



Land use and cover effects on an ecosystem engineer

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ABSTRACT

Human induced land-use change in the form of urbanization and agriculture are rapidly transforming our planet's terrestrial landscapes and causing the loss of species at unprecedented rates. Studies documenting the impacts of development are extensive; however, less is known about the scale at which species respond to development and specific features of altered landscapes that make them vulnerable. This shortcoming may be due to the difficulty of collecting data across large spatial extents, but filling these information gaps are critical, particularly for species that have a disproportionate influence on ecosystems, such as ecosystem engineers. One such species, the southeastern pocket gopher (*Geomys pinetis*), has been declining throughout its range (southeastern United States) and continued loss will likely have strong effects on the imperiled longleaf pine ecosystem in which it is closely associated. Using range-wide data from presence-absence surveys and publicly available presence-only data, we used recent advances in species distribution modeling to understand this ecosystem engineer's associations with extensive land use and cover changes. Our study showed that pocket gophers inhabit a variety of land-use types, including regions with low levels of anthropogenic development, but are largely absent from intensely urbanized areas and closed-canopy forests. Conservation planning to reduce the spread of extensive development and forest management strategies to reduce closed-canopy systems will be instrumental in reducing the decline of the species and ultimately protection of the longleaf pine ecosystem. The approach used in this study will be increasingly beneficial for understanding species response to land-use change.

1. Introduction

Across the globe, species are being lost at an unprecedented rate due to human activities (De Vos et al., 2014; Pimm et al., 2014; Ceballos et al., 2015) and declines are expected to continue for the foreseeable future (Pereira et al., 2010). The loss of biodiversity is often coupled with loss of important ecological interactions, which can accelerate the demise of other species (Koh et al., 2004) and reduce community resilience (Ives and Cardinale, 2004). These ecological interactions are often lost prior to extinction of the species, with reduced abundance leading to functional extinction (Valiente-Banuet et al., 2015). Extinction, species or functional, is particularly concerning with species that

have a disproportionate influence on the structure and function of an ecosystem, such as keystone species (Paine, 1969; Mills et al., 1993) or ecosystem engineers (Jones et al., 1994; Jones et al., 1997), which either directly or indirectly influence organization and diversity of ecological communities.

A major threat to all species, regardless of their ecological functionality, is human induced land-use change (Foley et al., 2005; Newbold et al., 2015). Human dominated land uses are expanding at alarming rates due to the rapid increase in human populations and rates of urbanization (Foley et al., 2005; Song et al., 2018). Land-use changes often result in changes to land-cover, a key determinant of ecosystem processes (Foley et al., 2005). Recent land-cover changes have been

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extensive and rapid (Foley et al., 2005; Lambin and Geist, 2006), resulting in not only species loss (Pimm and Raven, 2000; Newbold et al., 2015), but also soil loss (Jie et al., 2002), climate changes (Arneeth et al., 2017), and overall reduced ecosystem functionality (Vitousek et al., 1997; Allan et al., 2015). Studies documenting global changes (Foley et al., 2005; Song et al., 2018) are extensive; however, much less is known about the scale at which species respond to land-use changes or how species respond to specific features within the altered landscape (Jackson and Fahrig, 2015; McGarigal et al., 2016).

Historically, the Coastal Plain of the southeastern United States consisted of an open landscape dominated by pines (*Pinus* spp.) with a diverse understory of warm season grasses, herbs, and forbs maintained by frequent disturbance (Platt et al., 1999). These communities began to disappear as the landscape was converted for human use including agriculture, intensive forestry, and urban development (Noss, 1989; Frost, 1993; Noss et al., 1995; Trani, 2002). Today, only approximately 4 percent of the historic longleaf pine forest remains (Frost, 2007). The portions of forest left have been threatened by the encroachment of woody understory and groundcover vegetation and increased tree canopy density due to a history of fire suppression and intensive forestry practices (Frost, 1993; Van Lear et al., 2005). These combined threats have been detrimental to the native and endemic flora and fauna that have evolved in the region (Noss, 1989; Frost, 1993; Noss et al., 1995; Trani, 2002).

Southeastern pocket gophers (*Geomys pinetis*; SEPG) are fossorial mammals native to the Coastal Plain and have strong influences on the ecosystems in which they live (Huntley and Inouye, 1988; Reichman and Seabloom, 2002; Clark et al., 2018). Pocket gophers have been shown to substantially alter the physical environment by their extensive tunnel building and mounding behavior, which aerate soils, cycle nutrients through the system, and increase plant diversity (Huntley and Inouye, 1988; Reichman and Seabloom, 2002; Clark et al., 2018). Specifically, SEPGs within the nutrient limited longleaf pine ecosystem aid in the conservation of nitrogen, phosphorus, and other nutrients important to the system (Clark et al., 2018). Populations of SEPGs appear to be declining (Scott, 2008) however, a comprehensive assessment of the current distribution is lacking. Given the ecological role of SEPG, loss of the species is likely to have cascading effects on the longleaf pine soil dynamics potentially decreasing nutrient availability and subsequently plant community structure. The species is currently listed as a high priority species of conservation concern in all three states in the range (Alabama Department of Conservation and Natural Resources, 2005; Georgia Department of Natural Resources, 2005; Florida Fish and Wildlife Conservation Commission, 2012; Ozier and Morris, 2016). Species listing, conservation, and management of SEPG has been limited by a lack of information about its ecology and factors influencing the distribution, particularly at broad spatial scales. Previous research has focused on local and home range scales where they are known to occur (Gates and Tanner 1988; Warren et al., 2017a, 2017b). At these scales, suitable habitat includes soils with low clay content (Warren et al., 2017b) and open canopies with sufficient understory growth to accommodate foraging opportunities (Ford, 1980). However, we currently do not understand if and how land-use and forest feature changes are influencing the species.

One way forward is to use the vast amount of publicly available species occurrence data from museums and citizen science projects coupled with remotely sensed environmental data. Species occurrence data of this type are generally referred to as presence-only data (PO), as typically there is no information about where the species is absent. Given this type of data, several modeling approaches use background data to characterize the environments in the study area or to generate contrasts against the known presence locations assuming presence is unknown at the background locations (see Elith et al. (2006) for discussion of these methods). However, sampling bias is often associated with collection of PO data, which can be problematic for accurately constructing distribution models (Araújo and Guisan, 2006; Phillips

et al., 2009). Presence-only data is often incomplete, particularly for secretive or rare species, and collected opportunistically, creating a potential bias in sampling locations near areas more frequented by the observer, such as roads (Phillips et al., 2009). Recent advances in species distribution modeling have addressed these concerns by allowing for the integration of PO data with presence-absence (PA) survey data to estimate species distributions (Dorazio, 2014; Fithian et al., 2015; Fletcher et al., 2016; Fletcher et al., 2019; Miller et al., 2019). These methods are typically derived from an extension of point-process models that focus on the intensity or density of a species in a bounded area or region from which the probability of occurrence can be estimated (Dorazio, 2014; Fithian et al., 2015; Fletcher et al., 2016). The models, called integrated distribution models (ISDMs; Fletcher et al., 2016), mitigate the sample bias present in PO data by leveraging the use of PA survey data and conversely improve PA data by increasing the number and extent of occurrence localities with PO data (Dorazio, 2014; Fithian et al., 2015; Fletcher et al., 2016).

