Effect of High-Intensity Wildfire and Silvicultural Treatments on Reptile Communities in Sand-Pine Scrub

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Abstract: ***We tested whether the herpetofaunal response to clearcutting followed by site preparation was similar to high-intensity wildfire followed by salvage logging in sand-pine scrub. Herpetofaunal communities were compared in three replicated 5- to 7-year post-disturbance treatments and mature sand-pine forest The three disturbance treatments were (I) high-intensity wildfire, salvage-logging, and natural regeneration; (2) clearcutting, roller-chopping, and broadcast-seeding; and (3) clearcutting and bracke-seeding. Animals were trapped over a Id-month period using pitfall traps with drift fences. Microhabitat features were measured along line transects. Because amphibian (frog) occurrence appeared to be unaffected by treatment, this paper focuses only on reptile communities. Six species of lizards and one snake species were numerically dominant. Reptile species richness, diversity, and evenness did not differ among treat-***

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Efecto de los incendios naturales de alta intensidad y de los tratamientos de silvicultura sobre las comunidades de reptiles en un brozal de ambiente arenoso

Resumen: ***Se analizó si la respuesta de la herpetofauna a la tala seguida de la preparación del los sitio, fue similar a la respuesta a incendios naturales de alta intensidad seguidos por una tala de rescate, en un brozal de pinos de ambiente arenoso. Se compararon las comunidades de herpetofauna en 3 tratamientos (con réplicas), luego de 5 a 7 años de finalizada la pertubacidn en bosques maduros de pinos de ambientes arenosos. Los tres tratamientos de perturbación fueron (I) incendio natural de alta intensidad, tala de rescate y regeneración natural, (2) tala, "roller-chopping" y "broadcast-seeding" y (3 j tala y "bracke-seeding". Los animules fueron atrapados a lo largo de un período mayor a 14 messes, utilizando trampas disimulados. Las caracteristicas de microhábitat fueron medidas a lo largo de transectos lineales. Dado que la ocurrencia de anfibios (ranas) parecid no estar afectada por el tratamiento, este tra-***

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ments or mature forest. Species composition differed markedly, however, between mature forest and disturbance treatments. Typical open scrub species such as Cnemidophorus sexlineatus, Sceloporus woodi, *and* Eumeces egregius, were *dominant in high-intensity burn, roller-chopped, and bracke-seeded stands but scarce in mature forest, and they were positively correlated with bare sand and other microhabitat features typical of open scrub. Conversely,* Eumeces inexpectatus *was most abundant in mature forest and was correlated with ground litter and other features typical of mature forest. With respect to the species sampled, especially the lizards (including endemic species) of open scrub, clearcutting appeared to mimic high-intensity wildfire followed by salvage-logging by creating microhabitat features such as bare sand In a mirror image of the usual concept, forest maturation historically served as the fragmenting agent of an extensive open-scrub landscape matrix that was maintained by high-intensity wildfire. Hence, the patchwork of age classes created by current clearcuttingpatterns could serve as a barrier to lizard dispersal and impede metapopulation dynamics. The absence of a true control (unsalvaged burns) suggests caution in interpreting the results of this study.*

bajo se centra sdlamente en las comunidades de reptiles. Seis especies de lagartijas y una especie de serpiente fueron numéricamente dominantes. La riqueza, diversidad y distriburi de las especies de reptiles, no difirió entre los tratamientos o el bosque maduro. Sin embargo, la composición de especies difirió marcadamente entre el bosque maduro y los tratamientos depertubacidn. Las especies típicas de brozales tales como Cnemidophorus sexlineatus, Sceloporus woodi, y Eumeces egregius, *fueron dominantes en las parcelas con quemas de alta intensidad, "roller cboped" y "brake-seeded': pero fueron escasas en los bosques maduros y estuvieron positivamente cowelacionadas con arenas desnudas y otras características de microhábitat típicas del brozal. Contrariamente,* Eumeces inexpectatus *fue más abundante en el bosque maduro y estuvo cowelacionada con la broza y otras caracteristicas típicas del bosque maduro. Con respecto a las especies muestreadas, especialmente las lagartijas (incluyendo las especies endémicas) de los brozales abiertos, la talaparece imitar incendios de alta intensidad, seguidospor tala de rescate creando micro-hábitats con caracteriticas similares tales como arenas desnudas. Como una reflección del concepto usual, la maduración del bosque siwid históricamente como el agente de fragmentacidn de una extensa matriz de paisaje de brozales abiertos, que era mantenida por incendios naturales de alta intensidad. Por lo tanto, el trabajo de parches de las clases de edades creado por los patrones de tala actuales, puede servir como bawera para la dispersión de las lagartijas e impedir la dinámica de la metapoblacidn. La ausencia de un verdadero tratamiento control (incendios no controlados) sugiereprecaucidn en la interpretación de los resultados de este trabajo.*

Introduction

The species richness of North American herpetofauna is notably high in the southeastern United States (Kiester 1971), and the scrub supports several species found nowhere else on earth (Neil1 1957; Auffenberg 1982; Christman &Judd 1990). The largest remaining patch of Florida scrub occurs in the Ocala National Forest in central Florida, an area where human population growth, forestry, and related developments are stressing both the native ecosystems and the agencies responsible for managing them.

