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Multi-scale responses of fox squirrels to land-use changes in Florida: Utilization mimics historic pine savannas

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ABSTRACT

Pine savanna ecosystems in the southeastern United States are highly fragmented and degraded. Within these ecosystems, southeastern fox squirrels (*Sciurus niger* spp.) appear to be excellent bioindicators and serve important ecological roles. However, because of the loss of these areas, fox squirrel populations are patchily distributed and they are thought to be declining. To determine factors influencing their distribution, we conducted a multi-scale occupancy study throughout the range of the Sherman's fox squirrel (*S. n. shermani*) in Florida. We surveyed 40 landscapes comprised of 200 grids and 1800 camera-trap points. We recorded 3170 camera-trap photos of fox squirrels at 8 of the 21 land cover classes surveyed, at 26 landscapes (65.0%), 70 grids (35.0%), and 210 of the camera-trap points (11.7%). At the landscape scale (7.65 km^2), the occurrence of fox squirrels increased as the amount of interspersion in tree cover increased, but decreased with increasing tree cover, supporting the need for open canopied areas interspersed with hardwoods and hardwood thickets at broad scales. At the finer grid scale (5.3 ha), their occurrence increased with pine and oak densities and proximity to urban and residential development and was also negatively influenced by tree cover. At the grid and point scales, fox squirrels were more likely to occur in areas with increased canopy closure, supporting their association with patches of oak trees imbedded in open canopy forests similar to the pine savannas that once dominated the region. Fox squirrels' occurrence was negatively influenced by woody understory and woody ground cover at all scales. Their preference for a midstory with an open canopy and clear understory also suggest a reliance on frequent disturbance such as fire to maintain their habitat. Fox squirrels appear to be highly adaptable as they occurred in land cover types and altered landscapes (e.g., developed, agriculture) outside of natural pine savannas. But, as indicators of pine savanna ecosystem health, their conservation along with other wildlife tied to these forests will necessitate management practices that include or emulate a fire regime to reduce tree canopy densities and the encroachment of the understory layer and woody ground cover, but also to maintain heterogeneity that intersperses requisites (food, shelter, and cover) across the landscape.

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1. Introduction

Over the past century pine forests in the southeastern United States (hereafter, Southeast) have been lost at an alarming rate. Between 1936 and 1980, Florida' pine forests (predominately longleaf pine [*Pinus palustris*]) diminished by 90% (Bechtold and Knight, 1982; Brown and Thompson, 1987). Today, the native pine forests in the Southeast occupy ≤3% of their historic range and what remains is highly fragmented and degraded (Frost, 1993). The ongoing conversion of pine forests to agriculture, intensively managed tree plantations, and urbanization has forced wildlife species reliant on these forests into remnant patches (Noss, 1989; Frost, 1993; Landers et al., 1995; Van Lear et al., 2005). Within these remnants, wildlife face additional threats from altered disturbance regimes, including the exclusion or suppression of fire (Weigl et al., 1989). These threats will continue to reshape the Southeast into the future; for example, within the next 50 years, the human population in Florida is projected to more than double and approximately three million ha of land will be converted for human habitation, increasing habitat fragmentation and heightening the scarcity of resources for wildlife (Zwick and Carr, 2006).

Southeastern pine forests were historically shaped by frequent fires that created an open canopy savanna with a sparse understory

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(Outcalt and Sheffield, 1996; Steele and Koprowski, 2001; Van Lear et al., 2005). At a broad scale, fire creates a heterogeneous landscape with patches of differing vegetation. Fire intensity and duration vary with site-specific and weather conditions and create dynamic landscapes that shift between savannas, woodlands, and other vegetative communities (Peet and Allard, 1993; Landers et al., 1995; Van Lear et al., 2005). Today, the application of fire is increasingly difficult because of air quality concerns (Ryan et al., 2013), threats to human structures, and excessive buildup of fuels that can lead to crown fires and forest destruction (Weigl et al., 1989). Many remaining tracts of pine forests are severely degraded and succeeding to homogenized, closed canopy hardwood-dominated forests which are unsuitable to many wildlife species (Engstrom, 1993).

One species that is important to the health of southeastern pine ecosystems is the fox squirrel (*Sciurus niger*). Six subspecies (*Sciurus n. vulpinus, S. n. niger, S. n. shermani, S. n. bachmani, S. n. avicennia*, and *S. n. cinereus*) are often grouped together as 'southeastern fox squirrels' because of their similarities in morphology and habitat use (Loeb and Moncrief, 1993). Southeastern fox squirrels are excellent bioindicators (Weigl et al., 1989) and are ecologically important as seed dispersers, seed predators, and prey for other species (Steele and Koprowski, 2001). They also have a coevolutionary relationship with the pine-oak systems by spreading hyphae and spores of fungi that require animal dispersal (Trappe and Maser, 1977; Weigl et al., 1989). Some southeastern mycorrhizae species have been documented to establish on pine seedling roots after exposure to fox squirrel feces (Gamroth, 1988). Southeastern fox squirrels may require large areas of forested pine savanna habitat and appear to be negatively influenced by changes in forest structure, especially by fragmentation and deforestation (Weigl et al., 1989; Chamberlain et al., 1999; Conner et al., 1999). Not surprisingly, many southeastern fox squirrel populations that were once common are now sparsely distributed and thought to be declining (Weigl et al., 1989; Loeb and Moncrief, 1993; Wooding, 1997). Today, three of six southeastern fox squirrel subspecies have a conservation status of protection: in Florida, the Sherman's fox squirrel (*S. n. shermani*) is a state listed Species of Special Concern and the Big Cypress fox squirrel (*S. n. avicennia*) is State Threatened (Humphrey and Jodice, 1992; Loeb and Moncrief, 1993). In the northeastern U.S., the Delmarva fox squirrel (*S. n. cinereus*) was recently (16 November 2015) delisted as federally endangered under the U.S. Endangered Species Act (1973 [as amended]; U.S. Fish and Wildlife Service, 1993) but remains state-listed in Delaware Maryland, and Virginia (U.S. Fish and Wildlife Service, 2015).

