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Changes in a Northwestern Florida Gulf Coast Herpetofaunal Community Over a 28-y Period

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Abstract.—Population declines of amphibians and reptiles throughout the world have led to the initiation of projects to monitor their status and trends. Historical collections give an indication of which species occurred in an area at one time, although the ambiguity surrounding locations and environmental conditions associated with collection decreases the value of this information source. Resampling using the same general protocols can give valuable insights to changes in community structure. However, this is only feasible when sampling methodology and exact site locations are known. From 2002–2005 we resampled 12 sites in St. Marks National Wildlife Refuge in Florida's panhandle, an area in which intensive herpetological surveys were conducted in 1977–1979. We documented a general decrease in species richness among the diversely managed sites, changes in dominant species and diversity and an increasing trend toward homogeneity of the herpetofaunal community among habitats. Changes were attributed to four causes: 28-y of forest community succession, changes in management practices, non-detection of species due to variation in sampling conditions and a decrease in occupancy by four amphibians and three reptiles. The use of population and habitat-related indexes helped define possible influences on community change and can be used to target species for monitoring. Declines of these seven species are of concern, especially considering the protected status of the refuge and its increasing isolation as surrounding landscapes are converted to urbanized settings.

Introduction

Landscape changes have been profound during the last several decades and increasing attention has been directed at ascertaining how these changes have affected native fauna and flora. Monitoring programs have been designed to track the status of biodiversity and community function (Dodd *et al.*, *in press*), yet biologists are acutely aware that baseline historical data are often lacking or were imperfectly collected. Early surveys of geographic distribution and relative species abundance often paid scant attention to concurrent sampling covariates, such as details of habitat complexity, land use and the environmental conditions under which individual animals were collected. In addition, exact locations were often poorly delineated before the advent of global positioning systems, making it difficult to determine how species and populations have changed in distribution through time.

Amphibians and reptiles are important components of many ecosystems because their sheer numbers and biomass affect ecosystem function through complex trophic interactions. Many of these species throughout the world are declining from a variety of causes (Gibbons *et al.*, 2000; Houlahan *et al.*, 2000). Efforts at documenting the current status and trends of amphibians and reptiles in the face of massive biotic and abiotic habitat changes that have occurred during the last century often focus on resurveys of areas previously collected, coupled with an examination of museum specimens (Lannoo *et al.*, 1994; Busby

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and Parmelee, 1996; Christiansen, 1998; Brodman *et al.*, 2002; Lips *et al.*, 2004; Hossack *et al.*, 2005). Yet, the effectiveness of *a posteriori* methods to measure change is directly related to the duration of the resurvey effort and the quality of the historical information (Skelly *et al.*, 2003).

Researchers are rarely able to employ the exact same methods to surveys conducted >20 y apart, primarily because the methodology of early surveys often was not recorded or collecting was haphazard. As a result, resurveys sometime focus on coarse measures of status, such as changes in species richness over a geographic area (*e.g.*, Lannoo *et al.*, 1994; Busby and Parmelee, 1996; Hossack *et al.*, 2005), rather than on a rigorous assessment of changes in local abundance. Resurveys that have been able to use methods similar to the original survey and at the same study sites (*e.g.*, Bradford *et al.*, 1994; Beebee, 1997; Gibbs *et al.*, 2005) have a much greater predictive power to document trends in status and species richness than those without access to such information.

In the late 1970s information on the distribution and relative abundance of amphibians and reptiles was collected by biologists working for the U.S. Fish and Wildlife Service (USFWS) at St. Marks National Wildlife Refuge, Florida (U.S. Fish and Wildlife Service, 1980). The objective of their study was to quantify the relationships among forestry management practices and the diversity and relative abundance of non-game wildlife. Although the results were never published, the data were archived at the USFWS National Ecology Research Center, the predecessor of the USGS Florida Integrated Science Center.

During the course of surveying St. Marks in connection with the USGS Amphibian Research and Monitoring Initiative (Corn *et al.*, 2005; Muths *et al.*, 2005), the availability of the data collected in the 1970s offered us the opportunity to assess possible changes in the herpetofauna over a 28-y period, using the exact same study sites and general sampling techniques. Coupled with ongoing sampling from throughout the refuge, the results offer insights into factors influencing the long-term structure of a protected herpetofaunal community. These comparative data are important, inasmuch as the region surrounding the refuge is rapidly being converted from a rural, silviculture-dominated economy to one focused on recreation, housing and retirement development (Ziewitz and Wiaz, 2004).

STUDY AREA

St. Marks National Wildlife Refuge (SMNWR) is located in Florida's panhandle approximately 42 km south of Tallahassee. Established in 1931 to provide wintering habitat for migratory birds, SMNWR extends for 72 km along the Gulf Coast in Taylor, Jefferson and Wakulla counties. For management purposes SMNWR is divided into three major sections or units: St. Marks, Wakulla, and Panacea (Fig. 1). Each unit contains a number of different habitats, although each is dominated by a particular community type. The refuge complex comprises 27,500 ha of diverse upland and wetland habitats. About 8200 ha of the refuge have been designated as a federal wilderness area.

Summers are hot and humid at SMNWR and winters are generally mild and dry. Most rainfall occurs during the spring and summer months, although significant rainfall may occur in the winter associated with periodic cold fronts. Significant and sometimes catastrophic storms reach the northern Gulf Coast during the summer and autumn hurricane season. For example, in recent years SMNWR was affected by tropical storm Bonnie (Aug. 2004) and hurricanes Frances (Sept. 2004), Jeanne (Sept. 2004) and Dennis (Jul. 2005). Depending on the amount of storm surge, salt water intrusion may occur at considerable distances from Apalachee Bay and freshwater sheet flooding may extend nearly throughout the eastern and central portions of the refuge.

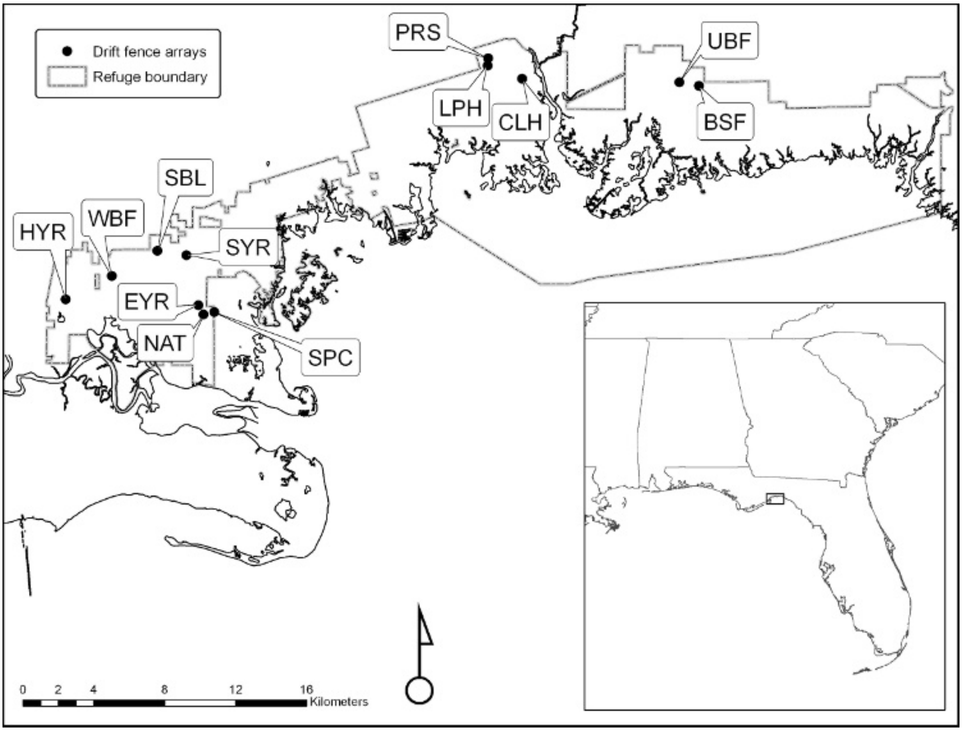

FIG. 1.—Map showing the locations of study sites at St. Marks National Wildlife Refuge, Florida. St. Marks Unit (BSF, UBF), Wakulla Unit (CLH, LPH, PRS), Panacea Unit (all remaining sites)

