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EFFECTS OF HURRICANES IVAN, KATRINA, AND RITA ON A SOUTHEASTERN LOUISIANA HERPETOFAUNA

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Abstract: Tropical weather disturbances are a major influence on coastal wetlands in North America. However, studies of their impact on biotic communities are rare. The abundance and species composition of amphibians and reptiles were investigated within levee, herbaceous marsh, and forested swamp habitats in southeastern Louisiana from 2002 to 2004 and again in 2005 to 2006. During the course of this study, three major hurricanes (Ivan, Katrina, and Rita) affected our study sites. This allowed us to opportunistically document the effect of major storm disturbances by comparing species richness, diversity, community assemblage, and abundance of amphibians and reptiles before and after hurricane events. We also used a previous study conducted in the same area during the late 1980's to assess long-term community composition changes. We documented the highest species richness in the forested swamp habitat (23 species), but the most diverse assemblage was found in marsh habitat ($H' = 2.082$). Overall, herpetofaunal diversity decreased and evenness increased in each habitat following hurricanes Ivan and Katrina/Rita. Drastic decreases in overall abundance of amphibians occurred, while the effect on reptile abundance varied with habitat. Reduced abundance of reptiles in marsh was recorded over the course of the study, while abundances in adjacent levee habitat increased, suggesting displacement of certain reptiles from the marsh to the levee. Significant saltwater intrusion was recorded in marsh and levee habitats, but not in the forested swamp. The hurricanes altered community composition and increased species evenness within each habitat, potentially affecting long-term community dynamics and species interactions.

Key Words: conservation, disturbance, diversity, marsh, saltwater intrusion, tropical storm, wetland

INTRODUCTION

Herpetofaunal species richness is high in the southeastern United States (Duellman and Trueb 1986, Gibbons and Stangel 1999, Gunzburger et al. 2005), but this region has experienced high rates of wetland loss, especially in Louisiana (Dahl 2006). Habitat degradation is linked to the current global amphibian and reptile decline (Duellman and Trueb 1986, Gibbons et al. 2000, Young et al. 2004). Thus, monitoring herpetofaunal community dynamics in the southeastern United States is especially important.

Natural disturbances, such as tropical storms and hurricanes substantially influence coastlines and coastal marshes, and may affect resident amphibians and reptiles. Tropical storms bring in nutrient rich sediment that facilitates soil accretion and biotic productivity, but the force of any storm surge may transform marsh into areas of open water (Dingler et al. 1995), cause extensive damage to vegetation (i.e., tree uprooting and branch breakage, Wright et al. 1970), and deposit salts (Jackson et al. 1995). Damage from a hurricane event can be influenced by the physical topographical structure of the habitat, severity of the storm, velocity of storm movement, diameter of the storm, and susceptibility of the ecosystem to damage (Tanner et al. 1991). While physical alterations are visually obvious, effects on biota are not. Possible outcomes of disturbance from storms on animal communities are changes in species richness, community composition, and abundance.

Louisiana has a long history of hurricanes (Stone et al. 1997, Roth 2003). Wetlands of the Lake Pontchartrain basin in southeastern Louisiana have sustained prolonged degradation and subsequent decline from a combination of natural and anthropogenic factors over the past 50 years that have left the ecosystems in poor condition. The Manchac Wildlife Management Area (MWMA) on the west

[1] Deceased

side of Lake Maurepas has been impacted by logging of *Taxodium distichum* L. (bald cypress), introductions of non-native species (e.g., nutria *Myocastor coypus* Kerr), saltwater intrusion, and subsidence of the land due to channelization of the Mississippi River and reduced sediment input. Salinity increases have shifted marsh communities from salt intolerant plant species to more salt tolerant species since 1956 (Barras et al. 1994) and sections of the MWMA now contain *Spartina patens* (Aiton) Muhl (saltmeadow cordgrass), a brackish marsh species associated with salinity intrusion (Platt 1988). These factors make wetland habitats more vulnerable to storm damage (Shaffer et al. 2003).

In October 2002, we initiated a herpetofaunal monitoring study in the MWMA and nearby Alligator Island (AI) forested swamp to document and assess community composition and species abundance. Our study had the initial goal of comparing data with a study previously conducted by Platt et al. (1989) that qualitatively (i.e., common, uncommon, and rare) documented herpetofaunal species richness within the same area. However, during our monitoring, Hurricanes Ivan in 2004 and Katrina and Rita in 2005 caused severe flooding and wind damage to the study area. These hurricane events provided a rare opportunity to examine pre- and post-hurricane reptile and amphibian populations.

We conducted surveys over the course of five years (2002–2005) in three habitat types, levee and herbaceous marsh of MWMA, and forested swamp on AI. Specific objectives of this study were: 1) to compare herpetofaunal species richness, abundance, and composition among the different habitats of MWMA and AI, 2) to determine the effects of Hurricanes Ivan and Katrina/Rita on species richness and community composition, and 3) compare our species list with an earlier survey by Platt et al. (1989) to identify changes in species assemblage over the past 17 years.

METHODS

Study Sites

Historically MWMA and AI (Figure 1) were part of an extensive continuous tract of freshwater forested swamp habitat (Platt et al. 1989). However, only small remnants of healthy forested swamp remain, including AI. MWMA has changed primarily to intermediate salinity marsh (Platt et al. 1989). Additionally, numerous levees constructed across the area for cypress tree logging and navigation are permanent scars in the landscape. Herbaceous marshes, levees, and forested swamps are now all major habitat types in Southeastern Louisiana (Chabreck and Linscombe 1978, Sasser et al. 2008).

