ANTHROPOGENIC IMPACTS AND LONG-TERM CHANGES IN HERPETOFAUNAL DIVERSITY AND COMMUNITY COMPOSITION ON A BARRIER ISLAND IN THE SOUTHEASTERN UNITED STATES

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Abstract.—We determined the impacts of human development on the herpetofauna of Kiawah Island, a barrier island in South Carolina, USA. We used drift fence arrays with pit and snake traps, cover boards, and visual encounter surveys to sample herpetofauna at twelve sites along a gradient of developmental density (low, moderate, and high) in two dominant habitats (forest and sand dune). We found the highest species richness in the low development area with 16 species, while we found 14 species in the moderate area and 13 species in the high area. We also found that abundance was the highest in the low development area with 587 individuals encountered. However, we found no statistically significant differences in richness and abundance across development areas. Diversity indices and evenness were significantly higher in the moderate and high development area when we compared them to the low development area, which we attributed to the large numbers of a few amphibian species that we found in the low development area. Community composition was fundamentally different between development areas; we encountered the largest number of families and sensitive species in the low development area. Furthermore, we found four unique species in the low development area, whereas we found one unique species in the moderate area and none in the high area. We found that species richness and abundance were significantly higher in forest habitats when compared to sand dunes, however we found two species only in the sand dunes. When we compared the results of our survey to a survey completed a few decades ago, we found that Kiawah may have lost two species but has retained 29 other herpetofaunal species and has gained two more species. We found that a variety of vegetative and environmental characteristics were important for predicting richness and abundance within each habitat. Overall, our results indicate that a mixture of various levels of development and types of habitat with certain characteristics (e.g. plant species richness, canopy cover, etc.) may have the ability to maintain the greatest herpetofaunal diversity on barrier islands.

Key Words.-amphibian; biodiversity; community ecology; conservation; development; reptile

INTRODUCTION

Anthropogenic development can transform and destroy natural habitats, representing a cause of worldwide biodiversity declines and a significant problem for protecting wildlife (Vitousek et al. 1997; Brooks et al. 2002; Lovelock 2006; Wilson 2006). While sometimes leading to complete habitat destruction, human development can also turn contiguous natural areas into fragmented patches. This habitat fragmentation can lead to myriad negative effects, including a decrease in overall habitat area (Saunders et al. 1991; Flather and Bevers 2002), increases in edge effects (Yahner 1988; Suarez et al. 1997), facilitation of exotics (Suarez et al. 1998; Lockwood et al. 2007), and a cascade of other biotic and abiotic changes (Harrison and Bruna 1999; Watling and Donnelly 2008) that typically reduce species richness, abundance, and diversity, and alter species composition (Bell and Donnelly 2006). Reducing species richness, abundance, and altering community composition threatens ecosystem integrity by altering biotic interactions, abiotic processes, and resiliency to further

environmental change (Ehrlich 1994; Tilman et al. 1997; Chapin et al. 2000; Fornara and Tilman 2008).

Although anthropogenic disturbance has clear impacts on natural ecosystems, species vary in their tolerances to human development. Declines in reptile and amphibian species richness and abundance often follow habitat loss and transformation (Shine 1991; Buhlmann 1995; Glor et al. 2001; Driscoll 2004; Stuart et al. 2004). The decline of amphibian and reptiles due to human development happens for several reasons (Alford and Richards 1999; Gibbons et al. 2000). First, a suite of biological traits makes herpetofauna vulnerable to pathogens, environmental contaminants, climate change, and invasive species (Vitt et al. 1990; Marco et al. 1999; Shine 2005). Second, they have limited mobility, which increases road mortalities and limits dispersal (Semlitsch and Ryan 1998; deMaynadier and Hunter 2000). Finally, they have narrow habitat tolerances and breeding requirements (Cushman 2006) such that environmental and vegetation variables play important roles in structuring and maintaining herpetofaunal communities (How and Dell 2000). This is especially true for amphibians, which often have specific breeding

needs, moisture requirements, and sensitivity to temperature because of their highly permeable, glandular skin (Findlay and Houlahan 1997). The narrow habitat requirements of amphibians often exacerbate the negative effects of habitat transformation, degradation, and edge effects that follow human disturbance and habitat fragmentation (Semlitsch 2000; Cushman 2006). These characteristics also make reptiles and amphibians excellent indicators of overall environmental health (Mullin and Seigel 2009).