Factors including historical biogeography, age, edaphic factors, and fire history (Myers 1990) affect plant and animal species composition and gave a unique character to each Florida scrub (Neil1 1957; Telford 1965; Jackson 1973; Auffenberg 1982; Christman & Judd 1990; Webb 1990). The Ocala scrub is unusual in its high density of sand pine relative to other scrubs. In recent decades, fire suppression has changed the landscape by facilitating large-scale forest maturation. Although spatially variable, however, sand-pine density was probably high prior to human interference (Hill 19 16; Webber 1935), perhaps due to relatively lower fire frequency or other historical influences. Nonetheless, the edaphic and habitat-structure requirements of the Ocala sand-pine scrub biota are the same as those of other xeric Florida scrubs.

Historically, the most prominent natural disturbance in the Florida scrub appears to have been infrequent, high-intensity wildfire that swept over large areas of landscape, creating a temporally shifting age-class mosiac (Myers 1990). Anecdotal evidence suggest that early successional stages of scrub may well have constituted the landscape matrix within which isolated patches of mature sand pine (*Pinus clausa*) occurred (Bartram 1791; Rawlings 1933). Post-fire recovery is rapid in scrub. Woody plants that were dominant before wildfire regain dominance within a few years by seeding or resprouting (Abrahamson 1984*a*, 1984*b*). In the short term, a similar response is observed following clearcutting and site preparation (Greenberg 1993). Following both of these high-intensity disturbances a low, open habitat structure is maintained for several years, and a sparse herbaceous ground cover permits large areas of bare sand to remain exposed until shrubs, lichens, and leaf litter replace it as the canopy closes.

The influence of vegetation structure and substrate on the composition of lizard communities composition has been well documented in other ecosystems (Pianka 1973; Fuentes 1976; Lillywhite 1977*a;* Cody & Mooney 1978; Mushinsky 1985; Braithewaite 1987; Mushinsky & Gibson 199 1). These factors affect cover availability, microclimate, productivity and prey availability, and they also have important implications for thermoregulatory, locomotory, burrowing, and egg-laying requirements, which differ among species. Several studies suggest that the herpetofauna of fire-dependent ecosystems such as chaparral (Lillywhite 1977*a,* 1977*b;* Simovich 1979), longleaf pine (*Pinus palustris*)-wiregrass (*Aristida stricta*) sandhills (Mushinsky 1985), and sand-pine scrub (Campbell & Christman 1982a) increase in diversity or density following fire but decline in long-unburned sites.

In the Ocala National Forest, current forest management for sand-pine scrub entails clearcutting stands of 8-25 ha. Heavy machinery used during the clearcutting operation crushes and kills nearly all above-ground vegetation. Site preparation commonly entails either roller-chopping (100% soil disturbance) and broadcast-seeding or bracke-seeding, which creates low beds and disturbs approximately 30% of the soil surface (Outcalt 1990). Because the economic value of sand pine was recognized only recently (1950–1970), only "virgin," previously unmanaged stands are being harvested.

Clearly, the landscape pattern created by clearcutting small patches does not mimic the dominant large-scale landscape dynamics of the natural disturbance regime. Campbell and Christman (1982*a*) suggest, however, that with respect to reptile habitat, clearcutting mimics wildfire by creating similar habitat features. We compared reptile communities of silviculturally disturbed stands (clearcut followed by one of two site-preparation treatments), stands that were burned by crown fires and salvage-logged, and mature sand-pine scrub to test the hypothesis that the reptile community responds similarly to both high-intensity silvicultural and wildfire-caused disturbance.

Study Area and Methods

The Ocala National Forest covers over 180,000 ha in Marion, Lake, and Putnam counties in central Florida (Fig. 1). It is bounded by the Ocklawaha River to the west and north, the St. John's River to the east, and extensive wetlands to the south. Elevations range from 2 to 49 meters above mean sea level. Sand-pine scrub occupies over 100,000 ha of the forest as a southeast-northwest oriented strip, approximately 60 km long and 10-20 km wide. Soils supporting sand-pine scrub are excessively drained aeolian or marine sands classified as the hyperthermic, uncoated families of Spodic (Paola series) and Typic Quartzipsamments (Astatula series).

In mature forest, the canopy is limited to a single tree species, sand pine. Historically, the even age structure of Ocala sand pine was maintained by infrequent, stand-replacing crown fires and by subsequent shedding of copious quantities of seeds (recorded as more than 2.47 million/ha) from semi-serotinous cones (Cooper et al. 1959).

The shrub layer is dominated by myrtle oak (*Quercus myrtifolia*), sand live **oak** (*Quercus* ***geminata),*** Chapman's **oak** (*Quercus* ***cbapmanii),*** fetterbush (*Lyonia ferruginea*), and two palmetto species (*Serenoa repens* and *Sabal etonia*). This area receives approximately 1300 mm of rainfall annually, with over half falling between June and September. Average daily temperatures range from 20–32° C between April and October and 1 1–23° between November and March (Kalisz & Stone 1984).

We sampled herpetofauna in replicated stands ($n = 3$ stands per treatment; 12 stands total) for each of three 5- to 7-year post-disturbance treatments and in mature forest (Fig. 1). Treatments were (1) high-intensity wildfire, salvage-logging, and natural regeneration (HIB); (2) clearcutting, roller-chopping, and broadcast-seeding (RC): and (3) clearcutting and bracke-seeding (BK). Mature (≥55 years) virgin forest stands that had been naturally regenerated following a stand-replacing fire in 1935 were used as a control (MF).

