# Fire, Habitat Structure and Herpetofauna in the Southeast

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Abstract.—In this paper I review studies of herpetofauna in two fire-maintained, xeric pineland southeastern U.S. ecosystems, longleaf pine-turkey oak sandhills and Florida sand pine scrub. I address evolutionary adaptations of herpetofauna to these xeric environments, and how fire disturbance influences herpetofaunal community composition by structuring habitat. Where data are available I examine how anthropogenic disturbance such as fire suppression, clearcutting, and restoration treatments can affect herpetofaunal community composition, and whether some anthropogenic disturbance types can mimic natural disturbance in their effects. I also address possible reasons why detection of population response is more difficult for amphibians than for common reptile species.

Natural disturbance is an important force in shaping the habitat structure of ecosystems within southeastern United States. However, type, frequency, intensity, and scale of natural disturbance varies among ecosystems. Wind, ice, insect and disease outbreaks, or fire can be dominant disturbance types in some southeastern ecosystems, acting at scales ranging from single-tree death to thousands of hectares. Disturbance regimes and the habitat structure they maintain exert selective pressure on life history strategies, physical, and behavioral adaptations of resident flora and fauna (Denslow 1980). Hence, biotic components that characterize and distinguish ecosystems often provide clues to the most common habitat structure, and dominant disturbance regime that historically shaped it.

Interference with disturbance regimes can alter the habitat structure of ecosystems by disrupting processes that shape, maintain, and perpetuate them. Major structural alterations to habitat can, in turn, potentially adversely affect characteristic flora and fauna. Similarly, introduction of anthropogenic disturbance types to ecosystems that do not resemble or mimic the results of natural disturbance regimes can adversely affect their biota.

Fire is an integral disturbance type to many southeastern ecosystems that drives their process, function, and many of their defining floral and faunal components (Myers and Van Lear 1998). However, fire characteristics vary among ecosystems. In the southeastern Coastal Plain, the longleaf pine-wiregrass ecosystem was historically maintained by low-intensity, high frequency (3-5 year intervals), large-scale groundfires that killed many young, invading hardwoods. This burning regime maintained a low density of mature longleaf pine, scattered understory oaks, and an abundance of sunlight at ground level that promoted a continuous groundcover dominated by wiregrass and a high diversity of herbaceous plants (Myers 1990). Fire suppression is more aptly viewed as a disturbance in sandhills than is fire itself, as it disrupts a process that maintains and perpetuates this habitat structure. In the absence of fire a dense hardwood understory develops, leaf litter and shade increase, and wiregrass becomes sparse (see Table 1).

Conversely, the sand pine scrub ecosystem in peninsular Florida was maintained by high-intensity, low frequency (10-100 year intervals) wildfires that killed virtually all above-ground vegetation, followed by rapid resprouting of shrubs (Abrahamson 1984; Greenberg et al. 1995). During long fire-free intervals a thick shrub layer developed, and even-aged stands of sand pine matured at densities that varied dramatically among scrubs.

Herpetofaunal assemblages differ among southeastern ecosystems and physiographical regions according to historical biogeography, and physiological and environmental constraints that adapt each species to specific or generalized habitats. Species exhibiting specialized traits often are also restricted in their local distribution by habitat type and condition. Reptile and amphibian species in xeric sandhills and scrub include widespread generalists and species having narrow habitat requirements, usually typical of recent post-fire conditions. Because the habitat condition in xeric sandhills and sand pine scrub is sculpted by fire, herpetofaunal distribution and abundance is closely tied to disturbance regime.

Surprisingly few studies examine differences in habitat characteristics between fire-suppressed and fire-maintained sandhills or sand pine scrub, and how habitat structure affects herpetofauna. However, even an intuitive understanding of fire effects and ecological requirements of herpetofauna would suggest that there are impacts. Species having specialized adaptations to structural features of fire-maintained habitat, such as bare ground, could be at a disadvantage in fire suppressed habitat. Gopher tortoises are abundant in regularly burned sandhills, where a dense layer of wiregrass and herbaceous groundcover provide plentiful food, and the light level is adequate for nest sites (Diemer 1992). This might be expected to adversely affect gopher tortoise burrow commensals, but only if burrows are a limiting resource. By reducing root density in uplands (by reducing tree density), fire likely

