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Fox squirrel response to forest restoration treatments in longleaf pine

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Restoration of the longleaf pine (*Pinus palustris*; LLP) ecosystem and its associated fauna is a principal goal of many land-management agencies in the southeastern United States. Prescribed fire and herbicide application are 2 common methods of LLP restoration. We employed a multi-scale approach to investigate how occurrence of fox squirrels (*Sciurus niger*) was influenced by fire frequency and herbicide application in LLP communities of northern Florida. We sampled 9-point, 4-ha grids of camera traps with 106 grids in fire treatments, 23 herbicide treatment grids, and 27 control grids. We evaluated a priori models for occurrence of fox squirrels at point, 4-ha patch, and home-range scales, and the influence of fire and herbicides on vegetation structure. Fox squirrel occurrence was positively associated with densities of turkey oak (*Quercus laevis*) at the patch scale, which were significantly less abundant in herbicide-treated areas. Fox squirrel occurrence was negatively correlated with fire interval and positively correlated with oak densities at a localized point scale. Additionally, fox squirrel point occurrences declined over time since the last fire. Fire produced habitat more favorable for fox squirrels than did herbicide treatments.

Key words: Florida, herbicide, occupancy, *Pinus palustris*, prescribed fire, *Quercus laevis* restoration, *Sciurus niger*

Fire suppression has helped cause shrub encroachment and increased woody biomass in savannas throughout the globe (Bragg and Hulbert 1976; Gilliam and Platt 1999; Miller and Rose 1999; Van Auken 2000; Cabral et al. 2009). Frequent fires limit tree and shrub densities, allowing understories to become dominated by grasses and herbaceous plants (Provencher et al. 2000; Peterson and Reich 2001). These changes to vegetation communities are likely to induce subsequent effects in mammalian communities (Blaum et al. 2007; Darracq et al. 2016).

Prescribed fire and herbicide application commonly are used to reduce woody biomass in encroached savannas (Ansley and Castellano 2006; Freeman and Jose 2009; Havstad and James 2010). Prescribed fire, generally applied in longleaf pine (LLP) on a 2- to 3-year interval (Lewis and Harshbarger 1976; Walker and Peet 1983; Waldrop et al. 1992), imitates natural processes and is a cost-effective restoration method that gradually decreases woody biomass (Provencher et al. 2000, 2001a, 2001b; Hiers et al. 2014). Most prescribed fires have been conducted during the dormant season because they are easier to manage (Glitzenstein et al. 1995), but growing-season fires have become more common (Streng et al. 1993; Glitzenstein et al. 1995). Nevertheless, prescribed fire may require decades to reverse woody biomass (Brockway and Outcalt 2000) and may be ineffective if encroachment is severe (Kush et al. 2004). Herbicide may be used when prescribed fire is no longer effective, or when the rapid reduction of woody biomass is desired (Brockway and Outcalt 2000; Provencher et al. 2001b; Kush et al. 2004). Herbicide has been effective at reducing woody biomass (e.g., oaks; *Quercus* spp.), but can result in plant communities that may not represent historic conditions (Wilkins et al. 1993; Hiers et al. 2014).

In savannas, woody biomass often has been removed in an attempt to bolster abundance and diversity of wildlife (Plentovich et al. 1998; Hiers et al. 2014). However, the responses of wildlife to fire and herbicide are complex and species-specific (Lautenschlager 1993; Fontaine and Kennedy 2012). The frequent use of these approaches to reduce woody biomass, coupled with our inability to predict responses of wildlife, necessitates a better understanding of their influence on wildlife species.

Because they both maintain and are sensitive to disturbances in forests, tree squirrels are an ideal group of organisms through which to understand the influence of forest-management practices (Carey 2000). We investigated the response of fox squirrels (*Sciurus niger*) to fire and herbicide application in LLP savannas. Longleaf pine savannas once dominated the southeastern United States, but recent land-use changes have reduced LLP savannas to < 3% of their original extent (Frost 1993), leading to the extirpation of fox squirrels from much of their former range (Kantola and Humphrey 1990; Hafner et al. 1998). Historically, the persistence of LLP savannas was maintained with fire return intervals of 2.2–5 years (Henderson 2006; Huffman 2006; Stambaugh et al. 2011); however, human population growth and land-use changes since the early-mid 1900s resulted in widespread fire suppression of LLP savannas (Frost 1993; Gilliam and Platt 1999), leading to systematic increases in woody biomass (Hartnett and Krofta 1989; Boyer 1990; Gilliam and Platt 1999).

Although they are not found exclusively in the southeastern United States (Fig. 1), fox squirrels are key dispersers of seeds and fungal spores in LLP savannas (Weigl et al. 1989; Steele and Koprowski 2001). Within LLP savannas, fox squirrels use areas with an open understory (Chapman 1894; Perkins and Conner 2004), but also commonly use vegetation that contributes to increased woody biomass. Fox squirrels use oaks (*Quercus* spp.) for food (Moore 1957; Conner et al. 1999; Perkins et al. 2008), rearing offspring (Weigl et al. 1989), and daytime refugia (Conner and Godbois 2003). Few oak species can survive the frequent fires that characterized LLP ecosystems historically (Hiers et al. 2014); however, fire suppression and less-frequent fires allow fire-intolerant mesic oak species (i.e., *Quercus virginiana*, *Q. hemisphaerica*, and *Q. nigra*) to invade the ecosystem (Hiers et al. 2014). Increased oak densities result in decreased floral diversity of the understory (Gilliam and Platt 1999; Hiers et al. 2007) and extirpation of fire-associated wildlife (Walters 1991). In response, managers commonly remove all oaks (Boyer 1990; Brockway et al. 1998; Kush et al. 1999), including fire-tolerant "pyrophytic" species like turkey oak (*Q. laevis*), potentially negatively influencing fox squirrels.

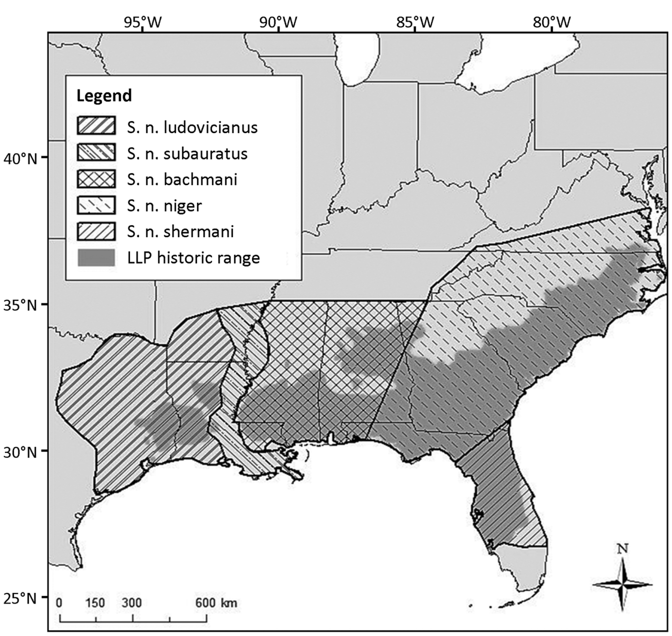

Fig. 1.—Distribution of fox squirrel (*Sciurus niger*) subspecies that occur within the historic range of the longleaf pine (LLP) ecosystem (adapted from Moncrief et al. 2010).