The conservation and management of pine forests for southeastern fox squirrels has been constrained by a lack of reliable information on their population trends (Greene and McCleery, 2017) and the factors contributing to their patchy distributions at broad scales. Previous research has focused on local (e.g., population level) and home range scales where they are known to occur, particularly in upland pine savannas (i.e., sandhill and pine flatwoods communities) (Moore, 1957; Kantola and Humphrey, 1990; Chamberlain et al., 1999; Conner and Godbois, 2003; Perkins and Conner, 2004; Prince et al., 2016). At these scales, we have a good understanding of the vegetation structure favorable to fox squirrels, such as reduced understory and woody ground cover (Conner et al., 1999). However, the proportion and distribution of oaks and pines across the landscape has been debated (Weigl et al., 1989; Kantola and Humphrey, 1990; Chamberlain et al., 1999; Perkins and Conner, 2004). These differences may stem from a lack of information about fox squirrels' response to broader vegetation patterns across the landscape. In fact, we know little about how landscape features and characteristics in a rapidly

changing region of the country may contribute to the distribution of fox squirrels.

Maintaining a forest with diverse faunal components is a critical conservation need for the functioning of the southeastern pine forests. A thorough approach to understanding how wildlife can persist in southeastern pine forests should account for changes in the environments at multiple spatial scales (Wiens, 1989). Features that are favorable at one scale may have little importance or be a deterrent at another scale (Ciarniello et al., 2007). Accordingly, our goal for this study was to use the distribution of the Sherman's fox squirrel in Florida at different biologically relevant scales to understand how land-use change, fire suppression, and other environmental factors shape their distribution in the Southeast.

2. Material and methods

2.1. Survey area

We conducted field surveys throughout the range of Sherman's fox squirrels in North and Central Florida on public and private lands (Fig. 1). The vegetation communities at our sites were highly variable and included open grasslands, pine-dominated forests, pine–hardwoods, hardwood hammocks, bottomland hardwood forests, and pine clear cuts. The canopy trees varied between sites, but the dominant pine trees included longleaf, slash (*P. elliottii*) and loblolly (*P. taeda*), and the dominant oaks were turkey (*Quercus laevis*), live (*Q. virginiana*), laurel (*Q. laurifolia*), and water (*Q. nigra*). The sites varied in their vegetation management practices which included grazing, mowing, burning, cropland agriculture (e.g., sorghum) and no active management. Most sites with pines outnumbering hardwoods were managed for timber.

2.2. Field surveys

To assess the influence of environmental features on the distribution of fox squirrels, we surveyed using a nested (hierarchal) design at three spatial scales: landscape, grid, and survey point. First, we generated random points throughout North and Central Florida using ArcGIS 10.1 (ESRI, Redlands, CA). Around each random point, we created a 7.65 km^2 buffer which represented the landscape scale. Then, we used a stratified random approach to select 40 landscapes (Fig. 1) within three categories (hereafter, *landscape class*) as either sandhill, flatwoods, or random, determined from their *land cover class* (Florida Natural Areas Inventory, 2010). Of the 40 landscapes, we selected 10 in upland pine or sandhills, 10 in mesic/shrubby flatwoods, the primary land cover classes within the pine savannas where fox squirrels are most common (Moore, 1957; Kantola and Humphrey, 1990), and the remaining 20 without regard to land cover class. When a randomly selected landscape could not be surveyed (permission was denied, hunting or a prescribed burn was scheduled), a new site was selected until the 40 landscapes were proportionally allocated. Survey areas on three landscapes were located entirely on private properties, one was divided on private and public lands, and the remainder were primarily public, many with private properties interspersed.