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**Table 1.—Mean (±SE) percent cover of select habitat characteristics and basal area (BA) of trees in hardwood-invaded (HI) versus savanna-like (SL) longleaf pine-wiregrass sandhills surrounding eight isolated, ephemeral ponds in the Ocala National Forest, Florida. Percentage data were square root-arcsine transformed for t-tests but are presented as untransformed values (adapted from Greenberg in press)**

| | Upland matrix | | | |
|---|---|---|---|---|
| | HI | SL | df | P |
| Wiregrass (% cover) | 11.6± 6.0 | 66.5±8.6 | 25.0 | <0.0001 |
| Herbaceous (% cover) | 4.5 ± 1.4 | 21.5±4.7 | 25.0 | 0.0002 |
| Leaf litter (% cover) | 99.3± 0.5 | 68.5±9.6 | 12.7 | 0.0023 |
| Bare ground (% cover) | 0.4 ± 0.2 | 9.4±3.7 | 13.3 | 0.0072 |
| Coarse woody debris ≥12.5 cm (% cover) | 0.7 ± 0.4 | 1.2±0.6 | 25.0 | 0.6208 |
| Shrub <2.5 cm (% cover) | 47.5±8.2 | 27.8±6.4 | 25.0 | 0.0548 |
| Light (%) | 22.8±3.7 | 54.0±4.9 | 25.0 | <0.0001 |
| Longleaf pine BA ($m^2$) | 4.5 ±1.2 | 4.8±1.1 | 25.0 | 0.8475 |
| Hardwoods & sand pine BA ($m^2$) | 2.8±0.7 | 0.9±0.5 | 25.0 | 0.0357 |
| Snag BA ($m^2$) | 0.7±0.3 | 0.5±0.3 | 25.0 | 0.5677 |

facilitates burrowing conditions for primary underground excavators (such as gopher tortoises and pocket gophers) and thereby secondary burrow- and tunnel users such as Florida gopher frogs and striped newts. Historically, fire probably maintained and deepened ephemeral wetlands that are used as breeding sites by xeric pineland amphibians by killing encroaching trees and shrubs, and burning peat and vegetation buildup during dry periods. Fire also maintained a low density of mature trees in uplands surrounding ponds by killing young trees. Lower tree density reduces transpiration, but may increase evaporation from ponds. Hardwood invasion may affect hydroperiod and water depth of shallow ponds by altering the balance between transpiration and evaporation (Sharitz and Gresham 1998).

In this paper I will review studies of herpetofauna in two fire-maintained xeric pineland ecosystems, longleaf pine-turkey oak-wiregrass sandhills and Florida sand pine scrub. I will specifically address some evolutionary adaptations of herpetofauna to xeric environments of these fire-maintained ecosystems, and how disturbance influences herpetofaunal community composition by structuring habitat. I also will discuss possible reasons why detection of population response is more difficult for amphibians than for common reptile species. Where data are available I examine how anthropogenic disturbance such as fire suppression, clearcutting, and restoration treatments can affect herpetofaunal community composition, and whether some anthropogenic disturbance types can mimic natural disturbance in their effects.

Although reptiles and amphibians often are generically lumped together as "herpetofauna," they are phylogenetically as distinct from one another as are mammals from birds. Amphibians (class *Amphibia*) have permeable, moist skin that for many serves a respiratory function, and increases their susceptibility to desiccation. Many species also require water for egg deposition and larval development. Taxa vary considerably in their vulnerability to desiccation. For example, anurans are more tolerant of high temperatures (Stebbins and Cohen 1995), and can store and reabsorb larger amounts of water in their bladders than salamanders (Zug 1993). Some salamanders are lungless, and some are completely terrestrial (DeMaynadier and Hunter 1995). Many amphibian species have small home ranges (Duellman and Trueb 1986) and poor dispersal capabilities (Sinsch 1990). Conversely, most reptiles (class *Reptilia*) require warm temperatures (associated with higher light levels) for egg incubation and successful development of hatchlings (Deeming and Ferguson 1991). Reptiles have dry, scaly skin that protects them from desiccation. Clearly, response to disturbance might be expected to differ between the two classes, and among species within them.

