drawn from a Bernoulli trial using the annual persistence probability estimated from inputs representing future conditions, given that the population had persisted in the previous year.

We used similar outputs and procedures as in the current persistence model to characterize future resiliency, redundancy, and representation from the projection model. We calculated the future persistence probability for each population as the percentage of model iterations where the population was persisting (z = 1) in 2080 and grouped populations into the same five categories of persistence probability. We summed the number of populations at or above a persistence threshold in 2080 and used all model iterations to calculate the mean (the most likely prediction) and 95% credible intervals for the number of persisting populations in each representative unit and range-wide each year through 2080. Lastly, we characterized future representation using the spatial distribution of populations likely to persist in 2080, relative to current and historical distributions.

See Supplemental material for our R and JAGS code and associated datasets for the current and future persistence analysis.

3. Results

3.1. Summary of southern hognose snake records and populations

We obtained 2227 southern hognose snake occurrence records from years 1880–2018. Many early occurrence records only had spatial precision to the county level. We delineated 222 southern hognose snake populations across the range (Fig. 1). The number of populations per representative unit ranged from 4 (Alabama Central) to 58 (Upper Coastal Plain [GA/FL]; Fig. 1). Of the total dataset, 31 occurrence records, grouped into 18 populations, fell outside of the area used in the habitat suitability analysis (Crawford et al., 2020). Because we did not have habitat metrics to inform predictions of persistence for these populations, all 31 records were prior to 1975, and our future scenarios did not consider reintroductions, we counted all 18 populations as extirpated currently and in the future for all summaries. We used the remaining 2196 occurrence records, grouped into 204 populations, to fit the persistence model and project future persistence. Within the 69-

year time frame of the current persistence model (1950–2018), southern hognose snakes were found 2.67 (range = 1 to 45) times in a population, on average. From the search effort dataset, the number of observer-days per year per population ranged from 0 to 82 (mean = 0.167), and records of non-target species came from 124 of 204 (60.8%) populations analyzed.

3.2. Current persistence and species status

The persistence model showed adequate convergence and fit to the data. Estimated persistence varied considerably by population but was positively influenced by mean habitat suitability and number of populations within 10 km (Table 3). Persistence was also positively influenced by the percentage of protected land, but the effect was not as strong as the other predictors, with the 95% BCIs slightly overlapping 0 (Table 3). Mean annual persistence rates were similar across

Table 3
Parameter estimates (means and 95% Bayesian credible intervals [2.5 to 97.5 percentile of the posterior distribution]) for the persistence model predicting the probability of persistence and detection between 1950 and 2018 for 204 populations of southern hognose snakes. Posterior parameter estimates that do not overlap zero are interpreted as ecologically important.

Parameter	Mean	Lower 95%	Upper 95%
Persistence			
μ_{rep}			
Upper Coastal Plain (Carolinas)	0.967	0.944	0.984
Upper Coastal Plain (GA/FL)	0.969	0.952	0.982
Atlantic Coastal Plain (Carolinas)	0.969	0.949	0.985
Atlantic Coastal Plain (GA/FL)	0.933	0.874	0.974
FL Peninsula	0.939	0.896	0.970
FL Ridge	0.928	0.856	0.973
AL/FL Panhandle	0.943	0.904	0.971
West (AL/MS)	0.933	0.864	0.976
β_{HSI}	3.074	1.595	4.682
$\beta_{protect}$	0.748	-0.079	1.643
β_{near}	3.782	2.208	5.445
Detection			
μ_{mean}	0.012	0.009	0.014
β_{trend}	0.043	0.038	0.049
β_{effort}	0.007	-0.045	0.053

Parameter notations: μ_{rep} – representative unit intercepts (presented on probability scale); β – covariate effects on persistence and detection; and μ – intercept.