Currently, the marsh and water management program at SMNWR includes water level manipulation in 682 ha of manmade impoundments. Salt water is pumped into the impoundments periodically to control plant growth. Controlled burning is used to reduce trees and other woody growth and herbicides are used to control cattails (*Typha* sp.). The fire and forest management program is designed to establish multi-age timber stands using both commercial harvesting and prescribed burning applications. Approximately one-third of the fire-dependent habitats on the refuge are burned each year using a combination of summer and winter burns. Planting is used to restore the historic fire-dependent longleaf pine (*Pinus palustris*)/wiregrass (*Aristida beyrichiana*) ecosystem. Feral hogs (*Sus scrofa*) cause considerable damage to understory vegetation and leaf litter in some areas. Major invasive plants include cogon grass (*Imperata cylindrica*), cattail and Chinese tallow (*Sapium sebiferum*). Human recreation is extensive on the refuge, featuring both intensive consumptive (hunting and fishing) and non-consumptive (photography, bird watching and hiking) activities.

The diversity of upland and wetland habitats at SMNWR potentially supports 40 species of amphibians (21 frogs and 19 salamanders) and 68 species of reptiles (13 lizards, 34 snakes, 20 turtles and one crocodilian) (Conant and Collins, 1991). Amphibians and reptiles are active year-round, depending on weather conditions. The amphibian community, in particular, contains both winter-spring (for example, *Ambystoma cingulatum*, *Pseudacris ornata*) and spring-summer (for example, *Hyla cinerea*, *Rana heckscheri*) breeders. The timing of reproduction varies with temperature and rainfall. Amphibians may skip breeding during drought conditions when wetlands do not fill.

METHODS

FIELD DATA COLLECTION 1977–1979

No specific site selection criteria or quantitative habitat analyses are available for the 12 sites selected for intensive pitfall trapping (U.S. Fish and Wildlife Service, 1980). Of the 12 sites (Table 1), two (BSF, UBF) were located in the slash pine (*Pinus elliottii*) flatwoods-dominated St. Marks Unit, three (CLH, LPH, PRS) in mesic and hydric loblolly pine (*P. taeda*)-cabbage palm (*Sabal palmetto*) hammocks in the Wakulla Unit and the remaining 7 sites in the mostly longleaf pine sandhill (*P. palustris*) uplands of the Panacea Unit. Site descriptions, locations, and sampling dates are in Tables 1 and 2. Site descriptions, fire history and notes from the 1970s are based on information reported in U.S. Fish and Wildlife Service (1980) and on photographs taken during those surveys now archived at the USGS Florida Integrated Science Center, Gainesville.

Two adjacent trapping arrays were installed at each sampling location. Each array consisted of four sections of 7.6 m long galvanized metal flashing arranged in a ''+'' pattern (Campbell and Christman, 1982). A 19-l bucket was sunk flush with the ground surface at the end of each metal section, for eight buckets per array. Two wire-mesh screen funnel traps (76 × 20 cm) were placed along each metal arm of the array. Both buckets and funnel traps were partially shaded and sponges were placed in each bucket and funnel trap and moistened as necessary to prevent desiccation.

Traps were opened between Nov. 1977 and Jul. 1979, depending on location (Table 2). Arrays were checked at approximately 7-d intervals. The buckets were never closed, thus allowing animals to enter and potentially escape throughout the sampling period. When arrays were checked, however, all captured animals were preserved and the specimens deposited in the Florida Museum of Natural History.

FIELD DATA COLLECTION 2002–2005

Beginning in Oct. 2002 single drift fence arrays were installed at the 12 sites described above. Each array was configured the same as those from the previous study. Except for Nov. 2003, we opened traps at the arrays monthly, usually for 7 consecutive days, from Oct. 2002 through Dec. 2003. During 2004–5 the arrays were opened for 8 consecutive nights in Mar. (spring) and Jun. (summer) and 6 nights in Sept.–Oct. (fall) and Feb. (winter). Sampling effort is summarized in Table 2.

For each captured animal, we measured snout-vent length (SVL) and determined sex when possible. We marked all captured animals (except snakes) by toe clipping (no more than two toes were clipped on any individual) with a site-specific mark. Animals were released in the general vicinity but away from the arrays. Information on the extent of flooding was available from refuge personnel and by comparing river stages recorded from USGS monitoring stations on the St. Marks River near Newport and on the Sopchoppy River near Sopchoppy with known flooding events, particularly flooding resulting from Hurricanes Ivan (2004) and Dennis (2005).

DATA SUMMARY AND ANALYSIS

We tabulated numbers of amphibians and reptiles collected at the two closely-spaced arrays (A and B) at each site in the 1970s and compared them using the Wilcoxon Signed Rank test. Inasmuch as there were no significant site-based differences in counts between arrays A and B (amphibians: $Z = -0.204$, $P = 0.838$; reptiles: $Z = -1.868$, $P = 0.062$; Fig. 2), we combined these data in subsequent analyses. Because the 1970s counts represent a removal sampling protocol, we excluded recaptures in the 2000s results when computing catch per unit effort, and in the calculation of diversity, dominance and similarity indexes. The numbers of individual amphibians and reptiles recorded during sampling in the 1970s and 2000s were standardized (catch per unit effort, CPUE). We used a metric based on the number of days the buckets were actually open.

DOMINANCE AND DIVERSITY

Species diversity was calculated using Margalef's Diversity Index and species dominance was calculated using the Berger-Parker Index (Magurran, 1988). Diversity and dominance indices were calculated separately for amphibians and reptiles by sampling years.

SIMILARITY

We computed Bray-Curtis Index values using square-root transformed count data for amphibians and reptiles separately (Beals, 1984; Magurran, 1988) by site for both the 1970s and 2000s using Program Primer-E (Clarke and Gorley, 2001). We examined similarity relationships using two ordination methods, cluster and MDS, in this program. Additionally, we used the SIMPER routine in Primer-E to compute the overall percentage contribution that each species made to the dissimilarity between groups determined in the cluster analysis. The outcome is a list of species in their decreasing order of importance in discriminating between all possible pairs of dissimilarity coefficients within the cluster (Clarke and Gorley, 2001).

We used Program EstimateS version 7.5 to compute an expected species accumulation curve, the Mao Tau (with 95% confidence limits), based on the analytical formulas of Colwell *et al.* (2004; also *see* Ugland *et al.*, 2003). The Mao Tau is a sample-based rarefaction curve which provides a graphic estimate of expected species accumulation. We then computed both incidence-based (ICE) and abundance-based (ACE) coverage estimates of species richness among sampling sites. The derivation and use of these estimators is discussed by Chazdon *et al.* (1998) and Colwell (2005). Species accumulation curves were generated separately for amphibians and reptiles for both historic (1970s) and recent (2000s) surveys.