Within each landscape, we randomly selected five grids. On each grid, we placed nine survey points in a 3 × 3 arrangement. We spaced survey points at 115 m intervals to capture fine-scale differences in vegetation features between grids, which yielded a grid size of 5.3 ha. To maximize grid independence and to reduce spatial autocorrelation, we separated grids by ≥500 m; the pooled mean maximum distance moved from southeastern fox squirrel trapping and radio-telemetry studies (Greene and McCleery, 2017), which yielded the 7.65 km^2 for a landscape.
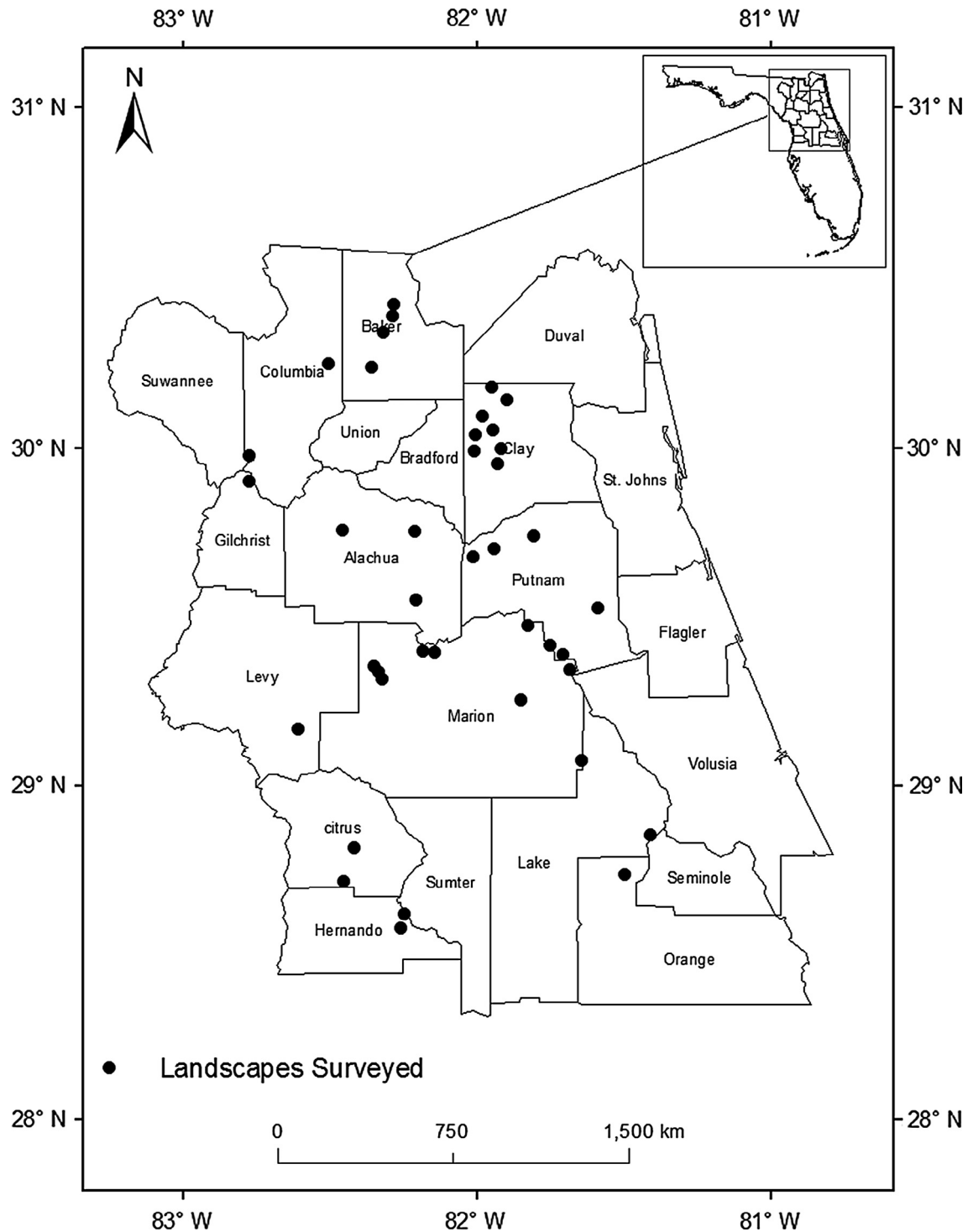
Fig. 1. The distribution of the 40 landscapes surveyed in a multi-scaled study of habitat use and selection of Sherman's fox squirrels in North and Central Florida, USA, 2013–2014.

We "trapped" each survey point using a game camera (Bushnell Trophy Cam model 119436, Bushnell Outdoor Products, Overland Park, KS), which has been shown to significantly increase the probability of detecting fox squirrels compared to live-trapping or visual-based survey methods (Greene et al., 2016). To assess the presence of fox squirrels, we placed each camera 50 cm above the ground and angled it towards a bait pile of pecans and cracked corn 2.5 m from the camera which we placed on the first day. We equipped cameras with an 8 GB SanDisk memory card (SanDisk

Corporation, Milpitas, CA) and used the camera's 'normal' sensitivity setting to take three photos every 10 s when triggered. We left cameras in the field for up to 8 days (average 6.44 [SD = 1.04] including cameras [n = 74] that malfunctioned during the survey period), unless there were site access limitations. We defined our camera-trapping days to be based upon the 24-h period beginning when the camera was activated. We conducted our surveys from 01 January to 01 July in 2013 and 2014, a period of increased activity for southeastern fox squirrels (Moore, 1957; Weigl et al.,

1989) and when detections are more likely to occur (Greene et al., 2016).

2.3. Vegetation features

To capture variation in forest structure, we measured vegetative features along four strata at each survey point: (1) canopy layer; (2) midstory and overstory trees (≥10 cm at 137 cm diameter at breast height); (3) understory cover; and (4) ground cover. At the canopy layer, we used a concave spherical densitometer (Lemmon, 1957; Forestry Suppliers, Inc., Model-C) to measure the density of forest canopy (*canopy closure*) at each survey point. Our intent was to capture fine scale differences in canopy closure between pines and oaks; we predicted canopies in pine forests would be less dense than fire-suppressed areas dominated by hardwoods. To survey mid- and overstory trees, we used the point-center quarter method (Cottam and Curtis, 1956) at each survey point to measure the densities (trees per hectare) of pines (*pine density*) and oaks (*oak density*). We truncated surveys for each quarter to only include the closest trees ≤100 m from a survey point, and used a correction factor to account for quarters where pine or oak trees were missing (Warde and Petranka, 1981).

To capture variation in fire histories, we measured the amount of understory cover using the line-intercept method (Canfield, 1941) by placing a 10-m line along each cardinal direction from a survey point. We measured any obstruction ≥1 cm wide along each transect between 45 cm and 2 m in height, which included grasses, ferns, forbs, vines, woody shrubs, down trees, limbs, and branches, and pooled these into a single variable (*understory cover*). Second, we measured the ground cover density by surveying 5, ½ m × ½ m quadrats (Daubenmire, 1959), with one placed 1 m behind the survey point and one 10 m from the camera in each cardinal direction. We visually estimated ground cover vegetation (<45 cm in height) to create three variables: *open ground*, *herbaceous ground cover*, and *woody ground cover*.