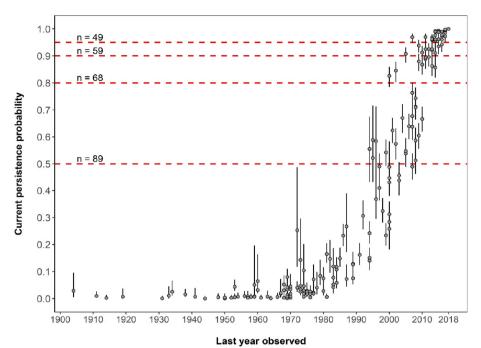


Fig. 3. Mean (\pm 95% credible intervals) probability of persistence in the current year (2018) for southern hognose snake populations (N=204) related to the last year an individual was observed in a population. Horizontal red dashed lines indicate persistence thresholds of 50, 80, 90, and 95%, and n values indicate the number of populations with mean current persistence probabilities at or above each threshold. Each point represents a population with the exception that the point with 100% persistence probability in 2018 represents 18 populations where snakes were observed that year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

representative units. Current persistence probability was equal to 1 for populations where southern hognose snakes were observed in 2018 and generally decreased with years since the last observation (Fig. 3). The estimated mean detection rate was low (0.01) with a positive effect of a linear temporal trend and weak evidence of a positive effect of search effort on detection (Table 3).

Measures of current resiliency, redundancy, and representation have decreased from historical conditions. Range-wide, a majority (133 [60%]) of 222 total delineated populations had a current persistence probability < 50%, meaning they were more likely than not to be extirpated, while only 89 (40%), 68 (31%), 59 (27%), and 49 (22%) had a current persistence probability > 50%, 80%, 90% and 95%, respectively (Fig. 1). The mean number of persisting populations across model iterations was 89. Populations with higher (> 50%) current persistence probabilities were distributed across the species' range but exhibited a degree of spatial clustering (Fig. 1). The geographic extent occupied by the species has likely decreased as all populations in the northeast and western edges of the range are likely extirpated at present, including all populations in the West (AL/MS) and Alabama Central representative units. Within each of the other representative units, between 50 and 86% of populations had an estimated current persistence probability < 50% (Fig. 1). See U.S. Fish and Wildlife Service (2019, section 4.2, Appendix B) for additional results for current conditions.

3.3. Future persistence and species status

Future scenarios varied in the degree that urbanization, sea level rise, and management affected land cover and fire frequency, which influenced mean changes in predicted HSI across populations (see U.S. Fish and Wildlife Service, 2019, Table B-7). On average, HSI within populations decreased between 3.9 and 4.9% for the three stressor scenarios. For all other scenarios, the mean change in HSI from current conditions ranged from a decrease of 7.5% (Decreased Management) to an increase of 4.9% (Protect Even More Populations).

Future resiliency, redundancy, and representation were predicted to decrease from current conditions in all scenarios to varying degrees. We present results for the mean number of persisting populations from all model iterations (Fig. 4) to illustrate predicted trends; the same trends were predicted using the number of populations above a certain persistence threshold (see U.S. Fish and Wildlife Service, 2019, Section 4.2,

Appendix B). There was substantial overlap in the credible intervals between scenarios. Currently (in 2018), the mean number of persisting populations was 89 out of 222 (40%). The mean number of persisting populations was predicted to decrease to 56 (25%) for all three stressor scenarios by 2080 (Fig. 4; lines for these scenarios all overlap). Relative to stressor scenarios, the mean number of persisting populations in 2080 was slightly lower for the Decreased Management scenario (54: 24%), slightly higher for the Improved Management scenario (58: 26%), and higher for the Protect More Populations (64: 29%) and Protect Even More Populations (66: 30%) scenarios (Fig. 4). Within each representative unit, the number of populations at or above all persistence probability thresholds (50, 80, 90, and 95%) decreased from current conditions in all scenarios. Using the number of populations with a > 90% future persistence probability, no representative unit was predicted to have a population meeting this threshold under the Decreased Management scenario, two units had at least one population meeting this threshold under the three stressor scenarios and Increased Management scenario, and five units had at least one population meeting this threshold under the Protect More Populations and Protect Even More Populations scenarios (Fig. 5). Additionally, one representative unit (Atlantic Coastal Plain [GA/FL]) had only one population with a > 50% future persistence probability in all scenarios except the Protect Even More Populations scenario (two populations), indicating a higher risk of unit-wide extirpation and loss of representation, relative to other units. See U.S. Fish and Wildlife Service (2019, Section 5.2, Appendix B) for additional results for future conditions.