Given the secretive nature of this fossorial mammal and the difficulty in modeling the distribution, ISDMs could prove useful in understanding more about their response to land use and cover change. Therefore, our goals were to implement recent advances in integrated species distribution modeling and planned survey data to understand SEPG association with land use and cover changes in order to fill critical gaps in knowledge of the species distribution at broad spatial scales. Specifically, we hypothesize that: 1) SEPG occurrence would be higher in forest and lower in areas of high human use (agriculture, low development, and high development); and 2) that suitable habitat for SEPG consists of open canopy forest, which promotes early successional plants for forage, and with low clay content soil conducive to creating and maintaining burrow systems.

2. Methods

2.1. Presence-absence surveys

Because SEPGs are fossorial and create visible surface mounds above their burrows (Supplementary Materials, Fig. A.1), we employed transect sampling based on signs of the species to assess presence and absence. Similar methods have been successfully used to survey species where sightings of the animal are rare (Smith et al., 2009). To identify transects, we used a pseudostratified random sampling design to capture major land cover communities potentially used by SEPGs on public and private properties across their range (Fig. 1). Land-cover sampling categories were identified from the National Landcover Database (NLCD; U.S. Geological Survey, 2011), which included barren land/sand/clay, evergreen forest, mixed forest, shrub/scrub, grassland/herbaceous, pasture/hay, cultivated crops, open development, low intensity development, medium intensity development, and high intensity development at a 30 × 30 m spatial grain. We did not include areas periodically saturated with water (woody and emergent herbaceous wetlands), as these areas are inhabitable by pocket gophers (Pembleton and Williams, 1978) because the soil is too wet to construct tunnels and water saturation can cause the animals to drown. We used the NLCD (U.S. Geological Survey, 2011) because it was a consistent source of data across the species range. We overlaid a 1-km² grid over the historic extent of the SEPG range (IUCN; Cassola, 2016) and randomly selected 50 to 75 grids from each state to sample the entire distribution. We selected grids with ≥50% of the above land-cover classifications to survey using the Data Management Tool in ArcMap version 10.2 (ESRI, 2011). If the sites were not accessible, as was the case for some grids on privately owned lands, we chose sites more opportunistically by finding sites as close as possible to the original randomly selected grid square. We conducted one field survey of each grid in which two surveyors independently walked a 500 × 500 m square (2000 m transect). If SEPG mounds were observed along the transect, the mound cluster center was geo-referenced and the species

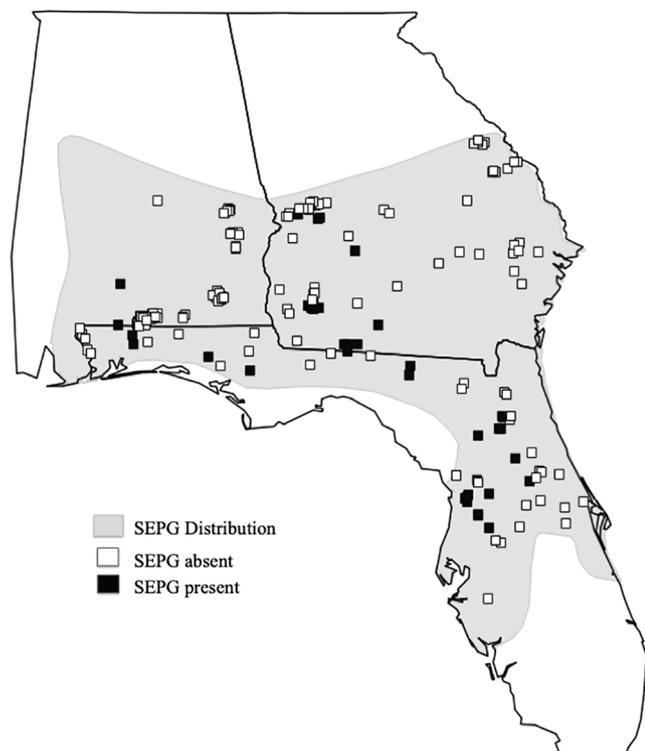


Fig. 1. Presence-absence (PA) surveys (N = 182) for *Geomys pinetis* (squares) across the historic range (IUCN; Cassola, 2016) highlighted in grey. Black squares indicate presence locations (N = 43) and white squares indicate absence locations (N = 139).

was recorded as present in the 1-km² grid. If there were no mounds observed along the transect the species was recorded as absent in the grid. We conducted surveys during the growing season March–Sept in 2016 and 2017. Because PA data from planned surveys can suffer from false negatives, we initially used an occupancy modeling approach (MacKenzie et al., 2002; MacKenzie et al., 2006) to calculate the probability that a cluster of SEPG mounds was detected by our two independent surveys. Finding scant evidence for false absences (probability of detection = 0.995), we confirmed that detectability was high and would not introduce bias into our models.

2.2. Presence-only occurrences

We assembled occurrence records of SEPGs throughout their geographic range across Florida, Georgia, and Alabama in two ways. First, we developed and promoted an iNaturalist application (<https://www.inaturalist.org/projects/southeastern-pocket-gophers>) and a web-based tool (<http://southeasternpocketgopher.weebly.com/>) for professionals and the public to record georeferenced, latitude and longitude locations of SEPG mounds. All presence locations required an image to be uploaded with each georeferenced point. We assembled sightings from March 2016 to December 2017. We (SID, EIP, JTP) verified each photo for potential misidentification of mounds.

Second, we compiled high-resolution (4 decimal places) latitude and longitude georeferenced locations from databases housed by the Florida Museum of Natural History and Alabama Department of Natural Resources. After removing duplicates and occurrence points of the locations recorded prior to 2014, which matched as closely as possible to the survey sampling time frame and that of the variables used in the models, the data set consisted of 1485 presence locations. We selected the 1-km² grid square containing at least one of the PO occurrence points for further land use analyses, which resulted in 316 PO grids.

2.3. PA/PO integrated distribution modeling

We implemented two modeling approaches to understand the SEPGs associations with land use and cover change. First, we modeled broad-scale land-use associations using ISDMs, integrating our PO and PA datasets. Second, we conducted a binary probit-regression model with the PA data to interpret vegetation and soil features associated with the presence of SEPGs. While this information can be included in ISDM, given the large PA sample size and geographic coverage, there would be no benefit in estimation (e.g. Fletcher et al., 2019). Therefore we use a separate model to provide more tractable insight into the features specifically at the PA survey locations.