We investigated responses of fox squirrels to the management of woody biomass in LLP. Specifically, we tested 2 predictions: 1) fox squirrels would occur less frequently in LLP treated with herbicide than in nontreated areas because of their use of oak trees for nesting, and 2) fox squirrels would occur most frequently in areas experiencing a short fire return interval because these areas have open understories and an oak component. Additionally, to investigate the mechanisms by which these restoration practices differentially influenced fox squirrel occurrence, we investigated how herbicide and fire influenced vegetative structure and composition, and how these changes influenced fox squirrel occurrence.

Materials and Methods

Study area.—We conducted research at 5 sites within north-central and the panhandle regions of Florida: Jennings State Forest (JSF), Camp Blanding Joint Training Center (CBJTC), Ocala National Forest (ONF), St. Marks National Wildlife Refuge (SMNWR), and Eglin Air Force Base (EAFB; Fig. 2). We combined CBJTC and JSF into a single site for analysis due to their shared border, creating 4 sites. All of our sites were managed with prescribed fire, whereas herbicide was used to treat woody biomass only on JSF and EAFB. The eastern (JSF) and western (EAFB) extent of our sites represented extremes in temperature and rainfall. Summer temperatures peaked in July and were similar at 21.9–33.2°C (JSF) and 21.6–33.4°C (EAFB—NOAA 2015). Total annual rainfall accumulations also were similar between EAFB (1.349 m) and JSF (1.347 m—NOAA 2015). Dry seasons occur at both sites (EAFB: September–November; JSF: October–January), but JSF has a more pronounced dry season than EAFB (NOAA 2015).

All of our sites were classified as sandhill communities (Florida Natural Areas Inventory 2010). Soils within these LLP sandhill communities were sandy and well drained (Kalisz and Stone 1984; Overing et al. 1995; Provencher et al. 2000). Elevations ranged from 0 to 100 m above sea level (Kalisz and Stone 1984; Provencher et al. 2001b). Common shrub and understory species on our sites included persimmon (*Diospyros virginiana*), pawpaw (*Asimina* spp.), gopher apple (*Licania michauxii*), broomsedge (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), and wiregrass (*Arisaema stricta*—Kalisz and Stone 1984; Rodgers and Provencher 1999; Provencher et al. 2001b). Fire-suppressed portions of our sites were characterized by decreased herbaceous groundcover, increased detritus, and oak encroachment (Engstrom et al. 1984; Varner et al. 2000). Our herbicide-initiated LLP restoration areas were treated with hexazinone (3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione), which has been successfully used to control oak encroachment

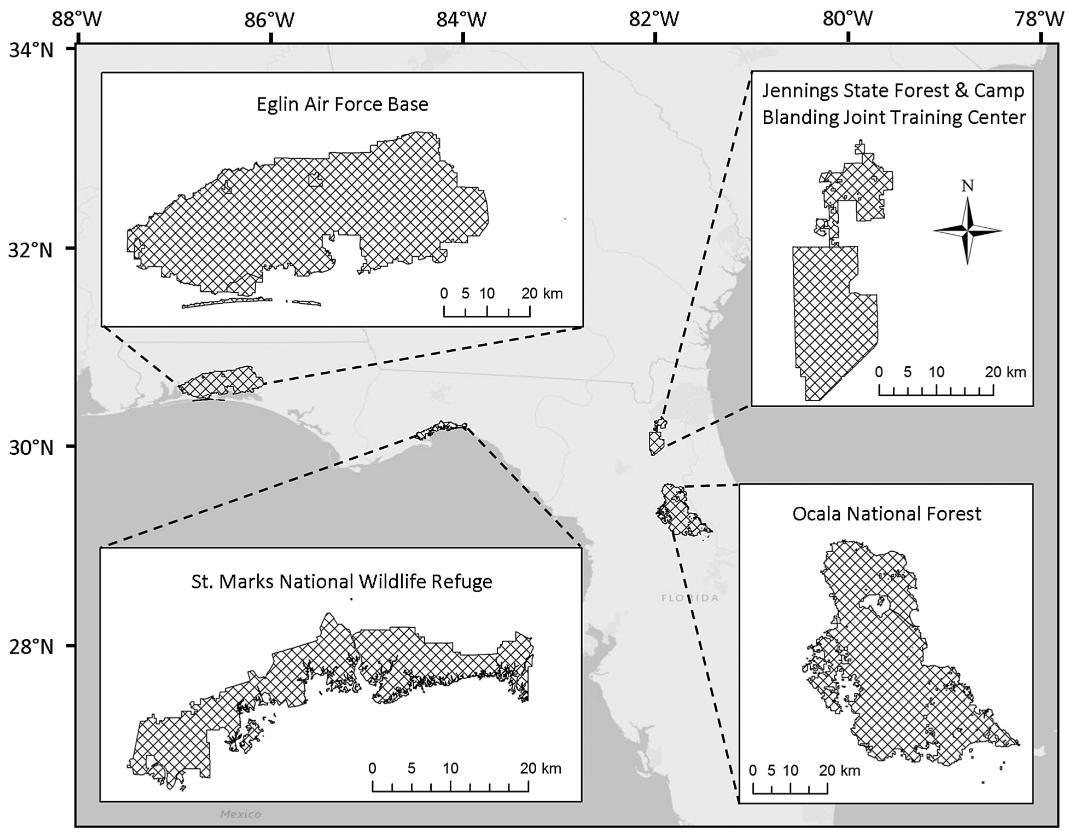

Fig. 2.—Fox squirrel (*Sciurus niger*) research locations in Florida utilized in 2013 (St. Marks NWR, Jennings State Forest, and Camp Blanding JTC) and 2014 (Eglin AFB and Ocala National Forest). All research occurred on public lands.

(Brockway et al. 1998; Provencher et al. 2001a; Freeman and Jose 2009).

Study design.—To understand fox squirrel response to fire and herbicide treatments, we sampled fox squirrels on camera-trapping grids. Grids consisted of 3 lines of 3 points each with 100 m between points (4 ha). We measured responses of fox squirrels to fire and herbicide at the point scale, at the patch scale (4-ha trapping grids), and at a home-range scale (23.76 ha, radius = 275 m from patch center—Weigl et al. 1989; Fig. 3). The point scale allowed us to infer what specific features fox squirrels may avoid or select. The broader patch scale is likely a better indication of the general forest conditions (i.e., fire regime, tree density, etc.) that influenced their presence. Finally, the home-range scale should indicate how fire and herbicide may attract or repulse squirrels from large areas.