4. Discussion

Approaches for estimating population persistence (i.e., through PVA) have long been recommended and used to generate quantitative information for status assessments, conservation planning, and designation on national or international threatened species lists (Beissinger and Westphal, 1998; Akçakaya and Sjögren-Gulve, 2000; Morris et al., 2002; Rodrigues et al., 2006; McGowan et al., 2017; Smith et al., 2018). Still, persistence modeling approaches have recently faced criticism for being too data-intensive to be implementable for many at-risk species petitioned for listing (Wolf et al., 2015). At the same time, citizen science databases of plant, invertebrate, fish, and wildlife species have

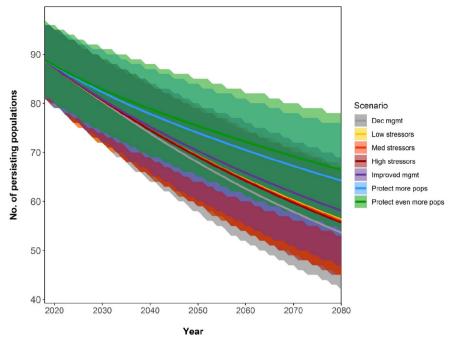


Fig. 4. Predicted mean (\pm 95% credible intervals) number of persisting southern hognose snake populations between the present year (2018) and 2080, given seven scenarios of threats and management actions.

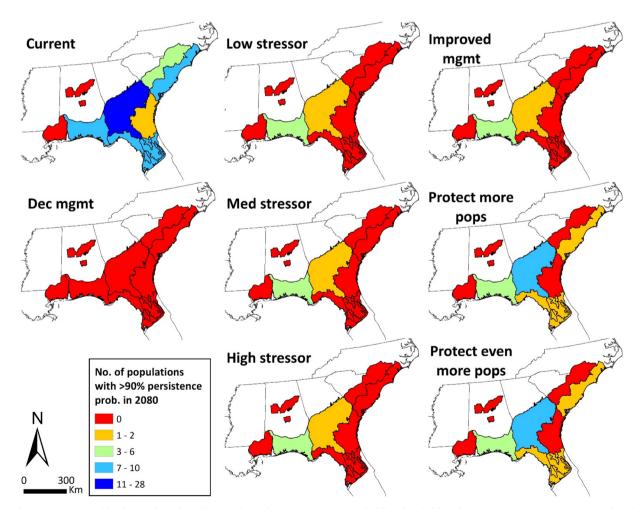


Fig. 5. Redundancy, measured by the number of populations above the 90% persistence probability threshold, within representative units for the southern hognose snake currently and in the year 2080 under seven future scenarios of stressors and management.

become increasingly populated and accessible, and studies have begun developing approaches to use these datasets to better estimate certain parameters like habitat suitability and occupancy (e.g., Kéry et al., 2010; Peach et al., 2017; Robinson et al., 2018). Our work contributes an additional example of using citizen science data of non-target species as inferred absences when target species data are limited, but it also demonstrates a method for using these minimal inputs to estimate persistence to inform status assessments and conservation decisions. Estimating persistence allowed us to characterize the southern hognose snake's overall status and revealed several patterns in resiliency, redundancy, and representation: (i) a majority (60%) of all known populations have likely become extirpated by 2018, (ii) the species has likely experienced a range contraction as two of nine representative units are likely extirpated, and at least one additional unit is at risk of extirpation by 2080, and (iii) although more populations are predicted to become extirpated in the future under all scenarios tested, management strategies to acquire and improve habitat on currently unprotected lands with existing populations could lessen the rate of population declines.

It is important to acknowledge that persistence models and estimates, however rigorous, do not solely determine any listing or conservation decision for a species. These decisions involve other elements such as stakeholders' values and risk tolerance that cannot be addressed with scientific information. However, using a persistence modeling approach like ours ensures the methods used to characterize a species' status are transparent and replicable, the results explicitly capture extinction risk and uncertainty, and any subsequent policy decisions are based on the best available scientific information. While persistence probability for a population offers a straightforward metric to compare with a decision maker's risk tolerance level, persistence can further serve as the basis for summarizing other metrics important for characterizing a species' status at broader scales. In our study, we used multiple persistence probability thresholds (analogous to levels of risk tolerance) to capture principles of redundancy and representation across the southern hognose snake's range. We expressed these principles as the number of populations predicted to persist and the number and extent of ecological settings predicted to be occupied by populations, respectively. These results provide evidence regarding the species' ability to withstand large-scale catastrophic events and changes in genetic or ecological breadth of the species under current and future conditions that is valuable for listing and conservation planning decisions for at-risk species (Shaffer and Stein, 2000; Wolf et al., 2015; Smith et al., 2018).