For the ISDM, we considered land use and distance from roads as covariates for modeling SEPG distribution. We reclassified the 11 land-use categories from the NLCD (U.S. Geological Survey, 2011) into these four major land cover types (forest (mixed and evergreen), low development (open and low intensity), high development (medium and high intensity), and agriculture (pasture/hay, cultivated crops, herbaceous grassland) using the Spatial Analyst Tool in ArcMap (ESRI, 2011). We used the Zonal Statistics Tool in ArcMap (ESRI, 2011) to tabulate the percentage of each land-use type within the 1-km² grids. Because there is little information about the ecology and extent of pocket gopher movement and dispersal across broad spatial scales, we selected three scales to assess the appropriate scale for modeling SEPG distribution. In addition to the 1-km² scale used in the PA surveys, we included the same covariates for land use at 5- and 10-km² scales. The 5- and 10-km² grids were created by generating a square buffer for each respective scale around each 1-km² grid surveyed. We tested for associations between the percentages of each land-use category in the PO and PA data using Pearson's product moment correlation. Positive correlation values for all pairs of land-use categories were < 0.70, so all were included in the integrated models (Supplementary Materials, Table A.1). Because PO data does not have information on species absences, background data using environmental covariates was used to estimate the site-specific presence and absence probabilities. For the background data used in the model, we randomly generated 10,000 points across the extent of the study area using the Data Management Sampling Tool in ArcMap. We created 1-, 5- and 10-km² grids by generating a square buffer around each point for each scale.

Distance to roads were used to account for PO sample bias, as PO occurrence points are often collected opportunistically and may be biased towards easily accessible areas, such as along roadsides (Phillips et al., 2009). Distance to road was derived from the TIGER/Line Primary and Secondary Road dataset (U.S. Census Bureau, 2016). We calculated distance from each grid centroid to the closest primary or secondary road using the Analysis Tool in ArcMap (ESRI, 2011). Using distance to road and land cover categories, we fitted 14 models

Table 1

Presence-absence (PA) and presence-only (PO) integrated distribution models tested to explain *Geomys pinetis* distribution.

PA/PO Integrated Distribution Models
Forest
Agriculture
Low Development
High Development
Forest + Agriculture
Forest + High Development
Forest + Low Development
Agriculture + High Development
Agriculture + Low Development
Forest + Agriculture + Low Development
Forest + Agriculture + High Development
Agriculture + High Development + Low Development
Forest + High Development + Low Development
Forest + Agriculture + Low Development + High Development

(Table 1) using the *multispeciesPP* package (Fithian, 2014) in R version 3.4.1 (R Core Team, 2019) at all three spatial scales. We used model ranking to determine the most relevant scale for explaining SEPG distribution. We ranked models using Akaike's information criterion (AIC) and considered models with $\Delta i \leq 2$ (Burnham and Anderson, 2004) to be competing. The relative importance and significance of each variable were evaluated by standardized coefficients and confidence intervals. We considered variables with 95% CIs that did not cross zero to be meaningful predictors of SEPG occurrence. We used the complementary log–log (cloglog) function to predict probability of occurrence from model output of intensity values (Fithian et al., 2015). We plotted predicted response of meaningful variables to understand their biological relevance to SEPG distributions. To model predictive performance, we used cross-validation by partitioning the PA data into four-folds using the *kfold* function in the R package *dismo* (Hijmans et al., 2017). We measured the discriminatory ability of the model with area under a curve AUC (ranging from 0 to 1). A value of 0.5 indicates that the model performs no better than random while values greater than 0.5 indicate better discriminatory capabilities as the value approaches 1 (Hosmer and Lemeshow, 2000). Each partition was used as testing data separately and the AUC values were averaged for each test. Model predictive performance was performed in the package *pROC* with the function *auc* (Robin et al., 2011).

2.4. Probit regression of PA data

After determining the most relevant scale and land-use types using the integrated distribution model, we used our intensive field surveys to identify vegetation and soil characteristics associated with SEPG presence. We modeled PA data using binary probit regression at the 10-km scale because that scale best-explained SEPG presence in the integrated distribution models for the land-use categories. We used U.S. Forest Service Tree Canopy analytical layer (Jin et al., 2013) from the NLCD (U.S. Geological Survey, 2011) to estimate mean and standard deviation of tree density (percent tree cover) from 30×30 m pixels. We used the gridded soil survey geographic database (gSSURGO: U.S. Department of Agriculture, 2015) to estimate mean percent clay in each grid from 10×10 m pixels using Zonal Statistics in ArcMap (ESRI, 2011). We used SEPG presence or absence in each 10-km quadrat as the response variable and forest cover (mean and standard deviation of canopy cover) and soil (percent clay) as explanatory variables. We constructed eight binary regression models including a null model, three models with only a single covariate, a full model including all covariates, and additive models of mean canopy cover and percent clay and standard deviation of canopy cover and percent clay. We also considered an interactive model of all three covariates. The general linear model analysis was conducted with the *glm* function in the *glmm* package (Knudson, 2017). We ranked models using Akaike's information criterion corrected for small sample size (AICc) and evaluated variables within competing models ($\Delta i \leq 2$). Model selection was performed with the *AICc* function in the *MuMIn* v1.40.4 package (Bartón, 2018) in R 4.0.1 (R Core Team, 2019). Relative importance and significance of each variable, predicted probability of presence, and model performance was evaluated by methods described above.

3. Results

3.1. PA/PO integrated distribution modeling

We conducted 182 surveys across the SEPG's historic range (FL: $n = 55$, GA: $n = 70$, AL: $n = 57$) (Fig. 1). SEPGs were present at 43 of the 182 survey sites. Our PO data set included $n = 316$ presence-only records. The full model (Table 1) was the most parsimonious model describing SEPG intensity for the integrated models at 1-km, 5-km, and 10-km (Tables 2–4), with an additional competing model at the 5-km scale that included forest, agriculture, and high development (Table 3).

In all of these models, the variables were meaningful (95% CI did not include 0) with a positive relationship between SEPG intensity and percentage forest, agriculture, and low development, and a negative relationship with the percentage of high development (Table 5). There was no evidence for road-biased sampling in the PO locations used in models at any spatial scale (Table 5).

Examining across scales, the most parsimonious model explaining SEPG distribution was the full model (Table 4) at the 10-km scale (AIC: 1-km = -936.8 , 5-km = -947.3 , 10-km = -985.3). Percent forest was positively and most strongly correlated with SEPG intensity ($\beta = 0.577$, SE ± 0.070 ; Table 5). Probability of occurrence increased from approximately 10% when percent forest was 0 to 65% when percent forest was > 40 (Supplementary Material; Fig. A.2). SEPG intensity was also positively associated with percent agriculture ($\beta = 0.281$, SE ± 0.414 ; Table 5), with an increase in probability of occurrence from approximately 15% when percent agriculture was 0 to 60% when percent agricultural area was > 40 (Supplementary Material; Fig. A.2). There was also a positive association in SEPG intensity in areas with increasing low levels of development ($\beta = 0.648$, SE ± 0.107 ; Table 5), with an increase from 15% probability of occurrence at 0% low level of development to almost 90% probability of occurrence when the percent of low development areas > 15 (Supplementary Material; Fig. A.2). High levels of development were negatively correlated with SEPG intensity ($\beta = -2.044$, SE ± 0.070 ; Table 5) with probability of occurrence decreasing from approximately 15% to near 0 when the percent of high development increased from 0% to approximately 1% (Supplementary Material; Fig. A.2).

