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Long-term effects of prescribed fire on reptile and amphibian communities in Florida sandhill

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Long-Term Effects of Prescribed Fire on Reptile and Amphibian Communities in Florida

Sandhill

by

Neal Thomas Halstead

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Sciences
University of South Florida

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Long-Term Effects of Prescribed Fire on Reptile and Amphibian Communities in Florida Sandhill

Neal Thomas Halstead

ABSTRACT

I examined the effects of fire frequency on reptile and amphibian community composition in a periodically burned sandhill habitat in west-central Florida. Plots burned in 2003 had lower species richness, diversity, and evenness indices than plots that had not been burned during the previous six years. Community composition was different among plots burned at different times and followed a gradient of change that corresponded to the time since the last fire. *Aspidoscelis sexlineata* were the most abundant lizards in recently burned plots, while *Scincella lateralis* and *Plestiodon inexpectatus* were relatively more abundant in unburned plots. *Gopherus polyphemus* were least abundant in unburned plots. Community composition among plots was correlated with mean leaf litter cover and herbaceous ground cover. Mean percent cover of leaf litter and herbaceous vegetation responded to the time since the last fire. Fire indirectly affects community composition through changes in environmental variables, such as percent coverage of leaf litter and herbaceous vegetation.

Additionally, I examined annual variation in reptile and amphibian community composition over a period of four years in the mid 1980s and again in 2004. Differences existed in number of individuals captured, diversity, and evenness among years. Community composition was different between all consecutive years except 1986 and

1987. Number of individuals captured per year and annual differences in community composition were correlated with summer rainfall. The annual pattern of variation in community composition over time was no different in unburned experimental plots than in experimentally burned treatments. The power to detect such a difference is low, however, because of low replication. No apparent loss of species occurred between the 1980s and 2004, but the abundances of two non-native species were significantly higher in 2004 than in the 1980s. A third exotic species was documented at the site for the first time in 2004. Because of the increasing number of exotic reptiles and amphibians in Florida, the site is at risk of invasions of other species.

Fire Affects Herpetofaunal Community Composition Through Variation in Microhabitat Variables that Respond to the Time Since the Last Fire

Introduction

Florida high pine habitats, such as sandhills and clayhills, are characterized by having a natural fire return interval ranging from 1-10 years, which maintains 1) a sparse overstory of longleaf pine (*Pinus palustris*) or slash pine (*P. elliottii*), 2) a dense understory of herbaceous vegetation dominated by wiregrass (*Aristida stricta*), and 3) a low density midstory of hardwoods, usually turkey oak (*Quercus laevis*) (Myers, 1990). Less than 3% of the original high pine habitats in Florida remain, and the vast majority of the existing high pine is highly fragmented and degraded (Kautz, 1993; Myers, 1990). Approximately 75% of fragments are less than 40 ha in area and 30% are less than 8 ha. Many of these habitat fragments exist within a matrix of urban and suburban developments (Heuberger and Putz, 2003).

Ecological processes often are altered in fragmented habitats, including increased likelihood of invasion by non-native species, increased susceptibility to extinction for populations occurring within the fragment, and altered groundwater levels and nutrient input (Heuberger and Putz, 2003). Habitat fragmentation contributes to decreases in species richness and diversity across several taxa (Dickman, 1987; Kjoss and Litvaitis, 2001). Fire suppression in Florida sandhill habitats causes an increase in hardwood density, canopy cover and leaf litter depth and a concomitant decrease in herbaceous

understory vegetation (Brockway and Lewis, 1997; Kautz, 1993; Mushinsky, 1985, 1992; Myers, 1990).

The effects of prescribed fire on species richness and diversity have been studied in several ecological systems. Increased plant species richness and evenness occurs in longleaf pine communities subjected to moderate to high fire frequencies (Mehlman, 1992). Reintroduction of fire to longleaf pine sandhills at Eglin Air Force Base in northwest Florida increased species richness of plants, arthropods, herpetofauna, and birds (Provencher et al., 2003). Effects of fire on reptile and amphibian populations vary. For example, prescribed fire had significant negative short-term (1-2 years) effects on amphibian populations in South Carolina pine flatwoods (Schurbon and Fauth, 2003). Potential negative and positive effects of prescribed burning exist for amphibian populations, but more rigorous research is needed (Pilliod et al., 2003; Russell et al., 1999). Diversity of reptiles and amphibians on burned plots in a west-central Florida longleaf pine sandhill, however, was higher than on unburned plots (Mushinsky, 1985).

To enhance our understanding of the effects of fire on reptile and amphibian communities, I examined its effects on herpetofauna at the University of South Florida's (USF) Ecological Research Area (ERA) to answer the following questions. 1) What effects do different prescribed fire frequencies have on species richness and diversity indices? 2) What is the effect of different prescribed fire treatments on community composition? 3) Does community composition, by retaining species identities throughout analysis, show a different response to fire frequency than univariate richness, diversity, and evenness indices? I found that species richness, diversity, and evenness were all

higher in plots that were not burned recently, and that community composition of reptile and amphibian species was different among plots burned at different times.

Materials and Methods

Study Site

The USF ERA is approximately 245 ha of riverine swamp, pine flatwoods, and sandhill located in Hillsborough County, west-central Florida (28°05' N, 82°20' W). My study was conducted in approximately 13 ha of upland sandhill habitat with an overstory of *P. palustris*, a midstory of *Q. laevis*, and an understory dominated by *A. stricta*, numerous forb species, and scattered clumps of saw palmetto (*Serenoa repens*) (Mushinsky, 1985, 1992). Experimental burn plots (0.7 – 1.9 ha) with various prescribed fire frequencies were established in the 1970's in 12.4 ha of sandhill along the southern border of the ERA. Replication of four prescribed fire treatments (one-, two-, five- and seven-year fire return intervals) began in the mid-1980s, with two replicate plots in each treatment (Fig 1). All one-, two-, and five-year plots were most recently burned in November 2003. The seven-year plots were burned in 1998 (Schmidt, 2005). The two reference plots (CE and CW) have not been burned since 1965 or earlier (Mushinsky, 1985).

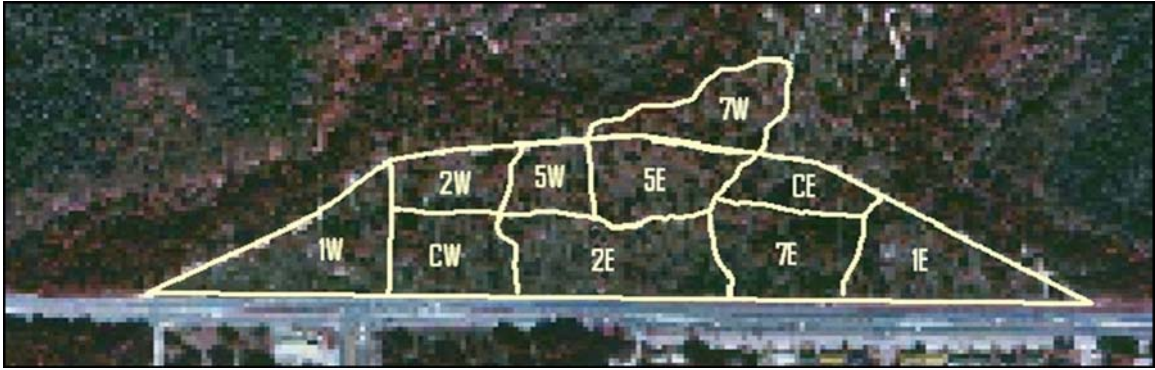


Figure 1. Map of USF ERA. Outlines indicate boundaries of experimental plots.

Experimental Design

Five drift fence/pitfall trap arrays were placed in each plot approximately 20-30 m apart with a random orientation (Mushinsky 1985, 1992). Each trap array consisted of a 6 m long by 0.5 m high drift fence (aluminum flashing), buried on edge 10-15 cm in the ground. At both ends of each drift fence, a 19 L plastic bucket was placed in the ground with the top edge at ground level. Holes were drilled in the bottom of the buckets to allow for drainage of rainwater, and pieces of Styrofoam or cellulose sponge (approximately 10 x 10 x 2 cm) were placed in each bucket as a shade cover/flotation device. A cover object of 2 m long by 0.5 m wide galvanized roofing material was placed on the ground within 5 m of each trap array (Mushinsky 1985, 1992).

In addition to pitfall traps, two funnel traps were placed along both sides of each drift fence near the center. Funnel traps were constructed from 0.6 cm mesh hardware cloth and consisted of a rectangular trap body (approximately 20 x 20 x 50 cm) with two funnels of the same material (approximately 30 cm diameter outer opening to 4 cm diameter inner opening) inserted into both ends of the trap body. Funnel traps were placed flush against the drift fence and buried approximately 2 cm into the soil to hold

them in place and provide a smooth transition into the funnel entrance. Pieces of wet cellulose sponge were placed inside the trap body to help prevent desiccation of organisms. Shade covers constructed from vinyl siding (approximately 60 x 30 cm) were placed over the top of each funnel trap body.