To compare herpetofaunal community dynamics among marsh, levee, and forested swamp we randomly established seven study sites. At MWMA, we selected two levee sites and four marsh sites, and at AI we selected one forested swamp site. Marsh habitats were dominated by bull tongue (*Sagittaria lancifolia* L.), saltmeadow cordgrass (*S. patens*), and common reed (*Phragmites* sp.), the levee sites by palmetto (*Saber* sp.) and Chinese tallow (*Sapium sebiferum* L.), and the forested swamp site by bald cypress (*T. distichum*), water tupelo (*Nyssa aquatica* L.), blackgum (*Nyssa* sp.), and alligator weed (*Alternanthera philoxeroides* Mart.). The sites in MWMA corresponded to habitats surveyed for herpetofauna by Platt et al. (1989) from June 1986 to April 1989; their dataset provided a historical record of amphibians and reptiles.

Herpetofaunal Surveys

For this study, 301 herpetofaunal surveys were conducted in MWMA or Alligator Island (Figure 1). Surveys were conducted at one forested swamp site and two marsh sites beginning October 2002 and at two additional marsh sites and two levee sites beginning in March 2003. All seven sites were surveyed through November 2004. After the hurricanes, sites were re-sampled from March 2005 through November 2006. Three survey layouts were used to acquire herpetofaunal abundance, species richness, and community composition (Figure 1). Marsh and forested swamp sites were approximately 200 m away from any canal edges, but levee transects were placed along the center of the levee running parallel to canals. Survey lines were constructed with string strung between trees, or PVC pipes when trees were unavailable.

Herpetofaunal species richness, abundance, and composition at sites were obtained by conducting visual and acoustic encounter surveys (Heyer et al. 1994, Rödel and Ernst 2004), including refuge examination (e.g. under logs, tree holes, etc.), diurnally and nocturnally in each site, approximately monthly (excluding January), to encompass different activity patterns of the herpetofauna. Each survey lasted approximately 1 hour (mean ± SE: 60 ± 28 min). Two observers (1.5 m away from either side of the transect line) walked slowly and identified and recorded all individuals in the area between the observers and the transect line. Thus the total search area encompassed a 3 m swath along the length of

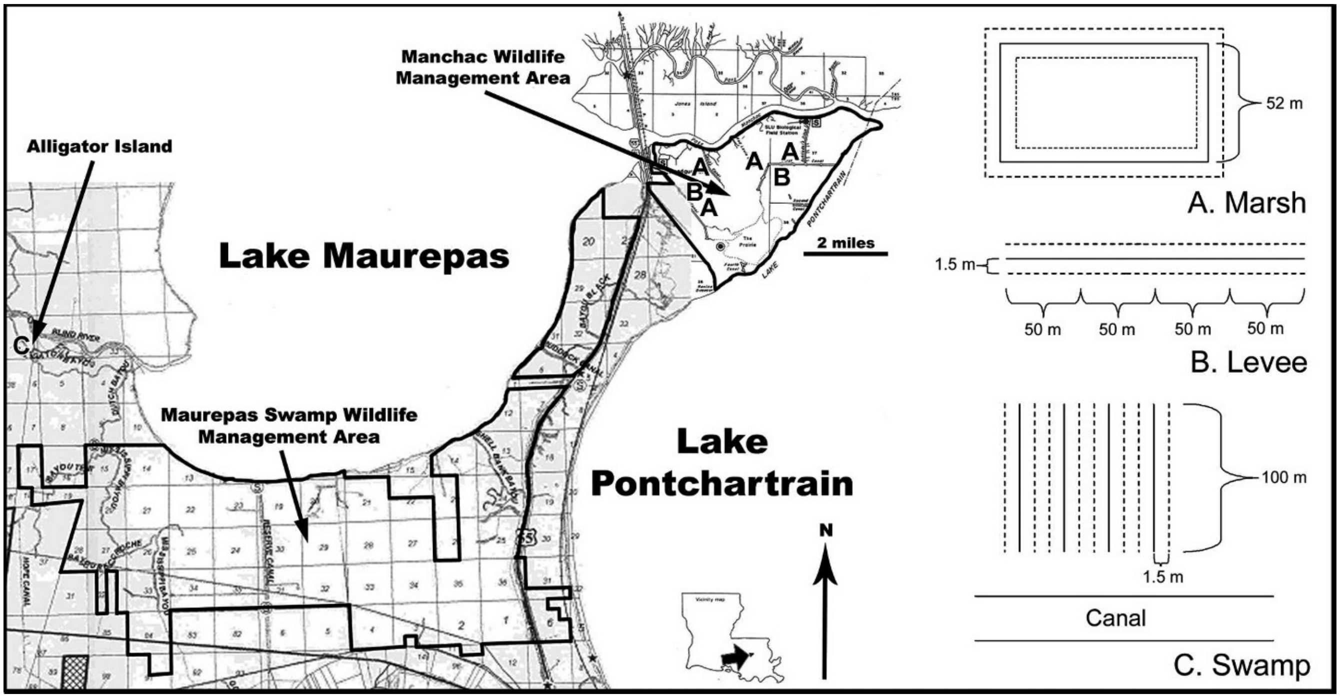

Figure 1. The Manchac Wildlife Management Area and Alligator Island (redrawn from Louisiana Department of Wildlife and Fisheries July 2006). Study site location and transect layout denoted by letter corresponding to habitat type.

each transect (e.g., 3 × 50 m long transect = 150 m^2 × 4 transects = 600 m^2 searched). Animals that could not be positively identified to species in the field were collected and identified in the laboratory; those individuals were returned to the capture site within a few days. During each survey we recorded environmental conditions that could influence herpetofaunal activity including air and water temperature (°C), water salinity (parts per thousand [ppt]), cloud cover, and wind speed (using a modified Beaufort scale). Salinity is particularly important because osmotic stress caused by a rise in salt concentration can result in direct mortality or slow growth and development of amphibian larvae (Gomez-Mestre et al. 2004, Chinathamby et al. 2006).