We used the full model at 10-km to predict and visualize relative probability of SEPG occurrence across the species range (Fig. 2). Occurrence probabilities were low across the range with the majority of probability of occurrence values $< 50\%$ (Supplementary Material; Fig. A.3). Higher probabilities of occurrence generally aligned with heavily forested regions particularly in the northern part of the range (Fig. 2). Low probability of occurrence was predicted in regions with high levels of human development (e.g., large cities).

3.2. Probit regression PA data

The most parsimonious regression models using the PA data set included the model with only mean canopy cover (AICc = 168.795) and the full model (AICc = 168.178) (Table 6). However, in the full model, only mean canopy cover and standard deviation of canopy cover had estimates with 95% CIs that did not cross zero (Table 7). Both models performed well with the full model AUC = 0.816 and the model with mean canopy cover AUC = 0.7758. Mean canopy cover was negatively associated with SEPG probability of occurrence ($\beta = -0.072$, SE ± 0.014 ; Table 7) with a decrease in occurrence from approximately 95% to almost 0 when mean canopy cover was $> 35\%$ (Supplementary Material; Fig. A.4). Standard deviation of canopy cover also had a negative relationship with SEPG probability of occurrence ($\beta = -0.095$, SE ± 0.017 ; Table 7) with a decrease in occurrence from 60% to 10% when standard deviation of canopy cover was $> 20\%$ (Supplementary Material; Fig. A.4). At the 10-km spatial scale, percent clay was not a meaningful predictor ($\beta = 0.028$, SE ± 0.033) of SEPG distribution (Table 7). Southeastern pocket gopher probability of occurrence values across the range were generally low (Supplementary Material; Fig. A.5). Occurrence probabilities were greatest in the Central Ridges and Uplands of Florida, the Southern Gulf Coastal Plain in Alabama, and the Sandhills of Georgia (Fig. 3).

4. Discussion

Globally, the amount of urbanized land is increasing rapidly and causing substantial and often irreversible alterations to the landscape (Foley et al., 2005; Song et al., 2018). We show that pocket gophers, an important ecosystem engineer of longleaf savanna (Clark et al., 2018),

Table 2

Model selection results for integrated models that explain *Geomys pinetis* distribution at the 1-km scale. Table codes include k = number of parameters in model; AIC = Akaike's Information Criterion; Δ AIC = AIC for model *i*-minAIC. Spatial grain of covariates was 30 × 30m. The most parsimonious model is highlighted in grey.

Model 1km	Deviance	k	AIC	Δ AIC
Forest + Agriculture + Low Development + High Development	-944.801	4	-936.8	0.0
Forest + Agriculture + High Development	-922.188	2	-918.2	18.6
Forest + High Development + Low Development	-922.332	2	-918.3	18.5
Forest + Agriculture + Low Development	-906.256	2	-902.3	34.5
Forest + High Development	-905.993	2	-902.0	34.8
Forest + Agriculture	-903.720	1	-901.7	35.1
Agriculture + High Development + Low Development	-904.236	2	-900.2	36.6
Agriculture + High Development	-891.516	2	-887.5	49.3
High Development	-889.442	1	-887.4	49.4
Forest	-880.036	1	-878.0	58.8
Forest + Low Development	-880.070	2	-876.1	60.7
Agriculture	-857.267	1	-855.3	81.5
Agriculture + Low Development	-858.027	2	-854.0	82.8
Low Development	-854.807	1	-852.8	84.0

are highly sensitive to intensive urbanization, where negative effects were 2 × greater than other covariates we considered in modeling. High intensity urban environments are characterized by large areas of impervious surface, artificial surfaces made of impenetrable materials including asphalt and compacted soils, which reduce and fragment area

available to wildlife (McCleery et al., 2014). SEPGs are likely sensitive to presence of impervious surfaces because they are dependent on suitable soils for creating and maintaining burrows. The associated loss and fragmentation of suitable habitat can negatively influence the population dynamics, dispersal abilities, and the genetic structure of

Table 3

Model selection results for integrated models that explain *Geomys pinetis* distribution at the 5-km scale. Table codes include k = number of parameters in model; AIC = Akaike's Information Criterion; Δ AIC = AIC for model *i*-minAIC. Spatial grain of covariates was 30 × 30 m. The most parsimonious models are highlighted in grey.

Model 5km	Deviance	k	AIC	Δ AIC
Forest + Agriculture + High Development	-951.314	2	-947.3	0.0
Forest + Agriculture + Low Development + High Development	-953.551	4	-945.6	1.8
Forest + Agriculture + Low Development	-941.583	2	-937.6	9.7
Forest + Agriculture	-938.747	1	-936.7	10.6
Forest + High Development + Low Development	-939.969	2	-936.0	11.3
Forest + High Development	-938.644	2	-934.6	12.7
Forest + Low Development	-925.839	2	-921.8	25.5
Forest	-918.654	1	-916.7	30.7
High Development	-893.973	1	-892.0	55.3
Agriculture + High Development + Low Development	-894.077	2	-890.1	57.2
Agriculture + High Development	-893.976	2	-890.0	57.3
Low Development	-877.575	1	-875.6	71.7
Agriculture + Low Development	-877.642	2	-873.6	73.7
Agriculture	-854.314	1	-852.3	95.0

Table 4

Model selection results for integrated models that explain *Geomys pinetis* distribution at the 10-km scale. Table codes include k = number of parameters in model; AIC = Akaike's Information Criterion; ΔAIC = AIC for model *i*-minAIC. Spatial grain of covariates was 30 × 30 m. The most parsimonious model is highlighted in grey.

Model 10km	Deviance	k	AIC	Δ AIC
Forest + Agriculture + Low Development + High Development	-993.251	4	-985.3	0.0
Forest + High Development + Low Development	-977.113	2	-973.1	12.1
Forest + Agriculture + High Development	-969.595	2	-965.6	19.7
Forest + High Development	-957.406	2	-953.4	31.8
Forest + Agriculture	-953.792	1	-951.8	33.5
Forest + Agriculture + Low Development	-953.793	2	-949.8	35.5
Forest + Low Development	-953.248	2	-949.2	36.0
Forest	-933.712	1	-931.7	53.5
Agriculture + High Development + Low Development	-917.359	2	-913.4	71.9
High Development	-905.592	1	-903.6	81.7
Agriculture + High Development	-905.655	2	-901.7	83.6
Low Development	-870.701	1	-868.7	116.6
Agriculture + Low Development	-870.702	2	-866.7	118.5
Agriculture	-853.861	1	-851.9	133.4

Table 5

β coefficient estimates with mean standard errors (SE), p value (P), and 95% confidence intervals for the most parsimonious integrated distribution model at the 1-km, 5-km, and 10-km scale for *Geomys pinetis* distribution. Covariates associated with intensity tested in the model include low development, high development, forest, and agriculture. The bias covariate in the model is road distance.