Behavioral or physical adaptations to xeric upland environments likely reduce the vulnerability of the native herpetofauna to fire and consequent habitat alterations (Means and Campbell 1981). Among reptilian sandhill and sand pine scrub inhabitants, several species exhibit specialized behavioral or anatomical traits for surviving in a xeric, open, loose-sand environment (Campbell and Christman 1982a;

**Table 2.—Mean (± SE) number of select reptile species captured using drift fences and pitfall traps during August 1991 - September 1992 in three treatments and mature forest controls (n = 3 per treatment and control) in sand pine scrub, Ocala National Forest, Florida**

| Species | Burn & Salvage | Clearcut & Rollerchop | Clearcut & Bracke-Seed | Mature Forest | P |
|---|---|---|---|---|---|
| Six-lined Racerunner | 5.7 ± 1.2[a,b] | 12.3 ± 1.2[a] | 13.0 ± 5.2[a] | 2.3 ± 1.5[b] | 0.0752 |
| Mole Skink | 11.0 ± 2.1[a] | 16.7 ± 3.5[a] | 9.7 ± 3.5[a] | 1.3 ± 0.3[b] | 0.0237 |
| Southeastern Five-lined Skink | 1.3 ± 1.3[a] | 1.0 ± 0.6[a] | 1.0 ± 0.6[a] | 13.3 ± 1.7[b] | 0.0001 |
| Ground Skink | 2.0 ± 1.0[a,b] | 0.7 ± 0.7[a] | 0.0 ± 0.0 | 3.7 ± 0.3[b] | 0.0140 |
| Scrub Lizard | 12.0 ± 6.5[a,b] | 25.0 ± 11.0[a,c] | 38.3 ± 2.6[c] | 1.7 ± 0.3[b] | 0.0194 |
| Peninsula crown snake | 2.0 ± 1.2[a] | 7.7 ± 2.4[a,b] | 8.7 ± 1.3[b] | 3.7 ± 2.2[a] | 0.0977 |

Greenberg et al. 1994; Stout et al. 1998). For example, sand skinks, mole skinks, and crown snakes are "sand swimmers," requiring loose, bare sand for semifossorial movement. Short-tailed snakes (Campbell 1992) and pine snakes (Conant and Collins 1991) use underground burrows extensively. Six-lined racerunners and scrub lizards are cursorial, and the mechanics of movement are apparently facilitated by open, bare sand.

Behaviors that exploit cool, moist microhabitats also are apparent in many reptile species inhabiting sandhills and scrub. Gopher tortoises dig burrows that are used as retreats by at least 23 reptile species, including pine snakes and sand skinks, and 9 amphibian species, including gopher frogs and narrowmouth toads (Jackson and Milstrey 1989). Several species, including southern, eastern narrowmouth, and spadefoot toads avoid heat and desiccation by burrowing underground, or by using pre-existing burrows, tunnels and root channels (Russell et al. 1999). Nocturnal foraging, that may allow some species to tolerate extreme conditions of temperature and drought. Selective pressure "pre-adapts" many species to their environments and the disturbance regimes that shape them.

Many reptile species appear to respond to fire-maintained habitat features such as the amount of bare ground, rather than to plant associations *per se* (Campbell and Christman 1982; Greenberg et al. 1994). In sand pine scrub, scrub lizards, sand skinks, six-lined racerunners, mole skinks, and crown snakes are more abundant in open scrub habitat with a high proportion of bare sand than in mature, forested scrub (Campbell and Christman 1982; Greenberg et al. 1994; Means and Campbell 1982). Scrub lizards ($r^2 = 0.44$; $p = 0.0182$) and six-lined racerunners ($r^2 = 68$; $p = 0.0010$) are positively correlated, whereas southeastern five-lined skinks are negatively correlated ($r^2 = 0.75$; $p = 0.0003$) to the amount of bare sand (Greenberg et al.1994).

Reptile response to anthropogenic and natural disturbances may be similar in some ecosystems if the resulting post-disturbance habitat structure is similar. For example, the relative abundance of mole skinks, scrub lizards, and six-lined racerunners was similar in sites that had been recently burned and salvage-logged, clearcut with low-intensity site preparation, and clearcut followed by roller-chopping, but lower in mature forested sand pine scrub (Greenberg et al. 1994). Conversely, generalist species that are common in many southeastern ecosystems, such as ground skinks and southeastern five-lined skinks were widespread among scrub age classes or more abundant in mature sand pine forest than in young, open scrub (Table 2) (Greenberg et al. 1994). This suggests that high-intensity natural disturbance was an important selective pressure on physical or behavioral adaptations by herpetofauna.