Microhabitat variables [percent cover of: bare sand, leaf litter, herbaceous vegetation, woody vegetation, and woody deadfall; woody stem density; leaf litter depth; leaf litter type (oak/pine); presence/absence of canopy cover; and canopy type (oak/pine)] were measured at the end of the sampling period in eight 1 m² quadrats, with one quadrat immediately adjacent to each pitfall and funnel trap and one quadrat 1 m from each pitfall and funnel trap at each trap array. Mean and standard deviation of each microhabitat variable was calculated over the eight quadrats for each trap array.

Trap arrays were checked several days per week from November 2003 through June 2005. All captured individuals were identified to species and marked individually by toe-clipping (Waichman 1992). Snakes were scale-clipped or marked with passive-integrated transponder (PIT) tags (AVID Technology, Tewksbury, MA).

Data Analysis

Because the purpose of this study was to examine patterns of change in community composition associated with prescribed fire, species abundances at each trap array were correlated with distance to the nearest wetland edge. Species that were significantly correlated with distance to wetland were removed from analysis. This exercise eliminated any potential effect on community composition of location of the experimental plots relative to the wetland.

Species richness was estimated using the observed count of number of species (S). Hill's diversity numbers N_1 and N_2 (Hill, 1973) were used to measure species diversity as recommended by Ludwig and Reynolds (1988). Simpson's index ($1-\lambda'$; Simpson, 1949) and the Shannon-Weaver index (H' ; Shannon and Weaver, 1949) also were calculated for diversity because of their common use in the literature and their relation to N_2 and N_1 , respectively. Evenness of relative abundances was measured with the modified Hill's ratio ($F_{2,1}$; Alatalo, 1981). Overall differences in index values among plots were tested using the randomization technique described by Solow (1993). When the randomization test indicated a difference in index values, pairwise comparisons were made by bootstrapping 95% confidence intervals for each fire frequency.

Nonparametric analyses of community composition, retaining all species identities, were performed using PRIMER (version 6; PRIMER-E Ltd, 2006). Similarity between sampling units (trap arrays, plots, and treatments) was calculated using the Bray-Curtis index (Bray and Curtis, 1957) on square-root transformed counts of species abundances. Square-root transformation was used to down-weight the effect of very abundant species (Clarke and Gorley, 2006).

Cluster analysis was performed using the unweighted complete linkage method (Ludwig and Reynolds, 1988) with a post-hoc randomization procedure to identify groups of plots with different community compositions, assuming no a priori structure among experimental plots. The post-hoc randomization test was accomplished through the SIMPROF routine in PRIMER. The SIMPROF procedure tests for significant differences in community composition at each node in the cluster dendrogram (Clarke and Gorley, 2006). Complete linkage was used as the clustering technique because the

goal of the procedure was to identify groups that were the most different. Because species-abundance patterns were nonlinear, nonmetric multidimensional scaling (NMS) was used for ordination, as recommended by Ludwig and Reynolds (1988).

Differences in community composition among plots, burn frequencies, and time since the last fire treatments were tested for by analysis of similarities (ANOSIM). ANOSIM is a nonparametric analogue to ANOVA in that it tests against the null hypothesis that there is no difference in community composition among treatments. The test statistic used in ANOSIM is R , which is a measure of the observed differences among rank similarities between treatments relative to the observed differences among rank similarities within treatments. Under the null hypothesis of no treatment effect, R would approach 0. If all rank similarities within treatments are greater than all rank similarities between treatments R is equal to 1. The null distribution of R is calculated in PRIMER by repeatedly randomly shuffling all sample labels and recalculating R for each permutation. A one-tailed test of significance is determined by calculating the proportion of randomized R statistics that are greater than the observed value of R . The ANOSIM test calculates the observed R statistic among all treatments (Global R), as well as R statistics between each pairwise combination of treatments. Like ANOVA, if the Global R statistic is not significant, then pairwise comparisons are ignored (Clarke and Warwick, 2001).

The existence of a directional change in community composition along a gradient of fire frequency treatments was determined by constructing a model matrix consisting of the distance in years between prescribed burns between all pairs of plots. The rank dissimilarities from the observed Bray-Curtis similarity matrix were correlated with the model matrix, using the RELATE function in PRIMER. Significance was determined

using a Monte Carlo randomization technique that repeatedly calculated the Spearman rank correlation of the observed Bray-Curtis similarity matrix with the model matrix for 999 permutations of randomly reassigned plot labels in the observed Bray-Curtis matrix (Clarke and Gorley, 2006). A similar model matrix was constructed to test for change in community composition following the pattern of years since the last fire.

Species that contributed to differences in community composition between different groups were identified using the similarity percentages (SIMPER) routine in PRIMER (Clarke and Gorley, 2006). Species that contributed most to the overall pattern of Bray-Curtis similarity were identified using a modified BIOENV procedure in PRIMER that calculated the Spearman rank correlation values between Bray-Curtis similarity values from progressively larger subsets of species and the Bray-Curtis similarity matrix from the full species set. Randomization tests that randomly shuffled plot labels and recalculated the Spearman rank correlation were used to determine significance of r_S for each number of species in the subset (Clarke and Warwick, 2001).

Microhabitat variables were normalized, and the BIOENV procedure in PRIMER was used to calculate the Spearman rank correlation between the Euclidean distance matrix (using various combinations of normalized variables) and the Bray-Curtis similarity matrix of transformed species abundances between all pairs of trap arrays. To account for potential covariation among microhabitat variables, principle components analysis was performed on the normalized microhabitat variables, and the BIOENV procedure was performed using the weights of trap arrays on each PC axis to produce Euclidean distance matrices. Mean values for each microhabitat variable were also calculated for each plot and fire frequency treatment and the above procedures were repeated for those scales of

analysis. The randomization test described above was used to determine significance for each combination of environmental variables (Clarke and Gorley, 2006). ANOSIM was used to test for differences in environmental variables among fire frequency treatments, and RELATE was used to test for directional change in microhabitat variables among fire frequency treatments.

Results

A total of 1415 individuals from 23 species were used for analysis (Table 1). Variation in species richness was not different among fire frequency treatments ($s^2 = 4.7$; $p = 0.380$). Diversity indices were higher in seven-year treatments and reference plots than plots burned in November 2003 ($p < 0.05$; Table 1). Within the group of recently burned plots, diversity was higher in two-year treatments than in five-year treatments, although the difference was not as great as the difference between recently burned and unburned plots. Evenness was higher in plots not burned recently than in plots burned in 2003 ($p < 0.05$; Table 1). Evenness was not different among plots of different fire frequencies burned in 2003.

Table 1. Number of individuals captured (N), species richness (S), and Hill's diversity (N_1 , N_2) and evenness ($F_{2,1}$) numbers with upper and lower 95% confidence interval limits for each fire frequency. Confidence intervals were not calculated for species richness because no difference was detected by a randomization test.

Fire Frequency (years)	N	S	N_1			N_2			$F_{2,1}$		
			Observed value	95% Confidence Interval		Observed value	95% Confidence Interval		Observed value	95% Confidence Interval	
				Lower	Upper		Lower	Upper		Lower	Upper
1	356	14	3.73	3.16	4.20	2.19	1.93	2.50	0.44	0.41	0.49
2	327	14	4.73	4.00	5.32	2.76	2.37	3.20	0.47	0.44	0.53
5	257	14	3.34	2.74	3.85	1.96	1.71	2.26	0.41	0.39	0.47
7	270	19	7.77	6.58	8.48	5.58	4.78	6.30	0.68	0.64	0.75
no fire	205	15	6.79	5.70	7.46	5.12	4.38	5.75	0.71	0.68	0.78

Community composition was different among fire frequency treatments and among plots with different times since the last fire (TSF). Cluster analysis in conjunction with the SIMPROF test revealed two groups of experimental plots with different community composition, those that were burned in November 2003 and plots that had not been recently burned, that differed in community composition ($p = 0.05$; Fig 2). A similar pattern was revealed by NMS (stress = 0.05; Fig 3), although the 7W plot appears to be more similar to the more recently burned plots.