1-km	β Estimate	SE	P	95% CI Lower Upper	
				Lower	Upper
Intercept	-1.995	0.215	< 0.001	-2.416	-1.573
Low Development	0.407	0.074	< 0.001	0.262	0.553
High Development	-2.644	0.731	< 0.001	-4.077	-1.211
Forest	0.420	0.069	< 0.001	0.285	0.556
Agriculture	0.323	0.068	< 0.001	0.190	0.456
Road Distance	0.055	0.057	0.335	-0.057	0.167
5-km	β Estimate	SE	P	95% CI Lower Upper	
				Lower	Upper
Intercept	-1.839	0.177	< 0.001	-2.185	-1.492
Low Development	0.218	0.137	0.111	-0.050	0.486
High Development	-1.028	0.363	< 0.001	-1.739	-0.316
Forest	0.496	0.068	< 0.001	0.363	0.629
Agriculture	0.254	0.069	< 0.001	0.119	0.389
Road Distance	0.025	0.059	0.668	-0.091	0.141
10-km	β Estimate	SE	P	95% CI Lower Upper	
				Lower	Upper
Intercept	-2.015	0.185	< 0.001	-2.378	-1.652
Low Development	0.648	0.107	< 0.001	0.438	0.858
High Development	-2.044	0.414	< 0.001	-2.855	-1.234
Forest	0.577	0.070	< 0.001	0.439	0.714
Agriculture	0.281	0.070	< 0.001	0.145	0.418
Road Distance	0.027	0.059	0.648	-0.089	0.143

species (McCleery et al., 2014). Additionally, pocket gophers are considered pests and are often persecuted in areas inhabited by humans (Prakash, 2018). Given regional projected increases in human population growth and urbanization (Cutter et al., 2014), SEPG are likely to see considerable declines in usable areas within their range.

We found that other land-use categories reflecting low levels of human development, low intensity urban and agricultural areas, were positively correlated with SEPG occurrence. Low human disturbance likely mimics the frequent disturbance of pine savannas in which the species evolved (Greene and McCleery, 2017). Natural disturbances in open pine systems, such as frequent fire, create open canopies and an understory with a high abundance of early successional plant species (Frost, 1993). Similarly, landscaping and maintenance of residential and agricultural areas typically involve removal of trees and shrubs and an increase in plant diversity (McKinney, 2008), particularly grasses and herbs (Marzluff and Ewing, 2001), which are early successional plant species that pocket gophers prefer for forage (Behrend and Tester, 1988; Connior et al., 2010). Evidence that SEPGs are more prevalent in areas of low urbanized land-use categories because of open canopies was supported by our investigation into features positively associated with occurrence in our PA models. As percent canopy cover increased occurrence decreased (occurrence drops to zero at ~ > 35% mean tree density). Positive associations to low levels of human development have been shown in SEPGs (highway shoulders; Avise and Laerm, 1982) and in other species of pocket gophers, (alfalfa fields, Patton and Brylski, 1987; grazing lands and hayfields, Connior et al., 2010; non-native grasslands, Reichman and Smith, 1985; Broussard, 1996; Connior et al., 2010; lawns, Connior et al., 2010). The trend also occurs in other mammals endemic to the region (Greene and McCleery, 2017).

Response to canopy cover and ultimately the understory vegetation is a conservation concern for the species. Many open pine canopy forests in the southeastern United States have transitioned into hardwood-encroached, closed canopy forests due to a history of fire suppression, some forest management practices (Frost, 1993; Jose et al., 2007; McIntyre et al., 2019), and increased atmospheric CO₂ that favors C₃

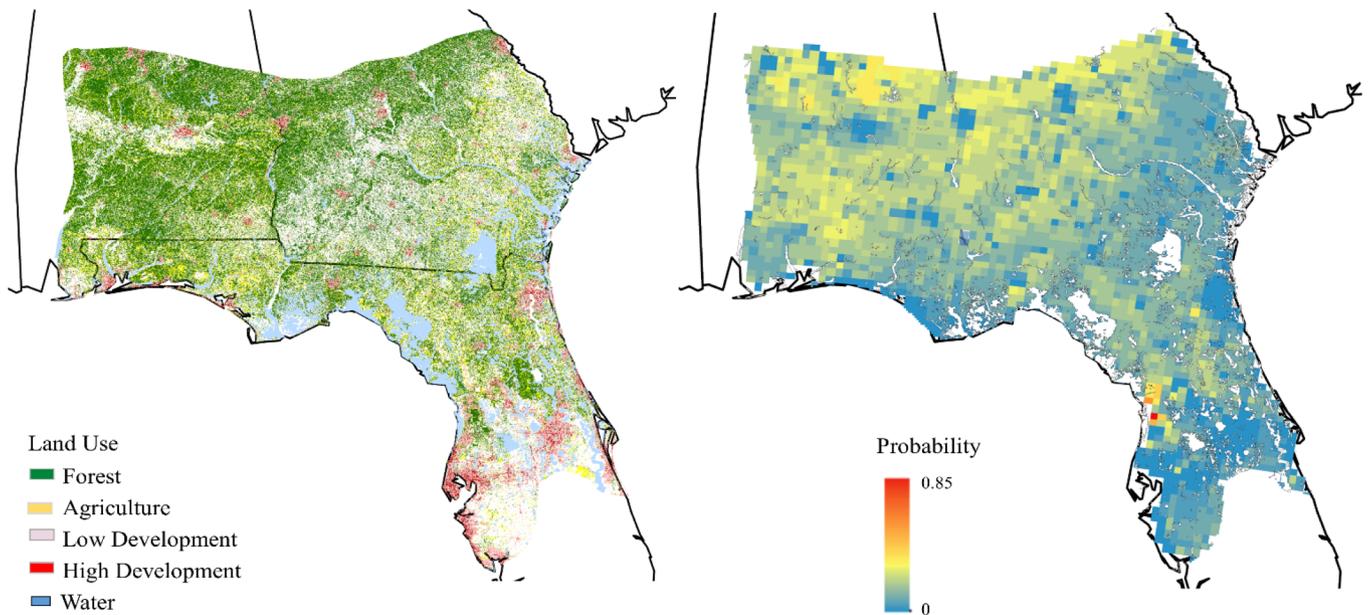


Fig. 2. Land use covariates across the range of *Geomys pinetis* (left panel). Integrated distribution model (10-km full model (Forest + Agriculture + Low Development + High Development; right panel) predicted probability of occurrence for *Geomys pinetis* (right panel). Occurrence probability values are represented as a color gradient with warmer shades representing higher probability of occurrence.