Finally, we examined the overlap of species composition and richness with a variety of habitat variables, including dominant forest community, soil types, maximum, minimum and mean air temperature, rainfall, flooding events, salinity and land management practices using available GIS overlays and data from USGS stream gauge and nearby weather stations. We found no herpetofaunal distributional patterns correlated with salinity, soil types, rainfall or maximum, minimum or mean air temperatures, so these variables will not be discussed further.

RESULTS

A total of 29 species (1821 individuals) of amphibians and 36 species (1576 individuals) of reptiles was found during pitfall trapping from 1977 to 1979. Although total individual counts did not vary between paired arrays, the number of species captured sometimes varied by >5 species per array (UBF for amphibians; BSF and HYR for reptiles); counts at most arrays, however, did not differ by more than one or two species (Fig. 3). Differences in species richness were most often observed when only one individual of a particular species was captured at a site. Corresponding values for the 2002 to 2005 sampling period were 24

TABLE 1.—Sampling site locations and general habitat characteristics, St. Marks National Wildlife Refuge, Florida

Site	UTM (all zone 16)	Site description (1970s)	Site description (2000s)	Fire 1970s	Fire after 1979	Fire 2000s	Notes 1970s	Notes 2000s
BSF	777716E 3337735N	Burned slash pine flatwoods	Mesic pine flatwoods	1973; Nov. 77	Changed to summer burns	May 03	Thinned 1977	Thinned by 75%; 27 y growth
CLH	767730E 3337878N	Coastal loblolly pine hammock	Coastal loblolly pine hammock				More hydric than LPH	No change
EYR	749814E 3324508N	8 y old longleaf pine sandhill	35 y old longleaf pine sandhill; plantation; mixed oaks			Feb. 04		27 y succession
HYR	742317E 3324648N	100 y old longleaf pine flatwoods	130 y old longleaf pine flatwoods	Winter 1969; Aug. 78		Jul. 03	Heavy ground cover	No change
LPH	765767E 3338562N	Loblolly pine hammock	Loblolly pine hammock	1974			Mesic; no lumbering in >40 y	Under- and midstory became more grassy
NAT	750125E 3323984N	Widely spaced 50–60 y old longleaf pines; not thinned in 40 y	Widely spaced 80–90 y old longleaf pines; not thinned in 70 y; large Turkey oaks	None from 1967 to 1977				Grassy understory changed to open sand; mature overstory
PRS	765790E 3338989N	Pine regeneration shelterwood	Pine regeneration shelterwood 30 y old; mixed oaks				Heavily thinned in 1977; widely spaced 40 y old loblolly pines	Less ground cover; overstory and midstory present; 27 y succession
SBL	747418E 3327553N	60–70 y old longleaf;moderately spaced	90–100 y old longleaf; moderately spaced	Aug. 78; Aug. 79	Fire managed	Apr. 03	Thinned 1975	More open; fewer oaks
SPC	750729E 3324137N	Site-prepped clearcut	Site-prepped clearcut; stunted widley spaced 30 y old longleaf pines mixed with oaks	Spring 1977		Mar. 04	Clearcut spring 1977; replanted Jan. 78	27 y pine growth; mixed oaks

TABLE 1.—Continued

Site	UTM (all zone 16)	Site description (1970s)	Site description (2000s)	Fire 1970s	Fire after 1979	Fire 2000s	Notes 1970s	Notes 2000s
SYR	749070E 3327336N	60–70 y old longleaf pine; moderately spaced	90–100 y old longleaf pine; moderately spaced	Jan. 78		Oct. 02, May 04	Thinned 1971	More open; fewer oaks
UBF	776608E 3337911N	Unburned slash pine flatwoods	Hydric slash pine flatwoods	Jan. 79		May 03, Jan. 03, Feb. 05	Thinned 1971	Fewer larger trees; understory the same
WBF	744888E 3326039N	70 y old longleaf pine flatwoods	100 y old longleaf pine flatwoods	Winter 1968	Changed to summer burns	Jul. 03	Thinned 1974	Fewer larger trees

TABLE 2.—Sampling dates and survey effort, St. Marks National Wildlife Refuge, Florida. CPUE is catch per unit effort

Site	Sampling frame (1970s)	Sampling effort (1970s) (2 arrays/night)	Actual number of days checked	CPUE amphibians (1970s)	CPUE reptiles (1970s)	Sampling frame (2000s)	Sampling effort (2000s) (1 array/night)	CPUE amphibians (2000s)	CPUE reptiles (2000s)
BSF	12/5/78–7/25/79	464	28	0.143	0.054	10/22/02–02/21/05	96	1.167	0.406
CLH	12/6/78–7/25/79	462	25	0.485	0.312	11/19/02–02/21/05	92	0.171	0.458
EYR	12/14/77–7/9/79	1144	70	0.04	0.14	10/23/02–02/20/05	95	0.695	0.589
HYR	12/15/77–7/9/79	1142	69	0.088	0.139	10/23/02–02/20/05	94	1.436	0.298
LPH	12/6/78–7/25/79	462	26	0.957	0.253	10/22/02–02/21/05	96	3.833	0.365
NAT	11/9/77–7/9/79	1214	75	0.043	0.122	10/23/02–02/20/05	95	0.621	0.779
PRS	12/8/78–7/25/79	462	25	0.522	0.208	10/22/02–02/21/05	96	5.365	0.313
SBL	11/29/78–7/10/79	446	24	0.099	0.159	10/23/02–02/20/05	95	0.884	0.347
SPC	11/9/77–7/9/79	1214	74	0.07	0.117	10/23/02–02/20/05	95	0.779	0.474
SYR	12/15/77–7/10/79	1144	68	0.052	0.141	10/23/02–02/20/05	95	1.642	0.589
UBF	12/5/1978–7/25/79	464	27	0.442	0.3	10/22/02–02/21/05	96	0.781	0.323
WBF	11/29/78–7/9/79	444	24	0.295	0.223	10/23/02–02/20/05	94	1.17	0.255

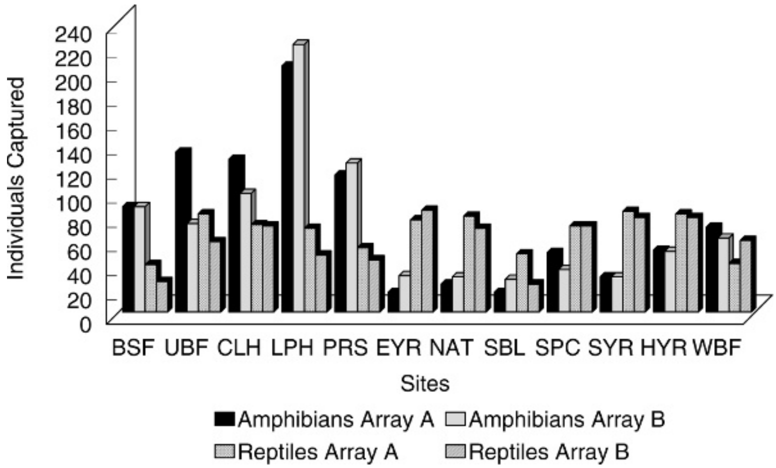

FIG. 2.—Comparison of trapping results at paired arrays A and B, 1977–1979, at 12 study sites at St. Marks National Wildlife Refuge

species of amphibians (2037 individuals) and 29 species of reptiles (541 individuals). CPUE increased dramatically (as much as 10 fold) between the historic and recent sampling (Table 2).