The persistence and detection components of our model framework have limitations that should be considered when interpreting results. As stated previously, our adaptation of the Cormack-Jolly-Seber model (Lebreton et al., 1992; Brooks et al., 2000) lacked a recolonization mechanism typical of occupancy models (MacKenzie et al., 2003; Kéry et al., 2010). We also assumed persistence probability responded only to landscape-based site predictors (habitat suitability, proportion of population area in protected status, number of nearby populations) and not to internal population attributes commonly used in PVAs (e.g., population growth or recruitment rates: McGowan et al., 2017). These more complex frameworks require basic life history and demographic information that have not been estimated for southern hognose snakes. Within the context of our study (focused on a small-bodied species with low detection and limited dispersal), it is reasonable to assume colonization rates are negligible and population dynamics are more strongly influenced by annual persistence rates in the model, which account for internal processes of survival and recruitment. Therefore, it is reasonable that our model can yield accurate estimates of persistence over a given time frame that are valuable for assessing risk for species with

Our model hinged on accounting for imperfect detection with citizen science data of non-target species, which required other assumptions. In addition to the assumptions stated previously (see Section

2.2), we assumed that records of non-target snake species within southern hognose snake population boundaries indicate that preferred habitat of the southern hognose snake was searched. Although many non-target species are also found in more mesic habitats that may occur in population boundaries but are not used by southern hognose snakes, the list of 13 non-target species includes those most commonly found during surveys targeting southern hognose snakes according to expert judgment and previous work (Enge and Wood, 2002). Applying our approach for other species will require careful consideration of the set of non-target species used to most accurately represent cases where appropriate searches were conducted but the target species was not detected. We also note that we retained the effect of search effort in the model even though it had a small (but still positive) effect on detection probability in order to demonstrate its potential application for other studies using citizen science data. This estimate may have been reduced by the inclusion of the temporal trend effect, as the two effects may have been correlated. The number of non-target records generally increased over the 69-year period modeled due to many social and technological factors (e.g., emergence of citizen science databases, improvement of georeferencing software on phones). Although including both effects may have slightly influenced the precision of parameter estimates in this study, other studies focused on shorter temporal scales (< 10 years) would likely not require a trend effect and could better estimate the isolated effect of search effort. Additional work could explore any interactions between search effort and temporal or spatial trends that could relate to the ability of citizen scientists to detect target species. Lastly, we caution that although citizen science data can be effectively integrated in models to estimate population persistence, improving the quality and quantity of data through systematic surveys (e.g., detection-non-detection data) and other research efforts (e.g., telemetry, mark-recapture) will reduce the number of required model assumptions and greatly improve the accuracy of estimates needed for status assessments and conservation planning for atrisk species.

The results from the current persistence model offer insights into the effects of site conditions on risk of extinction for southern hognose snake populations. Relationships between persistence probability and site predictors agree with life history studies and expert judgment that the species uses and survives best in fire-dependent, xeric habitat (e.g., longleaf pine sandhills: Tuberville et al., 2000; Beane et al., 2014; Willson et al., 2018) - attributes that were associated with a higher HSI (Crawford et al., 2020). Still, a specific site may have additional factors, such as presence of non-native invasive species or a history of overcollection (Tuberville et al., 2000), that may influence estimates but were not able to be captured in this analysis. It is reasonable that populations on protected lands likely have a reduced risk to direct threats such as habitat loss, road mortality, and collection, especially if protected lands have been established and managed for conservation goals over longer periods, which would cause higher population persistence probabilities. This relationship supports previous findings of Tuberville et al. (2000) that many southern hognose snake populations on protected lands appeared to be stable. The strong relationship between number of populations within 10 km and persistence could support that nearby populations may provide opportunities for "rescue" where recolonization can occur after a catastrophe or could provide a signal that there are localized conditions (e.g., geological, climatic, management practices) that promote long-term population persistence that have not been otherwise captured in our analyses. However, we caution that this relationship is somewhat phenomenological without further research into dispersal capabilities of the species (but see Willson et al., 2018) or influential spatial attributes at local scales. Lastly, the current persistence model also estimated higher than average persistence probabilities for certain populations that had favorable site-level conditions (i.e., high habitat suitability, percentage of protected land) but no record of southern hognose snakes or non-target species (i.e., no search effort) in many years (Fig. 3). These sites could be prioritized for

surveying to better estimate their current status.