Table 6

Model selection results for logistic regression models that explain *Geomys pinetis* distribution at the 10-km scale. Table codes include df = degrees of freedom, AICc = Akaike’s Information Criterion corrected for small sample size, ΔAIC = AIC for model *i* - minAIC. The spatial grain of mean and standard deviation of canopy cover was 30 × 30 m and percent clay was 10 × 10 m. The most parsimonious models are highlighted in grey.

Model 10 km	df	AICc	ΔAIC
Mean Percent Tree Canopy + Standard Deviation Percent Tree Canopy + Mean Percent Clay	4	168.2	0
Mean Percent Tree Canopy	2	168.8	0.6
Mean Percent Tree Canopy + Mean Percent Clay	3	170.5	2.3
Mean Percent Tree Canopy * Standard Deviation Percent Tree Canopy * Mean Percent Clay	4	172.5	4.3
Null	1	201	32.2
Mean Percent Clay	2	202.6	34.4
Standard Deviation Percent Tree Canopy	2	202.9	34.1
Standard Deviation Percent Tree Canopy + Mean Percent Clay	3	204.5	36.3

woody plant growth (Bond and Midgley, 2000). Hardwood encroachment has many consequences including the reduction of shade intolerant early successional species, which make up the diverse grass-dominated herbaceous understory characteristic of the open pine systems. SEPGs are likely highly sensitive to woody encroachment, as loss of herbaceous understory decreases available forage. Forb cover has been found to be the most important variable in habitat selection in another species of pocket gopher, *Geomys breviceps*, in the longleaf pine system (Wagner et al., 2017). Additionally, hardwood root systems require the expenditure of significant amounts of energy to create and maintain underground burrow systems (Ford, 1980).

In addition to negative consequences of woody encroachment to the ecosystem, effects may be exacerbated by loss of the SEPG itself, as the pocket gophers are known to play a functionally important role in the system (Huntley and Inouye, 1988; Reichman and Seabloom, 2002; Clark et al., 2018). Therefore, management actions for SEPG should

Table 7

β coefficient estimates with mean standard errors (SE), p value (P), and 95% confidence intervals for the most parsimonious probit regression models for *Geomys pinetis* distribution at the 10-km scale.

Mean Canopy Cover	β Estimate	SE	P	95% CI	
				Lower Bound	Upper Bound
(Intercept)	3.013	0.799	< 0.001	1.447	5.772
Mean Canopy Cover	-0.072	0.014	< 0.001	-0.100	-0.045
Full Model				95% CI	
	β Estimate	SE	P	Lower Bound	Upper Bound
Intercept	6.631	2.054	< 0.001	2.605	10.658
Mean Canopy Cover	-0.087	0.017	< 0.001	-0.120	-0.055
Percent Clay	0.028	0.033	0.392	-0.036	0.093
Standard Deviation Canopy Cover	-0.095	0.046	0.038	-0.185	-0.005

reduce woody encroachment in the understory and open the canopy of the system. Management strategies that substantially reduce or delay woody encroachment will be those most effective at retaining the diverse herbaceous understory dominated by grass species in longleaf pine savannas. These strategies include implementing a fire regime that mimics the frequent disturbance historically present in the system (Frost, 1993) potentially coupled with mechanical thinning methods to allow light to reach ground level. Additionally, in areas where pines are planted it is important to manage for widely spaced trees with periodic thinning and fire to maintain the herbaceous understory (Harrington, 2011).

Surprisingly, SEPG presence does not appear to be associated with soil features at broad spatial scales. Studies have shown that soil, particularly clay content, is an important predictor of SEPG presence (Warren et al., 2017b; Bennett, 2018). Our finding is likely due to a lack of spatial resolution with gSSURGO data. The scale of the gSSURGO data may be too coarse to capture the microhabitat attributes suitable to SEPG (Bennett, 2018). However, our findings are consistent with studies on *Geomys bursarius*, in which sites with a high-density of

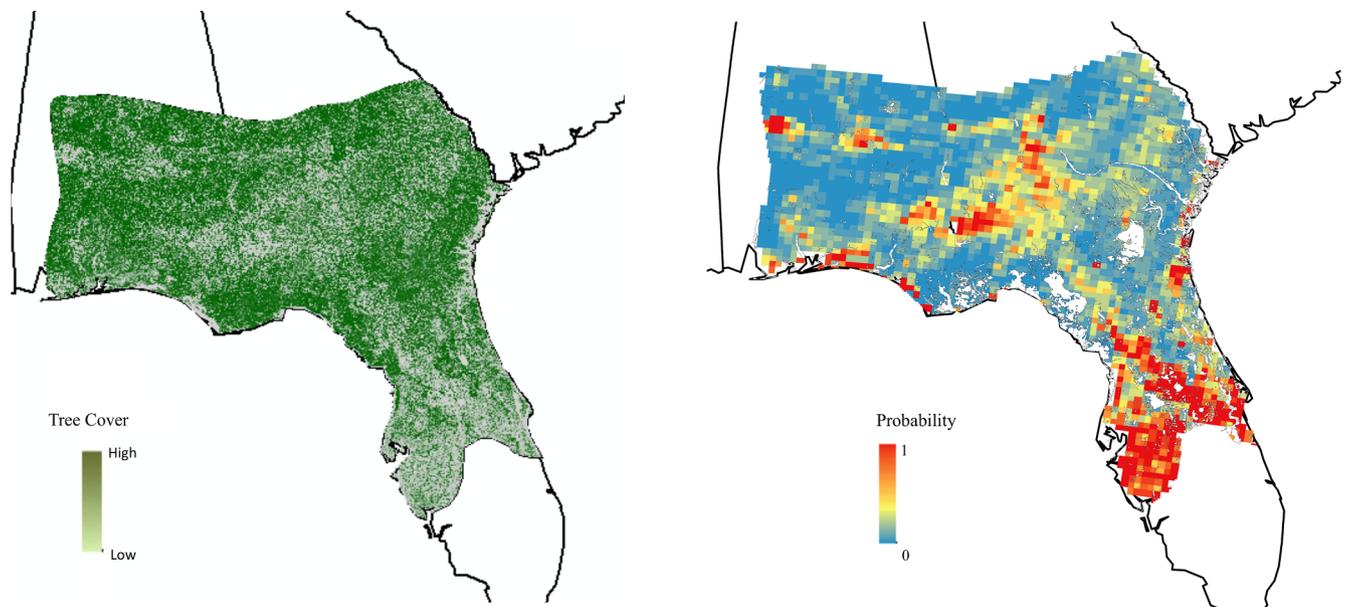


Fig. 3. Percent tree cover across the range of *Geomys pinetis* (left panel). Darker shades of green represent higher percentages of tree cover. The full (Mean Percent Tree Canopy + Standard Deviation Percent Tree Canopy + Mean Percent Clay) presence-absence (PA) probit regression distribution model (10-km) predicted probability of occurrence for *Geomys pinetis* (right panel). Occurrence probability values are represented as a color gradient with warmer shades representing higher probability of occurrence. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vegetation biomass, particularly grasses, are preferentially selected (Behrend and Tester, 1988) more so than specific soil conditions (Connior et al., 2010).