Stand-selection guidelines included (1) being located at least 0.9 km from permanent or known temporary water sources to reduce bias introduction by nearby aquatic habitat and (2) similarity in elevation, topography, and soil characteristics. Additional criteria for disturbance treatments included (1) similar lengths of time since treatment (± 1.5 years) and (2) same pretreatment age and disturbance history (identical to MF). All RC, BK, and MF stands were at least 13.8 ha; HIB stands were located in disparate areas of one 365-ha wildfire patch.

In MF, mean pine density was about 642 trees/ha, and trees averaged 16.7 meters in height. In HIB, RC, and BK treatments, mean pine density was 3080-4076 stems/ha, and mean tree height ranged from 1.9 to 2.8 meters (Greenberg 1993).

Trapping arrays (modified from Campbell & Christman 19826) consisted of eight, 7.6-meter lengths of erect 0.5-meter-high aluminum flashing spaced 7.6 meters apart and arranged in an "L" pattern (Fig. 2). Drift fences were buried 4-6 cm into the ground such that they were self-supporting. Two black 18.9-liter buckets with 1.25-cm holes drilled in the bottoms for drainage were sunk flush with the ground at each end of the fence. Sticks in the drill holes prevented animal escape. A sponge was placed into each bucket and damp-

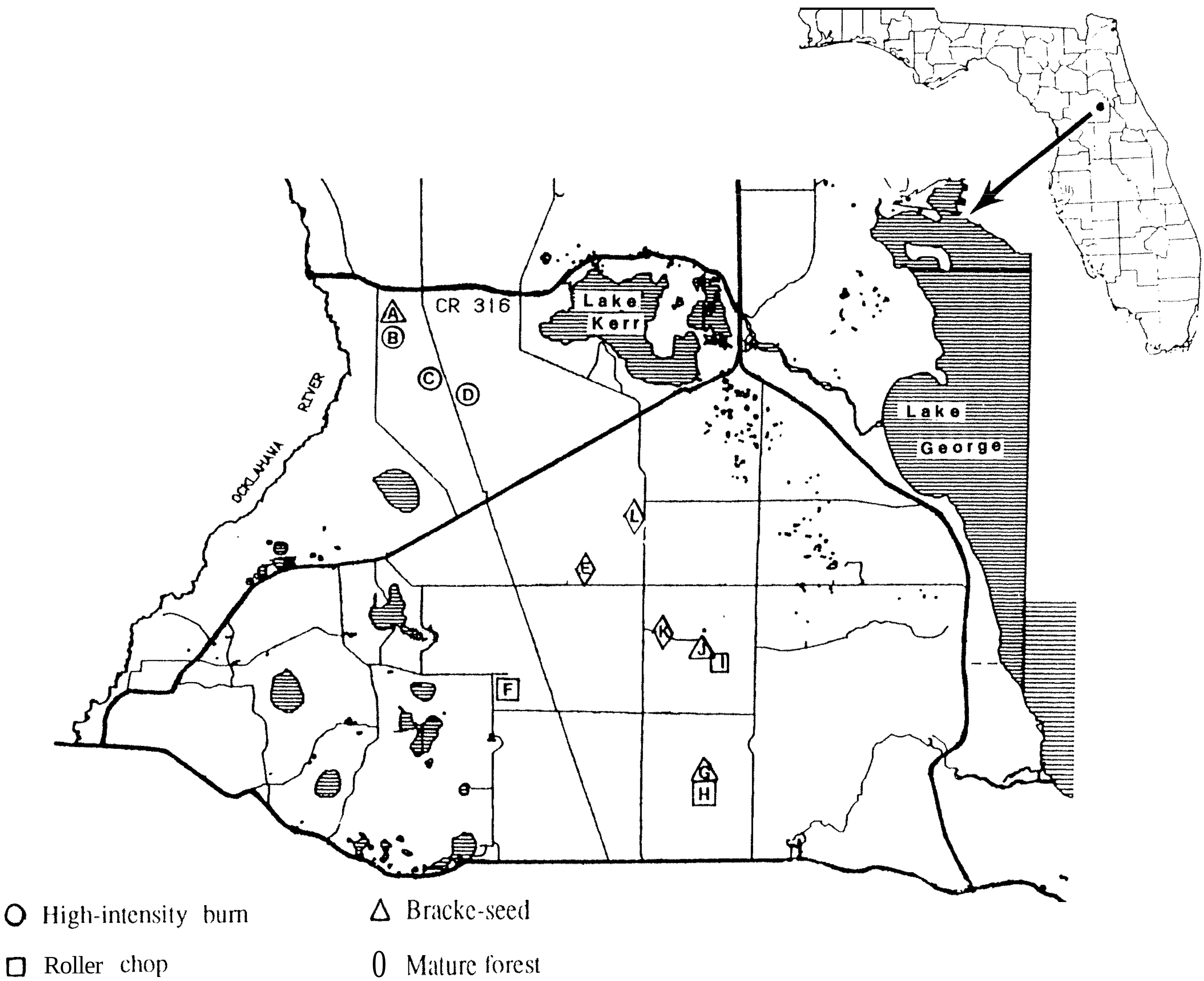

Figure 1. Map of Ocala National Forest with study site locations.

ened at each visit to reduce the probability of animal desiccation. One double-ended and one single-ended funnel trap were placed along either side of and immediately adjacent to each fence. Buckets were shaded by squares of pegboard slanted over the opening. Funnel traps were initially shaded by palmetto fronds were replaced by pegboard after several months.