2.4. Landscape features

To assess influences of forest structure, we created three variables. First, we quantified the total area of forest (*forest*) in each landscape using ArcGIS, where non-forested spaces represented areas converted to agriculture or development. Second, we used the U.S. Forest Service Tree Canopy analytical layer (Jin et al., 2013) from the 2011 National Land Cover Database to estimate the average percentage of tree cover (*tree cover*) at each scale from 30 × 30 m pixels. We used this environmental variable because fox squirrels are said to avoid closed-canopy forests typically associated with excessive hardwoods (e.g., Perkins et al., 2008). We used ArcGIS to extract the *tree cover* data within our landscapes, grids, and from a 100 × 100 m square buffer around each survey point. Third, we used the standard deviation of *tree canopy* calculated at each scale as a measure of forest heterogeneity (*interspersion*), which we predicted would capture the small hardwood patches within open pinelands that are favorable to fox squirrels (Perkins et al., 2008).

We assessed the influence of development two ways using Arc-GIS. First, we exported all land cover classes (Florida Natural Areas Inventory, 2010) and created a subset of Low Intensity and High Intensity Urban (hereafter, urban) and Medium and High Density Residential (hereafter, residential) land cover classes that were <20 km from a survey point. We calculated the distance from a survey point to the nearest urban and residential polygons using the R packages rgdal (Bivand et al., 2014) and rgeos (Bivand and Rundel, 2014) to create variables using the nearest distance to an urban area (*distance to urban*), residential area (*distance to residential*), or the nearest distance to either of these areas of development (*distance to development*). Second, we used the Percent Developed Imperviousness layer (Xian et al., 2011) from the 2011 National Land Cover Database to obtain measures of the impervious surfaces (*impervious*) around our landscapes. The effects of urbanization can extend beyond the boundary of an urban area and have yielded mixed responses from wildlife due to the presence of water, food supplements, and degree of the forest-urban mosaic which can alter animal movements (Hess et al., 2014). Therefore, to capture urbanized areas on the periphery of our survey sites, we added a 3.7 km buffer to each landscape, which is an average dispersal distance recorded for *S. n. shermani* (Wooding, 1997), then quantified the percentage of impervious surfaces from the bounded area.

2.5. Occupancy estimation

We created encounter histories of our camera-survey days (n = ≤8) and turned our environmental variables into covariates (n = 18) for each scale (see Supplementary Material, Table A.1 for full variable definitions). To improve model convergence, we standardized the continuous covariates (Kéry, 2010). We examined the relationships between our covariates at each scale and dropped 1 of the pair if their Pearson's correlation coefficient was >|0.70|.

We first analyzed our landscape- and grid-scale data in program Presence v8.3 (Hines, 2006) using a single-season model (MacKenzie et al., 2006) to assess the importance of the normalized covariates on the probability of occupancy (Ψ) and detection (*p*). Our null models indicated that we had near perfect detection after eight days (e.g., at the grid scale the probability of a false absence $[1 - p]^8 = 0.013$); therefore, we evaluated the influence of covariates on Ψ with binomial regressions in R (R Core Team, 2014). For the landscape scale analysis, we used generalized linear models, with point-scale data averaged across all grids within a landscape. For the grid scale analysis, we used generalized linear mixed-effects models (package lme4; Bates et al., 2015a,b), with point-scale data averaged within grids, and used landscape as a random effect to account for spatial autocorrelation.

We first assessed goodness-of-fit by the marginal and conditional R^2 values from our global models (Nakagawa and Schielzeth, 2013) using the R package MuMIn (Barton, 2016). Then, we generated a suite of a priori models for the landscape (Table 1) and grid (Table 2) scales. Our models were comprised of variables that were single, multiple, and interactive combinations. We assessed all continuous variables as a linear response, except pine density and oak density which we were included as linear and quadratic responses because fox squirrels are known to occur in forests with moderate forest cover. We determined the covariates predictive importance by inspecting the conditional beta coefficient (β) estimates and their 95% confidence intervals (CI), with significance defined as CIs for a variable that did not overlap zero. When a significant covariate became nonsignificant because of the high variance in additive or interactive models, we excluded them from the final candidate set of models. Models that had convergence issues were also deleted from the final model set.

We evaluated our candidate models using Akaike Information Criterion corrected for small sample size (AICc), where the level of importance was assessed by model weights. Most of our covariates were either described in the literature as being important predictors of fox squirrel occurrence or were needed to evaluate our biological predictions. Our goal was to understand their relative importance of these variables at each spatial scale; therefore, to avoid discounting variables known to influence fox squirrel occurrence, we considered all models that had significant beta coefficients. We used multimodel inference to account for sampling variance and model selection uncertainty by model averaging variables that occurred in >1 model (Buckland et al., 1997; Anderson,

Table 1
Candidate models with environmental covariates, Akaike's Information Criterion (AICc), difference in AICc (ΔAICc) between a model and the model with the lowest AICc Akaike weight (w_i), and number of parameters (k) for the candidate models used to estimate Sherman's fox squirrels' occurrence at the landscape scale in North and Central Florida, USA, 2013–2014.