We selected sampling locations for fire regime using a stratified random sampling approach. We defined frequent disturbance as a fire interval of 0–3 years, intermediate disturbance as 3–5 years, and reduced disturbance as > 5 years (Darracq et al. 2016). We used fire history data, including prescribed fires and wildfires, from the last 20 years and ArcGIS (Esri, Redlands, California) to randomly select 29–46 locations in each stratum (0–3 years, 3.01–5 years, > 5 years) based on available acreage. We spaced locations > 275 m apart to ensure the independence of fox squirrel detections (Weigl et al. 1989).

To understand how fox squirrels respond to herbicide treatment, we selected locations that had been treated with herbicide within the last 20 years and compared them to areas that

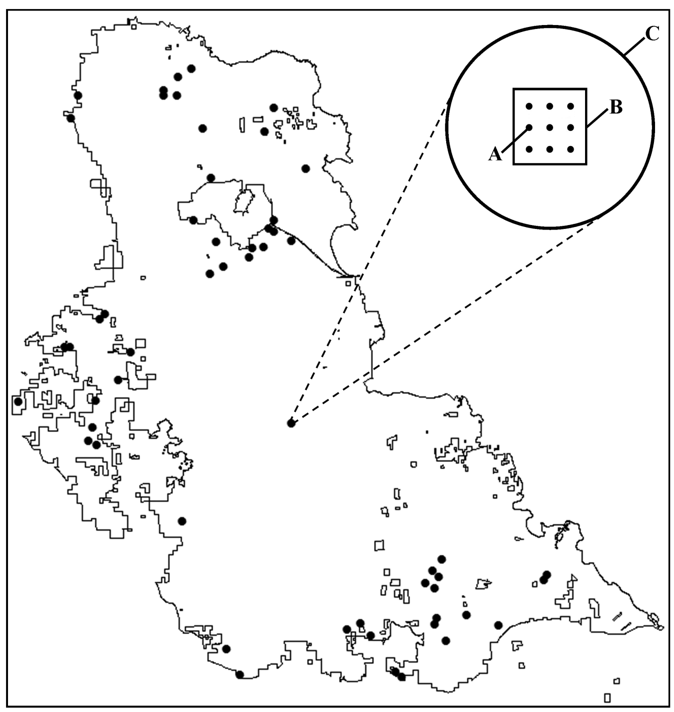

Fig. 3.—Covariates were collected at 3 scales (A, B, and C), while fox squirrel (*Sciurus niger*) sampling occurred at 2 scales (A and B); (A) point scale—individual camera points, (B) patch scale—9 camera points with 100-m spacing (4-ha grids), and (C) home-range scale—approximate area of a fox squirrel's home range (23.76 ha—Weigl et al. 1989) centered around each camera grid.

had never received herbicide. We determined areas that had been treated with herbicide (*Treatment*; herbicide-treated areas received a value of 1, whereas nontreated areas received a zero) by inspecting shapefiles provided by managers at each site. We randomly sampled 23 treated and 27 untreated areas on JSF and EAFB. We restricted all treated and untreated plots to areas that experienced fire 3–6 times in the last 20 years, reducing the potentially confounding effects of fire.

Camera trapping.—We measured fox squirrel occurrence on multiple scales by establishing a 3 × 3 grid of sampling points with 100-m spacing, covering each 4-ha patch. We placed a camera trap (Trophy Cam; Bushnell Outdoor Products, Overland Park, Kansas) at each grid point (Greene et al. 2016). At each grid point, camera traps were attached to the base of the nearest tree (< 10 m from point) ~45 cm above the ground, and were removed after 4 consecutive days. We removed vegetation from the camera trap's field of view to minimize camera misfires.

We sampled 5 sites for the fire component of our research, placing camera traps on 107 patches with 963 points from January to June in 2013 and 2014. We sampled 7, 25, 8, 51, and 16 patches at CBJTC, EAFB, JSF, ONF, and SMNWR, respectively. Sampling intensity varied between sites due to differences in the amount of LLP savanna available. To investigate the influence of herbicide application on LLP structure, and its subsequent influence on fox squirrel occurrence, we surveyed vegetation and placed cameras on 2 sites encompassing 50 patches with 450 points. We sampled 8 treated and 9 nontreated patches at JSF and 15 treated and 18 nontreated patches at EAFB. We camera trapped at JSF from March to June in 2013 and at EAFB from April to June in 2014.

Vegetative characteristics.—We characterized the vegetation structure and composition at all 9 points in each patch. We estimated the density of canopy (≥ 10 cm diameter at breast height) pine (*Pine*; cumulative for all *Pinus* spp.), oak (*Oak*; cumulative for all *Quercus* spp.), and turkey oak (*Quercus laevis*; *TurOak*) trees using the point-centered quarter method and standard calculations (Cottam et al. 1953; Mitchell 2007). We focused on *TurOak* because of its ability to endure fire (Heyward 1939) and importance to fox squirrels (Weigl et al 1989; Kantola and Humphrey 1990). We assessed shrub cover (*Shrub*) with the line-intercept method (Cook and Stubbendieck 1986; Aldridge and Brigham 2002; Caratti 2006) at a height of ≥ 45 cm along 4 transects extending 10 m in each cardinal direction from the center of each point. Additionally, we used a 0.5 × 0.5 m grid to measure the occurrence of ferns (Conner 1999) at the center of each point, and 10 m in each cardinal direction from each point.

Fire characteristics.—We obtained 20 years of fire history data, including prescribed fires and wildfires, for each site from land managers. We calculated the average time interval between fires over the last 20 years (*FireInterval*) at the point and patch scales using GIS. We generated a measure of fire interspersion at the home-range scale to determine if fox squirrel occurrence was influenced by heterogeneity in fire frequency. At the home-range scale, there was often a number of discrete areas with different fire return intervals that creating a mosaic. We first determined the total number of fires experienced by each discrete area within the home-range scale, and then estimated the average fire frequency for all the areas at that scale. We calculated our index of interspersion (*IntIndex*) by taking the absolute difference in fire frequency between each discrete area and the home range's average. Then, we multiplied the absolute differences by the discrete area's portion of the home-range scale and summed the totals for each home range. Additionally, we noted the number of years since the last fire (*YearsSinceLastFire*), and seasonality of the last fire (*Season*; April–September = growing season, October–March = dormant season) at the point and patch scale.

Herbicide characteristics.—To determine if fox squirrel occurrence was influenced by herbicide application, we used GIS to calculate an index of herbicide treatment at the home-range scale. We calculated percent of the home-range scale polygon treated with herbicide using herbicide application data provided by site managers, yielding an herbicide *Treatment* metric (*Herbicide%*).