Survey data were organized as counts of individuals per species, per habitat, per year. Three major hurricanes occurred during our study, so data were partitioned into periods of pre- and post-hurricanes. Categorizations were pre-Ivan: 14 Oct. 2002 to 26 March 2004; post-Ivan/pre-Katrina: 6 Nov. 2004 to 28 Aug. 2005; and post-Katrina: 29 Aug. 2005 to 8 Nov. 2006. Hurricane Rita (landfall 24 Sept. 2005) is included in the post-Katrina survey period because only one survey was conducted between the post-Katrina and pre-Rita landfall. Scientific and Standard English names of herpetofauna follow Crother (2008).

Data Analysis

We compared changes in species richness, diversity, evenness, and abundance among pre-Ivan, post-Ivan, and post-Katrina sampling periods, and within habitats. Species richness and abundance were standardized across habitats by multiplying each by a correction factor of 0.415584, derived as follows: (minimum number of surveys conducted in a habitat /maximum number of surveys conducted in a habitat [64/154 = 0.415584]). Data were normally distributed [Kolmogorov-Smirnov test (K-S test) and box plot examination]. ANOVA was used to determine differences among habitats and survey periods.

To determine wind and salinity differences among habitats, non-parametric Kruskal-Wallis tests (K-W) were used because of non-normality (K-S test). Air and water temperature data were normally distributed so we used ANOVA. Among survey periods, environmental variables (air and water temperature, salinity, and wind score) were not distributed normally, so we used K-W tests. Bonferroni comparisons were used, when applicable, to test specific differences between sample means. ANOVA, K-W, and K-S tests were performed with Systat (2002) statistical software 10.2.01.

Survey count data for amphibians and reptiles were analyzed separately and combined to produce a

Table 1. Comparison of amphibians and reptiles recorded in Manchac Wildlife Management Area from 1986–1989 (Platt et al. 1989) and in MWMA and AI from 2002–2006 during our study. Presence indicated by (+) and absence by (−).

	Platt et al. 1989		2002–2006		
	Manchac WMA		Manchac WMA		AI
	Levee	Marsh	Levee (n = 83)	Marsh (n = 154)	Forested Swamp (n = 64)
Amphibians					
Acris crepitans Baird	+	+	16	44	223
Amphiuma sp.	−	−	−	−	+**
Gastrophryne carolinensis Holbrook	+	+	2	+[A]	4
Hyla avivoca Viosca	−	−	−	−	74
Hyla cinerea Schneider	+	+	208	407	364
Hyla squirella Bosc	−	−	−	+[A]	−
Lithobates catesbeianus Shaw	+	−	1	1	+[A]
Lithobates clamitans Latreille	−	−	1	−	824
Lithobates grylio Stejneger	−	+	−	+[A]	+[A]
Lithobates sphenocephalus Cope	+	−	91	41	+[A]
Ollotis nebulifer Girard	+	−	1	1	−
Pseudacris crucifer Wield-Neuwied	−	−	−	−	1
Total amphibian species richness	6	4	7	8	10
Reptiles					
Agkistrodon piscivorus Lacepède	+	−	12	10	41
Alligator mississippiensis Daudin	−	+*	+[A]	+[A]	+[A]
Anolis carolinensis Holbrook	+	+	27	−	35
Chelydra serpentina Linnaeus	−	+*	−	−	−
Coluber constrictor Linnaeus	+	−	+[A]	−	−
Kinosternon subrubrum Lacepède	+	+	4	−	+[A]
Lampropeltis getula Linnaeus	+	−	+[A]	−	−
Macrochelys temminckii Troost *in* Harlan	+**	−	−	−	−
Nerodia cyclopion Duméril, Bibron, and Duméril	−	+	1	5	1
Nerodia erythrogaster Forster	−	+	−	−	−
Sternotherus odoratus Latreille	+	+*	−	−	−
Nerodia fasciata Linnaeus	−	+	1	5	26
Nerodia rhombifer Hallowell	−	+	1	−	−
Opheodrys aestivus Linnaeus	+	+	3	−	−
Pantherophis obsoletus Say	+	+	4	−	+[A]
Plestiodon fasciatus Linnaeus	+	−	1	−	5
Plestiodon laticeps Schneider	+	−	−	1	−
Regina rigida Say	−	+	−	−	1
Scincella lateralis Say *in* James	−	−	+[A]	−	+[A]
Storeria dekayi Holbrook	−	+***	−	−	1
Thamnophis proximus Say	+	+	6	5	8
Trachemys scripta Schoepff	−	+	−	+[A]	+[A]
Total reptile species richness	11	14	14	7	13
Total species richness	27		25		23

[A] Present by acoustic sampling or incidentally found, no abundances assigned.
*Observed in open water areas (major canals) outside immediate site locations.
** Only 1 individual was observed.
*** Questionable status on Platt et al. (1989) list because only 1 specimen was collected in Oct. 1985 after hurricane Juan. Platt speculated the snake was washed in from nearby forested upland habitats.