We sampled for 14 months (August 1991–September 1992) with traps opened and closed alternating 2-week intervals. When open traps were checked every 2-3 days. Animals observed near trapping arrays during sampling periods were hand-captured if possible, but numbers captured in this manner were insignificant. Reptiles were individually marked by clipping of toes (lizards) or ventral scales (snakes). All animals were released near the point of capture.

Microhabitat features, including percentage cover of leaf litter, woody debris, bare ground, herbaceous plants, shrubs, and pine, were measured along three, 10-meter line transects (Mueller-Dombois & Ellenberg 1974) in each of five randomly located lo-by-lo-meter quadrats per stand. In MF, pine cover was estimated using a spherical densiometer at the midpoint of each line transect.

We used analysis of variance (ANOVA) (SAS Institute 1985) to statisically compare stand richness, Shannon's diversity index, evenness (Brower & Zar 1977), total abundance, and relative species abundance of reptile communities among treatments and MF. Pairwise contrasts between least squares means were performed if there was a significant treatment effect. Data were log- or square-root-transformed when required to correct for nonnormality or heteroscedasticity. We computed Horn's Index of Community Similarity (Horn 1966) for all possible treatment pairs. Recaptures were excluded from the data set for the above calculations.

With ordinary least squares methods, linear regression lines were fitted to species with sample sizes larger

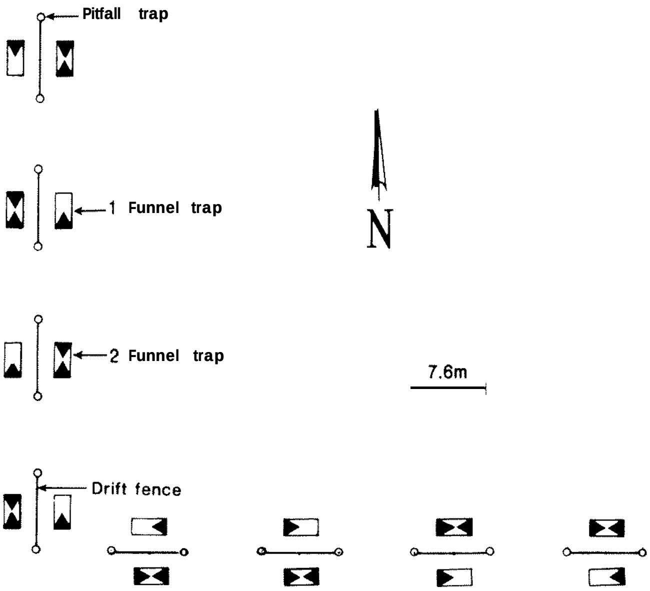

Figure 2. Schematic diagram of herpetofauna trapping arrays. Funnel traps are not to scale.

than 30 individuals. Microhabitat features were used as independent variables. The stand average of line transect measurements for each feature was used in the regression analysis.

Results

Species Richness and Diversity

Seventeen species of reptiles were captured in all treatments and MF combined (Table 1). Species richness, diversity, and evenness did not differ among treatments or MF for reptiles (Table 2). Four species of frogs also were captured, but because their occurrence did not appear to be related to treatment effects our discussion focuses on reptiles.

Community Composition

A total of 658 individual reptiles was captured a total of 940 times (Table 1). Total abundance did not differ among treatments, although reduced numbers in HIB and MF relative to clearcut treatments were suggested ($p = 0.0623$).

Among species (Table 1), ***Sceloporus woodi*** was trapped most often and composed 35% of all reptile captures, followed by ***Eumeces egregius* (*18%*)**, ***Cnemidophorus sexlineatus*** (15%), ***Tantilla relicta*** (10%), ***Eumeces inexpectatus*** (8%), and ***Anolis carolinensis*** (7%). Of the nine snake species captured, ***only Tantilla relicta,*** a small, semifossorial species, was common. We do not know whether this is an accurate reflection of relative abundance or a result of trap bias against large snakes (Greenberg et al. 1994).

Lizard species composition differed between MF and disturbance treatments (Table 1; Fig. ***3).*** Fewer ***Cnemidophorus sexlineatus, Eumeces egregius,*** and ***Sceloporus woodi*** occurred in MF than in disturbance treatments. Conversely, Eumeces ***inexpectatus*** and ***Scincella lateralis*** were more abundant in MF than in the disturbance treatments.

Two of seven ***Cnemidophorus sexlineatus*** (< *57* mm), two of four ***Eumeces egregius*** (< 34 mm), and

Table 1. Mean (±SE) number of reptiles captured from August 1991 through September 1992 in three treatments (HIB, RC, BK)* and mature forest (MF) in sand-pine scrub, Ocala National Forest, Florida.**