Model	AICc	ΔAICc	w_i	k
Tree cover	44.289	0.000	0.648	2
Woody ground cover	47.829	3.540	0.110	2
Herbaceous ground cover	47.992	3.703	0.102	2
Understory cover	49.838	5.550	0.040	2
Interspersion	50.591	6.302	0.028	2
Distance to urban	51.371	7.082	0.019	2
Landscape class	52.526	8.238	0.011	3
Canopy closure	53.387	9.098	0.007	2
Null model	53.901	9.612	0.005	1
Pine density	54.136	9.847	0.005	2
Impervious surface	54.578	10.289	0.004	2
Forest	54.700	10.411	0.004	2
Open ground	55.146	10.857	0.003	2
Number of land cover classes	55.746	11.458	0.002	2
Distance to development	55.812	11.523	0.002	2
Vine	56.118	11.829	0.002	2
Oak density	56.533	12.244	0.001	2

Table 2
Candidate models with environmental covariates, Akaike's Information Criterion (AICc), difference in AICc (ΔAICc) between a model and the model with the lowest AICc Akaike weight (w_i), and number of parameters (k) for the candidate models used to estimate the occurrence of Sherman's fox squirrels at the grid scale in North and Central Florida, USA, 2013–2014.

Model	AICc	ΔAICc	w_i	k
Woody ground cover	200.342	0.000	0.933	3
Landscape class	206.626	6.284	0.040	4
Understory cover	208.033	7.691	0.020	3
Tree cover + Canopy closure	212.763	12.421	0.002	4
Tree cover + Open ground	214.017	13.675	0.001	4
Distance to urban	214.030	13.687	0.001	3
Pine density	214.577	14.235	0.001	4
Distance to development	215.474	15.132	0.000	3
Pine density × Tree cover	215.701	15.359	0.000	5
Open ground	216.210	15.868	0.000	3
Herbaceous ground cover	218.286	17.944	0.000	3
Oak density	218.983	18.641	0.000	4
Tree cover	219.044	18.702	0.000	3
Null model	219.481	19.139	0.000	2
Canopy closure	219.858	19.516	0.000	3
Number of land cover classes	220.603	20.261	0.000	3
Vine	220.643	20.301	0.000	3
Interspersion	221.008	20.666	0.000	3

2008) using the R package AICcmodavg (Mazerolle, 2016). We generated plots of predicted values for the probability of occurrence as a function of our most influential variables at each spatial scale.

To increase our understanding of how the environmental covariates influenced the occurrence of fox squirrels at the point scale, we modeled Ψ and p using data from the landscapes where fox squirrels were detected. We used a Bayesian approach (Royle and Kéry, 2007; Kéry and Schaub, 2012) outlined by Kéry (2010) because it allowed us to fit complex models with covariates to our hierarchical data while accounting for spatial autocorrelation between camera-survey points on the same grid (Ries et al., 2004; Royle and Dorazio, 2008; Kéry, 2010; Govindan et al., 2012). We conducted our analysis in WinBUGS 1.4.3 (Lunn et al., 2000; Spiegelhalter et al., 2003) implemented in R using the package R2WinBUGS (Sturtz et al., 2005). We used non-informative priors (mean = 0, variance = 0.001) for all covariates and used the grid as a random effect on the occupancy component of the model to account for site effects (Ries et al., 2004).

We fit a global model on Ψ and used a stepwise approach to determine the influence of variables that we predicted would influence p, which included *understory cover, open ground, woody ground cover, and herbaceous ground cover*. We individually

removed the noninfluential variables on p if their 95% credible intervals (CRIs) included zero and continued until all variables were significant (Govindan et al., 2012; Kéry and Schaub, 2012). Then, we used the best parameterization of p to evaluate models with different parameterizations of Ψ for our environmental covariates. Again, we used a stepwise approach on a fully parameterized model on Ψ until we had a multivariate model with only significant variables. We used this approach because the Bayesian deviance information criterion (DIC) that is most often used as the model selection criterion (Spiegelhalter et al., 2002) has been shown to perform poorly with hierarchical models (Plummer, 2008; Millar, 2009; Kéry, 2010). For all models, we initiated Markov Chain Monte Carlo (MCMC) runs for each model for 75,000 iterations, a burn-in period of 20,000 iterations, three chains, and with a thinning rate of three. We assessed the convergence of the MCMC chains by visual assessment of trace plots in WinBUGS and examined the $\bar{R}$ statistic to ensure it was near one.

3. Results

The number of land cover classes at landscapes ranged between 15 to 54 (mean = 33.4, SD = 9.077). At our random landscapes,

cameras were in 1 to 6 land cover classes (mean = 3.25, SD = 1.618). Of the 21 land cover classes surveyed, we detected fox squirrels at 8 (Supplementary Material, Table A.2). In total, we surveyed for 11,795 camera-trap days. We detected fox squirrels at 26 of the landscapes (65.0%), 75 of the grids (37.5%), and at 218 of the survey points (12.1%). We used all environmental covariates except the average distance to a residential area because it was disproportionally represented in the pooled *distance to development* covariate and resulted in a high correlation (≥0.786) at all scales, likely because dwellings in the subclass of High Density Residential are often located in large urban areas or on the urban-rural fringe. Our marginal and conditional R^2 values at the landscape scale were 0.460 and 0.619 and at the grid scale 0.555 and 0.759, respectively.

For our landscape-scale analysis, our top model included one covariate, the percentage of *tree cover* (Table 1). The percentage of *tree cover* negatively influenced the probability of occurrence of fox squirrels (β = −1.563, 95% CI = −2.918 − −0.588), where occurrence declined from approximately 75% to 55% when tree cover was >50% on a landscape (Supplementary Material, Fig. A.1). Fox squirrels were more likely to occur in the sandhill *landscape class* (β = 2.603, 95% CI = 0.469–5.719) compared to flatwoods or randomly selected sites. Other significant variables were moderately weak in predicting occurrence. Of these, the probability of occurrence of fox squirrels decreased with increasing *woody ground cover* (β = −1.104, 95% CI = −2.144 − −0.321) and understory (β = −0.997, 95% CI = −2.176 − −0.190), both nearly identical in their predictions, with fox squirrel occurrence declining from approximately 70% to 50% as woody shrub and ground cover increased towards 100%. Fox squirrel occurrence was also positively influenced with increasing heterogeneity (*interspersion*) (β = 0.828, 95% CI = 0.133 − 1.658) and *herbaceous ground cover* (β = 1.611, 95% CI = 0.394 − 3.473), with fox squirrel occurrence increasing from approximately 50% to 70% as *herbaceous ground cover* and *interspersion* each increased towards 100%. All other estimates had 95% CIs that overlapped zero (Table 3).