Shannon-Wiener index of species diversity (H′) (Krebs 1999). These indices were compared within and among habitats across survey periods. H′ ranges from 0 to the theoretical maximum of log(s), where s is the number of species in the sample (Krebs 1999). Biological communities rarely exceed H′ = 5.0 (Washington 1984), so we used log base 2 to calculate diversity indices. Assemblage heterogeneity was estimated using Simpson's measure of evenness ($E_{1/D} = [1/D]/s$) (Krebs 1999).

We used Morisita's Index of Similarity (I_m) to assess community similarity between the habitat

Table 2. Observed and estimated species richness and detection probability under selected model using program CAPTURE. S = observed species richness, N′ = estimated species richness, SE (N′) = estimated standard error, CI (N′) = 95% confidence interval of estimated species richness, and P′ = estimated probability of capture (detection probability). M(o) is the null model, assuming every member of the population is equally detectable on every sampling occasion, M(t) assumes the probability of detection varies with time, and M(th) assumes detection probability varies by time and individual animal.

Habitat		Years	S	Model	N′	SE(N′)	CI(N′)	P′
Marsh	Herpetofauna	5	10	M(o)	10	0.3349	10–10	0.60
	Amphibians	5	5	M(o)	5	0.1793	5–5	0.64
	Reptiles	5	5	M(th)	6	1.7302	6–14	0.47
Levee	Herpetofauna	4	17	M(t)	19	1.5264	18–24	0.39
	Amphibians	4	7	M(o)*	8	1.3610	8–15	0.40
	Reptiles	4	10	M(o)	11	1.8528	11–20	0.38
Forested swamp	Herpetofauna	5	15	M(o)	15	0.3748	15–15	0.61
	Amphibians	5	6	M(o)	6	0.0909	6–6	0.73
	Reptiles	5	9	M(o)	9	0.4837	9–9	0.53

* Model M(tbh), which assumes probability of detection varies by time, behavioral response of captured animal, and individual, scored higher in the model test but no estimator for population size was available in CAPTURE program.

types because it is independent of sample size (Krebs 1999) or density (Morisita 1971). We estimated species richness among habitats with the model-fitting program CAPTURE (Rexstad and Burnham 1991; http://www.mbr-pwrc.usgs.gov/software/capture.html), which selects from eight closed population models using three combinations of unequal detection probabilities among species (Otis et al. 1978). We estimated species richness in two ways; 1) separately for amphibians and reptiles for each habitat using four (levee) or five (forested swamp and marsh) survey years as the number of occasions and 2) for total herpetofauna for each habitat and survey years. Estimates of species richness and detection probability from the models receiving the highest discriminate function score are presented.

Because sample sizes differed among survey periods within habitats we used rarefaction ($E[S_n]$) to assess species accumulation within habitats among survey periods (Analytic Rarefaction 1.3; http://www.uga.edu/~strata/software/Software.html). We produced three rarefaction curves, one for each sampling period for each habitat.

RESULTS

Species Richness and Diversity within Habitats

Herpetofaunal species richness, evenness, diversity, and abundance varied among levee, marsh, and forested swamp habitats. Forested swamp and levee exhibited higher observed species richness (23 species and 21 species, respectively) compared to the marsh habitat (15 species). However, excluding incidental species (individuals spotted just outside transect boundary), levee had higher species richness

Table 3. Mean (1 SD) environmental conditions during surveys conducted in marsh, levee, and forested swamp habitats.

Habitat	Survey Period	Mean Air Temp. (°C)	Mean Water Temp. (°C)	Mean Salinity (ppt)	Mean Wind Score*
Marsh		(n = 146)	(n = 135)	(n = 137)	(n = 62)
	pre-Ivan	24.1 (5.1)	25.9 (4.3)	1.18 (0.61)	0.6 (0.727)
	post-Ivan	25.6 (4.6)	29.3 (2.6)	2.21 (0.41)	1.5 (0.9)
	Post-Katrina	23.5 (5.6)	23.9 (4.7)	5.44 (1.06)	1.4 (1.1)
Levee		(n = 77)	(n = 70)	(n = 71)	(n = 82)
	pre-Ivan	24.3 (5.4)	27.1 (3.5)	1.20 (0.50)	0.5 (0.7)
	post-Ivan	25.5 (4.7)	30.1 (2.4)	2.05 (0.39)	1.4 (0.9)
	post-Katrina	22.7 (5.6)	24.5 (5.1)	5.29 (0.87)	1.7 (1.0)
Forested swamp		(n = 60)	(n = 57)	(n = 60)	(n = 62)
	pre-Ivan	23.1 (5.2)	23.2 (6.4)	0.11 (0.02)	0.4 (0.6)
	post-Ivan	24.8 (3.7)	26.3 (3.0)	0	0.8 (1.0)
	post-Katrina	23.0 (4.8)	24.9 (5.8)	0.37 (0.78)	0.7 (0.7)

* wind score: 0 = calm, 1 = light breeze, 2 = moderate breeze, 3 = very windy

Table 4. Standardized species abundance, richness, diversity, and evenness per habitat and survey period. Survey period categories: pre-Ivan: 14 Oct. 2002 to 26 March 2004; post-Ivan/pre-Katrina: 6 Nov. 2004 to 28 Aug. 2005; and post-Katrina: 29 Aug. 2005 to 8 Nov. 2006.