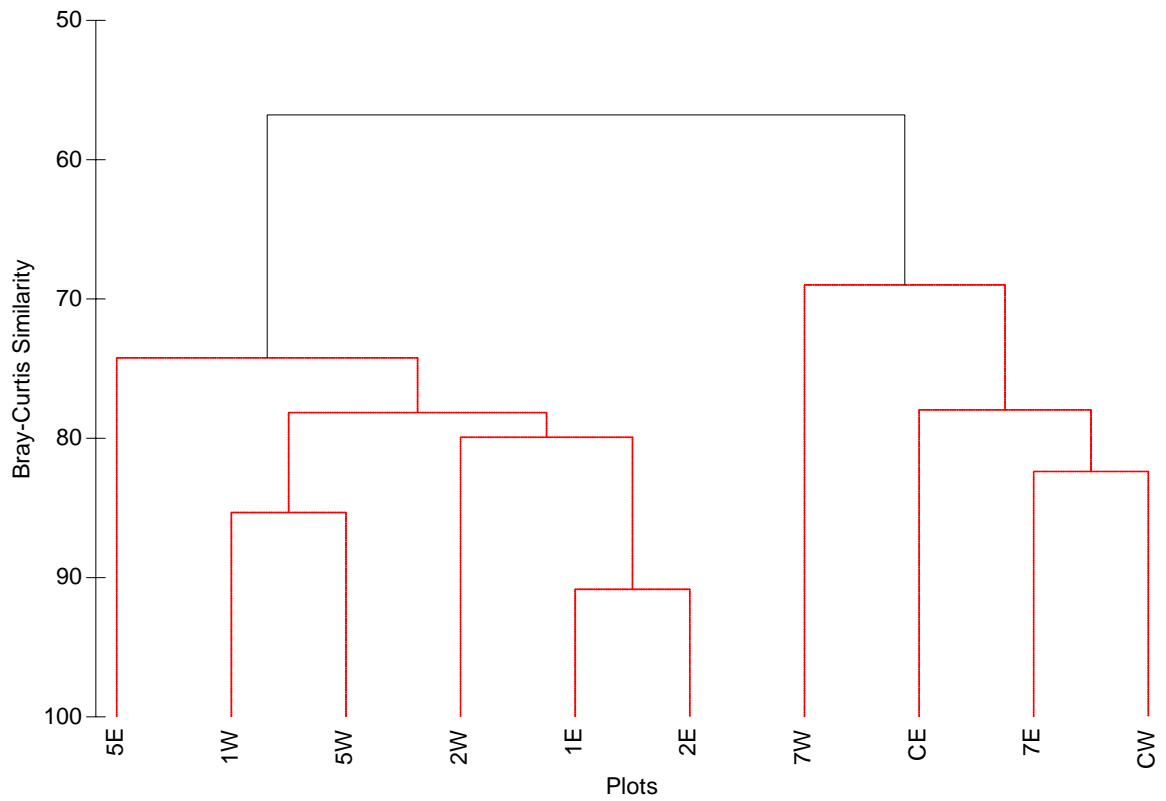


Figure 2. Cluster analysis dendrogram of experimental plots using the complete linkage method. Labels along the x-axis refer to plot designations. Solid black lines indicate significantly different clusters with $p \leq 0.05$.

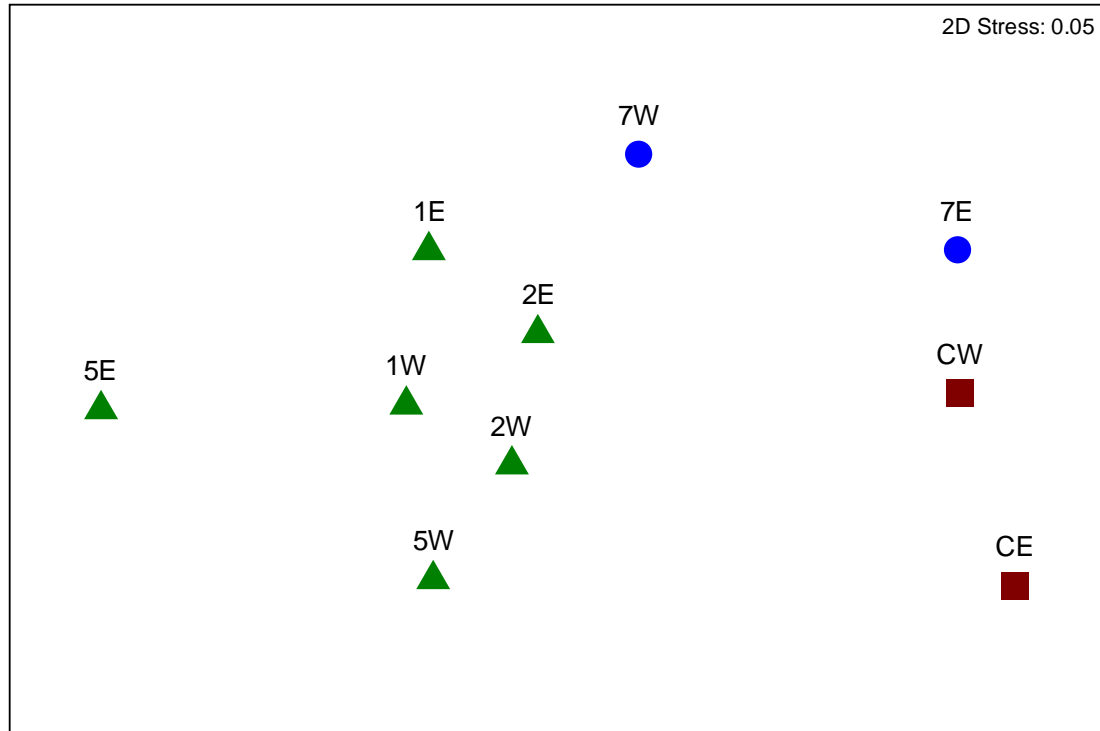


Figure 3. Nonmetric multidimensional scaling plot of experimentally burned plots. Labels are plot designations. Symbols refer to the time since the last fire (triangles = 1 year since fire; circles = 7 years since fire; squares = unburned reference plots). Stress measures the goodness-of-fit of the data to the pattern; lower stress indicates a better fit.

The separation between TSF treatments was significant (Global $R = 0.807$, $p = 0.002$) when accounting for variation among plots within TSF treatments, using a two-way nested ANOSIM with plots nested in time since fire treatments. Pairwise tests showed differences between plots burned in November 2003 and reference plots. Community composition in plots in the seven-year treatment was not different from plots burned in 2003 or from unburned reference plots (Table 2). Significance tests from randomization had low power to detect real differences because of the low number of replicates in each

fire frequency treatment. Because the two-way nested ANOSIM showed no difference in similarity among trap arrays in replicate plots within each TSF treatment (Global R = -0.007, $p = 0.52$), a one-way ANOSIM could be performed using trap arrays as replicates without risk of pseudoreplication (Clarke and Gorley, 2006). This reduced the overall separation among TSF treatments (Global R = 0.398, $p = 0.001$), but revealed significant pairwise differences in community composition between all TSF treatments (Table 2).

Table 2. Pairwise R values between plots with different time since the last fire from a two-way nested ANOSIM (replicate plots nested in TSF treatments); and from a one-way ANOSIM treating trap arrays as replicate samples.

Comparison	2-way nested ANOSIM, plots within time since the last fire treatments		1-way ANOSIM, trap arrays as replicates	
	R	p	R	p
1 vs. 7	0.656	0.071	0.335	0.001
1 vs. no fire	1	0.036	0.523	0.001
7 vs. no fire	1	0.333	0.185	0.020

Differences in community composition among fire frequency treatments were also significant, but less distinct than TSF treatments (two-way nested ANOSIM; Global R = 0.560; $p = 0.011$). As before, low replication resulted in pairwise comparisons without sufficient power to detect differences between fire frequency treatments (Table 3). Because community composition among trap arrays in plots within fire frequency treatments was not different (Global R = -0.018, $p = 0.587$), a one-way ANOSIM was performed using trap arrays as samples. Differences in community composition among fire frequency treatments were significant in the one-way analysis (Global R = 0.271, $p =$

0.001). Community composition was different among trap arrays in fire frequency treatments burned at different times (Table 3). Fire frequency treatments burned in November 2003 did not have different community composition (Table 3). Changes in community composition among plots were correlated with the pattern of differences in years between fire ($r_s = 0.559$, $p = 0.001$) as well as the pattern of differences in TSF ($r_s = 0.69$, $p = 0.003$).

Table 3. Pairwise R values between plots with different fire frequency treatments from a two-way nested ANOSIM (replicate plots nested in fire frequency treatments); and from a one-way ANOSIM treating trap arrays as replicate samples.

Comparison	2-way nested ANOSIM, plots within fire frequency treatments		1-way ANOSIM, trap arrays as replicates	
	R	p	R	p
1 vs. 2	-0.25	1.000	-0.076	0.911
1 vs. 5	0.25	0.667	0.034	0.259
1 vs. 7	0.75	0.333	0.361	0.001
1 vs. no fire	1	0.333	0.552	0.001
2 vs. 5	0	1.000	0.053	0.212
2 vs. 7	0.5	0.333	0.277	0.005
2 vs. no fire	1	0.333	0.506	0.001
5 vs. 7	0.5	0.333	0.337	0.002
5 vs. no fire	1	0.333	0.485	0.001
7 vs. no fire	1	0.333	0.185	0.030

The relative abundances of three lizard species, the six-lined racerunner, *Aspidoscelis sexlineata*, the southeastern five-lined skink, *Plestiodon inexpectatus*, and the ground skink, *Scincella lateralis*, and one turtle, the gopher tortoise, *Gopherus polyphemus*, accounted for the majority of the dissimilarity in community composition between TSF treatments. Plots burned in 2003 had relatively higher abundances of *A. sexlineata* and

lower abundances of *P. inexpectatus* and *S. lateralis* than plots that had not burned recently. Long-unburned reference plots had lower abundances of *G. polyphemus* than all other plots. Several other species were abundant on all plots but contributed less to the dissimilarity in community structure between TSF treatments, including the black racer, *Coluber constrictor*, the southern leopard frog, *Lithobates sphenoccephalus*, the green anole, *Anolis carolinensis*, and the ringneck snake, *Diadophis punctatus* (Table 4).

