Forest Ecology and Management 391 (2017) 42–51

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Daniel U. Greene *, Robert A. McCleery

Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA

ARTICLE INFO

Article history:
Received 30 September 2016
Received in revised form 27 January 2017
Accepted 3 February 2017
Available online 23 February 2017

Keywords:
Camera surveys
Camera traps
Fox squirrel
Habitat selection
Longleaf pine
Sciurus niger

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.

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

* Corresponding author at: Department of Natural Resources Management, Texas Tech University, Goddard Building, Box 42125, Lubbock, TX 79409, USA.
E-mail address: dgreene907@gmail.com (D.U. Greene).

http://dx.doi.org/10.1016/j.foreco.2017.02.001
0378-1127/

(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 $\geq$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.