	Manchac WMA						Alligator Island		
	Marsh			Levee			Forested Swamp		
	pre-Ivan (n = 78)	post-Ivan (n = 37)	post-Katrina (n = 39)	pre-Ivan (n = 41)	post-Ivan (n = 19)	post-Katrina (n = 23)	pre-Ivan (n = 37)	post-Ivan (n = 11)	post-Katrina (n = 16)
Amphibians									
Standardized abundance	188	16	1	106	17	10	546	56	17
Diversity (H′)	2.52	1.61	1.85	1.82	1.24	1.99	1.49	1.40	0.96
Evenness ($E_{1/D}$)	0.33	0.52	0.90	0.61	0.54	0.42	0.37	0.47	0.87
Standardized richness	2	2	1	1	2	2	2	2	2
Reptiles									
Standardized abundance	7	2	2	6	4	14	30	11	8
Diversity (H′)	0.75	2.08	1.11	2.17	1.06	0.75	1.02	0.83	0.85
Evenness ($E_{1/D}$)	0.88	0.80	0.75	0.38	0.63	0.55	0.54	0.57	0.78
Standardized richness	2	1	2	2	2	3	2	3	2
Herpetofauna									
Standardized abundance	195	17	4	112	21	24	576	67	26
Diversity (H′)	2.35	1.34	0.70	1.63	0.83	0.61	1.34	0.99	0.53
Evenness ($E_{1/D}$)	0.16	0.41	0.79	0.29	0.40	0.45	0.21	0.28	0.70
Standardized richness	4	2	2	3	4	5	5	5	4

(17 species) than forested swamp (15 species) and marsh (10 species, Table 1), although these differences were not significant (ANOVA: $F_{2,9} = 2.0$, $p = 0.246$, $R^2 = 0.507$). Modeled species richness estimates showed similar trends to those of observed species richness (Table 2). Species richness estimates were 19 species for levee, 15 species for forested swamp, and 10 species for marsh under models of M(t) (capture probability varies with time) and M(o) (equal capture probability), respectively. Reptile species richness was higher than amphibian richness, but amphibians were more abundant, contributing > 83% of total herpetofaunal abundance in all habitats. Abundance did not differ among habitats (ANOVA: $F_{2,8} = 0.8$, $p = 0.541$, $R^2 = 0.884$).

Overall, marsh habitat had higher species diversity (H′ = 2.08) than levee (H′ = 1.23) and forested swamp (H′ = 1.12), but these differences were not significant (ANOVA: $F_{2,9} = 3.9$, $p = 0.117$, $R^2 = 0.914$). Communities were dominated by a few abundant anurans, indicated by low evenness scores (marsh: $E_{1/D} = 0.10$; levee: $E_{1/D} = 0.06$; forested swamp: $E_{1/D} = 0.20$). All habitats were uneven and not significantly different from each other (ANOVA: $F_{2,9} = 0.3$, $p = 0.783$, $R^2 = 0.802$). However reptile species were more evenly distributed than overall herpetofauna (Bonferroni: $p = 0.009$). Our data do not show the expected increase in diversity with increase in richness because of the extreme abundances of recently metamorphosed frogs at some sites (e.g., marsh had the lowest richness, but the highest diversity). Diversity was slow to increase for levee habitats because of low species evenness from a relatively high incidence of *Hyla cinerea* (Green Treefrog) (55%).

Marsh and levee habitats were similar in community composition, sharing nine species ($I_m = 0.914$; marsh to forested swamp: $I_m = 0.394$, 6 species; forested swamp to levee: $I_m = 0.382$, 11 species). Forested swamp had more unique species than any other habitat (5 species; Table 1). Dominant amphibian species were *H. cinerea* in marsh and levee habitats and *Lithobates clamitans* (Green Frog) in the forested swamp, while dominant reptiles were *Anolis carolinensis* (Green Anole) in the levee and *Agkistrodon piscivorus* (Cottonmouth) in marsh and forested swamp habitats (Table 1).

Detection probabilities were low to moderate, but variable among habitats and species groups (Table 2). The inability to detect all species present in the sampled community/area can lead to biased species richness estimates (Nichols et al. 1998). However, our observed richness was congruent with the estimates from CAPTURE (Table 2).

Environmental Conditions

Environmental conditions of air and water temperatures and wind were expected to be similar among habitats because of regional proximity.