There is a dearth of information on how fire suppression affects herpetofauna of xeric sandhills. Potential effects appear difficult to detect, perhaps in part because habitat heterogeneity remains within hardwood-invaded sandhills for decades after commencement of fire suppression. Litt (1999) reported no difference in species richness, and few differences in relative abundance of species between fire-suppressed sandhills and three restoration treatments (mechanical girdling and felling; herbicide; and growing season fire) or frequently burned "reference" sandhills. Meshaka and Layne (pers. comm.) also found that during 1979-1994, species diversity and richness of herpetofauna in a fire-suppressed sandhill in Florida was similar to that reported for frequently burned Florida sandhills. They attributed the persistence of xeric-adapted reptiles such as six-lined racerunners and scrub lizards species to a frequent occurrence of shrub-free openings. The abundance of southeastern five-lined skinks increased during their study. Mushinsky (1985) reported higher abundance of six-lined racerunners on an annually burned sandhill site with low wiregrass and herbaceous cover relative to sites with longer burn intervals. Sandhill reptiles respond to subsets of microhabitat characteristics that are unique to each species or species group (Litt 1999; Mushinsky 1985). Habitat

heterogeneity within regularly burned sandhills permits the co-occurrence of post-disturbance specialists and generalists, and contributes to the high diversity of herpetofauna in sandhills and scrub relative to other Florida ecosystems (Campbell and Christman 1982).

Among the few studies comparing amphibian use of fire suppressed versus regularly burned xeric pinelands, none provide conclusive results. Clearly, amphibians that are characteristic of xeric, fire-climax pinelands also use fire-suppressed habitat (Greenberg 2001; Greenberg unpubl. data; Litt 1999; Mushinsky 1985). Palis (1998) reported high adult usage and egg mass deposition by gopher frogs at a pond within fire-suppressed longleaf pine-turkey oak sandhill uplands. Some studies provide anecdotal evidence of habitat preference. Palis (1998) reported a tendency for adult gopher frogs to immigrate to a breeding pond from the direction of an early successional bombing range versus a hardwood-invaded sandhill, suggesting heavier use of the more open habitat. Dodd (1996) reported more captures in open xeric hammock, fewer in closed xeric hammock, and as expected in sandhills if captures were proportional to trap effort.

Season of burn influences diversity patterns, percent cover, and flowering of several herbaceous sandhill species (Robins and Myers 1989). Few studies address whether season of burn affects herpetofaunal communities in sandhills. C.L. Hardy and associates (pers. comm.) applied dormant season burns to uplands surrounding one half of ephemeral ponds in sandhills, and growing season burns to the other half. Their preliminary results indicate no treatment differences in amphibian or reptile use of ponds.

Amphibian population response to disturbance or habitat condition appears to be difficult to detect in fire-adapted ecosystems such as sandhills and sand pine scrub, and may require long-term data. Although many species use uplands during much of their lives, the distribution and abundance of amphibians in uplands is closely tied to distance from water (Dodd 1995, 1996). Greenberg (1993) reported that the relative abundance of anurans was not significantly related to stand age or disturbance treatment in sand pine scrub, but was negatively correlated with distance from permanent water sources (lakes and wet prairies) ($r^2 = 0.5406$; $p = 0.0064$). This relationship was not consistent among individual species, possibly because some small, ephemeral wetlands were not detected, and because some species travel further from breeding sites than others (Dodd 1996). Dodd (1996) reported no significant correlation between the number of amphibians captured per trap and trap distance from nearest water body, but 83% of amphibians were captured within 600-m from water. Greenberg (1993) collected spadefoot toad tadpoles from a roadside puddle in sand pine scrub. This suggests larval developmental rates, precipitation, and the distribution of depressions as small as puddles (in this case, anthropogenically-created by clay-subsidized sand roads) can differentially affect the spatial and temporal distribution patterns of amphibians. Clearly, ephemeral ponds are critical centers of herpetofaunal diversity in sandhills (Dodd 1992; Moler and Franz 1987); most amphibian and several reptile species, such as turtles and swamp snakes, would not occur there in their absence.

Wetlands within sandhills function as a magnet to amphibians. Capture rates may reflect life history patterns such as longevity and strong breeding site fidelity, providing misleading representation of relative abundance among species, and sites, and years. Hydroperiod, water depth, and underwater dynamics of competition and predation also heavily influence annual recruitment and population fluctuations (Heyer 1976; Maiorana 1976), and further confound data interpretation.