The following amphibians were captured in the 1970s, but not in the 2000s: *Amphiuma means* (n = 3), *A. pholeter* (n = 2), *Hyla gratiosa* (n = 1), *Notophthalmus perstriatus* (n = 17), *Pseudacris crucifer* (n = 2), *Pseudobranchus striatus* (n = 15), *Rana capito* (n = 1) and *Siren intermedia* (n = 58). Four of these (*A. means, A. pholeter, P. striatus, S. intermedia*) are highly aquatic and very rarely found outside water. Two species (*Eleutherodactylus planirostris* [n = 12], *Rana clamitans* [n = 7]) were observed in the 2000s, but not in the 1970s. Ten species of reptiles were captured in the 1970s, but not in the 2000s: *Farancia abacura* (n = 6), *Heterodon simus* (n = 11), *Lampropeltis getula* (n = 8), *Ophisaurus attenuatus* (n = 6), *O. compressus* (n = 1), *O. ventralis* (n = 15), *Pituophis melanoleucus* (n = 1), *Regina alleni* (n = 1), *Storeria occipitomaculata* (n = 9), *Terrapene carolina* (n = 11). Two species (*Crotalus adamanteus* [n = 1], *Plestiodon fasciatus* [n = 5]) were found in the 2000 trapping, but not in the 1970 trapping. *Lampropeltis*, *Pituophis* and *Crotalus* are large-bodied and mostly surface-dwelling snakes as adults, and are not often captured in funnel traps; *Farancia* and *Regina* are aquatic snakes. *Plestiodon* is a semi-arboreal lizard. All of the other reptiles are ground surface dwellers.

DIVERSITY

The greatest diversity of amphibians was found in the Panacea Unit of SMNWR both in the 1970s and 2000s (Table 3). Site NAT had the greatest diversity during both sampling periods. WBF had the lowest diversity values in the 1970s, whereas PRS had the lowest values in the 2000s. In no case did amphibian diversity values increase between the 1970s and 2000s. Reptile diversity was lowest at site SBL and greatest at BSF and HYR in the 1970s, but lowest at NAT and greatest at WBF in the 2000s. Diversity increased at five sites through the years (UBF, EYR, SBL, SYR, WBF). Unlike amphibian diversity, there were no patterns in reptile diversity correlated with geography or forest community during either sampling period (Table 3).

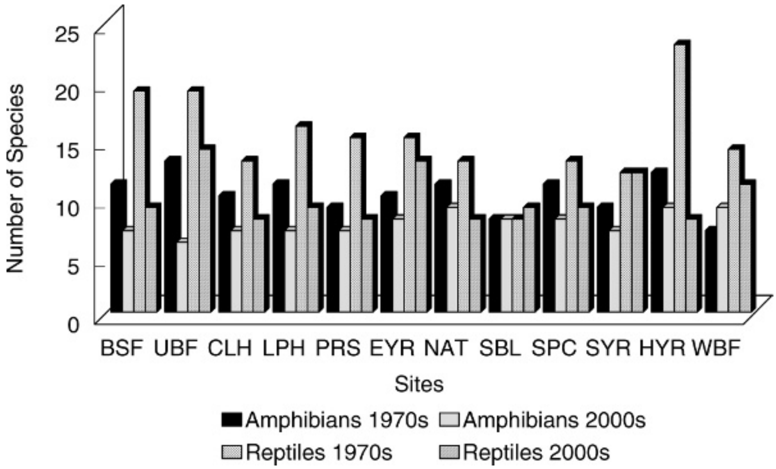

FIG. 3.—Comparison of amphibian and reptile species richness between the 1970s and 2000s at 12 study sites at St. Marks National Wildlife Refuge

DOMINANCE

Most sites had a rather diverse amphibian community not dominated by a particular species, at least in the 1970s (Table 3). Only at site PRS was the community overwhelmingly dominated by a particular species, the eastern narrow-mouthed toad (*Gastrophryne carolinensis*). This pattern changed in the 2000s, with 5 of the 12 sites with calculated values <2.0 (Table 3), suggesting dominance by one or more species, particularly the southern toad (*Bufo terrestris*) and *G. carolinensis*. The dominant species also changed through the years, with seven species forming the predominant group in the 1970s and only four during the 2000s. Salamanders dominated the amphibian communities at half of the sites in the 1970s, but were not dominant at any sites during our recent trapping effort. Indeed, the number of captures of the three formerly dominant species (*Ambystoma cingulatum, A. talpoideum, Notophthalmus viridescens*) decreased between surveys to almost insignificance (89 to 17, 128 to 8, 155 to 13, respectively). All three of these species have both terrestrial adult and aquatic larval stages. All captures of *A. cingulatum* in the 1970s were of larvae, whereas captures in the 2000s were of adults and juveniles.

For reptiles, the pattern was very different. In the 1970s, eight different species were dominant at the 12 sites, but only at SPC was the community overwhelmingly dominated by a single species, the six-lined racerunner (*Aspidocelis sexlineata*). This was not surprising since the racerunner is a heliothermic ground-dweller and site SPC had been recently clearcut. In the 2000s the eastern fence lizard (*Sceloporus undulatus*) was the dominant reptile at 7 of the 12 sites; this species was clearly the most common reptile at site PRS but, for the most part, the high dominance values suggest that the reptile community was rather evenly distributed in terms of species richness. The fence lizard is a common semi-arboreal lizard of the open sandhill community, especially within the Panacea Unit of SMNWR.

HERPETOFAUNAL COMMUNITIES IN RELATION TO HABITAT

Site similarity-index matrixes for amphibians and reptiles, both for the 1970s and 2000s, are presented in Tables 4 and 5. The amphibian community tended to become more similar

TABLE 3.—Results of species diversity (Margalef's) and dominance (Berger-Parker) analyses for amphibians (top) and reptiles (bottom) at 12 sites on St. Marks National Wildlife Refuge, Florida, 1977–1979 and 2002–2005. The Berger-Parker value represents an inverse relationship in that the lower the value, the more a community is dominated by a particular species

		Amphibians					
		1977–1979			2002–2005		
Refuge unit	Site	Margalef's	Berger parker	Dominant species	Margalef's	Berger parker	Dominant species
St Marks	BSF	1.94	2.49	*Ambystoma cingulatum*	1.39	2.88	*Gastrophryne carolinensis*
	UBF	2.25	4.02	*Notophthalmus viridescens*	1.37	2.38	*Rana sphenocephala*
Wakulla	CLH	1.66	2.24	*Rana sphenocephala*	1.49	1.70	*Rana sphenocephala*
	LPH	1.48	2.15	*Scaphiopus holbrookii*	1.03	1.70	*Gastrophryne carolinensis*
	PRS	1.46	1.37	*Gastrophryne carolinensis*	0.97	1.66	*Scaphiopus holbrookii*
Panacea	EYR	2.35	3.29	*Notophthalmus viridescens*	1.84	2.14	*Bufo terrestris*
	NAT	2.53	5.20	*Bufo terrestris*	2.15	1.78	*Bufo terrestris*
	SBL	1.85	2.44	*Ambystoma talpoideum*	1.65	2.30	*Scaphiopus holbrookii*
	SPC	2.25	5.31	*Gastrophryne carolinensis*	1.77	2.60	*Gastrophryne carolinensis*
	SYR	1.96	3.47	*Ambystoma talpoideum*	1.27	1.85	*Bufo terrestris*
	HYR	2.38	2.59	*Rana sphenocephala*	1.88	2.37	*Gastrophryne carolinensis*
	WBF	1.23	2.57	*Notophthalmus viridescens*	1.92	3.20	*Gastrophryne carolinensis*