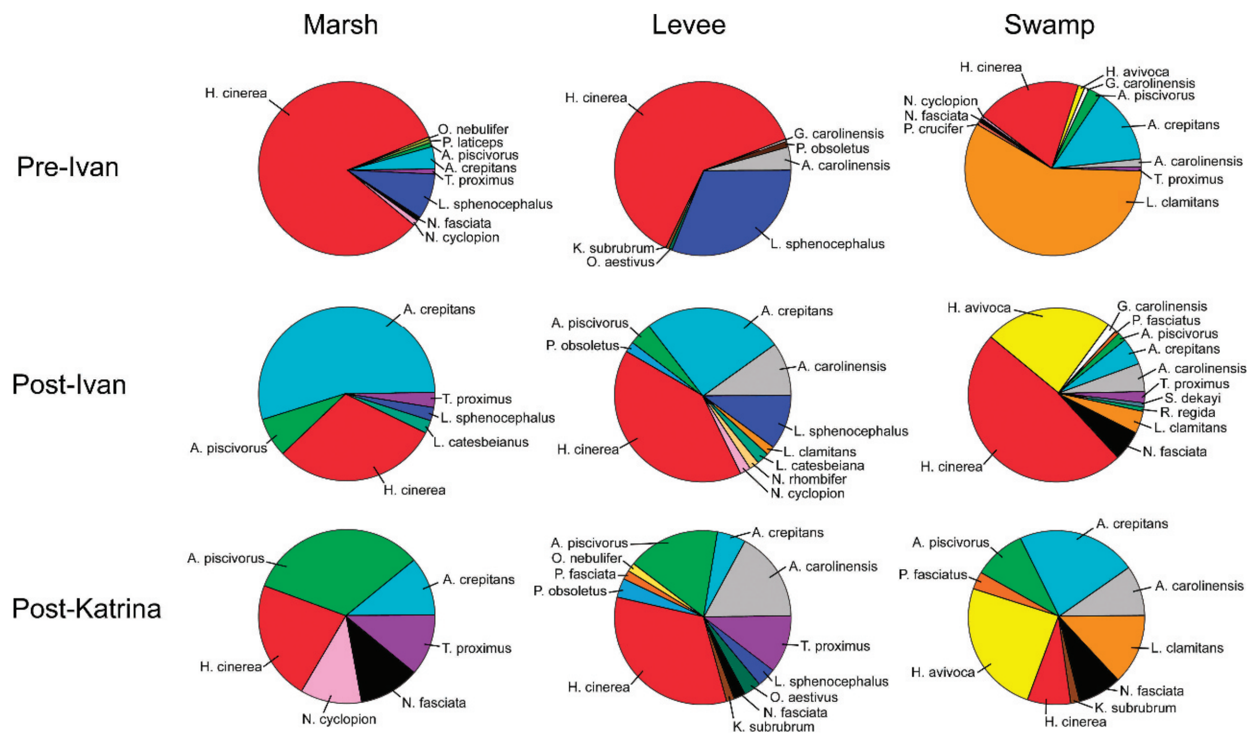

Figure 2. Community composition for marsh, levee, and forested swamp habitats during pre-Ivan, post-Ivan, and post-Katrina surveys. Each slice represents standardized abundance for each species.

However, two of these variables were higher in marsh and levee habitats than in the forested swamp, wind score (K-W test = 11.332, p = 0.003) and water temperature (ANOVA: $F_{2,253}$ = 3.8, p = 0.024, R^2 = 0.029). There was no difference in air temperature among habitats (ANOVA: $F_{2,265}$ = 0.7, p = 0.503, R^2 = 0.005, Table 3). Significant temporal differences existed for some environmental conditions. The warmest water (mean = 28.6°C, K-W test = 24.7, p < 0.001) and air temperatures (mean = 25.3°C, K-W test = 6.4, p = 0.041) occurred in post-Ivan surveys, and the windiest conditions were recorded in post-Katrina surveys (K-W test = 54.6, p < 0.001).

Hurricane Effects

The impacts of hurricanes were decreased abundance and diversity, and increased evenness of the herpetofaunal communities in marsh, levee, and forested swamp habitats. Abundance and diversity were significantly higher during surveys conducted pre-Ivan for all habitats compared to post-Ivan and post-Katrina surveys (diversity: $F_{2,9}$ = 17.5, p = 0.011, R^2 = 0.914; abundance: $F_{2,8}$ = 11.0, p = 0.042, R^2 = 0.884, Table 4) and all assemblages became more even ($F_{2,9}$ = 7.8, p = 0.041, R^2 = 0.802, Table 4). Species richness did not differ among survey periods ($F_{2,9}$ = 0.0, p = 0.982, R^2 = 0.507).

Species evenness was highest in post-Katrina marsh surveys and lowest in pre-Ivan marsh surveys when the community was dominated by *H. cinerea* (Table 4, Figure 2, Appendix 1). Prior to hurricane Ivan, *L. clamitans* was the most abundant frog in the forested swamp but its abundance was reduced by each hurricane event; eventually *Hyla avivoca* (Bird-voiced Treefrog) became the most abundant frog (Figure 2, Appendix 1). Levee reptile assemblages were less even than marsh or forested swamp reptile assemblages; *A. piscivorus* and *A. carolinensis* made up 67% of the levee reptile assemblage abundance. In general, habitats shifted from amphibian dominated communities before the hurricanes to more even amphibian and reptilian communities post-Katrina (Figure 2).

Pre-Ivan survey periods supported higher numbers of herpetofauna in every habitat, but surveys accumulated species slower than during the post-Ivan and post-Katrina periods (Figure 3a, b, and c). Rarefaction curves predict that levee and marsh habitats had highest species richness during the post-Katrina surveys (Levee: 10.9, 95% CI 9–13 species, n = 44; Marsh: 5.6, 95% CI 5–7 species, n = 8,