As an example, preliminary results of a study comparing herpetofaunal use of isolated, ephemeral ponds using intermittent drift fences with pitfall and funnel traps, indicate significant differences ($p < 0.05$) in the use of ponds within regularly burned sandhills ($n = 4$) versus hardwood-invaded sandhills ($n = 4$) by some amphibian species. Whereas significantly more adult eastern narrowmouth toads, leopard frogs, and southern toads used ponds within hardwood-invaded sandhills during 1994-1997, more adult striped newts used ponds in savanna-like sandhills (Table 3). Juvenile recruitment by oak toads and narrowmouth toads was higher in hardwood-invaded sandhills (Greenberg, unpubl. data), and recruitment by Florida gopher frogs was higher in savanna-like sandhills (Greenberg 2001) (Table 3). However, confidence in the biological significance of these results is compromised by a lack of clean distinction between upland matrix treatments. The level of hardwood invasion in the hardwood-invaded upland matrix is patchy (Table 1). Further, the distance (on one side) between 3 ponds in the hardwood-invaded upland matrix and the savanna-like upland matrix is < 30 m. Variation in pond use and recruitment among species, sites, and years is high. These and confounding factors associated with using ponds as trap foci suggests that detection of biologically meaningful differences in pond use among different habitat conditions requires long-term data and heavy replication.

In recent decades, recognition that fire is critical to xeric pineland ecosystems has led to implementation of control burning programs for sandhill on many public lands, where resources permit. In sandhills, the restoration goal commonly is to create a "park-like" environment dominated by longleaf pine and wiregrass, and virtually devoid of a hardwood midstory. This vision is inspired by some descriptions by early surveyors and naturalists (e.g., Vignoles 1823; Williams 1837; Harper 1911; Myers 1990), and by the narrow

**Table 3.—Mean (+ SE) adult use (entering and exiting individuals) and juvenile recruitment (exiting individuals only) of select pond-breeding amphibians using isolated, ephemeral ponds in hardwood-invaded (HI) (n = 4) and savanna-like (SL) (n=4) longleaf pine-turkey oak-wiregrass sandhills during February 1994 - January 1998, Ocala National Forest, Florida**