		Reptiles					
		1977–1979			2002–2005		
Refuge unit	Site	Margalef's	Berger parker	Dominant species	Margalef's	Berger parker	Dominant species
St Marks	BSF	4.31	4.33	*Plestiodon inexpectatus*	2.29	3.67	*Storeria dekayi*
	UBF	3.65	4.09	*Thamnophis sauritus*	3.90	3.50	*Thamnophis sauritus*
Wakulla	CLH	2.41	2.22	*Scincella lateralis*	2.06	5.00	*Thamnophis sirtalis*
	LPH	3.15	2.44	*Scincella lateralis*	2.82	4.25	*Scincella lateralis*
	PRS	3.07	4.36	*Coluber constrictor*	2.30	2.10	*Sceloporus undulatus*
Panacea	EYR	2.76	2.96	*Aspidocelis sexlineata*	3.17	2.93	*Sceloporus undulatus*
	NAT	2.40	3.61	*Anolis carolinensis*	1.75	2.45	*Sceloporus undulatus*
	SBL	1.64	2.84	*Sceloporus undulatus*	2.46	3.71	*Sceloporus undulatus*
	SPC	2.42	1.39	*Aspidocelis sexlineata*	2.25	2.92	*Sceloporus undulatus*
	SYR	2.16	2.37	*Scincella lateralis*	2.86	2.94	*Sceloporus undulatus*
	HYR	4.34	2.65	*Scincella lateralis*	2.26	3.67	*Sceloporus undulatus*
	WBF	2.83	4.71	*Cemophora coccinea*	3.24	5.50	*Plestiodon inexpectatus*

among sites between the 1970s and 2000s, although three sites (LPH, EYR, SPC) remained essentially the same and only one site (PRS) became more diverse (Table 6). Many of the increases in similarity were large, however, indicating substantial trends towards a more homogenous community. For reptiles, three sites became more similar to one another (BSF, SBL, SPC), three sites (UBF, LPH, WBF) became less similar and the remainder were

TABLE 4.—Matrix of Bray-Curtis Similarity Indexes for amphibians at 12 sites in St. Marks National Wildlife Refuge. The values in bold represent historical data (1977–1979) and the non-bold values represent collections made from 2002–2005. *See* the text for habitat type of individual sampling sites

	St. Marks		Wakulla			Panacea						
	BSF	UBF	CLH	LPH	PRS	EYR	NAT	SBL	SPC	SYR	HYR	WBF
BSF	—	**0.475**	**0.342**	**0.198**	**0.304**	**0.182**	**0.221**	**0.119**	**0.301**	**0.180**	**0.255**	**0.197**
UBF	0.549	—	**0.242**	**0.108**	**0.166**	**0.231**	**0.202**	**0.096**	**0.317**	**0.136**	**0.340**	**0.488**
CLH	0.397	0.553	—	**0.354**	**0.495**	**0.119**	**0.145**	**0.097**	**0.227**	**0.141**	**0.314**	**0.118**
LPH	0.189	0.144	0.213	—	**0.597**	**0.102**	**0.105**	**0.160**	**0.137**	**0.184**	**0.099**	**0.122**
PRS	0.170	0.066	0.075	0.771	—	**0.188**	**0.177**	**0.182**	**0.245**	**0.233**	**0.187**	**0.113**
EYR	0.586	0.278	0.227	0.058	0.092	—	**0.735**	**0.400**	**0.595**	**0.381**	**0.449**	**0.339**
NAT	0.444	0.355	0.352	0.285	0.219	0.327	—	**0.375**	**0.686**	**0.450**	**0.418**	**0.284**
SBL	0.598	0.378	0.407	0.144	0.136	0.559	0.512	—	**0.279**	**0.777**	**0.262**	**0.274**
SPC	0.613	0.201	0.216	0.200	0.197	0.500	0.444	0.466	—	**0.417**	**0.441**	**0.324**
SYR	0.567	0.289	0.257	0.073	0.103	0.814	0.368	0.619	0.487	—	**0.275**	**0.242**
HYR	0.575	0.330	0.346	0.186	0.153	0.375	0.457	0.618	0.505	0.483	—	**0.379**
WBF	0.374	0.235	0.267	0.100	0.092	0.343	0.391	0.517	0.331	0.495	0.696	—

essentially unchanged (Table 6). Most changes were less than 0.3 units, however, suggesting that the changes were minor.

There were distinct patterns within the matrixes of habitat similarity among sites. The amphibian communities in the 1970s were most similar to one another within management units, regardless of habitat type or ongoing management practice (Fig. 4). Indeed, community similarities scaled from an east to west direction, such that the two eastern sites sampled from the St. Marks Unit were more similar to the three sites from the adjacent Wakulla Unit and most different from site SBL, one of the farthest sampling sites in the Panacea Unit to the west. These relationships were maintained even within a management unit. For example, the two most distant sites within the Panacea Unit (WBF in the west, SYR in the east) were also the most dissimilar to one another in terms of their amphibian communities.

TABLE 5.—Matrix of Bray-Curtis Similarity Indexes for reptiles at 12 sites in St. Marks National Wildlife Refuge. The values in bold represent historical data (1977–1979) and the non-bold values represent collections made from 2002–2005. *See* the text for habitat types of each individual sampling site

	St. Marks		Wakulla			Panacea						
	BSF	UBF	CLH	LPH	PRS	EYR	NAT	SBL	SPC	SYR	HYR	WBF
BSF	—	**0.412**	**0.258**	**0.220**	**0.199**	**0.169**	**0.131**	**0.132**	**0.106**	**0.159**	**0.232**	**0.317**
UBF	0.467	—	**0.389**	**0.352**	**0.230**	**0.134**	**0.118**	**0.133**	**0.028**	**0.213**	**0.342**	**0.244**
CLH	0.540	0.491	—	**0.667**	**0.350**	**0.151**	**0.158**	**0.149**	**0.098**	**0.472**	**0.601**	**0.305**
LPH	0.320	0.273	0.340	—	**0.498**	**0.332**	**0.332**	**0.404**	**0.208**	**0.568**	**0.580**	**0.380**
PRS	0.222	0.167	0.196	0.263	—	**0.406**	**0.393**	**0.395**	**0.311**	**0.397**	**0.447**	**0.564**
EYR	0.184	0.099	0.119	0.085	0.373	—	**0.688**	**0.450**	**0.609**	**0.573**	**0.219**	**0.479**
NAT	0.203	0.113	0.179	0.233	0.468	0.525	—	**0.575**	**0.455**	**0.602**	**0.202**	**0.445**
SBL	0.206	0.129	0.185	0.115	0.536	0.674	0.590	—	**0.254**	**0.500**	**0.191**	**0.435**
SPC	0.250	0.216	0.182	0.188	0.500	0.713	0.630	0.707	—	**0.370**	**0.153**	**0.365**
SYR	0.208	0.141	0.189	0.098	0.523	0.714	0.600	0.759	0.813	—	**0.488**	**0.454**
HYR	0.364	0.327	0.385	0.359	0.605	0.263	0.375	0.386	0.348	0.364	—	**0.481**
WBF	0.364	0.327	0.192	0.359	0.372	0.342	0.417	0.246	0.377	0.364	0.409	—