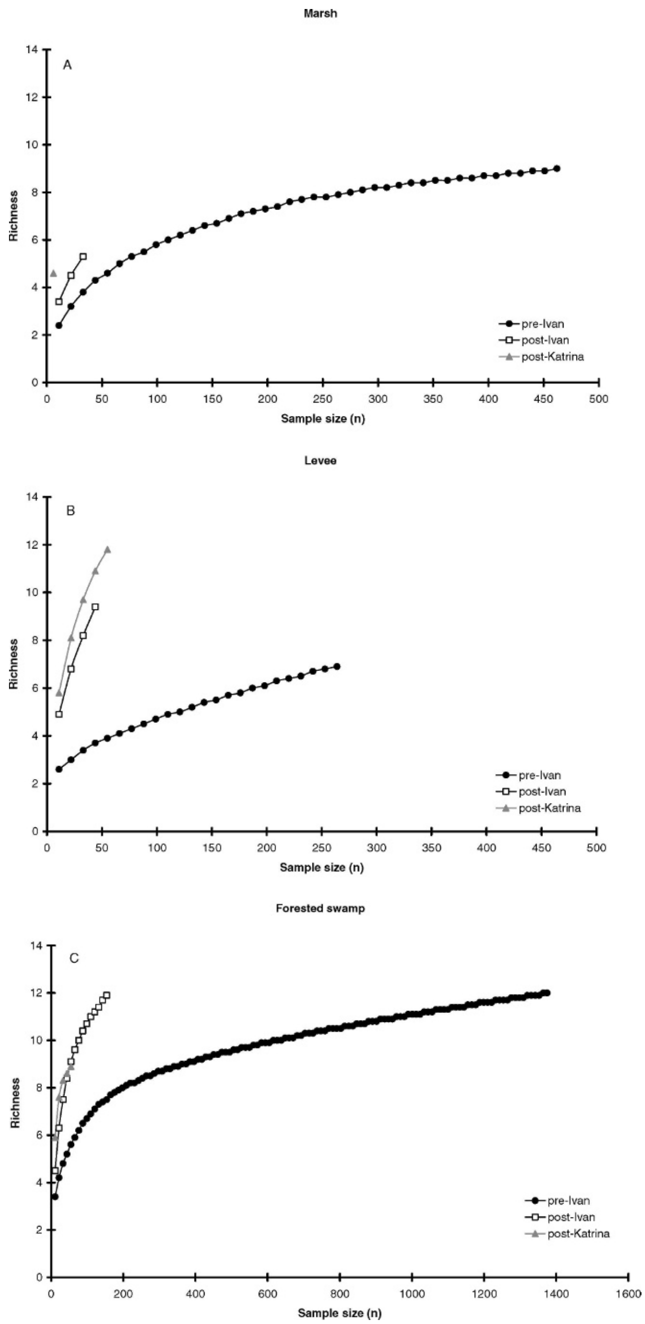

Figure 3. Rarefaction curves estimated for A) marsh, B) levee, and C) forested swamp habitats during three survey periods. Species richness was estimated by E(Sn) and sample size (n) was number of individuals. The slope describes the rate of relative species accumulation and the height was estimated species richness (Stewart et al. 2005).

Figure 3a, b) and forested swamp habitat had highest richness during post-Ivan surveys (9.1, 95% CI 9.1–11.3 species, n = 55 individuals, Figure 3c).

Hurricanes affected water salinities within habitats. Salinity was highly variable (range 0.0 to 8.10 ppt) but mean salinity increased during post-

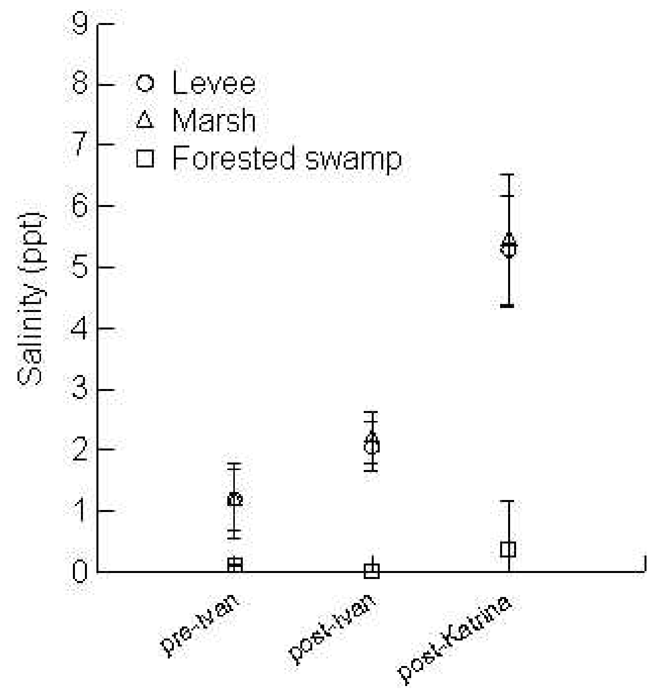

Figure 4. Mean salinity concentrations (ppt) and SD of survey period separated by habitat.

Katrina surveys (4.38 ppt) compared to either pre-Ivan (0.93 ppt) or post-Ivan surveys (1.70 ppt) (K-W test = 84.6, $p < 0.001$). Salinity in marsh and levee habitats was significantly higher than the forested swamp habitat (K-W test = 123.5, $p < 0.001$; Figure 4, Table 3).

Comparison to Platt et al. (1989)

We recorded 898 individuals during 167 survey hours in the MWMA during the five years of this study. We found 21 of the 27 species previously recorded by Platt et al. (1989), plus four additional species, *Scincella lateralis* (Little Brown Skink), *Kinosternon subrubrum* (Eastern Mud Turtle), *L. clamitans*, and *Hyla squirella* (Squirrel Treefrog, Table 1). *Hyla cinerea* was the most abundant amphibian in both studies. *Agkistrodon piscivorus* was common in our surveys, but Platt et al. (1989) considered the species rare or uncommon. Salamanders (Urodela) were absent from both this study and Platt et al. (1989).