At the grid scale, our top model included *woody ground cover* as the only covariate (Table 2). *Woody ground cover* negatively influenced the occurrence of fox squirrels (β = −1.653, 95% CI = −2.041 − −0.922), where the probability of occurrence declined rapidly from approximately 70% to 20% when woody ground cover was at 40%, and was approximately 0% as woody

ground cover increased further (Supplementary Material, Fig. A.2). Other parameter estimates (Table 4) indicated that fox squirrel was positively influenced by *canopy closure* (β = 1.026, 95% CI = 0.259 – 1.793), with the probability of occurrence increasing from approximately 10% with open canopies to 40% near closed-canopied areas. This relationship was likely influenced by the *oak density* (β = 0.948, 95% CI = 0.018 – 1.924), where fox squirrel occurrence increased from approximately 20% to 80% as tree densities increased from 0 to 600 trees per hectare (although uncertainty was relatively high as indicated by wide confidence intervals). Fox squirrels' occurrence also increased as the *distance to urban area* (β = −1.487, 95% CI = −3.331 – −0.385) and *distance to development* decreased (β = −0.981, 95% CI = −2.016 – −0.188), but occurrence was highly variable (e.g., at 60% occurrence, 95% CI = 30–100% at the periphery of development). *Understory cover* negatively influenced fox squirrel occurrence (β = −1.446, 95% CI = −2.447 – −0.624), with probabilities of occurrence decreasing from approximately 60% when shrub cover was absent, was 20% at 40% cover, and 0% when cover was 100%. Conversely, *open ground* (β = 0.706, 95% CI = 0.140–1.271) positively influenced occurrence. Fox squirrels' occurrence was positively influenced by pine density (β = 1.200, 95% CI = 0.377–2.661) and negatively influenced by *tree cover* (β = −1.075, 95% CI = −2.012 – −0.137); these variables also had a significant interaction (β = −0.920, 95% CI = −1.828 – −0.172). Plotted predicted values (excluding the upper 5% of outliers of pine tree density densities) under low (18%), medium (62%), and high (90%) *tree cover* indicated that although pines were important, too many diminished their value and decreased the probability of fox squirrel occurrence (Supplementary Material, Fig. A.3). Fox squirrels were more likely to occur in the sandhill *landscape class* (β = 4.235, 95% CI = 2.226–6.975) compared to flatwoods or random sites.

At the point scale, our best model included two variables affecting Ψ and one affecting p: Ψ(*canopy closure + woody ground cover*) p(*understory cover*). Our posterior mean of occupancy was 0.291 (CRI = 0.258–0.332) and the posterior mean of daily detection was 0.157 (CRI = 0.138–0.177), indicating overall probabilities of occurrence and detection were 29% and 16%, respectively. The variable *understory cover* decreased the probability of detecting fox squirrels (posterior mean = −0.771, CRI −0.945 – −1.495). Fox squirrel occurrence was positively influenced by *canopy closure* (posterior mean = 0.535, CRI = 0.415–0.897), with the probability

Table 3
Estimates of the beta coefficients (β), standard errors (SE), lower (LCI) and upper (UCI) 95% confidence intervals, z-value, and corresponding *P*-values for environmental covariates used to estimate the occurrence of Sherman's fox squirrels at the landscape scale in Central Florida, USA, 2013–2014.

Covariate	β	SE	LCI	UCI	z-value	*P*-value
Intercept	0.901	0.484	−0.015	1.296	1.809	0.062
Tree cover	−1.563	0.579	−2.918	−0.588	2.612	0.007[*]
Woody ground cover	−1.104	0.455	−2.144	−0.321	2.349	0.015[*]
Interspersion	0.828	0.379	0.133	1.658	2.114	0.029[*]
Landscape: sandhill	2.603	1.236	0.469	5.719	2.037	0.035[*]
Herbaceous ground cover	1.611	0.772	0.394	3.473	2.021	0.037[*]
Understory cover	−0.997	0.498	−2.176	−0.190	1.938	0.045[*]
Distance to urban area	−0.833	0.471	−2.022	−0.074	1.710	0.077
Canopy closure	−0.616	0.401	−1.493	0.106	1.485	0.125
Landscape: random	1.025	0.798	−0.515	2.666	1.242	0.199
Impervious surface	−0.413	0.346	−1.195	0.241	1.156	0.232
Forest	−0.430	0.386	−1.339	0.262	1.079	0.265
Pine density (linear)	−0.498	0.457	−1.454	0.370	1.053	0.276
Oak density (linear)	0.647	0.642	−0.549	2.039	0.975	0.314
Open ground	0.331	0.339	−0.329	1.035	0.946	0.329
Pine density (quadratic)	−0.359	0.517	−1.474	0.267	0.672	0.487
Number of land covers	0.133	0.222	−0.285	0.607	0.582	0.548
Distance to development	−0.186	0.335	−0.862	0.477	0.537	0.579
Oak density (quadratic)	−0.073	0.329	−0.678	0.900	0.216	0.824
Vine	−0.015	0.333	−0.683	0.803	0.043	0.964

[*] Indicates significant at α = 0.05.