An interesting pattern emerges when examining occurrence of SEPG across the species range in terms of land-use and features within land-use categories. At broad scales, SEPG can occupy a variety of land-use classifications including forests, agricultural areas, and low urban intensity environments. Predicted probability of occurrence is widespread across the range and high in northern portions of the range when examining land use covariates alone. However, when examining features within those land use categories, vegetation diversity and structure is clearly important in creating conditions that promote establishment of burrows and appropriate forage. Predicted probabilities from the PA models are highest in regions where there are large tracts of open canopy, characteristic of the Coastal Plain regions of the southeastern United States. Taken together, SEPGs are clearly absent from both intensely urbanized areas and closed canopy forest and the combination of both within the region likely explains the apparent decline. Conservation strategies to mitigate increased development will be an integral part of protecting the species. Additionally, forest management strategies to reduce closed canopy systems and maintain herbaceous groundcover will also be instrumental in reducing SEPG decline. Understanding factors that promote SEPG occurrence at broad spatial scales was a first step in addressing how best to conserve the species. Additional fine-scale studies will also be necessary to guide management strategies at the local level. Furthermore, we need increased understanding of the genetic health of the species by assessing the dispersal capabilities and connectivity of fragmented populations across the landscape.

5. Conclusions

As global species extinctions continue, understanding land-uses, environmental features and spatial scales associated with species declines are critical. Using integrated species distribution modeling coupled with survey and public and citizen science data, we generated meaningful information about factors that limit the SEPG range. Our study integrates both fine scale PA and broad scale PO data (see review by Fletcher et al. (2019)) to examine the variables that influence the

distribution of a species. This approach may be increasingly beneficial for understanding factors that drive the loss of species. The methods should be equally useful in helping to fill critical gaps in our understanding of the loss of other species critical to ecosystem functioning and curtailing the mass species extinction facing our planet.

6. Data statement

Raw data files will be deposited in Dryad Digital Repository.

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. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117642>.

References

Alabama Department of Conservation and Natural Resources, 2005. In: Alabama's

- Comprehensive Wildlife Conservation Strategy, Appendix 1–3. Species of Greatest Conservation Need, pp. 295–303.
- Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Grassein, F., Hölzel, N., Klaus, V.H., Kleinebecker, T., 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol. Lett.* 18, 834–843.
- Arnett, A., Sitch, S., Pongratz, J., Stocker, B.D., Ciais, P., Poulter, B., Bayer, A.D., Bondeau, A., Calle, L., Chini, L.P., Gasser, T., 2017. Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed. *Nat. Geosci.* 10, 79–84.
- Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* 33, 1677–1688.
- Avise, J.C., Laerm, J., 1982. Gophers of the southeastern United States. *Florida Nat.* 55, 7–10.
- Bartón, K., 2018. MuMIn: Multi-Model Inference. R Package Version 1.40.4.
- Behrend, A.F., Tester, J.R., 1988. Feeding ecology of the plains pocket gopher in east central Minnesota. *Prairie Nat.* 20, 99–107.
- Bennett, M., 2018. Assessing Occurrence and Habitat Characteristics of the Southeastern Pocket Gopher (*Geomys pinetis*) (M.S. Thesis). Auburn University.
- Bond, W.J., Midgley, G.F., 2000. A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Glob. Change Biol.* 6, 865–869.
- Broussard, D.R., 1996. The Relationships Between Population Demographics of *Geomys bursarius* and the Variability of Its Food Base (M.S. Thesis). Baylor University.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. *Soc. Methods Res.* 33, 261–304.
- Cassola, F., 2016. *Geomys pinetis* (Errata Version Published in 2017). *The IUCN Red List of Threatened Species* 2016. e.T42589A115192878.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253.
- Clark, K.L., Branch, L.C., Farrington, J., 2018. Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests. *PLoS One* 13, e021137.
- Connor, M.B., Kershner, A.A., Medlin Jr, R.E., Elrod, D.A., Sasse, D.B., Risch, T.S., 2010. Distribution and habitat attributes of an endemic subspecies of pocket gopher. *Am. Midl. Nat.* 164, 217–229.
- Cutter, S.L., Solecki, W., Bragado, N., Carmin, J., Fragkias, M., Ruth, M., Wilbanks, T.J., 2014. Ch. 11: Urban systems, infrastructure, and vulnerability. In: Melillo, J., Richmond, Terese (T.C.), Yohe, G. (Eds.), *Climate Change Impacts in the United States: The Third National Climate Assessment*. U.S. Global Change Research Program, pp. 282–296.
- De Vos, J.M., Joppa, L.N., Gittleman, J.L., Stephens, P.R., Pimm, S.L., 2014. Estimating the normal background rate of species extinction. *Conserv. Biol.* 29, 452–462.
- Dorazio, R.M., 2014. Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Glob. Ecol. Biogeogr.* 23, 1472–1484.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.
- Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? *Global Ecol. Biogeogr.* 24, 52–63.
- Fithian, W., 2014. multispeciesPP: Multispecies Poisson Process Models. R Package Version.
- Fithian, W., Elith, J., Hastie, T., Keith, D.A., 2015. Bias correction in species distribution models: pooling survey and collection data for multiple species. *Methods Ecol. Evol.* 6, 424–438.
- Fletcher Jr., R.J., McCleery, R.A., Greene, D.U., Tye, C.A., 2016. Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landscape Ecol.* 31, 1369–1382.
- Fletcher Jr., R.J., Hefley, T.J., Robertson, E.P., Zuckerberg, B., McCleery, R.A., Dorazio, R.M., 2019. A practical guide for combining data to model species distributions. *Ecology* 100, e02710.
- Florida Fish and Wildlife Conservation Commission, 2012. Florida's Wildlife Legacy Initiative. Florida's State Wildlife Action Plan.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., 2005. Global consequences of land use. *Science* 309, 570–574.
- Ford, C.R., 1980. The Status and Preservation of the Colonial Pocket Gopher (Thesis). University of Georgia, Athens, USA.
- Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. *Proc. Tall Timbers Fire Ecol. Conf.* 18, 17–43.
- Frost, C., 2007. History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), *The Longleaf Pine Ecosystem*. Springer, New York, pp. 9–48.
- Gates, C.A., Tanner, G.W., 1988. Effects of prescribed burning on herbaceous vegetation and pocket gophers (*Geomys pinetis*) in a sandhill community. *Florida Sci.* 51, 129–139.
- Georgia Department of Natural Resources, 2005. A Comprehensive Wildlife Conservation Strategy for Georgia. Georgia Department of Natural Resources-Wildlife Resources Division, Social Circle, GA.
- Greene, D.U., McCleery, R.A., 2017. Multi-scale responses of fox squirrels to land-use changes in Florida: utilization mimics historic pine savannas. *For. Ecol. Manage.* 391, 42–51.
- Harrington, T.B., 2011. Overstory and understory relationships in longleaf pine plantations 14 years after thinning and woody control. *Can. J. For. Res.* 41, 2301–2314.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. dismo: Species Distribution Modeling. R Package Version 1.1-4.
- Hosmer, D.W., Lemeshow, S., 2000. In: *Applied Logistic Regression*. John Wiley & Sons Inc., New York, pp. 164.
- Huntley, N., Inouye, R., 1988. Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38, 786–793.
- Ives, A.R., Cardinale, B.J., 2004. Food web interactions govern the resistance of communities after non-random extinctions. *Nature* 429, 174–177.
- Jie, C., Jing-Zhang, C., Man-Zhi, T., Zi-tong, G., 2002. Soil degradation: a global problem endangering sustainable development. *J. Geogr. Sci.* 12, 243–252.
- Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., Xian, G., 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sens. Environ.* 132, 159–175.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. In: Samson, F.B., Knopf, F.L. (Eds.), *Ecosystem Management*. Springer, New York, pp. 130–147.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Jose, S., Jokela, E.J., Miller, D.L., 2007. The longleaf pine ecosystem. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), *The Longleaf Pine Ecosystem*. Springer, New York, pp. 3–8.
- Knudsen, C., 2017. glmm: General Linear Mixed Models via Monte Carlo Likelihood. R Package Version 1.2.2.
- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis. *Science* 305, 1632–1634.
- Lambin, E.F., Geist, H.J., 2006. *Land-Use and Land-Cover Change: Local Processes and Global Impacts*. Springer-Verlag, Berlin.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, London.
- Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Rest. Ecol.* 9, 280–292.
- McCleery, R.A., Moorman, C.E., Peterson, M.N., 2014. *Urban Wildlife Conservation: Theory and Practice*. Springer, New York.
- McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol.* 31, 1161–1175.
- McIntyre, R.K., Conner, L.M., Jack, S.B., Schlimm, E.M., Smith, L.L., 2019. Wildlife habitat condition in open pine woodlands: field data to refine management targets. *For. Ecol. Manage.* 437, 282–294.
- McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176.
- Miller, D.A., Pacifici, F., Sanderlin, J.S., Reich, B.J., 2019. The recent past and promising future for data integration methods to estimate species' distributions. *Methods Ecol. Evol.* 10, 22–37.
- Mills, L.S.M., Soulé, M.E., Doak, D.F., 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43, 219–224.
- Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50.
- Noss, R.F., 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Nat. Areas J.* 9, 211–213.
- Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. *Endangered Ecosystems of the United States: a Preliminary Assessment of Loss and Degradation Vol. 28 US Department of the Interior, National Biological Service, Washington, DC, USA.*
- Ozier, J., Morris, K., 2016. *George C. Georgia's State Wildlife Action Plan. Appendix C. Mammals Technical Team Report*. Georgia Department of Natural Resources-Wildlife Resources Division, Social Circle, GA.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *Am. Nat.* 103, 91–93.
- Patton, J.L., Brylski, P.V., 1987. Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. *Am. Nat.* 130, 493–506.
- Pembleton, E.F., Williams, S.L., 1978. *Geomys pinetis*. *Mamm. Species* 86, 1–3.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W., Chini, L., et al., 2010. Scenarios for global biodiversity in the 21st century. *Science* 330, 1496–1501.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Pimm, S.L., Raven, P., 2000. Biodiversity: extinction by numbers. *Nature* 403, 843–845.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752.
- Platt, W.J., Carr, S.M., Reilly, M., Fahr, J., 1999. Pine savanna overstorey influences on ground-cover biodiversity. *Appl. Veg. Sci.* 9, 37–50.
- Prakash, I., 2018. *Rodent Pest Management*. CRC Press, Boca Raton, FL.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. URL: R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Reichman, O.J., Seabloom, E.W., 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends Ecol. Evol.* 17, 44–49.
- Reichman, O.J., Smith, S.C., 1985. Impact of pocket gopher burrows on overlying vegetation. *J. Mamm.* 66, 720–725.
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M., 2011. pROC: an Open-source Package for R and S+ to Analyze and Compare ROC Curves. R Package.