TABLE 6.—Changes in the Bray-Curtis Similarity Indexes for amphibians and reptiles captured during surveys in 1977–1979 and 2002–2005. The first number indicates a change (usually minor) in the index when one site is compared among other sites, whereas the second number indicates a substantial change (arbitrarily defined as 0.3 units or greater). An increase suggests that habitats became more similar in the intervening years; a decrease, the opposite. Thus, 9(5) would indicate that substantial changes occurred at 5 of 9 sites where some change occurred

	Amphibians		Reptiles	
Site	Increase	Decrease	Increase	Decrease
BSF	9(5)	2(0)	11(0)	0
UBF	7(2)	4(0)	4(0)	7(0)
CLH	8(2)	3(1)	5(2)	6(0)
LPH	5(0)	6(0)	1(0)	10(2)
PRS	2(0)	9(1)	6(0)	5(0)
EYR	6(2)	5(1)	5(0)	6(0)
NAT	8(0)	3(1)	6(0)	5(0)
SBL	7(4)	4(0)	8(1)	3(0)
SPC	6(1)	5(0)	10(2)	1(0)
SYR	7(2)	4(0)	5(1)	6(2)
HYR	8(3)	3(0)	6(0)	5(0)
WBF	8(1)	3(0)	3(0)	8(0)

The pattern changed somewhat in the 2000 sampling period. Instead of a similarity based on east to west location, amphibian community similarities appeared to be based on dominant community type (Fig. 4). Thus, the amphibians at sites BSF and UBF (slash pine, mesic or hydric soils) remained closely similar, and clustered with site CLH (loblolly pine, hydric soils). The two drier loblolly sites (LPH, PRS) clustered together, as did the longleaf pine sites with dry soils (the remaining seven sites). Even within the longleaf sites, some of the amphibian communities appeared similar among sites based on shared habitat characteristics: >100 y old trees with summer burns (HYR, WBF); 60–110 y old trees at sites with highly disturbed histories (NAT [open, no fire], SPC [mostly clearcut in 1970s]). A close examination of the cluster sets suggests that relationships between amphibian communities often remained intact from the 1970s to the 2000s, for example, BSF and UBF and LPH and PRS (Fig. 4). However, even when similarities were maintained, the site similarity index increased between sampling periods (BSF/UBF, 0.475 to 0.549; LPH/PRS, 0.579 to 0.771; Table 4) suggesting that the amphibian communities at even these sites were becoming more similar to one another than they had been nearly 28-y previously.

For amphibians, eight species in the 1970s survey accounted for 92% of the contribution to dissimilarity between groups determined in the cluster analysis: *Gastrophryne carolinensis* (21%), *Rana sphenocephala* (20%), *Bufo terrestris* (16%), *Notophthalmus viridescens* (11%), *Ambystoma talpoideum* (10%), *B quercicus* (6%), *Scaphiopus holbrookii* (3%), *Eurycea quadridigitata* (3%). In contrast, only six species accounted for 91% of dissimilarity in the 2000s: *G. carolinensis* (37%), *B. terrestris* (21%), *R. sphenocephala* (18%), *B. quercicus* (6%), *Hyla femoralis* (5%), *S. holbrookii* (4%).

For reptiles, there were no discernable patterns related to geography, major habitat type or management practice either in the 1970s or the 2000s (Fig. 5). Sites BSF and UBF retained similar habitat similarity indexes (0.412 versus 0.467; Table 5), despite the fact that BSF became more similar to CLH in the 2000s than it had been in the 1970s. For reptiles, 13

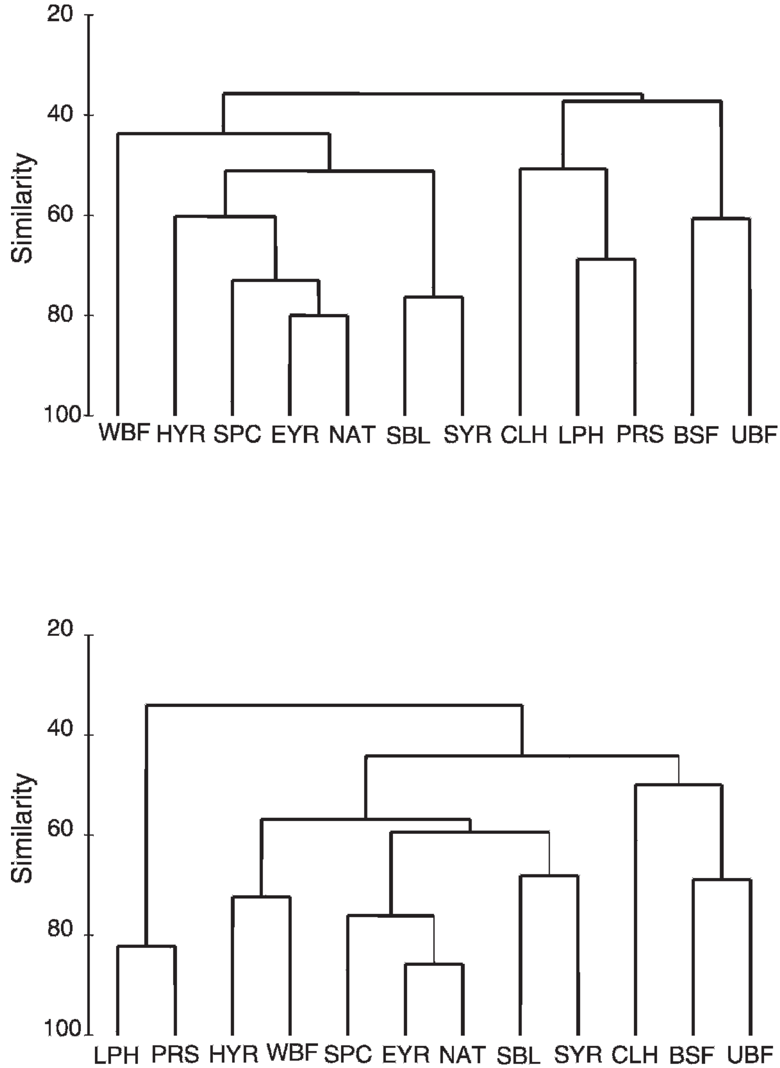

FIG. 4.—Cluster dendrograms based on square-root transformed Bray-Curtis Similarity Index values showing the relationship among habitat types and the amphibian community at 12 study sites at St. Marks National Wildlife Refuge. The cluster at top shows relationships in 1977–1979, whereas the cluster at the bottom shows the relationships in 2002–2005

species in the 1970s survey accounted for 90% of the contribution to dissimilarity between groups determined in the cluster analysis, but only three accounted for >10%: *Scincella lateralis* (21%), *Aspidocelis sexlineata* (12%), *Coluber constrictor* (11%). In contrast, 10 species accounted for 90% of dissimilarity in the 2000s, and five species accounted for more than 10% of this dissimilarity: *Anolis carolinensis* (15%), *C. constrictor* (14%), *Sceloporus undulatus* (14%), *A. sexlineata* (12%), *Cemophora coccinea* (10%).