Data analysis.—First, we examined the separate influences of fire and herbicide on the structure and composition of vegetation at the patch level. We ran generalized linear models (GLMs) in Program R (R version 3.1.1, www.r-project.org, accessed 27 September 2014) using package lme4 (version 1-1.7, http://cran.r-project.org/web/packages/lme4/index.html, accessed 15 January 2015) to determine the influence of *FireInterval* and *Season* on the vegetation of fire patches, and the influence of *Treatment* on the vegetation of herbicide patches. We evaluated the response of 4 vegetative variables (*Pine*, *Oak*, *TurOak*, and *Shrub* density) we believed would be influenced by either fire or herbicide.

We investigated how fire, herbicide, and heterogeneity in vegetation structure influenced the occurrence of fox squirrels at point, patch, and home-range scales using an occupancy modeling approach that accounts for imperfect detection (MacKenzie 2006; Royle and Dorazio 2008). We account for imperfect detection to offset changes in observed occupancy that may result from variable detection probability (e.g., irregular camera ranges). For both data sets (fire and herbicide), we reviewed camera-trap photos to determine occurrence at each point during the 4 consecutive days starting when cameras were placed at each point (Ahumada 2011). For patch and home-range scale analyses, we aggregated binary (1 = present, 0 = absent) measurements of daily fox squirrel occurrence within each patch. We modeled the influence of *Fern* and *Shrub* on detectability for herbicide and fire sampling areas using Program Presence (version 8.3, http://www.mbr-pwrc.usgs.gov/software/presence.html, accessed 5 February 2015) to determine if fox squirrel detection was influenced by site variables. Additionally, we investigated how *YearsSinceLastFire* influenced detection on fire sampling areas. We integrated the best predictor of detection in each of 22 a priori models, including a null and global model, comprised of point or patch (*Fern*, *FireInterval*, *Oak*, *Pine*, *Season*, *Shrub*, *Site*, *TurOak*, and *YearsSinceLastFire*) and home-range (*IntIndex*) scale variables (Table 1). We used 8 patch and home-range variables (*Fern*, *Herbicide%*, *Oak*,

Table 1.—Competing occupancy models investigating the response of fox squirrels (*Sciurus niger*) to prescribed fire conducted on 107 patches in sandhill communities across north-central Florida and the panhandle from January to June 2013 and 2014. Number of parameters (*K*), ΔAICc, and model weight (*w*) from models investigating the influence of 10 variables, including Fern (presence = 1, absence = 0), FireInterval (average interval between fires over the preceding 20 years), IntIndex (interspersion of FireIntervals within 275 m of patch center), Oak (oak density), Pine (pine density), Season (growing = 1, dormant = 0), Shrub (shrub cover; %), Site (where research was conducted), TurOak (turkey oak density), and YearsSinceLastFire (# of years since last fire) on fox squirrel detection and occupancy. Only models with ΔAICc < 2 and the null model are shown.

Model	*K*	ΔAICc	*w*
Psi(*FireInterval* + *TurOak*), *p*(*Shrub*)	5	0.00	0.393
Psi(*FireInterval* + *Season* + *TurOak*), *p*(*Shrub*)	6	1.01	0.237
Psi(*FireInterval* + *Oak*), *p*(*Shrub*)	5	1.59	0.178
Psi(.), *p*(*Shrub*)	3	10.32	0.002

Table 2.—Competing occupancy models investigating the response of fox squirrels (*Sciurus niger*) to herbicide application conducted on 50 patches on sandhill sites in Florida during March–June of 2013 and April–June of 2014. Number of parameters (*K*), ΔAICc, and model weight (*w*) from models investigating the influence of 8 variables, including Fern (presence = 1, absence = 0), Herbicide% (percent of area within 275 m of patch center treated with herbicide), Oak (oak density), Pine (pine density), Shrub (shrub cover; %), Site (where research was conducted), TurOak (turkey oak density), and Treatment (treated = 1, nontreated = 0) on fox squirrel detection and occupancy. Only models with ΔAICc < 2 and the null model are shown.

Model	*K*	ΔAICc	*w*
Psi(*TurOak* + *Site*), *p*(*Shrub*)	5	0.00	0.267
Psi(*TurOak* + *Pine*), *p*(*Shrub*)	5	0.79	0.180
Psi(*TreatmentBySite* + *TurOak*), *p*(*Shrub*)	7	0.84	0.176
Psi(*TreatmentBySite* + *Oak*), *p*(*Shrub*)	7	1.78	0.110
Psi(.), *p*(*Shrub*)	3	9.46	0.002

TurOak, *Pine*, *Shrub*, *Site*, and *Treatment*) to generate 17 a priori models to determine the influence of herbicide on fox squirrel occurrence (Table 2). These suites of models included single variable, additive, and interactive effects models. We ranked models using Akaike's information criterion accounting for small sample size (AICc), and considered models with ΔAICc < 2 to be highly supported competing models (Akaike 1973; Burnham and Anderson 2002). We conducted full-model averaging on the cumulative suite of patch-scale occupancy models (Lukacs et al. 2010; Symonds and Moussalli 2010). We considered variables with 95% confidence intervals (*CI*s) that did not overlap zero to be important for explaining observed variation in fox squirrel occurrence in LLP sandhills at the patch and home-range scales.

We assessed the probability of fox squirrel occurrence at the point scale using a Bayesian occupancy modeling approach (Gelman et al. 1995). This approach accounted for the lack of spatial independence in our point-scale data (9 points were nested within each patch—Gelman et al. 1995; Kéry 2010). We examined the relationship between 3 variables (*Fern*, *Shrub*, and *YearsSinceLastFire*) for fire, and 2 variables (*Fern* and *Shrub*) for herbicide, and the probability of detecting a fox squirrel at the point scale using the R package R2WinBUGS (Gelman et al. 2005) to run models in WinBugs (v1.4.3, http://www.mrc-bsu.cam.ac.uk/software/bugs/, accessed 10 February 2016). We then investigated the influence of 9 fire variables (*Fern*, *FireInterval*, *Oak*, *Pine*, *Season*, *Shrub*, *Site*, *TurOak*, and *YearsSinceLastFire*) and 8 herbicide variables (*Fern*, *Herbicide%*, *Oak*, *TurOak*, *Pine*, *Shrub*, *Site*, and *Treatment*) on point-scale fox squirrel occurrence. We parameterized models with uniform priors (Gelman et al. 1995; Gilks et al. 1996) and ran 3 Markov chains, each with 30,000 iterations for each model. We discarded the 1st 20,000 iterations and retained every 10th of the final 10,000 iterations. We assessed convergence using the Rhat statistic where values < 1.05 indicate convergence (Gelman and Rubin 1992). We evaluated models using stepwise selection starting from a global model (Kéry and Schaub 2012) where variables with 95% credible intervals (CRIs) not passing through zero were retained (Kéry and Schaub 2012).