- Scott, J., 2008. In: Survey of the Current Distribution of the Southeastern Pocket Gopher (*Geomys pinetis*) in Georgia. Final Report to the Georgia DNR, pp. 42.
- Song, X.P., Hansen, M.C., Stehman, S.V., Potapov, P.V., Tyukavina, A., Vermote, E.F., Townshend, J.R., 2018. Global land change from 1982 to 2016. *Nature* 560, 639–643.
- Smith, L.L., Linehan, J.M., Stober, J.M., Elliott, M.J., Jensen, J.B., 2009. An evaluation of distance sampling for large-scale gopher tortoise surveys in Georgia, USA. *Appl. Herpetol.* 6, 355–368.
- Trani, M.K., 2002. Southern Forest Resource Assessment highlights terrestrial ecosystems and wildlife conservation. *J. For.* 100, 35–40.
- U.S. Census Bureau, 2016. TIGER/Line Shapefiles (machine readable data files)/prepared by the U.S. Census Bureau, 2016. (accessed 7-7-2018). <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.2016.html>.
- U.S. Geological Survey, 2011. 20141010, NLCD 2011 Land Cover (2011 Edition) – National Geospatial Data Asset (NGDA) Land Use Land Cover: U.S. Geological Survey. <https://www.mrlc.gov/data/nlcd-2011-land-cover-conus-0> (accessed April 14, 2018).
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- U.S. Department of Agriculture, Soil Survey Staff, 2015. Gridded Soil Survey Geographic (gSSURGO) Database for the Conterminous United States. Natural Resources Conservation Service. Available online at <https://gdg.sc.egov.usda.gov/>. November 16, 2015 (FY2016 official release) (accessed May 5, 2018).
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, D., Gómez, J.M., Jordano, P., Medel, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307.
- Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *For. Ecol. Manage.* 211, 150–165.
- Wagner, R.O., Connor, M.B., Melder, C.A., Cooper, B.S., Hightower, D., Pearce, S., 2017. Movement and resource selection of Baird's pocket gopher within a longleaf pine ecosystem. *Southeast. Nat.* 16, 397–411.
- Warren, A.E., Conner, L.M., Castleberry, S.B., Markewitz, D., 2017a. Home range, survival, and activity patterns of the Southeastern pocket gopher: implications for translocation. *J. Wild. Manage.* 8, 544–557.
- Warren, A.E., Castleberry, S.B., Markewitz, D., Conner, L.M., 2017b. Understory vegetation structure and soil characteristics of *Geomys pinetis* (Southeastern Pocket Gopher) habitat in Southwestern Georgia. *Am. Midl. Nat.* 178, 215–225.