Table 4
Estimates of the beta coefficients (β), standard errors (SE), lower (LCI) and upper (UCI) 95% confidence intervals, z-value, and corresponding *P*-values from the environmental covariates used to estimate the occurrence of Sherman's fox squirrels at the grid scale in Central Florida, USA, 2013–2014.

Covariate	β	SE	LCI	UCI	z-value	*P*-value
Intercept	−1.155	0.520	−2.041	−0.087	2.211	0.026*
Woody ground cover	−1.653	0.404	−2.537	−0.922	4.064	< 0.001*
Landscape: sandhill	4.235	1.141	2.226	6.975	3.690	< 0.001*
Understory cover	−1.446	0.462	−2.447	−0.624	3.114	0.002*
Canopy closure	1.026	0.389	0.259	1.793	2.623	0.009*
Open ground	0.706	0.287	0.140	1.271	2.444	0.015*
Tree cover	−1.075	0.477	−2.012	−0.137	2.247	0.025*
Pine density × Tree cover	−0.920	0.412	−1.828	−0.172	2.218	0.026*
Distance to development	−0.981	0.451	−2.016	−0.188	2.164	0.030*
Distance to urban area	−1.487	0.701	−3.311	−0.385	2.109	0.454*
Pine density (linear)	1.200	0.581	0.377	2.661	2.056	0.014*
Oak density (linear)	0.948	0.476	0.018	1.924	1.980	0.046*
Herbaceous ground cover	0.542	0.291	−0.049	1.117	1.852	0.062
Pine density (quadratic)	−0.828	0.458	−1.932	−0.177	1.796	0.071
Landscape: random	1.455	0.921	−0.315	3.538	1.569	0.114
Oak density (quadratic)	−0.176	0.141	−0.459	0.123	1.239	0.213
Number of land covers	−0.416	0.436	−1.319	0.420	0.948	0.340
Vine	0.264	0.352	−0.214	1.130	0.745	0.454
Interspersion	0.174	0.236	−0.303	0.633	0.733	0.461

Indicates significant at $\alpha = 0.05$.

of occurrence increasing from approximately 5% to 15% from open to closed canopies (Supplementary Material, Fig. A.4). Fox squirrel occurrence was also negatively influenced by *woody ground cover* (posterior mean = −1.963, CRI = −3.861 − −0.158), and decreased from approximately 20% to 0% as woody vegetation dominated the ground cover (Supplementary Material, Fig. A.5).

4. Discussion

The environmental variables used in our study did not influence the occurrence of fox squirrels uniformly across our three ecological scales. Fox squirrels occurred in areas that were structurally similar to historic pine savannas, but they did not appear to need large swaths of forest that once covered the southeastern United States. Fox squirrels had been thought to need large tracts of land (Edwards, 1986; Hilliard, 1979; Weigl et al., 1989; Kantola and Humphrey, 1990) and the loss of pine forests has been a common explanation for their declines; however, we found no evidence that the amount of forest influenced fox squirrel occurrence at the landscape scale. Fox squirrels were adaptable and inhabited many land cover classes (e.g., coniferous plantations, pastures and croplands, and scrub) other than native pine forests (i.e., sandhills and pine flatwoods). Land cover classes where fox squirrels were not detected does not indicate a lack of use and was likely influenced by sample sizes (Supplementary Material, Table A.2). Concurrent research supports those land cover classes are occupied by fox squirrels in Florida (Greene and McCleery, unpublished data). Generally, fox squirrels' occurrence was associated with forested land cover classes or near clusters of hardwoods away from forests (e.g., in pastures and around cropland edges where hardwoods were frequent along fences). Within our study area, the patchy distribution of fox squirrels at the broad scale was better explained by stand-level metrics such as decreased tree cover and increased heterogeneity (*interspersion*), rather than the local scale variables typically studied. At the finest (point) scale, relationships between fox squirrels' occurrence and environmental variables was much weaker, likely due to the low percentage (~12%) of points having a detection.

On all landscapes, the most important feature influencing the patchy distribution of fox squirrels was the amount of tree cover. While fox squirrels were associated with trees at all scales, it was too much tree cover, rather than too little, that reduced the

occurrence of fox squirrels. Southeastern fox squirrels evolved in the frequently burned pine-savannas with open canopies (Kiltie, 1989, 1992; Weigl et al., 1989). Fox squirrels are known to avoid closed canopy forests (Conner et al., 1999), possibly because of the loss of pine nuts, a major seasonal source of food (Weigl et al., 1989). In the absence of fire, tree cover increases because hardwoods encroach and replace the overstory pine trees, eventually rendering the habitat unsuitable for southeastern fox squirrels (Conner et al., 1999). Conversely, frequent, but variable burn regimes create landscape heterogeneity in the pine-hardwood matrix that likely distributes resources spatially and temporally. Frequent fires likely explain the positive relationship with increased heterogeneity (*interspersion*) at our landscape scale. Increased heterogeneity across landscapes would include areas such as hardwood patches that would still represent tree cover, which likely explains the moderately weak relationship with tree cover and the probability of occurrence of fox squirrels.

Closed canopy forests are also the preferred habitats of eastern gray squirrels (*Sciurus carolinensis*) which appear to out-compete fox squirrels (Edwards et al., 1998). The small body size of eastern gray squirrels increases their ability to move throughout the dense tree canopies to avoid predators, but the large body size of southeastern fox squirrels reduces arboreal agility. Within the southeastern pine savannas favored by southeastern fox squirrels, the patchy nature of the trees and the discontinuous tree canopies often requires fox squirrels to travel on ground when escaping predators, moving across the landscape, and while foraging (Weigl et al., 1989). However, fox squirrels need cover (e.g., in oak thickets) from predators, for refuge, and nest habitat, which we believe explains the positive relationship with canopy closure at the grid scale in our study.