*Species' * **	*HIB*	*RC*	*BK*	*MF*	*p-Value*
Cnemidophorus sexlineatus	$5.7^{a,b}$ ± 1.2	12.3" ± 1.2	13.0^{b} ± 5.2	2.3^{a} ± 1.5	0.0752
Eumeces egregius	11.0" ± 2.1	16.7" ± 3.5	9.7^{b} ± 3.5	1.3" ± 0.3	0.0237
E. inexpectatus	1.3" ± 1.3	1.0" ± 0.6	1.0" ± 0.6	13.3^{b} ± 1.7	0.0001
Scincella lateralis	$2.0^{a,b}$ ± 1.0	0.7" ± 0.7	0.0 ± 0.0	3.7" ± 0.3	0.0140
Anolis carolinensis	3.3 ± 1.2	3.0 ± 1.5	6.7 ± 1.3	3.0 ± 0.6	0.2751
Sceloporus woodi	$12.0^{a,b}$ ± 6.5	$25.0^{b,c}$ ± 11.0	38.3" ± 2.6	1.7" ± 0.3	0.0194
Gopher-us polyphemus	*1.0* ± 0.6	X	X	0.0	
Coluber constrictor	0.7 ± 0.3	1.0 ± 0.6	0.0	0.7 ± 0.3	
Crotalus adamanteus	*0.0* ± *0.0*	*X*	*0.0*	*0.0*	
Elaphe guttata	*0.0* ± *0.0*	*0.3* ± 0.3	0.0	0.7 ± 0.3	
Heterodon platyrhinos	0.3 ± 0.3	0.0 ± 0.0	0.0	0.0	
Masticophis flagellum	*X*	0.7 ± 0.3	0.7 ± 0.3	0.0	
Micrurus fulvius	*0.0*	0.3 ± 0.0	0.0	0.3 ± 0.3	
Opheodrys aestivus	0.3 ± 0.3	0.0	0.0	0.0	
Pituophis melanoleucus	*0.0*	0.3 ± 0.3	0.0	0.0	
Rhineura floridana	0.3 ± 0.3	0.0	0.0	0.0	
Sistrurus miliarius	0.7 ± 0.3	0.0 ± 0.0	0.7 ± 0.7	0.3 ± 0.3	
Tantilla relicta	2.0" ± 1.2	$7.7^{a,b}$ ± 2.4	8.7^{b} ± 1.3	3.7" ± 2.2	0.0977
Total	$40.7^{a,b}$ ± 12.2	69.0 ^{b,c}± 18.7	78.7' ± 17.4	31.0" ± 1.7	0.0623

* *HIB = high-intensity bum; RC = roller-chopped; and BK = bracke-seeded.*

. * *Species observed but not captured are indicated by an X.*

*** *Different letters within a row denote significant differences among treatments ($p < 0.100$). Within-row value having the same letter do not significantly differ.*

Table 2. Number of species captured, mean (±SE) species richness, diversity, and evenness of reptiles in three treatments (HIB, RC, BK)* and mature forest (MF) in sand-pine scrub, Ocala National Forest, Florida.

Treatment	*Species Captured*	*Richness*	*Diversity (H')*	*Evenness*
HIB	13	9.0 ± 1.2	0.78 ± 0.04	0.83 ± 0.04
RC	12	8.3 ± 1.2	0.70 ± 0.05	0.77 ± 0.05
BK	9	6.7 ± 0.9	0.61 ± 0.04	0.77 ± 0.02
MF	11	x.7 ± 0.9	0.75 ± 0.04	0.80 ± 0.03
p-value		0.4445	0.1026	0.6433

• *HIB = high-intensity burn; RC = roller-chopped; and BK = bracke-seeded*

three of five ***Sceloporus woodi*** (<40 mm) captured in MF stands were immature, suggesting that mature forest may be minimally used during dispersal or as temporary, suboptimal habitat. Reduced numbers of ***Cnemidophorus sexlineatus*** and ***Sceloporus woodi*** in HIB were suggested ($p < 0.10$).

Horn's Index of Community Similarity indicated a high degree of reptile community overlap among the three disturbance treatments and low overlap of any disturbance treatments with MF (Table 3).

Microhabitat Features

Figure 4 depicts differences in microhabitat features among treatments and mature forest. Although some significant differences in percentage cover of microhabitat features existed among disturbance treatments, differences were small in scale relative to MF. The unexpected differences in percentage cover of woody debris were attributable to silvicultural practices. A significantly reduced level of woody debris in RC was caused by its fragmentation and partial burial by roller-chopper blades and a consequent accelerated rate of decomposition. In contrast, scattered piles of logging debris were left on HIB and BK stands. Natural limbfalls treefalls contributed to larger diameter and less clumped distributions of wood in MF relative to HIB or BK.

Simple linear regression analysis (Table 4) generally indicated a positive correlation of ***Cnemidophorus sexlineatus***, ***Eumeces egregius***, and ***Sceloporus woodi*** abundances with open-scrub features such as bare ground, and a negative correlation with mature-forest features such as leaf litter and pine cover. The abundance of ***Eumeces inexpectatus*** exhibited the opposite trend, occurring in greater numbers in association with microhabitat typical of MF. ***Scincella lateralis*** also was captured more commonly in MF than in disturbance treatments, but sample sizes were low. No species was significantly correlated with woody debris ($p \geqslant 0.14$) Among species analyzed, only ***Eumeces inexpectatus*** was significantly correlated ($p = 0.0020$; $r^2 = 0.63$) with herbaceous cover (predominantly terrestrial lichens, characteristic of mature forest).

Discussion

Absence of differences in reptile species richness and diversity among treatments suggest that, in the short term at least, reptile "biodiversity" per se is not diminished by current clearcutting and site preparation techniques in sand-pine scrub. The integrity of the open-scrub reptile community, however, is diminished in mature forest. Reptile species characteristic of recently disturbed open scrub are scarce in mature sand pine forest where, instead, forest generalists are numerically dominant.