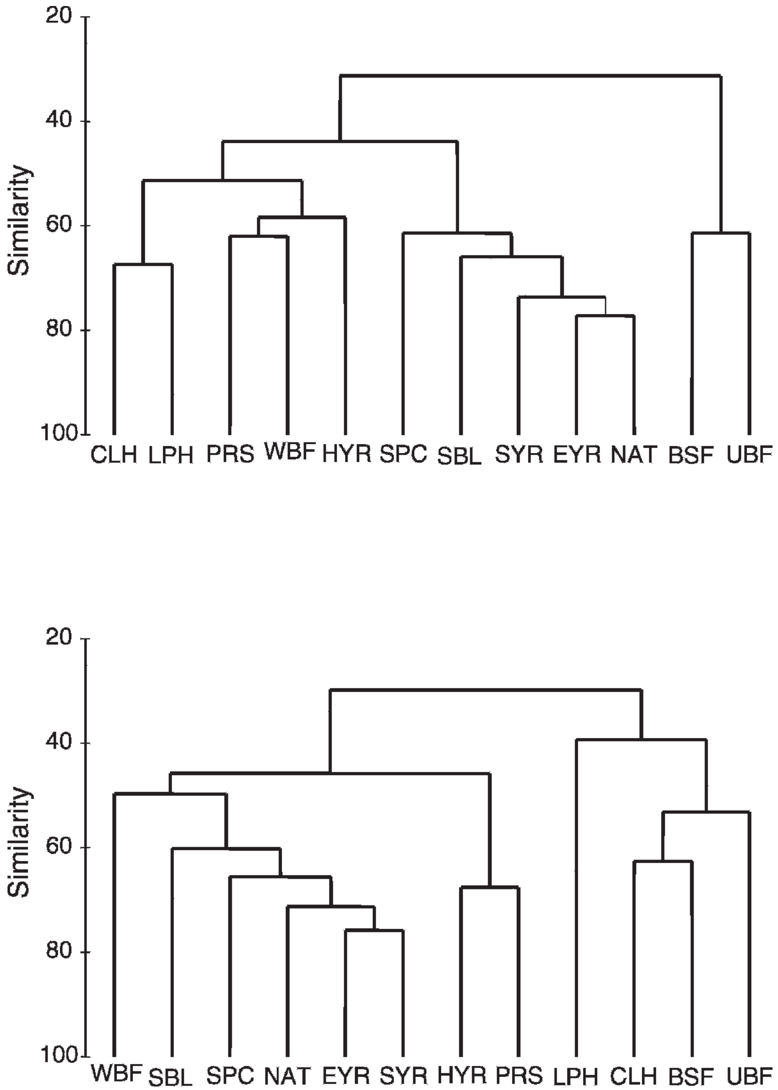

FIG. 5.—Cluster dendrograms based on square-root transformed Bray-Curtis Similarity Index values showing the relationship among habitat types and the reptile community at 12 study sites at St. Marks National Wildlife Refuge. The cluster at top shows relationships in 1977–1979, whereas the cluster at the bottom shows the relationships in 2002–2005

SPECIES RICHNESS

Species accumulation curves suggest that fewer species of amphibians and reptiles (Fig. 6) were expected in the 2000s than in the 1970s. In the 1970s, the curves predict that 29 species of amphibians might be present throughout the sampling sites, but only 19 in the 2000s. In the 1970s, 35 species of reptiles were predicted, but only 28 in the 2000s. The actual values were 29/35 (1970s) and 24/29 (2000s) for amphibians/reptiles.

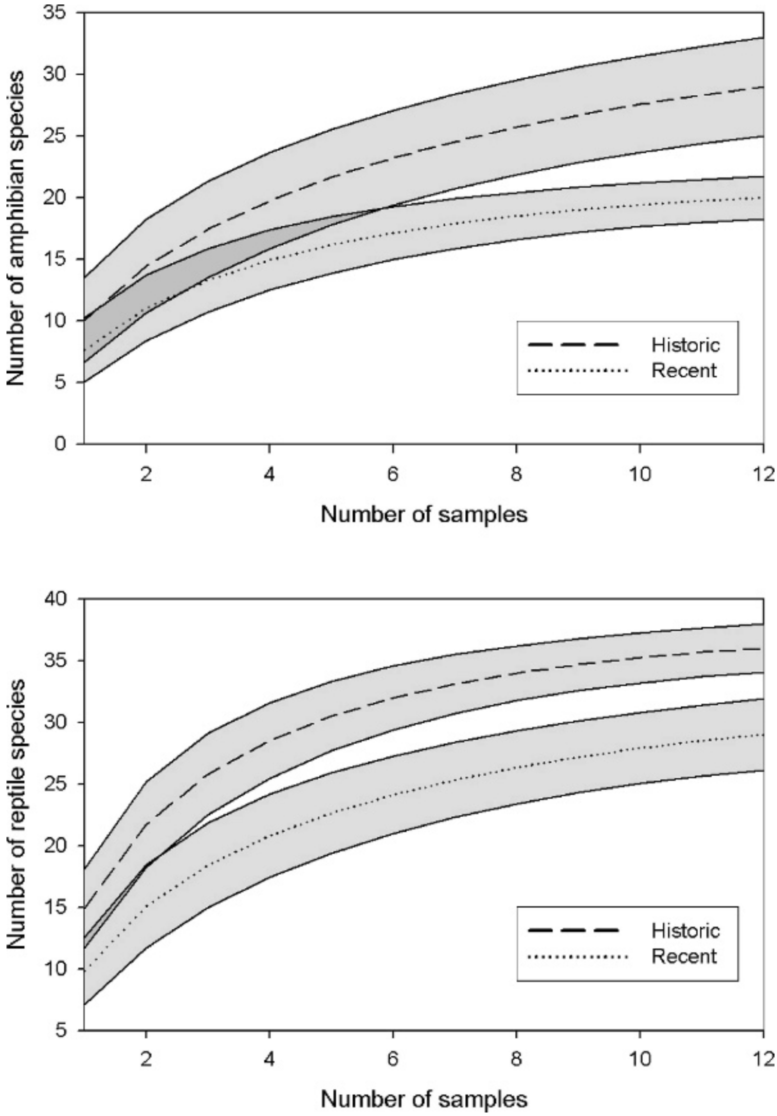

FIG. 6.—Species accumulation curves, with 95% confidence intervals, for amphibians (top) and reptiles (bottom) sampled at 12 study sites at St. Marks National Wildlife Refuge. The historic curve shows relationships in 1977–1979, whereas the recent curve shows the relationships in 2002–2005

DISCUSSION

Logistics, funding and record-keeping (or lack thereof) make large-scale resampling of herpetofaunal communities difficult, and each of these factors influenced our resurvey efforts at SMNWR. Still, valuable information on changes in the herpetofaunal community can be discerned from these paired surveys. Our results demonstrate that the herpetofaunal community changed over the course of 28 y at SMNWR. Given the dynamic nature of ecosystems in this region, this result is not surprising in and of itself.

Although the general community types remained the same (*i.e.*, as sandhill or mesic hammock), habitat succession and the adoption of different management practices resulted in a more homogenous and mature forest at SMNWR, regardless of location or previous land-use history. Although many studies have demonstrated short-term declines in species richness following disturbances (Gray, 1989), our results suggest that landscapes that change from a mosaic of disturbed and undisturbed habitats to a less frequently disturbed, more homogenous landscape might also be perceived as declining in species richness, at least for some taxa. What is important is the scale over which sampling occurs and the area of inference to which results can be extrapolated.