Table 4. Mean number of individuals captured per plot for eight species contributing to differences between the three time since the last fire treatments.

Species	Years Since The Last Fire		
	1	7	40
<i>Anolis carolinensis</i>	3.3	1.5	2.5
<i>Aspidoscelis sexlineata</i>	100.8	42	27
<i>Coluber constrictor</i>	12.8	15.5	10
<i>Diadophis punctatus</i>	2.2	3.5	3.5
<i>Gopherus polyphemus</i>	4.3	4	1
<i>Lithobates sphenoccephala</i>	13.3	16.5	5.5
<i>Plestiodon inexpectatus</i>	3.7	13.5	29
<i>Scincella lateralis</i>	11	27.5	18

Bray-Curtis similarity matrices calculated from the abundances of *Aspidoscelis sexlineata* ($r_S = 0.76$, $p = 0.004$) alone or *Plestiodon inexpectatus* ($r_S = 0.719$, $p = 0.01$) alone were both correlated with the Bray-Curtis similarity matrix from the full species set. Subsets of two or more species also produced significant correlations with the Bray-Curtis similarity matrix from the full species set, although different combinations of species gave similar results. In general, the best combinations included, in addition to at least one of the first two species, *Scincella lateralis*, *Lithobates sphenoccephalus*, *Diadophis punctatus*, *Rhadinaea flavilata*, and *Gopherus polyphemus*.

Mean percent leaf litter cover at each trap array produced a Euclidean distance matrix that had an $r_S = 0.404$ ($p = 0.01$) with the Bray-Curtis similarity matrix of transformed abundances. Inclusion of additional microhabitat variables decreased the Spearman rank correlation. Performing a principle components analysis to account for covariation among the normalized microhabitat variables did not increase the rank correlation when principle component axes were used to calculate Euclidean distances in the BIOENV procedure.

Bray-Curtis similarities of community composition among plots were correlated with a Euclidean distance matrix produced from mean percent herbaceous ground cover in each plot ($r_S = 0.795$, $p = 0.01$). No combination of principle component axes produced Euclidean distance matrices with a higher Spearman rank correlation than that produced from herbaceous ground cover alone.

Leaf litter cover was not different among fire frequency treatments (Global $R = 0.21$, $p = 0.138$) when plots were nested in fire frequency treatments in a 2-way nested ANOSIM. However, leaf litter cover was different among plots burned at different times (Global $R = 0.584$, $p = 0.032$) in a 2-way nested ANOSIM. Pairwise comparisons had low power, but indicated that plots burned in 2003 were different from reference plots (Table 4). Leaf litter cover among plots within TSF treatments was not different (Global $R = 0.073$, $p = 0.136$). A one-way ANOSIM using trap arrays as replicates indicated that leaf litter cover was different among plots with different times since the last fire (Global $R = 0.324$, $p = 0.001$), and that leaf litter cover was different between recently burned plots and plots not burned in 2003 (Table 5). The same pattern of differences among plots burned at different times but not among fire frequency treatments was true for one-way

ANOSIM of herbaceous ground cover among plots, as well as for the Euclidean distance matrices for any combination of environmental variables that was significantly correlated with the Bray-Curtis similarities among plots.

Table 5. Pairwise R values between plots with different fire frequency treatments from a two-way nested ANOSIM (replicate plots nested in fire frequency treatments) on Euclidean distances calculated from normalized mean percent leaf litter cover; and from a one-way ANOSIM treating trap arrays as replicate samples.

Comparison	2-way nested ANOSIM, plots within time since the last fire treatments		1-way ANOSIM, trap arrays as replicates	
	R	p	R	p
1 vs. 7	0.271	0.250	0.195	0.020
1 vs. no fire	0.938	0.036	0.500	0.001
7 vs. no fire	-0.5	1.000	0.035	0.240

Aspidoscelis sexlineata was positively correlated with bare sand and herbaceous vegetation, and negatively correlated with leaf litter, woody deadfall, and canopy cover, and leaf litter depth (Table 6). *Plestiodon inexpectatus* and *Scincella lateralis* were negatively correlated with bare sand and herbaceous vegetation, and positively correlated with leaf litter cover and depth, woody deadfall cover, and canopy cover (Table 6). *Gopherus polyphemus* was positively correlated with herbaceous vegetation and negatively correlated with leaf litter cover (Table 6). Most environmental variables were significantly correlated with other environmental variables, with the exception of woody vegetation cover, leaf litter composition, and canopy composition.

Table 6. Spearman rank correlations of number of individuals captured with environmental variables at each trap array for eight species associated with changes in community composition. Asterisks indicate correlations that are significant at $p = 0.05$.

Species		Bare sand cover	Leaf litter cover	Herbaceous ground cover	Woody deadfall cover	Canopy cover
<i>Anolis carolinensis</i>	r_s	0.057	0.065	-0.143	0.115	0.159
	p	0.693	0.652	0.322	0.426	0.271
<i>Aspidoscelis sexlineata</i>	r_s	.640(*)	-.743(*)	.509(*)	-.312(*)	-.424(*)
	p	0.000	0.000	0.000	0.027	0.002
<i>Coluber constrictor</i>	r_s	0.025	-0.021	-0.100	-0.122	-0.063
	p	0.862	0.887	0.489	0.398	0.663
<i>Diadophis punctatus</i>	r_s	0.110	-0.062	-0.163	-0.069	-0.153
	p	0.447	0.670	0.257	0.635	0.289
<i>Plestiodon inexpectatus</i>	r_s	-.533(*)	.579(*)	-.426(*)	.383(*)	.346(*)
	p	0.000	0.000	0.002	0.006	0.014
<i>Gopherus polyphemus</i>	r_s	0.138	-.362(*)	.422(*)	-0.053	-0.182
	p	0.340	0.010	0.002	0.712	0.206
<i>Lithobates sphenoccephala</i>	r_s	0.071	-0.186	0.128	-0.074	-0.057
	p	0.623	0.195	0.377	0.609	0.694
<i>Scincella lateralis</i>	r_s	-.306(*)	.476(*)	-.365(*)	.303(*)	.327(*)
	p	0.031	0.000	0.009	0.032	0.020

Discussion

Herpetofaunal community composition in Florida sandhill habitat responds to fire as an indirect effect of the response of microhabitat variables to the time since the last fire as well as the frequency with which plots are burned. It is difficult, however, to try to determine the exact mechanisms by which plant species are responding to fire because fire frequency and the time since the last fire are not independent variables. The time since the last fire can capture much of the variation associated with fire frequency because a plot that is burned annually will never have more than one year without fire, assuming prescribed burns occur on schedule, while plots with longer burn intervals can

have several years without fire. The frequency with which a plot is burned as well as the time of year during which the burn occurs, also can greatly influence the physical structure of sandhill habitat by permitting the persistence of greater or lower densities of hardwoods, herbaceous plants, leaf litter, and woody debris (Drewa et al, 2002, 2006; Glitzenstein et al, 1995, 2003). Obviously, both the time since the last fire and the frequency of fire can have significant effects on the physical structure of the habitat. It is unlikely that a plot burned every year, with a greater proportion of bare sand and herbaceous ground cover, and a plot burned every seven years, with greater leaf litter cover, canopy cover, and hardwood density, would have the same physical structure one year after a fire.

The one- and two-year fire frequency treatments were not burned between June 2000 and November 2003, which also confounds interpretation of the results presented here. A period of three years without fire has the potential to significantly alter the plant composition of the understory in longleaf pine systems. Understory vegetation was shrub-dominated in treatments with fire return intervals of three to four years as opposed to an herbaceous-dominated understory with intervals of one to two years in South Carolina flatwoods (Glitzenstein et al, 2003). Additionally, a switch from growing season fires in June to dormant season fires in November could also have affected the shrub layer in each burned plot. Dormant season fires have been associated with increases in hardwood densities in longleaf pine-dominated communities (Drewa et al, 2002, 2006; Glitzenstein et al, 1995).

The percent cover of woody vegetation near trap arrays was not different among fire frequency treatments 18 months after the November 2003 burn. The number of woody

stems resprouting from underground organs can reach pre-fire conditions within 12 months of growing season fires (Olson and Platt, 1995), supporting the hypothesis that the delay in prescribed burning may have altered the understory plant community in the one- and two-year fire frequency treatments. Historical data on densities of woody vegetation at the site are not available to test this hypothesis; the area of bare sand, however, decreased with increasing fire return intervals in 2005, matching patterns that existed in the 1980s (Mushinsky and Gibson, 1991). Furthermore, woody vegetation represented less than 8 percent of ground level vegetation in all fire frequency treatments in 2005, as opposed to bare sand and herbaceous vegetation which accounted for up to 25 and 50 percent cover, respectively. Therefore, whether the long history of frequent burning has maintained the structural composition of the understory among fire frequency treatments, or the three year delay in burning has allowed woody vegetation to significantly increase in the one and two year treatments, remains uncertain.