| | | Adults (No./100 trapnights) | | | Juveniles (No./100 trapnights) | | |
|---|---|---|---|---|---|---|---|
| | | Treatment | | | Treatment | | |
| Species | Year | HI | SL | P < 0.05 | HI | SL | P < 0.05 |
| Oak Toad | 1 | 0.61 + 0.1 | 0.12 + 0.08 | | 0.41 + 0.13 | 0.01 + 0.00 | * |
| | 2 | 0.19 + 0.09 | 0.09 + 0.05 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 3 | 0.52 + 0.51 | 0.11 + 0.06 | | 0.02 + 0.02 | 0.00 + 0.00 | |
| | 4 | 0.01 + 0.00 | 0.08 + 0.04 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 5 | 0.77 + 0.57 | 0.25 + 0.18 | | 0.12 + 0.12 | 0.00 + 0.00 | |
| Southern Toad | 1 | 0.17 + 0.07 | 0.03 + 0.01 | * | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 2 | 0.21 + 0.03 | 0.09 + 0.04 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 3 | 0.17 + 0.06 | 0.10 + 0.02 | | 0.15 + 0.14 | 0.04 + 0.04 | |
| | 4 | 0.09 + 0.01 | 0.08 + 0.04 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 5 | 0.20 + 0.11 | 0.10 + 0.02 | | 2.82 + 2.79 | 0.02 + 0.02 | |
| Eastern Narrowmouth Toad | 1 | 1.27 + 0.30 | 0.50 + 0.25 | * | 0.16 + 0.07 | 0.01 + 0.01 | * |
| | 2 | 0.47 + 0.16 | 0.27 + 0.09 | | 0.01 + 0.01 | 0.00 + 0.00 | |
| | 3 | 0.25 + 0.11 | 0.19 + 0.07 | | 0.01 + 0.00 | 0.00 + 0.00 | |
| | 4 | 0.13 + 0.03 | 0.18 + 0.09 | | 0.01 + 0.01 | 0.00 + 0.00 | |
| | 5 | 0.13 + 0.03 | 0.07 + 0.04 | | 0.01 + 0.01 | 0.00 + 0.00 | |
| Striped Newt | 1 | 0.00 + 0.00 | 0.01 + 0.01 | * | 0.00 + 0.00 | 0.01 + 0.01 | |
| | 2 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 3 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.00 + 0.00 | 0.01 + 0.01 | |
| | 4 | 0.00 + 0.00 | 0.10 + 0.08 | | 0.00 + 0.00 | 0.01 + 0.01 | |
| | 5 | 0.05 + 0.04 | 0.26 + 0.23 | | 0.06 + 0.03 | 1.23 + 1.19 | |
| Florida gopher frog | 1 | 0.04 + 0.01 | 0.02 + 0.01 | | 0.00 + 0.00 | 0.01 + 0.00 | * |
| | 2 | 0.01 + 0.00 | 0.02 + 0.01 | | 0.15 + 0.04 | 0.60 + 0.27 | |
| | 3 | 0.01 + 0.00 | 0.02 + 0.01 | | 0.07 + 0.03 | 0.33 + 0.14 | |
| | 4 | 0.00 + 0.00 | 0.01 + 0.00 | | 0.01 + 0.01 | 0.06 + 0.02 | |
| | 5 | 0.01 + 0.00 | 0.01 + 0.01 | | 0.32 + 0.04 | 0.72 + 0.27 | |
| Bullfrog | 1 | 0.00 + 0.00 | 0.01 + 0.00 | | 0.02 + 0.01 | 0.06 + 0.04 | |
| | 2 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.01 + 0.01 | 0.01 + 0.00 | |
| | 3 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.02 + 0.01 | 0.03 + 0.00 | |
| | 4 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.01 + 0.01 | 0.01 + 0.01 | |
| | 5 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.10 + 0.06 | 0.33 + 0.24 | |
| Pig Frog | 1 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 2 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.03 + 0.02 | 0.04 + 0.02 | |
| | 3 | 0.01 + 0.00 | 0.00 + 0.00 | | 0.02 + 0.01 | 0.07 + 0.03 | |
| | 4 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.03 + 0.02 | 0.15 + 0.11 | |
| | 5 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.05 + 0.02 | 0.03 + 0.02 | |
| Leopard Frog | 1 | 0.09 + 0.02 | 0.07 + 0.04 | * | 0.25 + 0.13 | 0.55 + 0.50 | |
| | 2 | 0.06 + 0.02 | 0.04 + 0.01 | | 0.11 + 0.03 | 0.14 + 0.07 | |
| | 3 | 0.04 + 0.01 | 0.03 + 0.00 | | 0.12 + 0.04 | 0.11 + 0.03 | |
| | 4 | 0.01 + 0.00 | 0.01 + 0.00 | | 0.01 + 0.01 | 0.01 + 0.01 | |
| | 5 | 0.03 + 0.01 | 0.01 + 0.01 | | 0.40 + 0.10 | 0.17 + 0.11 | |
| Spadfoot Toad | 1 | 0.31 + 0.21 | 0.73 + 0.47 | | 10.70 + 10.68 | 0.00 + 0.00 | |
| | 2 | 0.37 + 0.34 | 0.08 + 0.07 | | 4.58 + 4.54 | 0.00 + 0.00 | |
| | 3 | 0.10 + 0.10 | 0.02 + 0.01 | | 0.06 + 0.05 | 0.00 + 0.00 | |
| | 4 | 0.00 + 0.00 | 0.00 + 0.00 | | 0.00 + 0.00 | 0.00 + 0.00 | |
| | 5 | 0.19 + 0.17 | 0.10 + 0.05 | | 0.00 + 0.00 | 0.00 + 0.00 | |

habitat requirements of the endangered red-cockaded woodpecker (Carter et al. 1995). However, such descriptions may over-represent this sandhill variant because it was more easily (and commonly) traveled (Landers et al. 1990).

Palynological evidence suggests that the relative dominance of oak and pine has shifted many times within the past 20,000 years in the southeastern United States as a result of climatic and sea level changes that affects soil moisture and fire frequency (Watts 1971). Descriptions by early naturalists (see Myers 1990), plant composition and characteristics, and the presence of old-growth oaks suggest that even within recent centuries, fire in sandhills was spatially and temporally variable (Greenberg and Simons 1999; also see Myers 1990). Prior to fire suppression, patchiness in the intensity, season, frequency, and spatial extent of fire allowed some young oaks to reach fire-resistant size and occur in varying densities over time and across the sandhills landscape (Greenberg and Simons 1999).