We suggest that the changes in the herpetofaunal community at SMNWR may be attributed to four inter-related factors.

CHANGES IN HABITAT

Although detailed site descriptions and habitat measurements were not available, brief site descriptions in U.S. Fish and Wildlife Service (1980), archived photographs of each sampling site and discussions with individuals who conducted the 1970s surveys allowed us to qualitatively assess changes in the habitats at sampling sites. Changes generally followed a succession from a disturbed or young forest to a more stable and mature forest community (Table 1). For example, 28 y of managed succession took place at site SPC, taking it from a clearcut to a young mixed pine-oak forest; site PRS changed from an open shelterwood cut to a mixed oak-pine forest nearly 30 y old; site EYR changed from a very young open forest to a more mature longleaf pine forest; the already mature forest community at many sites (HYR, NAT, SBL, SYR, WBF) increased in age. None of the 12 sites we re-surveyed had been severely disturbed by clearcutting or shelterwood cutting over the 28-y interval.

CHANGES IN MANAGEMENT PRACTICES

During the 28-y interval between surveys, the U.S. Fish and Wildlife Service adopted management practices which decreased large-scale disturbances, such as site clearcutting. A fire management program was instituted that emphasized burning according to more natural regimes (for example, switching from winter to growing season burns; burning all habitats on a set rotation). A program was begun to restore the original longleaf pine forest rather than replanting slash pine as a row crop. All of these changes affected the sampling sites to one extent or another. Sites BSF and WBF were switched from winter to summer burns; fire management was begun at NAT and UBF; trees were thinned and, because of scheduled fire, leaf litter was often reduced (*e.g.*, sites BSF, LPH, NAT, PRS, SBL, SYR). Coupled with 28-y of growth, these management changes resulted in habitats becoming more similar in structure, if not in actual community composition. Thus, the overall herpetofaunal communities tended to become more similar to one another, even as individual species richness and dominance changed among sites.

Herpetofaunal response to changes in habitat structure is well documented (Mushinsky, 1986), and varies according to the life history requirements of individual species. The temporal and spatial use of fire and the amount of ground disturbance during silviculture may have profound effects on amphibians and reptiles (Mushinsky, 1985; deMaynadier and Hunter, 1995; Greenberg *et al.*, 1994; Means *et al.*, 1996; Chazal and Niewiarowski, 1998; McLeod and Gates, 1998; Russell *et al.*, 1999; Pilliod *et al.*, 2003). In the 1970s SMNWR included a diverse mosaic of habitats across the 12 sites sampled which contributed to the greater herpetofaunal species richness as compared with the 2000s. Changes in habitat structure resulting from both succession and management subsequently influenced herpetofaunal abundance, particularly of reptiles. For amphibians, changes in habitat structure may be less important in maintaining biodiversity than the retention of accessible breeding sites within a landscape through time (Russell *et al.*, 2002), at least as long as nearby terrestrial habitat remains for feeding and overwintering.

NON-DETECTION

It seems clear that a few species were not ''available'' to be sampled in the 2000s, although they were present in different habitats elsewhere on the refuge. During the 1970s survey, survey sites were flooded on several occasions, so much so that completely aquatic amphibians (*Amphiuma means*, *Siren intermedia*, *Pseudobranchus striatus*, larval *A. cingulatum*) were captured in wire-mesh funnel traps placed along drift fences. In the 2000s the sites did not flood during sampling, and hence these species were not captured. Ongoing simultaneous wetland surveys found these species, with the exception of *Notophthalmus perstriatus*, sometimes in abundance. Likewise, aquatic snakes (*N. fasciata*, *S. pygaea*), a turtle (*K. subrubrum*) and lizards favoring mesic habitats (*Ophisaurus* sp.) were found in the 1970s, but were not observed or only trapped in much lower numbers in the 2000s. Thus, temporary flooding allowed species that normally would not be observed to be captured in the earlier survey and, thus, influence estimates of richness, dominance and habitat similarity. Semi-aquatic species might also find it easier to disperse among wetlands in flooded forests, especially since movement between wetlands across uplands is important to many of these species (*e.g.*, Roe *et al.*, 2003).

DECLINING SPECIES

Some species appear to have declined significantly over the 28-y between surveys. These include four amphibians (*Ambystoma talpoideum*, *Eurycea quadridigitata*, *Notophthalmus perstriatus*, *N. viridescens*) and three small ground-dwelling reptiles (*Cemophora coccinea*, *E. egregius*, *Scincella lateralis*). Surveys elsewhere on SMNWR suggest a significant decrease in the number of wetland sites occupied by *A. talpoideum* and *N. viridescens* throughout the region; no *N. perstriatus* have yet been found on SMNWR in the 2000s at any previously verified breeding site. We suggest that these declines are real, but as yet we have not identified possible causative factors.

Determining the status of the reptiles is more difficult. We found far fewer individuals of three species (*Cemophora coccinea* 83 to 20; *E. egregius* 103 to 3; *S. lateralis* 339 to 16) than did the previous survey. Scarlet snakes and mole skinks may or may not be rare on the refuge, based on our subjective impressions during time constrained sampling. However, our impressions also suggest that the rarity of *S. lateralis* is real and not the result of stochastic or biased sampling results. This species accounted for 12% of the dissimilarity among habitat types in relation to changes in community structure, the highest of any species. The decline of small ground-dwelling reptiles in the Southeast may be the result of the introduction of fire ants (*Solenopsis*) (Mount, 1981; Allen *et al.*, 2004), armadillos (*Dasypus novemcinctus*) (Carr, 1994) and feral hogs, all of which are now common at SMNWR. More research needs to be directed toward understanding population changes of these reptiles.

CONSERVATION AND MONITORING IMPLICATIONS

Under ideal circumstances, surveys repeated years apart with the intent of detecting change should be replicated by using the same sampling procedures in a similar time frame at the exact locations. Even then, detection could be affected by habitat changes and differences in environmental covariates, such as temperature, rainfall and catastrophic storms and, thus, make interpretation of results difficult. Few studies of herpetofaunal communities have been able to replicate the collecting methods used 30 y or more in the past, yet historical distributional records may help to identify changes in species' status when coupled with current information on geographic range.

Indexes of similarity, diversity, dominance and species richness offer a means of critically examining changes in community composition when estimates of site occupation across a sufficient number of habitats or data on species abundance are not available, as is often the case when attempting to monitor status through time. In particular, the Bray-Curtis Similarity Index could prove useful in assessing the effects of habitat changes on herpetofaunal populations during monitoring programs, much as it has been used to address the success of restoration efforts and analyze geographic differences in biodiversity patterns (Bell and Barnes, 2000; Barnes and Lehane, 2001; Urbina-C. and Londroño-M., 2003; Ruiz-Jaen and Aide, 2005).

An index-based approach offers insights into potential, if not definitive causes of community change. Once potential causes are identified, research can then be designed to test hypotheses related to changes in species composition, especially in conjunction with future monitoring studies. Our results suggest that monitoring programs need to incorporate a rigorous evaluation of habitat structure and management procedures into data-collection protocols and that researchers must be acutely aware of the potential importance of stochastic or periodic environmental disturbances, such as storms and flooding, when interpreting species presence/not detected results. Simply counting individual animals or determining the percentage of site occupancy (MacKenzie *et al.*, 2005) may not be sufficient to understand changes in community composition through time.

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