Community composition was different among fire frequency treatments; this difference, however, was more distinct among plots burned at different times. Analysis of similarities revealed that treatments defined by the time since the last fire had greater separation than fire frequency treatments, although it is not possible to determine if the difference in the ANOSIM global R statistics from these two tests is significant. The same is true of the rank correlations of changes in Bray-Curtis dissimilarity with the patterns expected from directional change in composition across fire frequency or time since the last fire treatments. Furthermore, there was no difference in composition among plots of different fire frequencies that were burned at the same time. This finding provides further evidence that reptiles and amphibians may be responding more to

changes in the environment associated with the time since the last fire rather than the frequency of the fire itself. Because the most recently burned plots included the three most frequently burned treatments, however, it was not possible to distinguish differences in community composition as a function of fire frequency or time since the last fire separately. Further monitoring of both the herpetofaunal communities and the structural composition of the plots associated with plant communities needs to continue to capture variation associated with different experimentally burned treatments at various stages of post-burn succession. It is also important that prescribed burns occur on schedule and that fire frequency treatments are maintained.

Microhabitat variables are directly affected by fire frequency (Brockway and Lewis, 1997; Kautz, 1993; Mushinsky, 1985, 1992; Myers, 1990), although the data presented in this paper and others suggest that at least some microhabitat variables are responding to the time since the last fire (Glitzenstein et al, 2003; Guerin, 1993; Lemon, 1949; Olson and Platt, 1995). Percent cover of leaf litter alone accounted for 40% of the variation observed in community composition at individual trap arrays. At the plot level, cover of herbaceous vegetation explained nearly 80% of the variation in community composition. At this study site, composition of environmental variables was different among plots burned recently and plots not burned recently, but not among fire frequency treatments.

Lizard abundances accounted for the largest portion of the variation in community structure among treatments. Species have varied responses to these changes in microhabitat, but lizards respond most strongly to changes in ground cover (Mushinsky and Gibson, 1991; Table 6). Vegetation variables have been identified as important in structuring lizard communities in other systems (Dickman, 1987; Jellinek et al, 2004).

Six-lined racerunner, *Aspidoscelis sexlineata*, abundance responded positively to recently burned treatments that had little leaf litter cover and woody deadfall and more bare sand and herbaceous vegetation (Table 6). Orthopterans are a common prey item of adult racerunners, while juveniles tend to feed on small, cryptic, plant-dwelling arthropods (Paulissen, 1987). Arthropod abundance data were not collected during this study, but it is likely that the increased herbaceous cover in the most recently burned plots is also associated with an increase in the preferred prey items of this lizard. Insect (especially orthopteran) abundance and levels of herbivory increase near the edges (10 m from the edge) relative to the interior (500 m from the edge) of recently burned plots as vegetation recovers (Knight and Holt, 2005). Plots in this study were comparatively small (~1 ha), so it is likely that edge effects on insect herbivory occurred throughout the entire area of each plot. An increased area of bare sand in these treatments is also likely to improve the ability of racerunners to both see and pursue prey (Mushinsky, 1992). Inferences about relative abundances between treatments must be made cautiously, however, because increases in the area of bare sand may also increase the ability of lizards to encounter trap arrays. Analysis of mark-recapture data at the site would identify any differences in capture probabilities associated with changes in microhabitat variables.

Southeastern five-lined skinks, *Plestiodon inexpectatus*, and ground skinks, *Scincella lateralis*, were correlated with the same variables as *A. sexlineata*, but in the opposite direction (Table 6), and were more abundant in plots not burned recently. Both of these species are diurnal insectivorous lizards that rely strongly on chemosensory cues for prey recognition (Cooper et al, 2000; Cooper and Hartdegen, 1999) and actively forage for prey, often under litter (Mushinsky, 1992; Vitt and Cooper, 1986).

Gopher tortoises, *Gopherus polyphemus*, respond positively to the presence of herbaceous vegetation (Table 6) and were abundant in plots with less canopy cover and higher herbaceous ground cover. Gopher tortoises feed primarily on herbaceous species from several plant families (Macdonald and Mushinsky, 1988; Mushinsky and Gibson, 1991; Mushinsky et al, 2003). Open areas cleared by recent fire increase available forage for gopher tortoises by supporting greater species richness and biomass production of herbaceous plants (Brockway and Lewis, 1997; Platt et al, 2006), and also provide tortoises with sites for thermoregulation and egg deposition (Diemer, 1986). Consequently, increases in canopy cover and loss of herbaceous ground cover from a lack of prescribed fire reduce habitat quality for gopher tortoises (McCoy et al, 2006; Mushinsky and McCoy, 1994).

The lower degree of separation between individual trap arrays relative to plots or burn frequency treatments also suggests that communities at these smaller spatial scales are responding to differences in microhabitats that may exist within burn treatments. Other herpetofaunal species respond to different combinations of environmental cues than lizards or tortoises, or may be responding to similar cues at different spatial scales than the one measured (Table 6). The variation among species in responses to microhabitat variables supports recommendations to implement prescribed fire regimes that maximize heterogeneity in the structural components of the sandhill plant community in order to maximize diversity of reptile and amphibian species, as well as that of other taxonomic groups (Mushinsky, 1992; Mushinsky and Gibson, 1991; Van Lear et al, 2005).

Richness, diversity, and evenness indices did not have the discriminatory ability to distinguish differences in community composition between seven-year fire frequency

treatments and reference plots. These indices, however, revealed differences in the species-abundance patterns among plots burned in November 2003 that the compositional analyses did not detect. While diversity indices may more accurately describe species-abundance distributions, compositional analyses that retain species identities can be more sensitive in identifying differences among treatments with similar species-abundance distributions but different ranks of species abundance.

Annual Variation in Herpetofaunal Community Composition in a Periodically Burned Florida Sandhill

Introduction

Florida high pine habitats, such as sandhills and clayhills, are characterized by having a natural fire return interval ranging from 1-10 years, which maintains 1) a sparse overstory of longleaf pine (*Pinus palustris*) or slash pine (*P. elliottii*), 2) a dense understory of herbaceous vegetation dominated by wiregrass (*Aristida stricta*), and 3) a low density midstory of hardwoods, usually turkey oak (*Quercus laevis*) (Myers, 1990). Less than 3% of the original high pine habitats in Florida remain, and the vast majority of the existing high pine is highly fragmented and degraded (Kautz, 1993; Myers, 1990); approximately 75% of fragments are less than 40 ha in area and 30% are less than 8 ha. Many of these habitat fragments exist within a matrix of urban and suburban developments (Heuberger and Putz, 2003).

Ecological processes often are altered in fragmented habitats, including increased likelihood of invasion by non-native species, increased susceptibility to extinction for populations occurring within the fragment, and altered groundwater levels and nutrient input (Heuberger and Putz, 2003). Fire suppression in Florida sandhill habitats causes an increase in hardwood density, canopy cover and leaf litter depth and a concomitant decrease in herbaceous understory vegetation (Brockway and Lewis, 1997; Kautz, 1993; Mushinsky, 1985, 1992; Myers, 1990).

The effects of prescribed fire on species richness and diversity have been studied in several ecological systems. Reintroduction of fire to longleaf pine sandhills at Eglin Air Force Base in northwest Florida increased species richness of plants, arthropods, herpetofauna, and birds (Provencher et al., 2003). Diversity of reptiles and amphibians on burned plots in a west-central Florida longleaf pine sandhill was higher than on unburned plots in the early 1980s (Mushinsky, 1985). In 2004-5, however, diversity and evenness of reptile and amphibian communities were higher in plots that were not recently burned at the same study site (Halstead, in press).

To better understand the long-term effects of fire on reptile and amphibian communities, I examined herpetofaunal community composition at the University of South Florida's (USF) Ecological Research Area (ERA) to answer the following questions. 1) Is community composition constant over time? 2) If community composition varies over time, what environmental factors may affect it? 3) Does prescribed fire maintain a stable community composition? I found annual variation in community composition was correlated with summer rainfall. Fire frequency affects community composition, but the pattern of change in community composition over time is not different between experimentally burned plots and unburned reference plots.

Materials and Methods

Experimental Design

Experimentally burned plots (~ 0.5 – 1 ha) were established in an approximately 12 ha portion of longleaf pine sandhill in the University of South Florida's (USF) Ecological Research Area (ERA) in the mid-1970s. Originally, there were 11 experimental plots

with fire frequencies ranging from one- to nine-year fire return intervals, and two unburned reference plots (Fig 4). The experimental design was altered in 1982, combining plots and replicating fire frequency treatments so that there were eight experimental plots with two replicates of one-, two-, five- and seven-year fire return intervals. The two unburned reference plots, portions of both one-year plots, both five-year plots, and one seven-year plot remained unchanged (see Fig 1).