Results

Forest structure.—Shrub cover (*Shrub*) was significantly influenced by fire season (*Season*; Wald statistic = 3.150, $P = 0.004$). Shrub cover (*Shrub*) decreased in areas with growing-season fires compared to areas with dormant-season fires. Decreasing the fire return interval (*FireInterval*) also reduced shrub cover (Wald statistic = −0.318, $P < 0.001$). Neither fire season (*Season*) nor fire return interval (*FireInterval*) substantially influenced pine (*Pine*), oak (*Oak*), or turkey oak (*TurOak*) densities. Areas treated with herbicide had reduced oak (*Oak*; Wald statistic = 0.054, $P < 0.001$), turkey oak (*TurOak*; Wald statistic = 0.163, $P < 0.001$), and pine (*Pine*; Wald statistic = 0.002, $P < 0.001$) densities (Fig. 4). Herbicide application did not substantially influence shrub cover (*Shrub*; Wald statistic = −0.580, $P = 0.576$).

Fire–fox squirrel occurrence.—We detected fox squirrels at the patch level on 61 of 428 trap days (14.3%; 1 trap day = a patch of 9 active camera traps × 1 day) on 40 of 107 patches (37.4%). We captured 285 fox squirrel photos during the fire research component. Fox squirrel occurrence at the patch level was best explained by an additive model including fire return interval (*FireInterval*) and turkey oak density (*TurOak*; model weight = 0.393; Table 1). Fox squirrel occurrence was negatively associated with fire return interval (*FireInterval*; $\beta = -1.313$, 95% *CI* = −2.814 to 0.187), and positively associated with turkey oak density (*TurOak*; $\beta = 1.577$, 95% *CI* = −0.547 to 3.700), but they were not strong predictors of occurrence, with model averaged 95% *CI*s that contained zero. There were 2 additional highly supported models that included the covariates fire season (*Season*) and oak density (*Oak*; model weights = 0.273 and 0.178; Table 1). Fox squirrel occurrence was positively correlated with fire season (*Season*; $\beta = 0.9668$, 95% *CI* = −0.691 to 2.625) and oak density (*Oak*; $\beta = 2.545$, 95% *CI* = −0.612 to 5.702), but both had averaged 95% *CI*s that included zero. Home-range scale variables were not in any highly supported models (Table 1).

We detected fox squirrels at individual camera points during 78 of 3,852 trap days (2%; 1 trap day = 1 active trap × 1 day; 86 trap days excluded due to camera-trap failure) at 73 of 948 points (7.7%; 15 points excluded due to camera-trap failure). Point-scale fox squirrel occurrence was best explained by an additive model in which shrub cover (*Shrub*) influenced detection and fire return interval (*FireInterval*), turkey oak density (*TurOak*), and the number of years since the last fire (*YearsSinceLastFire*) influenced occurrence. Fox squirrel occurrence was negatively associated with fire return interval (*FireInterval*; Rhat = 1.012, β = −12.431, 95% CRI = −25.801 to −3.531; Fig. 5) and the number of years since the last fire (*YearsSinceLastFire*; Rhat = 1.022, β = −5.376, 95% CRI = −13.093 to −0.041; Fig. 5), but positively associated with turkey oak density (*TurOak*; Rhat = 1.015, β = 14.232, 95% CRI = 5.451 to 25.740; Fig. 5). Fox squirrel occurrence was not significantly influenced by other covariates at the point scale.

Herbicide–fox squirrel occurrence.—We detected fox squirrels during 22 of 200 trap days (11%) on 14 of 50 patches at the patch scale (28%). We detected fox squirrels on herbicide-treated patches during 5 of 92 trap days (5.4%) on 4 of 23 patches (17.4%) and during 17 of 108 trap days (15.7%) on 10 of 27 nontreated patches (37%). We captured 52 fox squirrel photos during the herbicide research component. Fox squirrel occurrence was best explained by an additive model containing site (*Site*) and turkey oak density (*TurOak*; model weight = 0.267; Table 2). Based on model averaged estimates turkey oak density (*TurOak*; β = 19.415, 95% *CI* = 2.892 to 35.938) was positively associated with fox squirrel occurrence, and the different sites strongly influenced fox squirrel occurrence (*Site*; β = 2.935, 95% *CI* = 0.515 to 5.356). While pine (*Pine*; β = −3.032, 95% *CI* = −6.927 to 0.863) and oak (*Oak*; β = 15.022, 95% *CI* = −8.525 to 38.568) densities were also components of highly supported models (model weights = 0.18, 0.11, and 0.07; Table 2), their 95% *CI*s overlapped zero. No other patch-scale models were well supported by the data, except the null model. We modeled EAFB independently because we found significant effects of site (*Site*) on fox squirrel occurrence. At EAFB, the model best supported by the data included only turkey oak density (*TurOak*; model weight = 0.31). However, the effect of turkey oak density (*TurOak*) on fox squirrel occurrence was not significant (β = 1.350, 95% *CI* = −0.467 to 3.166). There were no other highly supported models at the patch scale for EAFB.

We detected fox squirrels at the point scale during 25 of 1,748 trap days (1.4%; 52 trap days excluded due to camera-trap failure) on 22 of 444 points (5%; 6 points excluded due to camera-trap failure). We detected fox squirrels at herbicide-treated points during 6 of 798 trap days (0.8%) on 6 of 204 points (2.9%) and during 19 of 950 trap days (2%) on 16 of 240 points (6.7%). Fox squirrel detection and occurrence were not significantly influenced by any covariates at the point scale.

Discussion

As we predicted, at fine scales fox squirrels occurred most frequently in areas experiencing frequent fire. Additionally, fox squirrel occurrence rapidly decreased as fire interval increased; with occupancy at the point scale approaching zero when fire interval reached 8 years (Fig. 5). These findings were in agreement with previous research that associated fox squirrels with open pine savanna habitats (Kantola and Humphrey 1990; Perkins and Conner 2004), and highlight the importance of maintaining prescribed fire in LLP. While fox squirrels may occur in areas with fire intervals double the recommended 1–3 years, they did not occur in areas devoid of fire for long periods. The fox squirrel's reduced occupancy appeared to be associated with the loss of post-fire production of soft mast species (Hilmon 1969; Martin 1983), and a transition to shrub-dominated understory (Engstrom et al. 1984).