The lizard "succession" observed in Florida scrub (present study; Christman & Campbell 1982a; Anderson & Tiebout 1993) occurs also in other fire-dependent ecosystems such as chaparral (Lillywhite 1977*a*, 19776; Simovich 1979), Florida sandhills (Mushinsky 1985), and the wet-dry tropics of Australia (Braithwaite 1987). In each of these ecosystems, species composition appears to correspond with amount of bare ground and shrub cover and associated microclimate. These factors are in large part determined by the frequency, timing, spatial patterns, and intensity of fire.

Several scrub reptile species, including the endemics ***Sceloporus woodi*** (Jackson 1973) and ***Neoseps reynoldsi*** (a threatened species), as well as ***Cnemidophorus sexlineatus***, ***Eumeces egregius***, and ***Tantilla relicata***, primarily use open-scrub habitat with a high proportion of bare sand. These species are "xeric-adapted" (Campbell & Christman 1982*a*), exhibiting specialized behavioral and anatomical traits for surviving in a xeric, open, loose-sand environment. Conversely, ***Eumeces inexpectatus*** is not especially "xeric-adapted"; within sand-pine scrub it occurs primarily in the shadier, more mesic mature forest.

Differences in percentage cover of bare ground, litter layer, and/or size and distribution of woody debris might be expected to favor ***Eumeces inexpectatus*** over ***Cnemidophorus sexlineatus*** and ***Sceloporus woodi***. Anderson and Tiebout (1993) reported sightings of both ***Cnemidopborus sexlineatus*** and ***Sceloporus woodi*** on bare sand far in excess of its availability. In contrast, 67% of their ***Eumeces inexpectatus*** sightings (all in mature forest) were on recumbent logs that composed only 4% of the groundcover, indicating their high affinity with coarse, woody debris. Our results suggest that other forest features such as shade or litter layer also influence the distribution of ***Eumeces inexpectatus.*** Woody debris was available in HIB and BK (including some large-diameter logs), whereas few members of this species were captured in these treatment stands.

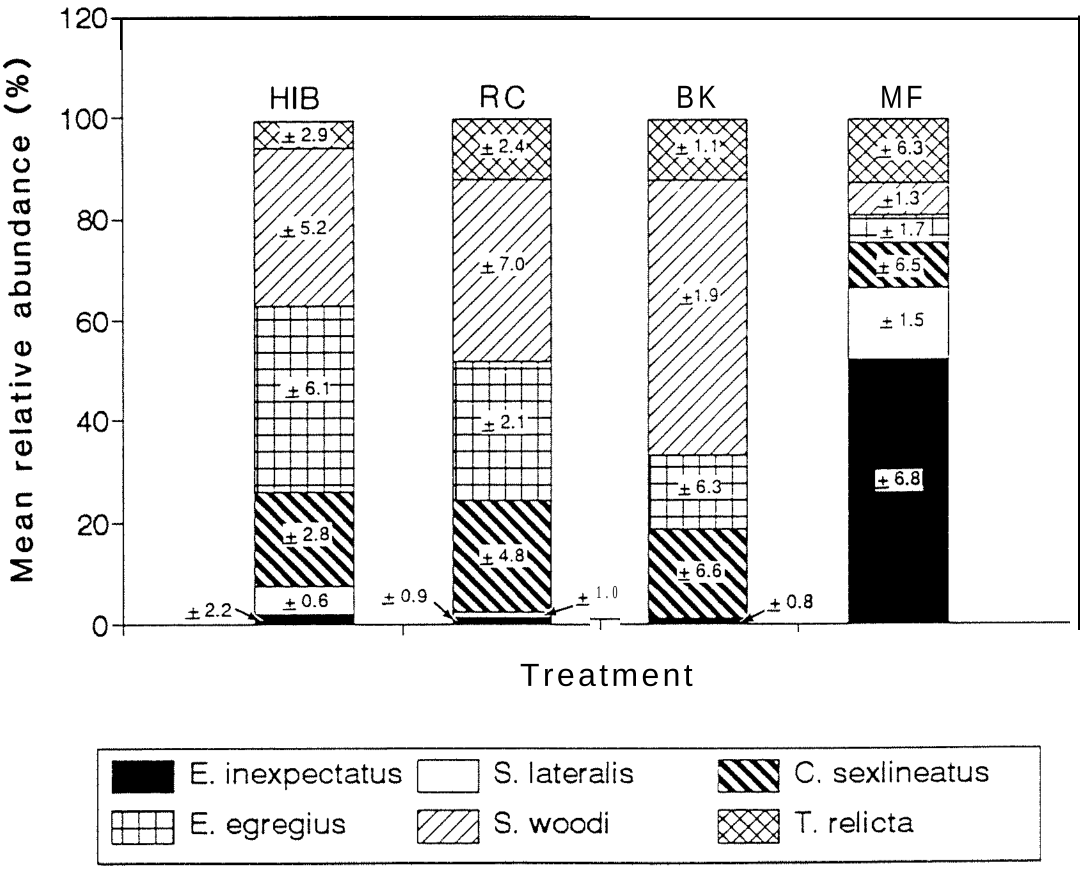

Figure 3. ***Mean relative abundance*** *of six commonly* ***trapped reptile species in high-intensity burn (HIB), roller-chopped (RC), and bracke-seeded (BK) treatments and mature forest (MF) in sand-pine scrub, Ocala National Forest, Florida***

Anderson and Tiebout (1993) suggest that piles of woody debris and the consequent reduced availability of bare ground may account for the reduced numbers of *Cnemidophorus sexlineatus* and ***Sceloporus*** *woodi* observed in young burn (which was salvage-logged and contained piles of woody debris) compared to a young clearcut (which had less woody debris). Their observation is not supported by our study. We detected no significant differences in numbers of either species among treatments with significantly higher levels of woody debris (HIB and BK) compared to minimal levels of woody debris (RC). But we did find a trend (p = 0.0977) of reduced numbers of these species and *Tantilla relicta* in burned stands.