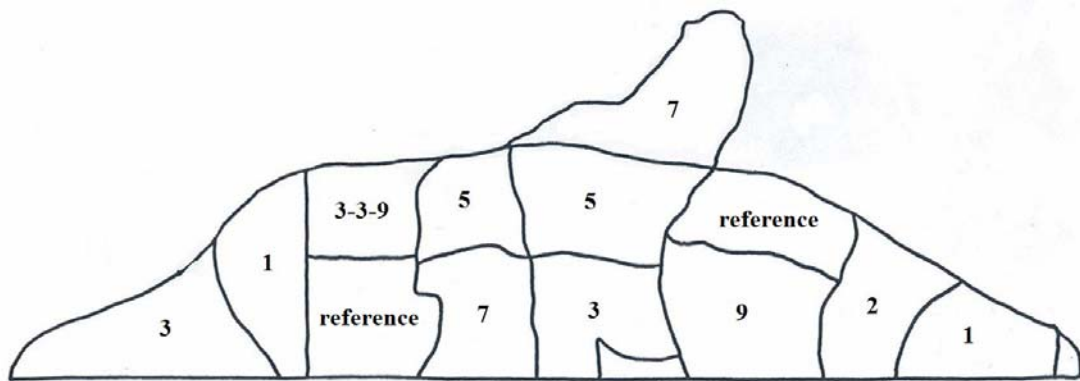


Figure 4. Map of experimentally burned plots in the USF ERA during the 1980s.

Numbers refer to fire return interval (years).

Five drift fence/pitfall trap arrays were placed in each plot approximately 20-30 m apart with a random orientation (Mushinsky 1985, 1992). Each trap array consisted of a 6 m long by 0.5 m wide drift fence (aluminum flashing), buried on edge 10-15 cm in the ground. At both ends of each drift fence, a 19 L plastic bucket was placed in the ground with the top edge at ground level. Holes were drilled in the bottom of the buckets to allow for drainage of rainwater, and pieces of Styrofoam or cellulose sponge (approximately 10 x 10 x 2 cm) were placed in each bucket as a shade cover/flotation

device. A cover object of 2 m long by 0.5 m wide galvanized roofing material was placed on the ground within 5 m of each trap array (Mushinsky 1985, 1992).

Trap arrays were checked several days per week from January 1984 through December 1987, and from January through December 2004. All captured individuals were identified to species and marked individually by toe-clipping (Waichman 1992). Snakes were scale-clipped or marked with passive-integrated transponder (PIT) tags (AVID Technology, Tewksbury, MA).

Data Analysis

Number of individuals captured per year was tested with a Kruskal-Wallis test, followed by pairwise Kolmogorov-Smirnov tests. Species richness was estimated using the observed count of number of species (S) and rarefaction (Hurlbert, 1971). Hill's diversity numbers N_1 and N_2 (Hill, 1973) were used to measure species diversity as recommended by Ludwig and Reynolds (1988). Simpson's index ($1-\lambda'$; Simpson, 1949) and the Shannon-Weaver index (H' ; Shannon and Weaver, 1949) were also calculated for diversity because of their common use in the literature and their relation to N_2 and N_1 , respectively. Evenness of relative abundances was measured with the modified Hill's ratio ($F_{2,1}$; Alatalo, 1981). Significant variation among index values was determined using the randomization technique described by Solow (1993). When differences among index values were suggested, 95% confidence intervals were bootstrapped around the index of interest for each year.

Nonparametric analyses of community composition were performed using PRIMER (v6, PRIMER-E, Ltd., 2006). Similarity between sampling units (trap arrays, plots, and

treatments) was calculated using the Bray-Curtis index (Bray and Curtis, 1957) on square-root transformed counts of species abundances. Square-root transformation was used to down-weight the effect of very abundant species (Clarke and Gorley, 2006).

Cluster analysis was performed using the unweighted complete linkage method (Ludwig and Reynolds, 1988) with a post-hoc randomization procedure to identify groups of plots with different community compositions. The post-hoc randomization test was accomplished through the SIMPROF routine in PRIMER. The SIMPROF procedure tests for significant differences in community composition at each node in the cluster dendrogram (Clarke and Gorley, 2006). Complete linkage was used as the clustering technique because the goal of the procedure was to identify groups that were the most different. Nonmetric multidimensional scaling (NMS) was used for ordination, as recommended by Ludwig and Reynolds (1988).

Analysis of similarities (ANOSIM) was performed to test for differences in community composition among years. ANOSIM is a nonparametric analogue to ANOVA in that it tests against the null hypothesis that there is no difference in community composition among treatments. The test statistic used in ANOSIM is R , which is a measure of the observed differences among rank similarities between treatments relative to the observed differences among rank similarities within treatments. Under the null hypothesis of no treatment effect, R would be close to 0. If all rank similarities within treatments are greater than all rank similarities between treatments R is equal to 1. The null distribution of R is calculated in PRIMER by repeatedly randomly shuffling all sample labels and recalculating R for each permutation. A one-tailed test of significance is determined by the calculating the proportion of randomized R statistics

that are greater than the observed value of R. The ANOSIM test calculates the observed R statistic among all treatments (Global R), as well as R statistics between each pairwise combination of treatments. Like ANOVA, if the Global R statistic is not significant, pairwise comparisons are ignored (Clarke and Warwick, 2001).

Species that contributed to differences in community composition between different groups were identified using the similarity percentages (SIMPER) routine in PRIMER (Clarke and Gorley, 2006). Species that contributed most to the overall pattern of Bray-Curtis similarity were identified using a modified BIOENV procedure in PRIMER that calculated the Spearman rank correlation values between Bray-Curtis similarity values from progressively larger subsets of species and the Bray-Curtis similarity matrix from the full species set. Randomization tests that randomly shuffled plot labels and recalculated the Spearman rank correlation were used to determine significance of r_s for each number of species in the subset (Clarke and Warwick, 2001). The BIOENV procedure in PRIMER was used to correlate the pattern of similarities in community composition with summer rainfall (Clarke and Gorley, 2006).

A further step in the analysis of long-term changes in community composition was to determine if the pattern of annual change in community composition was different in unburned plots than in burned plots. For this test, a second-stage analysis was performed. Second-stage analysis accounted for the main effect of yearly variation by calculating a Spearman rank correlation matrix of the pattern of annual change in Bray-Curtis similarity values for each replicate (Clarke et al, 2006). An NMS plot of these correlation values was then constructed to show the second-stage pattern. Replicates located close together on the NMS indicated that those replicates shared a similar pattern of annual

variation in community composition (Clarke et al, 2006). ANOSIM of the second-stage correlation matrix was used to formally test for differences in pattern of annual change in community composition among treatments. Second-stage analysis was also performed in a reversed direction that constructed a correlation matrix of the pattern of change in community composition among fire frequency treatments for each year. No formal test for differences among years was possible for this analysis because years were not replicated. Second-stage analyses were only performed for experimental plots that remained (at least in part) unchanged between the two sampling periods.

Results

The number of individuals captured per plot was higher in 2004 than in all other years ($p \leq 0.001$) and higher in 1985 than in 1984 ($p = 0.020$), 1986 ($p = 0.017$) and 1987 ($p = 0.009$; Table 7). Summer rainfall (May through September) was significantly correlated with number of individuals captured per plot ($R^2 = 0.99$, $p = 0.001$; Fig 5).

Table 7. Number of individuals captured (N), species richness (S), and Hill's diversity (N_1 , N_2) and evenness ($F_{2,1}$) numbers with upper and lower 95% confidence interval limits for each year. Confidence intervals were not calculated for species richness because no difference was detected by a randomization test.

Year	N	S	N_1			N_2			$F_{2,1}$		
			Observed value	95% Confidence Interval		Observed value	95% Confidence Interval		Observed value	95% Confidence Interval	
				Lower	Upper		Lower	Upper		Lower	Upper
1984	726	25	7.59	6.82	8.12	5.00	4.52	5.47	0.61	0.58	0.65
1985	1387	22	6.33	5.83	6.55	4.79	4.54	5.02	0.71	0.70	0.76
1986	720	21	6.42	5.83	6.84	4.57	4.19	4.94	0.66	0.63	0.70
1987	631	17	5.74	5.16	6.21	3.69	3.32	4.09	0.57	0.54	0.62
2004	2032	24	7.76	7.19	8.01	5.00	4.72	5.29	0.59	0.58	0.63