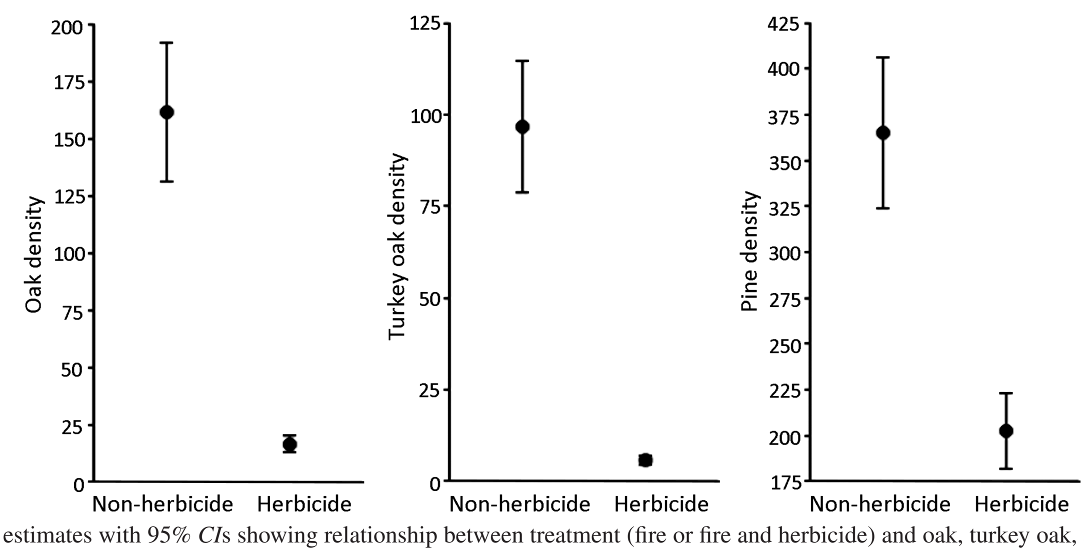

Fig. 4.—Point estimates with 95% *CI*s showing relationship between treatment (fire or fire and herbicide) and oak, turkey oak, and pine density. Research was conducted on 50 grids in sandhill communities across north-central Florida and the panhandle from March to June of 2013 and April to June of 2014.

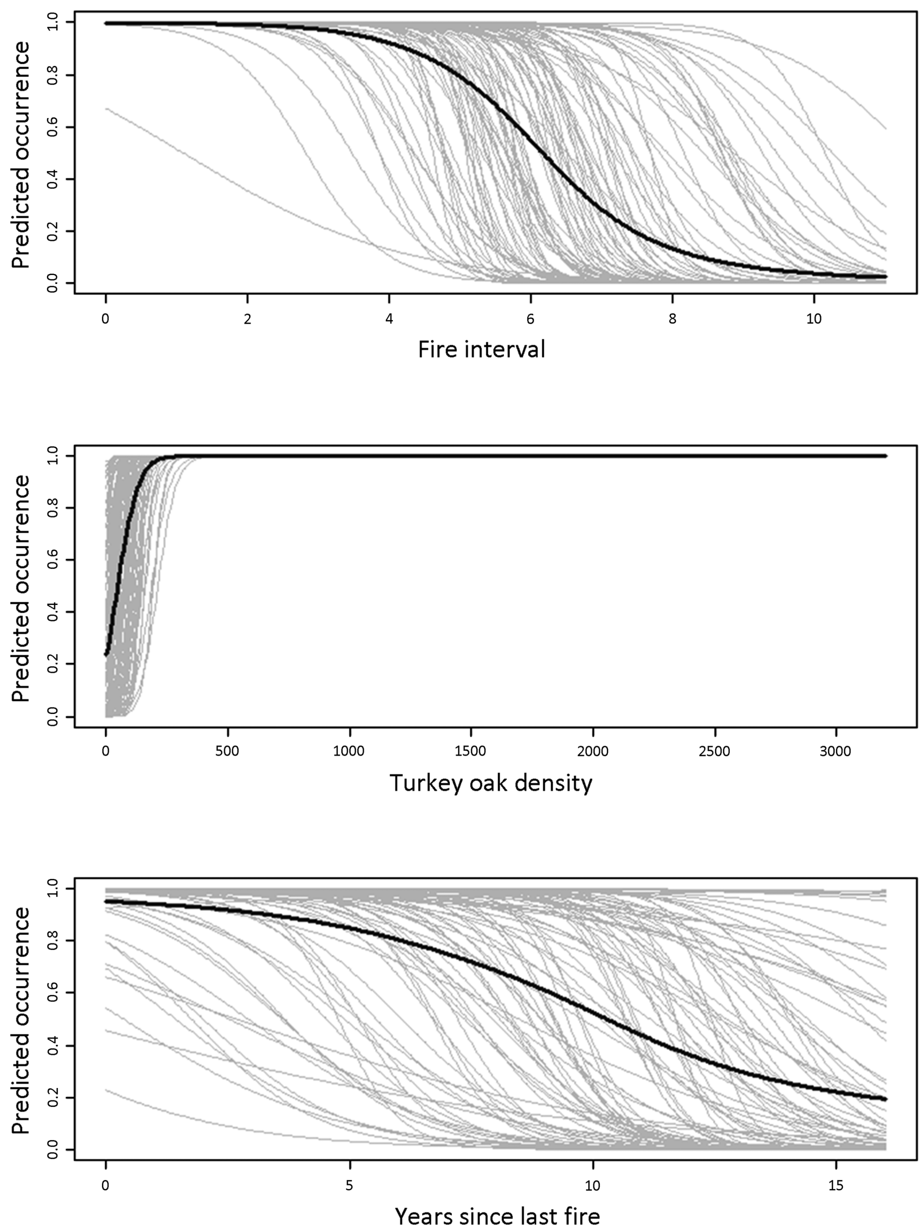

Fig. 5.—Predicted relationship between fire interval, turkey oak density (trees/ha), and years since the last fire occurred and the predicted occurrence probability of fox squirrels (*Sciurus niger*). Gray lines depict 250 randomly selected model runs, while the black line depicts the model average.

Fire produced habitat conditions more favorable to fox squirrel conservation than did herbicide treatment, as we predicted. The number of fox squirrel detections was 65% lower in areas treated with herbicide compared to nontreated areas. However, unexpectedly, no direct measure of herbicide application explained heterogeneity in fox squirrel occurrence. This may be the result of confounding effects associated with the method or rate of herbicide application, 2 variables not uniformly contained within the herbicide treatment records. We did find that areas treated with herbicide experienced marked declines in densities of turkey oaks compared to areas solely treated with fire. Hexazinone is a broad-leaf defoliant and has effectively reduced oak densities elsewhere (Brockway et al. 1998; Provencher et al. 2001a; Freeman and Jose 2009). The reduced occurrence of fox squirrels in herbicide-treated areas was likely related to changes in forest structure and composition, specifically the declines in turkey oak densities. Fox squirrels commonly use turkey oaks for food resources, daytime refugia, and nesting (Moore 1957; Weigl et al. 1989; Kantola and Humphrey 1990). Although fire may be effective at removing mesic oaks, it does so at lower rates than herbicide treatments, and did not eliminate pyrophytic turkey oaks in our study. In fact, the loss of naturally occurring oak species from the system has been seen as a potential detriment to faunal communities (Hiers et al. 2014). Thus, the potential deleterious effects of indiscriminately eliminating oaks from LLP forests, as proposed or executed in numerous studies (Brockway and Outcalt 2000; Provencher et al. 2001a, 2001b; Freeman and Jose 2009), may be a serious concern for wildlife populations.