Indeed, several lines of evidence suggest that tree-sized oaks were an integral part of the sandhill landscape (Greenberg and Simons 1999). Several oak species, including bluejack, turkey, and sand post oak are endemic to xeric pinelands, suggesting that they historically occurred there. The ability to reach tree size and reproduce sexually (as well as clonally) indicates that trees reached maturity frequently enough to retain the trait (Berg and Hamrick 1994; Landers et al. 1990; Myers 1990). The presence of acorn-dependent, xeric-pineland species such as Sherman's fox squirrels and red-headed woodpeckers suggests that hard mast was produced in sandhills. Clearly, stand conditions within these ecosystems historically were not homogeneous, but a heterogeneous matrix of stand ages and structural conditions.

The presence of both specialized, xeric-adapted species and wide-ranging generalist species in sandhills and scrub further indicate that historically, variable burning intensities, intervals, and spatial extent created a range of microhabitats and stand conditions (Campbell and Christman 1982). Braithwaite (1987) reported that lizard species in the wet-dry tropics of Australia were differentially favored in habitats created by various fire regimes. He suggested that no single fire regime was optimal for all species, but that a range of burning regimes would retain the entire lizard community.

Historically, fire frequency, intensity, and behavior as it interacted with fuel loads, wind, precipitation, topography, and pre-existing vegetation patterns was unlikely to sculpt homogeneous habitat structures across large landscapes. Whereas the scale of heterogeneity in stand age, tree or shrub density, and associated habitat features differed between sandhills (smaller habitat patches) and scrub (larger habitat patches), both ecosystems were a mosaic of stand conditions that shifted spatially and temporally across the landscape (Greenberg et al. 1994). Populations of xeric adapted reptiles probably became locally extinct, or persisted in low numbers within long-unburned habitat patches, exploiting young, open, suitable habitat through colonization and reproduction as it was created by fire.

Ideally, ecosystem management systems should be designed to incorporate silvicultural and land management systems that mimic natural disturbance (Hansen et al., 1991; Greenberg et al., 1994). A necessary corollary is the need to identify habitat characteristics that promote diversity and abundance of species (Hansen et al., 1991). More research on herpetofaunal response to natural disturbance and the associated changes in habitat structure is critically needed in order to gauge the success or failure of management.

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## List of Species Names

| | |
|---|---|
| **Vegetation** | |
| Wiregrass | *Aristida stricta* (Micheaux) |
| Turkey oak | *Quercus laevis* (Walt.) |
| Bluejack oak | *Quercus incana* (Bartr.) |
| Sand post oak | *Quercus margaretta* (Ashe) |
| Longleaf pine | *Pinus palustris* (Mill.) |
| Sand pine | *Pinus clausa* (Chapm. Ex Engelm.) Vasey ex Sarg. |
| **Birds** | |
| Red-cockaded woodpecker | *Picoides borealis* |
| Red-headed woodpecker | *Melanerpes erythrocephalus* |
| **Mammals** | |
| Sherman's fox squirrels | *Sciurus niger shermani* |
| **Herpetofauna** | |
| Six-lined racerunner | *Cnemidophorus sexlineatus* |
| Gopher tortoise | *Gopherus polyphemus* |
| Short-tailed snake | *Stilosoma extenuatum* |
| Pine snake | *Pituophis melanoleucus* |
| Scrub lizard | *Sceloporus woodi* |
| Sand skink | *Neoseps reynoldsi* |
| Mole skink | *Eumeces egregius* |
| Southeastern five-lined skink | *Eumeces inexpectatus* |
| Ground skink | *Scincella laterale* |
| Peninsula crown snake | *Tantilla relicta* |
| Oak toad | *Bufo quercicus* |
| Southern toad | *Bufo terrestris* |
| Striped newt | *Notophthalmus perstriatus* |
| Spadefoot toad | *Scaphiopus holbrookii* |
| Narrowmouth toad | *Gastrophryne carolinensis* |
| Florida gopher frog | *Rana capito aesopus* |
| Pig frog | *Rana grylio* |
| Bullfrog | *Rana catesbeiana* |
| Leopard frog | *Rana utricularia* |