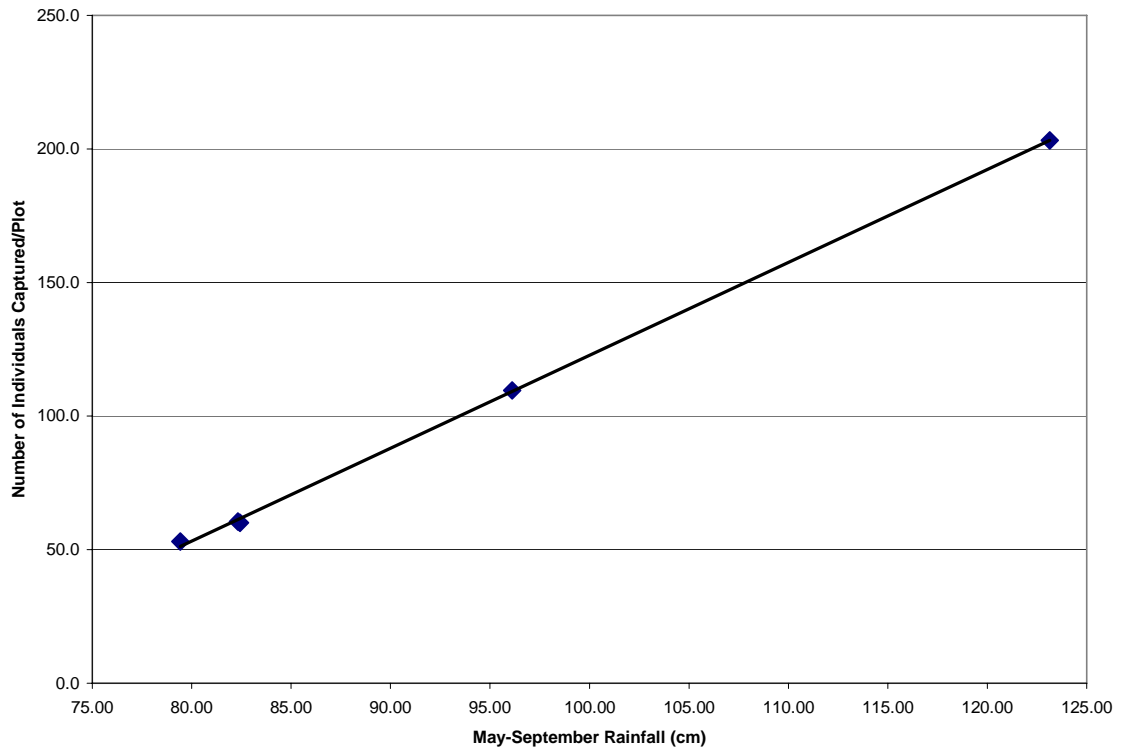


Figure 5. Mean number of individuals captured per plot (y-axis) versus summer rainfall (x-axis) for each year.

Species richness among years was not different ($p = 0.5076$). The number of abundant (N_1) and very abundant (N_2) species varied significantly among years ($N_1: p = 0.0001$; $N_2: p = 0.0001$), as did evenness ($F_{2,1}: p = 0.0014$). The number of abundant species was higher in 2004 than in all other years except 1984, and higher in 1984 than all years except 2004 and 1986 (Table 7). The number of very abundant species was lower in 1987 than all other years (Table 7). Evenness was higher in 1985 than all other years, and it was higher in 1986 than in all other years except 1985 and 1984 (Table 7).

Differences in community composition were greater between years than between fire frequency treatments. Cluster analysis in conjunction with the SIMPROF test revealed five distinct groups of experimental plots: one entirely of plots in 2004, one almost entirely of plots in 1985, and one large group that encompassed most of the plots in 1984, 1986, and 1987; the other two distinct groups consisted of a few plots in 1984 and 1987 that had distinct community compositions ($p < 0.05$). A similar pattern was revealed by NMS, showing a general shift in community composition between years with the largest separation between 2004 and all other years (stress = 0.16; Fig 6).

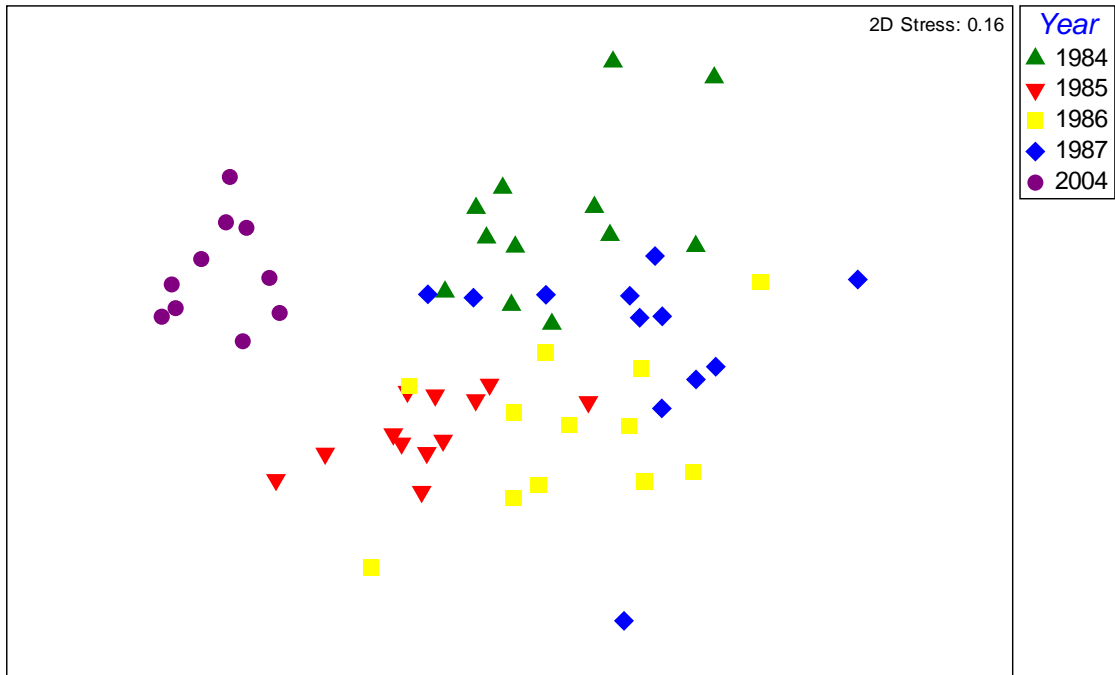


Figure 6. Nonmetric multidimensional scaling plot of experimentally burned plots among years. Stress measures the goodness-of-fit of the data to the pattern; lower stress indicates a better fit.

The separation among years was significant (Global $R = 0.759$, $p = 0.001$) across all fire frequency treatments, using a two-way crossed ANOSIM. Pairwise tests showed differences between all pairs of years except 1984 and 1987, and 1986 and 1987 (Table 8). The separation between fire frequency treatments across all years in the same two-way crossed analysis was smaller than the separation between years, but still significant (Global $R = 0.385$, $p = 0.001$). Pairwise comparisons of fire frequency treatments showed a more complicated pattern of differences (Table 9). The difference in community composition among years was also significantly correlated with summer rainfall ($r_s = 0.585$, $p = 0.01$).

Table 8. Pairwise R values between years from a two-way crossed ANOSIM.

Comparison	R	p
1984 vs. 1985	0.8	0.008
1984 vs. 1986	0.75	0.004
1984 vs. 1987	0.4	0.082
1984 vs. 2004	1	0.004
1985 vs. 1986	0.45	0.016
1985 vs. 1987	0.8	0.004
1985 vs. 2004	1	0.004
1986 vs. 1987	0.5	0.074
1986 vs. 2004	1	0.004
1987 vs. 2004	0.945	0.004

Table 9. Pairwise R values between fire frequency treatments from a two-way crossed ANOSIM. There were not enough replicates of the 2 and 9 year fire frequency treatments to make a pairwise comparison.

Comparison	R	p
1 vs. 2	-0.34	0.897
1 vs. 3	0.25	0.099
1 vs. 5	0.004	0.400
1 vs. 7	0.25	0.148
1 vs. 9	1	0.012
1 vs. no fire	0.5	0.016
2 vs. 3	-0.25	0.815
2 vs. 5	0.83	0.021
2 vs. 7	0.66	0.062
2 vs. no fire	0.83	0.021
3 vs. 5	0.313	0.148
3 vs. 7	-0.188	0.778
3 vs. 9	1	0.012
3 vs. no fire	0.125	0.321
5 vs. 7	0.35	0.025
5 vs. 9	0.5	0.185
5 vs. no fire	0.55	0.025
7 vs. 9	0.75	0.062
7 vs. no fire	-0.1	0.728
9 vs. no fire	1	0.012

In general, the change in abundance of *Gastrophryne carolinensis* was most characteristic of between-year differences in community composition. Other species that contributed to between year differences included *Aspidoscelis sexlineata*, *Tantilla relicta*, *Anaxyrus terrestris*, *Scincella lateralis*, and *Coluber constrictor*. However, the relative contribution of each species to the dissimilarity between pairs of years changed depending on the years being compared. Differences between years in the 1980s were more characterized by the relative abundances of *Scaphiopus holbrookii*, *Kinosternon baurii*, and *Plestiodon inexpectatus* than differences between 2004 and any year in the 1980s. Likewise, differences between 2004 and years in the 1980s were more influenced by the abundances of *Eleutherodactylus planirostris*, and *Anolis sagrei*, than differences between pairs of years in the 1980s.

The abundances of ten species could produce a pattern among Bray-Curtis similarities almost identical to that produced by the full species set ($r_s = 0.957$; $p = 0.01$). *Gastrophryne carolinensis* abundances alone produced Bray-Curtis similarities that had a Spearman rank correlation value of 0.527 with the Bray-Curtis similarity matrix from all species ($p=0.01$).

Second-stage analysis of patterns of annual variation within fire frequency treatments revealed no differences between long-term change in community composition in unburned plots relative to the pattern of annual variation in burned treatments (Global R = -0.019, $p = 0.543$; Fig 5). The second stage analysis of the pattern of similarity among fire frequencies within years suggested that there are differences between years in the pattern of among plot Bray-Curtis similarities, though no formal test was possible.

Discussion

Annual variation in summer rainfall has a large effect on community composition of reptiles and amphibians in a fire-maintained ecosystem. Separation among years was higher than among fire frequencies (ANOSIM Global R values of 0.759 and 0.385, respectively). Research in other fire-maintained systems has also shown annual variation in abundances of plants, small mammals, birds, and insects associated with changes in climate (Mushinsky and Gibson, 1991).