Fox squirrels did not respond to environmental variables at the home-range scale during the short time period of this study. Resources at the home-range scale may become more relevant over longer time periods than our 4-day monitoring period. Patch-scale selection only occurred within herbicide-treated areas. This scale of selection was likely only exhibited in areas treated with herbicide because they were completely devoid of turkey oaks. Fox squirrels in fire-treated areas selected increased densities of turkey oaks at the point scale, whereas fox squirrels in herbicide-treated areas did not, as there was little variation in densities of turkey oaks in plots that had received herbicide. Fox squirrels also selected for areas that experienced fire more frequently and more recently at the point scale. Frequent and recent fire resulted in reduced visual obstruction and may enable fox squirrels to better avoid predation. The lack of a significant relationship between pine density and fox squirrel occurrence across all scales was surprising. Previous research suggested that pines may be a more important food source for wildlife than oaks because LLP produces a more dependable mast crop (Wahlenberg 1946; Umber 1975; Kantola and Humphrey 1990). Our results may indicate that pine-related food resources, while important, may be interchangeable with other food resources. However, we believe this outcome was the result of our trapping season not overlapping masting periods when pine nuts are available.

Longleaf pine savannas are known for their open understory and high floral diversity (Peet and Allard 1993). Restoring this historic structure while maximizing floral diversity has become a common management goal (Brockway and Lewis 1997; Brockway et al. 1998), but does not necessarily provide resources vital to wildlife inhabitants. Our findings that herbicide application eliminated resources important to fox squirrels, namely turkey oaks, illustrated the need for further research into the effects of herbicide on faunal inhabitants. We recommend avoidance of herbicide application whenever possible. If herbicide application is deemed necessary, and wildlife conservation is a management goal, we recommend the selective treatment of individual oaks, opposed to broadcast (e.g., aerial) herbicide application. Prescribed fire should be preferentially used, as it most closely imitates natural processes in LLP savannas.

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Literature Cited

Ahumada, J. A., et al. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 366:2703–2711.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pp. 267–281 in Proceedings of the second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brooding habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

Ansley, R. J., and M. J. Castellano. 2006. Strategies for savanna restoration in the southern great plains: effects of fire and herbicides. Restoration Ecology 14:420–428.

Blaum, N., E. Rossmanith, A. Popp, and F. Jeltsch. 2007. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. Acta Oecologica 31:86–92.

Boyer, W. D. 1990. Growing-season burns for control of hardwoods in longleaf pine stands. United States Department of Agriculture Forest Service Research Paper SO-256.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19–24.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure, and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167–183.

Brockway, D. G., and K. W. Outcalt. 2000. Restoring longleaf pine wiregrass ecosystems: hexazinone application enhances effects of prescribed fire. Forest Ecology and Management 137:121–138.

Brockway, D. G., K. W. Outcalt, and R. N. Wilkins. 1998. Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills. Forest Ecology and Management 103:159–175.

Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Cabral, A. C., J. M. De Miguel, A. J. Rescia, M. F. Schmitz, and F. D. Pineda. 2009. Shrub encroachment in Argentinean savannas. Journal of Vegetation Science 14:145–152.

Caratti, J. F. 2006. Line intercept sampling method. Pp. LI 1–13 in Firemon: fire effects monitoring and inventory system (C. Duncan, R. Keane, J. Caratti, C. Key, N. Benson, S. Sutherland, and L. Gangi, eds.). United States Department of Agriculture Forest Service General Technical Report RMRS-GTR-164-CD.

Carey, A. B. 2000. Effects of forest management strategies on squirrel populations. Ecological Applications 10:248–257.

Chapman, F. C. 1894. Remarks on certain land mammals from Florida with a list of species known to occur in the state. Bulletin of the American Museum of Natural History 6:333–346.

Conner, L. M., and I. A. Godbois. 2003. Habitat associated with daytime refugia of fox squirrels in a longleaf pine forest. American Midland Naturalist 150:123–129.

Conner, M. C., J. L. Landers, and W. K. Michener. 1999. Fox squirrel and gray squirrel associations within minimally disturbed longleaf pine forests. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 53:364–374.

Cook, C. W., and J. Stubbendieck. 1986. Range research: basic problems and techniques. Society for Range Management, Denver, Colorado.

Cottam, G., J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population or randomly dispersed individuals. Ecology 34:741–757.

Darracq, A. K., W. W. Boone, and R. A. McCleery. 2016. Burn regime matters: a review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. Forest Ecology and Management 378:214–271.

Engstrom, R. T., R. L. Crawford, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. The Wilson Bulletin 96:437–450.

Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida: 2010 ed. Florida Natural Areas Inventory, Tallahassee, Florida.

Fontaine, J. B., and P. L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22:1547–1561.

Freeman, J. E., and S. Jose. 2009. The role of herbicide in savanna restoration: effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. Forest Ecology and Management 257:978–986.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proceedings of the Tall Timbers Fire Ecology Conference 18:17–43.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 1995. Bayesian data analysis. Chapman and Hall, New York.

Gelman, A., U. Ligges, and S. Sturtz. 2005. R2winbugs: a package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Journal of Statistical Science 7:457–472.

Gilks, W. R., S. Rochardson, and D. J. Spiegelhalter. 1996. Introducing Markov chain Monte Carlo. Pp. 1–20 in Markov chain Monte Carlo methods in practice (W. R. Gilks, S. Rochardson, and D. J. Spiegelhalter, eds.). Chapman and hall, New York.

Gilliam, F. S., and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology 140:15–26.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441–476.

Greene, D. A., R. A. McCleery, L. M. Wagner, and E. P. Garrison. 2016. A comparison of four survey methods for detecting fox squirrels in the southeastern United States. Journal of Fish and Wildlife Management 7:1–8.

Hafner, D. J., E. Yensen, and G. L. Gordon, Jr. 1998. North American rodents: status survey and conservation action plan. IUCN/SSC Rodent Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hall, E. R. 1981. The mammals of North America. 2nd ed. John Wiley and Sons, New York.

Hartnett, D. C., and D. M. Krofta. 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. Bulletin of the Torrey Botanical Club 116:107–113.

Havstad, K. M., and D. James. 2010. Prescribed burning to affect a state transition in a shrub-encroached desert grassland. Journal of Arid Environments 74:1324–1328.

Henderson, J. P. 2006. Dendroclimatological analysis and fire history of longleaf pine (*Pinus palustris* Mill.) in the Atlantic and Gulf coastal plain. Dissertation, University of Tennessee, Knoxville.

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20:287–304.

Hiers, J. J., J. J. O'Brien, R. E. Will, and R. J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecological Applications 17:806–814.