Table 3. Horn's Index of Community Similarity (R_o)* for reptiles in three treatments (HB, RC, BK)** and mature forest (MF) in sand-pine scrub. Ocala National Forest. Florida.

	Burn (HIB)	Chop (RC)	Bracke (BK)
NIB			
RC	0.919		
BK	0.876	0.950	
MF	0.654	0.588	0.540

* *Values closer to 1.0 indicate greater community similarity between treatments.*
** *HIB = high-intensity burn; RC = roller-chopped, and BK = hracke-seeded*

Lizards may require some optimal amount of vegetation (shrub) complexity. Many members of the genus ***Sceloporus*** use shrubs as perch sites for basking (Lillywhite & North 1974) or ambushing prey (Fuentes 1976). Dense clumps of scrub oaks serve as refuge for ***Sceloporus*** *woodi* (Jackson 1973). This lizard may require patchy environments where it can dart among shrubs to capture prey (Mushinsky 1992).

Reptiles that require open-scrub conditions probably evolved in an environment where such conditions were most available (Campbell & Christman 1982*a*). Populations avoided regional extirpation by shifting across the landscape as large-scale, high-intensity disturbances created suitable habitat.

In a mirror image of the usual concept (Harris 1984), forest maturation historically served as the fragmenting agent of an otherwise extensive matrix of disturbance-maintained open scrub. This raises questions of optimal clearcut size, spatial arrangement, and connectivity that

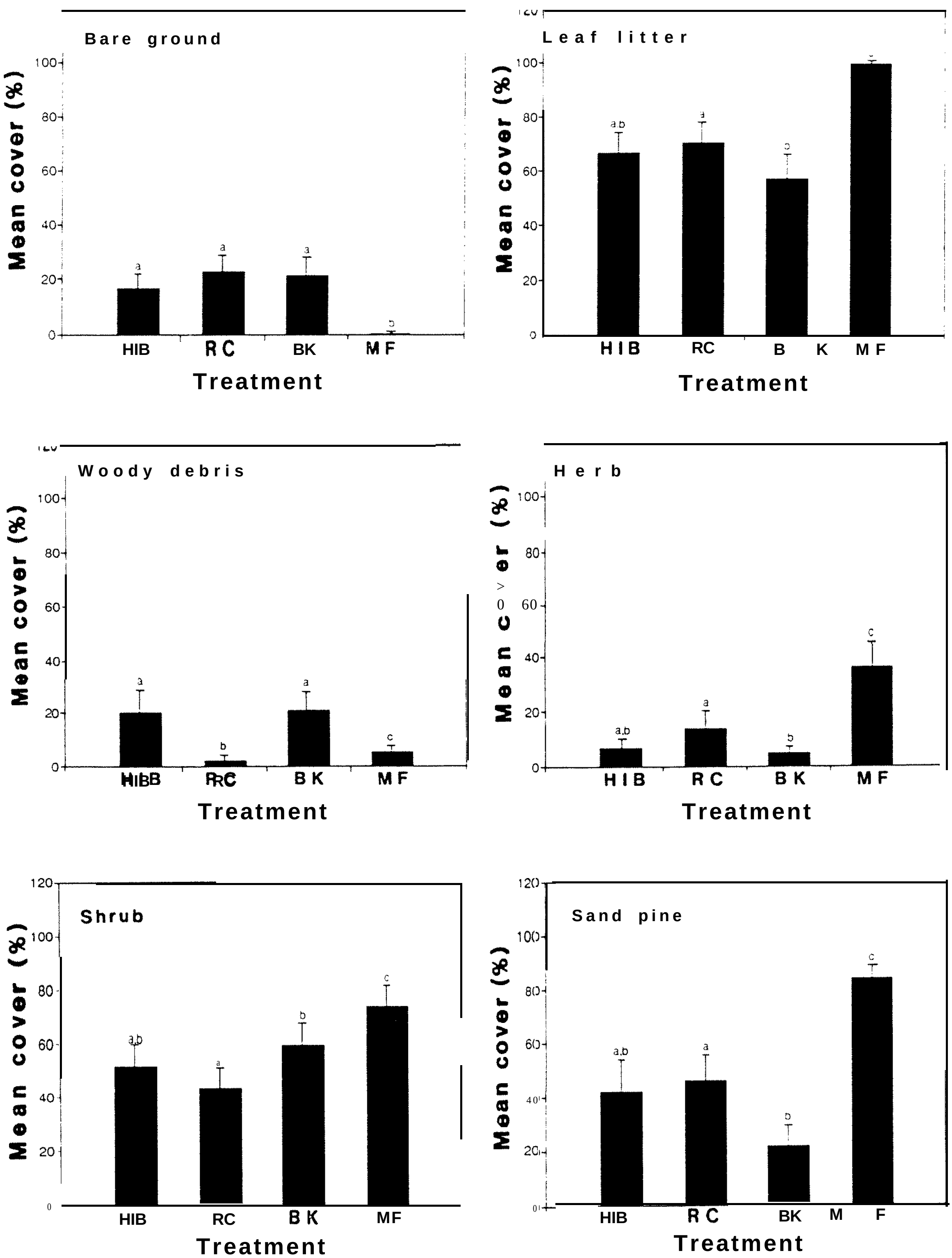

Figure 4. Mean percentage cover of bare ground, leaf litter, woody debris, herb, shrub, and sand pine in high-intensity burn (HIB), roller-chopped (RC), and bracke-seeded (BK) treatments and mature forest (MF) in sand-pine scrub, Ocala National Forest, Florida. Different letters denote significant differences among treatments ($p < 0.05$).