Summer rainfall explained nearly 60 percent of the variation in community composition among years, and 99 percent of the variation in number of individuals captured among years. Variation in number of individual reptiles captured per plot and number of amphibians captured per plot was still well-explained by summer rainfall when analyzed separately ($R^2 = 0.89$, and 0.98 , respectively). When captures of species were analyzed separately, 17 of the 35 species recorded were significantly positively correlated with annual rainfall.

The increase in abundances of most species in years with greater rainfall is likely because of increases in reproductive activity, hatching success, and/or juvenile survivorship. Most amphibian species require standing water to breed, and in relatively wet years standing water in the surrounding floodplain swamp expands to surround one side of the study site. Increases in captures of amphibians are probably a result of increased area of breeding habitat near the sampling area, increased reproductive effort by adults, and shorter distances required for both adults and juveniles to disperse into the nearby uplands from breeding sites. Future research at the study site could determine the

specific mechanisms by which amphibian captures increase during relatively wetter years.

Reptiles, however, do not require standing water for reproduction. An increase in rainfall can cause increases in soil moisture availability which can promote egg and hatchling survivorship (Overall, 1994; Philips and Packard, 1994; Socci et al, 2005; Warner and Andrews, 2002). Rainfall also is likely to influence vegetative growth, which can in turn increase prey abundance for both juvenile and adult reptiles and amphibians.

Only the southeastern five-lined skink, *Plestiodon inexpectatus*, exhibited a moderate (but non-significant) negative relationship with annual rainfall. Skinks were most abundant in 1984 and 1987, the two driest years, and least abundant in 2004, the wettest year. Skinks respond negatively to prescribed fire (Mushinsky, 1992), however, and 1984 and 1987 experienced a lower proportion of sites burned than in other years. Skink abundance was negatively correlated with the proportion of sites burned in each year, so it is likely that the negative relationship between skink abundance and summer rainfall is coincidental. By chance, summer rainfall and the proportion of plots burned were positively correlated for the five years presented here. Therefore, it is likely that some of the species that respond positively to recent fire, such as the six-lined racerunner, *Aspidoscelis sexlineata*, may not be responding as strongly to summer rainfall as the correlations suggest.

Community composition was usually different from one year to the next, with the exception of 1986 and 1987. Univariate measures of richness and diversity that do not retain species identities often failed to detect these changes. Species richness was not different among years. Hill's numbers of abundant species (N_1) and very abundant

species (N_2), and the modified Hill's evenness ratio ($F_{2,1}$) detected relatively few differences among pairs of years. Indices that describe species-abundance relationships are often useful for making broad comparisons between systems that share few, or no, species, but are less useful when making comparisons between sites within a habitat.

Within years, fire frequency has a significant effect on community composition. Despite this, the pattern of annual variation in community composition within different treatments is not different between experimentally burned and reference plots. This finding suggests that although burned plots have a significantly different composition of reptile and amphibian species than unburned plots, the long-term change within fire frequency treatments is not different. Because of the low number of replicates of each fire frequency treatment, however, the power to detect differences in the pattern of annual variation is low. Pairwise second stage ANOSIM R statistics suggest that there may be a trend toward frequently burned plots changing over time in a different manner than unburned plots. Further monitoring of amphibian and reptile communities at the site is needed to develop a longer time series to detect any real differences that may exist. Adding more replicates of experimentally burned plots would also be useful, but is unfortunately impractical at the site, given the limited availability of sandhill habitat.

No apparent loss of species was detected at the site, although the fragmented nature of the site may have increased the probability of extinction for species occurring in the study site. No species was consistently observed in the 1980s that was not also observed in 2004. Furthermore, most species abundances increased, with two notable exceptions. *Plestiodon inexpectatus* were not as abundant in 2004 as in the 1980s, which is likely a result of the high proportion of plots burned in 2003. The other exception was

Scaphiopus holbrookii, a species for which large fluctuations in observations of adults is well-documented (Gosner and Black, 1955; Greenberg and Tanner, 2004). The risk of extinction for several species, however, may have increased because of the fragmented nature of the study site, even though no loss of species was detected. Species that were uncommonly observed during the 1980s may well be locally extirpated at the study site. Continued monitoring is needed to determine if rare species are now absent from the site, and if other species that still occupy the site are experiencing long-term declines in abundance despite annual variation in abundance associated with rainfall.

Although the sandhill plant community remains intact and there are relatively few invasive plant species in the study site (Schmidt, 2005), the increasingly urban area surrounding the study site, in combination with fragmentation, has made it susceptible to invasions by non-native reptiles and amphibians. Two of three well-established non-native amphibians, and one of four reptiles, are present at the study site. Two non-native species, the greenhouse frog, *Eleutherodactylus planirostris*, and the brown anole, *Anolis sagrei*, have become more common at the site and were characteristic of differences in composition between 2004 and years in the 1980s. Changes in composition among years in the 1980s were characterized almost entirely by native species, although both non-native species were present at the site during the sampling period. A third non-native species, the Cuban treefrog, *Osteopilus septentrionalis*, observed in 2004 was not recorded during the initial sampling period.

Eleutherodactylus planirostris has been established in Florida since the early 1900s, so it is unlikely that the increase in abundance observed for this species was associated with their invasion. *Anolis sagrei* has experienced several introductions to mainland

Florida, and was established in Tampa as early as 1947 (Lee, 1985; Oliver, 1950).

Because the abundances of most other species also increased in 2004, it is uncertain whether the increased abundance of *A. sagrei* was associated with the annual variation in summer rainfall, or if it was associated with their establishment and subsequent invasion in Florida. *Osteopilus septentrionalis* was first recorded in mainland Florida in 1951 (Schwartz, 1952) and has subsequently expanded its range northward (Meshaka, 2001).

The appearance of *Osteopilus septentrionalis* at the study site since the 1980s almost certainly reflects the increasing range and abundance of this species in the state of Florida. This species has several attributes that make it a successful colonizing species, including high fecundity, short generation times, broad diet, few predators, and superior competitive ability, and its northward expansion is likely only limited by climate (Meshaka, 2001). It is most successful in hardwood hammocks, mangrove swamps, and areas of human disturbance. The northward expansion of the Tampa metropolitan area and the increased density of hardwoods in unburned areas of the USF ERA almost certainly facilitated the invasion of this species at the study site, and it is likely that Cuban treefrogs will continue to persist.

Cuban treefrogs have been associated with declines of native hylids in South Florida and the Everglades, especially in tropical hardwood hammocks and disturbed upland areas (Meshaka, 2001). It is likely that the impact of invasion of the Cuban treefrog will be more severe in natural areas farther north where it will compete with other native species that may have a greater overlap in habitat preference, such as the barking treefrog, *Hyla gratiosa*, and the pinewoods treefrog, *H. femoralis*. The larger size, broader diet (including other hylids), and high fecundity of the *O. septentrionalis* will

almost certainly have negative effects on these native hylids where their ranges overlap. *Hyla femoralis* occurs at the study site, which provides an opportunity to examine the response of this species to the invasion of the Cuban treefrog.

The giant toad, *Bufo marinus*, is locally abundant in Tampa and has been observed on the south side of Fletcher Avenue and the University of South Florida golf course (T. Piacenza, pers. comm.), both adjacent to the study site, but has not been documented inside the study site to date. Reptile species common in Tampa, but not observed in the study site, include the Mediterranean gecko, *Hemidactylus turcicus*, the Indo-Pacific gecko, *Hemidactylus garnotii*, and the Brahminy blind snake, *Ramphotyphlops braminus*, all of which occur most frequently on or near human habitations (pers. obs.).

Numerous other exotic species occur in Florida (Simberloff et al., 1997), including at least 28 lizard species (Butterfield et al., 1997). The majority of these species do not occur at the study site, but two lizard species in particular represent a serious threat of invading the site. The Nile monitor, *Varanus niloticus*, has been observed in southwest Florida as early as 1990, and is currently well-established and expanding its range, which could possibly include all appropriate habitats in peninsular Florida (Enge, et al., 2004). This large, carnivorous lizard does particularly well in areas disturbed by humans and adjacent to permanent water, so it is likely that the study site may be invaded if populations of *V. niloticus* become established in the Tampa area. The responses of native species to this invasion are largely unknown, but the Nile monitor is likely to have detrimental effects on populations of many species, especially burrowing species such as the gopher tortoise (Enge et al., 2004).

A more immediate threat to this study site is represented by the recent discovery of an apparently established population of the Argentine black and white tegu, *Tupinambis meriana*, southeast of Tampa (Enge, et al. 2006). Like Nile monitors, tegus also use burrows as refugia and juveniles in Florida have been trapped from gopher tortoise burrows. Although impacts of tegus on species indigenous to Florida have not been assessed, tegus are generally similar to monitor lizards in morphology (Losos, 1994) and probably represent at least as much of a threat to native species as the Nile monitor does (L. A. Fitzgerald, pers. comm.). The threat of invasion from these two large lizards at the study site underscores the need for continuous monitoring to determine the impact that invasion may have on native amphibians and reptiles, and also to develop potential management plans to help mitigate any detrimental effects on native species.

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