Summarizing persistence outputs from the estimation and projection models revealed past, present, and future trends of the southern hognose snake's range-wide status and provided information useful for prioritizing threats and management actions. There has been a widespread reduction in redundancy (i.e., the number of populations likely to persist) within each representative unit, which has led to a reduction in representation through the loss of all populations on the northeast and western edges of the range. It is very likely that the species has become extirpated in two of nine representative units (Alabama Central and West [AL/MS]), which includes all populations in Alabama and Mississippi where the species has not been detected since 1981 (U.S. Fish and Wildlife Service, 2019). However, many populations have a high persistence probability currently (> 95%), and, in general, these occur on protected lands with suitable habitat. For all future scenarios, many of these populations were predicted to have lower persistence probabilities due to the effects of urbanization and sea level rise. We note that the future projection model did not allow compatible land cover in protected lands to be removed by urbanization, but spatial inputs (and, therefore, habitat suitability and persistence) could still be influenced for populations on protected lands if (i) sea level rise removed compatible land cover or (ii) urbanization occurred adjacent to protected land boundaries and restricted fire frequency adjacent to protected land edges due to the wildland-urban interface (Theobald and Romme, 2007). Range-wide, we found evidence that resiliency, redundancy, and representation would decrease in the future under all scenarios evaluated - especially those that did not include additional management actions. Predicted status metrics were nearly identical among the three stressor scenarios due to minimal differences between scenarios in the amount of land cover loss, reduction in fire frequency, and HSI for populations, on average. Still, it may be initially surprising that persistence predictions were insensitive to the relatively high amount of uncertainty around rates of urbanization (Terando et al., 2014) and sea level rise (IPCC, 2013) in the southeastern U.S. Another important takeaway from future predictions was that the Improved Management scenario only slightly increased the number of persisting populations while the two higher management effort scenarios resulted in greater increases in the number of persisting populations, relative to stressor scenarios (Fig. 4). The protection for additional populations in the two highest effort management scenarios also reduced the risk of losing redundancy and representation, relative to all other scenarios, by yielding at least one population with a persistence probability > 90% in the Atlantic Coastal Plain (Carolinas), Florida Peninsula, and Florida Ridge representative units (Fig. 5). These results highlight the value of protecting additional populations, rather than solely managing populations on currently protected lands, if a management goal is to increase the number of persisting populations and minimize the loss of redundancy and representation for the southern hognose snake in the

Our work demonstrates an approach for estimating persistence for species when data are limited but conservation decisions are needed. We expect many at-risk species currently designated for status reviews and designations in the U.S. and internationally to have data limitations similar to the southern hognose snake, but citizen science data is becoming more abundant and accessible for scientific studies (Zipkin and Saunders, 2018). Therefore, our persistence model framework could be applied to overcome these challenges. As we did in this study, practitioners using this approach for other species could benefit from consulting species experts early in the process to identify appropriate lists of habitat-based or other factors for estimating persistence and nontarget species for estimating search effort and detection. Future scenarios could also be developed using input from species experts and other stakeholders and tailored to a particular decision context (Martin et al., 2012; Addison et al., 2013; Reside et al., 2019). For our study, we developed future scenarios to represent a range of plausible conditions, but our goal was to compare outcomes among broad strategies rather than guide management actions at specific sites. We acknowledge the feasibility of implementing management actions contained in scenarios is uncertain. For example, the ability to implement prescribed fire may be constrained in the future due to projected increases in temperature and decreases in precipitation in the southeastern U.S. (Mitchell et al., 2014). Our model framework could be used to inform site-specific management decisions by modifying scenarios to include local factors that could potentially influence persistence, which could be parameterized using published literature or expert judgment (e.g., McGowan et al., 2017).

CRediT authorship contribution statement

Brian A. Crawford: Methodology, Resources, Formal analysis, Writing - review & editing, Writing - original draft. **Melanie J. Olds:** Resources, Formal analysis, Writing - original draft. **John C. Maerz:** Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Clinton T. Moore:** Methodology, Formal analysis, Writing - original draft, Writing - review & editing.

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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