The positive influence of oak densities (grid scale) and canopy closure at finer scales (grid and point scales) supports the importance of oak trees and other hardwoods for fox squirrels. Oak trees have more structured canopies than pine trees, which increases the amount of canopy closure. Southeastern fox squirrels are dependent on oak trees for cover from predators (McCleery, 2009), seasonal sources of food (Weigl et al., 1989; Steele and Koprowski, 2001; Perkins et al., 2008), refuge, and hold approximately 80% of their nests (Kantola and Humphrey, 1990; Conner and Godbois, 2003). The positive linear relationship with fox squirrel occurrence and increasing oaks per hectare (reaching upwards of 600 trees per hectare) was likely inflated by detections in or near

dense oak patches, not in closed-canopy hardwood forests that are typically avoided by fox squirrels. Although fox squirrels are more common in areas with reduced tree cover, when foraging they often move and consume bulky food items near cover where they have reduced vulnerability to predators (Weigl et al., 1989).

At all scales, we found the occurrence of fox squirrels to concur with our understanding of their selection of areas with reduced woody understory cover and woody ground cover which has been consistently found in past studies. Fire has played an essential role in creating an open understory with reduced woody ground cover that is favorable to most mammals in the southeastern pine forests (Engstrom, 1993). Because fox squirrels are partially cursorial (Weigl et al., 1989; Steele and Koprowski, 2001; Ditgen et al., 2007), they may be reluctant to utilize areas with woody ground cover that minimizes their ability to see potential threats or reduce their efficiency of escaping predators (Weigl et al., 1989). While metrics of woody understory and ground cover were significance across scales, their influence on the occurrence of fox squirrels was greatest at the finer scales.

Like other studies, we found occurrence of fox squirrels increased around areas with moderate development (Jodice and Humphrey, 1992; Wooding, 1997; Lee et al., 2001; Ditgen et al., 2007). Residential areas and the urban fringe can provide vegetation structure favorable to fox squirrels, supplemental food, and water (Jodice and Humphrey, 1992; McCleery et al., 2007). Nonetheless, from a conservation perspective it is important that low density residential areas do not replace fox squirrels preferred upland pine forests (Weigl et al., 1989) and that the low intensity urbanization does not transition to high intensity urbanization that reduces the occurrence of fox squirrels (Tye et al., 2016).

The use of open canopy landscapes with closed forest patches by fox squirrels has implications for the health and structure of southeastern pine forests. Our results clearly illustrate that patches of oak trees and more broadly heterogeneity of vegetation structure and composition are important to fox squirrels within southeastern pine forests. Nonetheless, many southeastern forests are heavily managed to reduce or eliminate oaks or left to become closed canopy hardwood forests despite the importance of heterogeneity for native wildlife such as the fox squirrel (Weigl et al., 1989; Hiers et al., 2014; Prince et al., 2016). Regardless of the scale, the influences of forest structure on fox squirrels' occurrence clearly showed the need for open forest, commonly achieved through frequent fires. The vegetation structure in our study suggested wide variation in fire intervals. Some of our study sites received a recent (<1 month) prescribed burn before our survey or were on a frequent burn cycle (1–3 years) and therefore had reduced woody understory cover and woody ground cover vegetation; we frequently detected fox squirrels at these sites. Other sites had higher woody understory cover indicative of an intermediate fire frequency (e.g., 4–10 years) and were occupied by fox squirrels, but to a lesser extent. Lastly, we surveyed at many sites which had likely not been burned in nearly a century. These sites were closed canopy hardwood forests, but had indications of a preexisting pine forest from the early 1900s, including large remnant pines, catfaced pine snags, and artifacts of the turpentine industry such Herty turpentine cups. Fox squirrels were rarely detected at these sites.

Despite a 97% loss in the historic range of the longleaf pine ecosystem (Frost, 1993), fox squirrels appear to be a highly adaptable and resilient species as indicted by their occurrence around human development and numerous land cover classes. Furthermore, the long-held belief that southeastern fox squirrels have declined precipitously in the last century appears to be an artifact of survey designs and statistical methods used to estimate their densities, and while populations may no longer occur in areas heavily degraded or developed, their densities show little variabil-

ity in sandhill communities where they have been studied (Greene and McCleery, 2017). Nonetheless, fox squirrel densities throughout the southeastern United States appear to be substantially lower than previously considered (Greene and McCleery, 2017), and the areas where we found them mimicked the open savanna-type systems that are maintained by fire. As such, the conservation of fox squirrels and likely other pine savanna obligates will necessitate management practices which include or emulate a fire regime to reduce the encroachment of the woody understory and woody ground cover vegetation and to reduce tree canopy cover. Moreover, management for southeastern pine forests should retain hardwood components that contribute to increased overstory heterogeneity while simultaneously maintaining non-overlapping canopies typical of older pine stands. Future conservation efforts of fox squirrel populations and their habitats would benefit from an investigation of how individuals are influenced by habitat fragmentation, what defines a corridor between patches, and how corridors can be used to reconnect isolated populations and reoccupy vacant habitats.

5. Conclusions

We found fox squirrels to occur in multiple land cover classes and they were not restricted to the upland sandhill or flatwood communities where they have repeatedly been studied. Overall, fox squirrels appear to be resilient to the loss of the pine savannas and can be adaptable to land-use change. However, outside of the remaining pine savanna systems, fox squirrels are reliant on management practices which emulate frequent fires in the pine savannas where they evolved and future management practices should aim to create and maintain an open understory and ground cover with minimal woody vegetation.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.02.001.

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