Table 4. Slope direction, r^2, and p-value of simple linear regression analyses using capture rate of six reptile species as dependent variables and percentage cover of bare ground, leaf litter, shrub, and pine canopy cover as the independent variables.

	Bare Ground			Leaf Litter			Shrub			Pine Canopy		
Species	*Slope*	r^2	*p-value*	*Slope*	r^2	*p-value*	*Slope*	4	*p-value*	*Slope*	r^2	*p-value*
Anolis carolinensis	+	0.16	0.1983		0.24	0.1025	NA	0.01	0.7145	–	0.17	0.1762
Cnemidophorus sexlineatus	+	0.68	0.0010	–	0.38	0.0331	–	0.27	0.0834	–	0.57	0.0047
Eumeces egregius	+	0.24	0.1026	–	0.21	0.1327		0.48	0.0120	–	0.31	0.0596
Eumeces inexpectatus		0.75	0.0003	+	0.73	0.0004	+	0.80	0.0001	+	0.62	0.0024
Sceloporus woodi	+	0.44	0.0182		0.54	0.0069	–	0.22	0.1260	–	0.75	0.0003
Tantilla relicta	+	0.16	0.1908	NA	0.04	0.2471	NA	0.05	0.4720	–	0.34	0.0458

NA = not available.

are quite distinct from traditional forest management paradigms (Franklin & Forman 1987). A patchwork pattern of age classes created by current harvesting practices could pose a barrier to the dispersal of some reptile species and impede metapopulation dynamics.

Low-traffic roadways may provide additional avenues for open-scrub reptile exchange and colonization among stands (Anderson & Tiebout 1993; personal observation). Even among open-scrub reptiles, however, roads of different surface types may serve as selective filters. Paved or clay roads could pose a barrier to sand-swimmers such as *Tantilla relicta*, *Neoseps reynoldsi*, and *Eumeces egregius* while serving as an artery through otherwise inhospitable habitat-such as mature forest-for species such as *Sceloporus woodi* or *Cnemidophorus sexlineatus.* Number of roads and proximity to recent clearcuts or natural disturbances embedded in mature forest could affect population densities of open-scrub reptile species.

Conclusions

Our data support the hypothesis that under well-managed circumstances the effects of clearcutting are sufficiently similar to high-intensity wildfire followed by salvage-logging so as to commend it as an acceptable silvicultural treatment. At least in the short term it does not appear to threaten any species of the sampled reptile community typical of open sand-pine scrub.

These results highlight the importance of disturbance and consequent changes in microhabitat structure and/or microclimatic conditions to which most of the common scrub-reptile species are adapted. Provision of conditions similar to those following natural high-intensity disturbance, regardless of the means, appears to be a critical factor in maintaining the integrity of reptile communities typical of the open sand-pine scrub landscape. Harvesting techniques, such as selection cutting, that are designed to maintain mature forest conditions would probably eliminate the microhabitat features that many open-scrub reptile species apparently require.

Forest maturation historically served as the fragmenting agent of an otherwise extensive matrix of recently disturbed open scrub. The current size, shape, and juxtaposition of clearcuts rather than harvest and regeneration practices may disrupt landscape processes of reptile dispersal and impede metapopulation dynamics.

Because of the high endemicity and stenotopic habitat requirements of scrub biota, our results have important conservation implications. The dependence of open-scrub reptiles upon the ecosystem process of high-intensity disturbance and consequent habitat features renders the implications of our study pertinent to other Florida scrubs, despite the uniquely distinguishing character of each. In addition, we suggest that high-intensity disturbance, regardless of the means, may be the critical factor in maintaining the biotic integrity of other fire-dependent ecosystems, as well.

The limited scope of this study suggests cautious interpretation of these results. No true controls (unsalvaged burns) were available, nor were we able to obtain pretreatment data. Also, because our trapping techniques were biased against some taxonomic groups of herpetofauna, such as large snakes, fossorial species, and tree frogs (Greenberg et al. 1994), effects on untrappable species remain unknown.

Further study is required to evaluate and improve ecosystem management for herpetofauna in conjunction with timber harvesting in sand-pine scrub. Study needs include evaluation of (1) unsalvaged burns (a truly "natural" disturbance); (2) effect of various snag densities left on site; (3) effect of varying quantities, sizes, and distribution of woody debris left on site; (4) long-term effects of clearcutting and site preparation techniques, both within a rotation and spanning several rotations; (5) clearcut size and configuration with special reference to animal movement through the landscape mosaic of spatially and temporally shifting habitat; and (6) effects of roads and road substrate on selectively facilitating or impeding species movement across the landscape.

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