DISCUSSION

Our study documented change in herpetofaunal community composition, abundance, and diversity across three habitats impacted by three hurricanes over five years. We found that species diversity decreased and evenness increased with each hurricane event (Table 4), causing shifts in the dominant species. Evenness increased in habitats because abundance of rare species increased (e.g., *A. piscivorus* in marsh, and all reptiles in levee and forested swamp) and dominance of some species decreased (e.g., *H. cinerea*, *L. clamitans*). In forest canopy gaps created by Hurricane Opal in western North Carolina, higher reptile abundance, richness, and diversity was also detected (Greenberg 2001).

Successive years of poor reproductive success can lead to population extinction in amphibians (Semlitsch et al. 1996). Amphibians (adults, larvae, and eggs) are intolerant of saltwater because of their permeable membranes (Balinsky 1981, Duellman and Trueb 1986). Hurricanes Ivan, Katrina, and Rita inundated marsh at MWMA with saltwater at a time when vulnerable tadpoles were developing in marsh pools or had recently metamorphosed. A salinity increase would result in immediate tadpole mortality or prolonged developmental periods.

Reptiles were affected differently than amphibians. Habitat changes associated with the hurricanes Ivan and Katrina (i.e., decreased canopy cover, addition of saltwater via extensive flooding, and increase in debris) increased numbers for many species of reptile, while amphibians experienced drastic reductions. The snakes, *Thamnophis proximus* (Western Ribbonsnake) and *A. piscivorus*, two common habitat generalists (Dundee and Rossman 1989), showed an increase in abundance after the hurricanes in both levee and marsh habitats, although they decreased on AI. After Hurricane Floyd swept over the Bahamas, *Anolis sagrei* (Brown Anole) persisted possibly because their eggs can withstand inundation of saltwater for several hours (Losos et al. 2003). Reptiles may better survive because they are less dependent on freshwater than amphibians, are tolerant of saltwater (Andreone et al. 2003), and have sufficient mobility to escape flood water.

Forested swamp and levee habitats have considerable microhabitat heterogeneity from trees and shrubs and the associated refugia (debris, rotten logs, treeholes), which could account for higher species richness than in marsh. However, forested swamp habitat also supported the least diverse herpetofaunal community of all habitats because of three dominant amphibian species. Community compositions between marsh and levee habitats were most similar, probably because of close proximity.

In conclusion, hurricanes impacting the MWMA and adjacent forested swamp habitats in southeastern Louisiana significantly affected the herpetofaunal community composition, diversity, and abundance. These catastrophic events effectively reset the competition game board in terms of inducing greater species evenness in the herpetofaunal community, which could affect community dynamics. Our study demonstrates how long-term monitoring can offer unique opportunities to gain a better understanding of ecosystem function (Tinkle 1979, Cody and Smallwood 1996, Fitch 1999, Fitch 2006). This knowledge has obvious benefits to management and conservation of valuable habitats such as the threatened wetlands of Southeastern Louisiana.

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Appendix 1. Number of observed individuals and observed richness in Manchac Wildlife Management Area and Alligator Island, Louisiana during 2002–2006. Additional taxonomic detail on each species can be found in Table 1.

	Manchac WMA						Alligator Island		
	Marsh			Levee			Forested Swamp		
	pre-Ivan	post-Ivan	post-Katrina	pre-Ivan	post-Ivan	post-Katrina	pre-Ivan	post-Ivan	post-Katrina
Amphibians									
A. crepitans	20	23	1	0	13	3	201	8	14
G. carolinensis	0	0	0	2	0	0	1	3	0
H. avivoca	0	0	0	0	0	0	20	39	15
H. cinerea	392	13	2	169	20	19	282	77	5
L. catesbeianus	0	1	0	0	1	0	0	0	0
L. clamitans	0	0	0	0	1	0	809	7	8
L. sphenocephalus	40	1	0	84	5	2	0	0	0
O. nebulifer	1	0	0	0	0	1	0	0	0
P. crucifer	0	0	0	0	0	0	1	0	0
Abundance	453	38	3	255	40	25	1314	134	42
Observed richness	4	4	2	3	5	4	6	5	4
Reptiles									
A. carolinensis	0	0	0	12	5	10	20	9	6
A. piscivorus	4	3	3	0	2	10	32	3	6
K. subrubrum	0	0	0	1	0	1	0	0	1
N. cyclopion	4	0	1	0	1	0	1	0	0
N. fascista	4	0	1	0	0	1	12	9	5
N. rhombifer	0	0	0	0	1	0	0	0	0
O. aestivus	0	0	0	1	0	2	0	0	0
P. fasciatus	0	0	0	0	0	1	2	1	2
P. laticeps	1	0	0	0	0	0	0	0	0
P. obsoletus	0	0	0	1	1	2	0	0	0
R. regida	0	0	0	0	0	0	0	1	0
S. dekayii	0	0	0	0	0	0	0	1	0
Abundance	16	4	6	15	10	33	72	27	20
Observed richness	5	2	4	4	5	8	6	7	5
Herpetofauna									
Total abundance	469	42	9	270	50	58	1386	161	62
Observed richness	9	6	6	7	10	12	12	12	9