Hiers, J. K., et al. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. Journal of Wildlife Management 78:383–393.

Hilmon, J. F. 1969. Autecology of saw palmetto (*Serenoa repens*). Thesis, Duke University, Durham, North Carolina.

Huffman, J. M. 2006. Historical fire regimes in southeastern pine savannas. Dissertation, Lousiana State University, Baton Rouge.

Kalisz, P. T., and E. L. Stone. 1984. The longleaf pine islands of the Ocala National Forest, Florida: a soil study. Ecology 65:1743–1754.

Kantola, A. T., and S. R. Humphrey. 1990. Habitat use by Sherman's fox squirrel (*Sciurus niger shermani*) in Florida. Journal of Mammalogy 71:411–419.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, San Diego, California.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBugs: a hierarchical perspective. Academic Press, San Diego, California.

Kiltie, R. A. 1989. Wildfire and the evolution of dorsal melanism in fox squirrels. Journal of Mammalogy 70:726–739.

Kiltie, R. A. 1992. Camouflage comparisons among fox squirrels from the Mississippi River Delta. Journal of Mammalogy 73:906–913.

Koprowski, J. L. 1994. *Sciurus niger*. Mammalian Species 479:1–9.

Kush, J. S., R. S. Meldahl, and C. Avery. 2004. A restoration success: longleaf pine seedlings established in a fire-suppressed, old-growth stand. Ecological Restoration 22:6–10.

Kush, J. S., R. S. Meldahl, and W. D. Boyer. 1999. Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. Canadian Journal of Forest Research 29:1047–1054.

Lautenschlager, R. A. 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. Canadian Journal of Forest Research 23:2286–2299.

Lewis, C. E., and T. J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina coastal plain. Journal of Range Management 29:13–18.

Lukacs, P. M., K. P. Burnham, and D. R. Anderson. 2010. Model selection bias and Freedman's paradox. Annals of the Institute of Statistical Mathematics 62:117–125.

MacKenzie, D. I. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California.

Martin, P. 1983. Factors influencing globe huckleberry fruit production in northwestern Montana. International Conference on Bear Research and Management 5:159–165

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Mitchell, K. 2007. Quantitative analysis by the point-centered quarter method. Hobart and William Smith Colleges, Geneva, New York.

Moncrief, N. D., J. B. Lack, and R. A. Van Den Bussche. 2010. Eastern fox squirrel (*Sciurus niger*) lacks phylogenetic structure: recent range expansion and phenotypic differentiation. Journal of Mammalogy 91:1112–1123.

Moore, J. C. 1956. Variation in the fox squirrel in Florida. American Midland Naturalist 55:41–65.

Moore, J. C. 1957. The natural history of the fox squirrel *Sciurus niger shermani*. Bulletin of the American Museum of Natural History 113:1–71.

National Oceanic and Atmospheric Administration (NOAA). 2015. Climate Data Online. National Centers for Environmental Information, Silver Spring, Maryland.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera traps in animal ecology: methods and analyses. Springer, New York.

Overing, J. D., H. H. Weeks, J. P. Wilson, Jr., J. Sullivan, and R. D. Ford. 1995. Soil survey of Okaloosa County, Florida. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

Peet, R. K., and D. J. Allard. 1993. Longleaf pine-dominated vegetation of the southern Atlantic and eastern Gulf Coast region, USA. In Proceedings of the Tall Timbers Fire Ecology Conference (S. M. Hermann, ed.). Tall Timbers Research Station, Tallahassee, Florida 18:45–81.

Perkins, M. W., and M. Conner. 2004. Habitat use of fox squirrels in southwestern Georgia. Journal of Wildlife Management 68:509–513.

Perkins, M. W., M. Conner, and B. Howze. 2008. The importance of hardwood trees in the longleaf pine forest ecosystem for Sherman's fox squirrels. Forest Ecology and Management 255:1618–1625.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914–927.

Plentovich, S., J. W. Tucker, Jr., N. R. Holler, and G. E. Hill. 1998. Enhancing Bachman's sparrow habitat via management of red-cockaded woodpeckers. Journal of Wildlife Management 62:347–354.

Provencher, L., et al. 2001a. Longleaf pine and oak response to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. Forest Ecology and Management 148:63–77.

Provencher, L., et al. 2001b. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology 9:13–27.

Provencher, L., et al. 2000. Fire, herbicide, and chainsaw felling effects on arthropods in fire-suppressed longleaf pine sandhills at Eglin Air Force Base, Florida. Pp. 24–33 in The role of fire in nongame wildlife management and community restoration: traditional uses and new directions; proceedings of a special workshop. U.S. Forest Service, Nashville, Tennessee.

Rodgers, H. L., and L. Provencher. 1999. Analysis of longleaf pine sandhill vegetation in northwest Florida. Castanea 64:138–162.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. The analysis of data from populations, metapopulations, and communities. Academic Press, New York.

Stambaugh, M. C., R. P. Guyette, and J. M. Marschall. 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. Journal of Vegetation Science 22:1094–1104.

Steele, M. A., and J. L. Koprowski. 2001. North American tree squirrels. Smithsonian Institute, Washignton, D.C.

Stratman, M. R., and M. R. Pelton. 2007. Spatial response of American black bears to prescribed fire in northwest Florida. Ursus 18:62–71.

Streng, D. R., J. S. Glitzenstein, and W. J. Platt. 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. Proceedings of the Tall Timbers Fire Ecology Conference 18:227–263.

Symonds, M. R. E., and A. Moussalli. 2010. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Umber, R. W. 1975. Impact of pine plantation succession on sandhill wildlife in central Florida. Thesis, University of Florida, Gainesville.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

Varner, J. M., J. S. Kush, and R. S. Meldahl. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Tall Timbers Fire Ecology Conference 21:216–219.

Wahlenberg, W. G. 1946. Longleaf pine; its use, ecology, regeneration, protection, growth and management. Charles Lathrop Pack Forestry Foundation, Washington, D.C.

Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. Forest Ecology and Management 47:195–210.

Walker, J., and R. K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Plant Ecology 55:163–179.

Walters, J. R. 1991. Application of ecological principals to the management of endangered species: the case of the red-cockaded woodpecker. Annual Review of Ecology and Systematics 22:505–523.

Watts, D. E., I. D. Parker, R. R. Lopez, N. J. Silvy, and D. S. Davis. 2008. Distribution and abundance of endangered Florida key deer on outer islands. Journal of Wildlife Management 72:360–366.

Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. Miscellaneous Publication 24. Bulletin of Tall Timbers Research Station. Tall Timbers Research Station, Tallahassee, Florida.

Wilkins, R. N., W. R. Marion, D. G. Neary, and G. W. Tanner. 1993. Vascular plant community dynamics following hexazinone site preparation in the lower Coastal Plain. Canadian Journal of Forest Research 23:2216–2229.

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