Conversely, some biological traits of reptiles and amphibians may enable them to maintain viable populations in small, fragmented patches such as those by human development and caused habitat fragmentation. Compared with similar-sized terrestrial vertebrates, reptiles and amphibians have low energetic requirements, small home ranges, and the ability to persist in higher densities (Pough 1980; Bell and Donnelly 2006). Lizard distributions and abundances are not associated with fragment isolation or size (Dickman 1987; Burkey 1995; Jellinek et al. 2004), but instead are influenced by environmental and vegetation variables (Jellinek et al. 2004). In fact, some lizards favor edge environments (Schlaepfer and Gavin 2001) that would commonly follow habitat fragmentation. Thus, herpetofauna may be resistant to the effects of habitat fragmentation as long as the fragments maintain suitable habitat.

Isolated island ecosystems are more vulnerable to change than mainland ecosystems because of their small areas and their lack of major elements of the biota of (Henderson 1992; Vitousek continents 1998). Furthermore, the species that inhabit islands are more susceptible to decline than are mainland species because they generally have smaller populations, restricted genetic diversity, limited critical habitat, and are disproportionately negatively impacted by introduced species (Vitousek 1998). Barrier islands are elongated, shore-parallel features that are separated from the mainland by rivers and bays (Hayes 2005) and are a dominant geomorphic feature along the United States Atlantic and Gulf Coasts (Zhang and Leatherman 2011). The U.S. has the largest number of barrier islands worldwide, and approximately 24% of the total global length of barrier islands (Stutz and Pilkey 2011). Barrier islands are under tremendous development pressure, particularly in the United States (Stutz and Pilkey 2011). Taking into account the concentration of human populations and limited area, barrier islands are viewed as more vulnerable to human development than mainland ecosystems (Schlacher et al. 2007; Weinstein et al. 2007; Feagin et al. 2010). Despite the fact that the coastline of the southeastern U.S. (including barrier islands) has undergone rapid population growth for the past several decades and is predicted to continue growing (Crossett et al. 2004), few studies have

investigated the impacts of anthropogenic activities on barrier island herpetofauna in the southeastern U.S. (Gibbons and Coker 1978; Gibbons and Harrison 1981). This is particularly important because reptiles and amphibians are quite diverse (over 160 species) in the southeastern U.S.

Barrier island habitats exhibit a drastic decrease in physical stress and increase in complexity and vegetation cover landwards (McLachlan 1991) as the habitat transitions from sand dunes systems near the ocean to forested habitats more inland. Increased vegetation cover mediates temperatures, maintains moisture, creates stable microenvironments, and is responsible for general increases in habitat complexity (Hesp 1991). Habitats with high structural complexity typically support more species and individuals than nearby, less complex habitats (Bell et al. 1991). Complex habitats can reduce competition by providing more refuges or a greater spectrum of discrete resources and microhabitats, thereby allowing for enhanced niche partitioning (MacArthur and Levins 1964; Almany 2004).

We examined the impacts of human development on the herpetofauna of Kiawah Island, a barrier island in South Carolina, USA. This island has been progressively developed over the last several decades and thus we were able to identify a gradient of development and test its relationship with patterns of herpetofaunal richness, abundance and community composition. Additionally, a herpetofaunal survey was completed prior to extensive development on the island (Gibbons and Harrison 1981) allowing us to compare whole island species diversity before and after development. The island had two dominant habitats types that contain herpetofaunal communities, forest and sand dune, and we conducted sampling surveys in both. Finally, we measured a suite of microhabitat variables at each site because they are important for herpetofauna (Jellinek et al. 2004). Our study tests five hypotheses: (1) whole island species richness has decreased since the original survey; (2) areas of lower development will maintain higher herpetofaunal richness, abundance, diversity (i.e., higher exponential Shannon diversity and inverse Simpson diversity [Gotelli and Chao 2013] and evenness (a measure how equal are abundances of species) compared to areas of higher development; (3) forested habitats will have greater richness, abundance, diversity, and evenness than sand dune habitats; (4) forested habitats will have some unique species not found in the sand dunes habitats and vice versa; and (5) environmental and vegetation variables will have significant relationships with species richness and abundance within each habitat type.



FIGURE 1. A). Location of Kiawah Island, South Carolina, USA. B). Land use patterns on Kiawah Island in Charleston County. C) Locations of the 12 study sites on Kiawah Island in Charleston County, South Carolina.

MATERIALS AND METHODS

Study site.—Kiawah Island is a 3,330 ha barrier island located 45 km southwest of the Charleston peninsula in Charleston County, South Carolina, USA (32°36'N, 80°4'W; Fig. 1). The island consists of maritime forests, an extensive salt marsh dominated by Smooth Cordgrass (*Spartina alterniflora*), and a 16-km long, open beach

with associated dune systems. The Town of Kiawah Island is a gated tourist community with five 18-hole golf courses and over 1,100 full-time residents that live in low-density developments, but this population can exceed 10,000 people per day during the summer tourist season (Town of Kiawah Island. 2010. Comprehensive Plan: Population Element. Available from http://www.kiawah island.org/municipal-library [Accessed 26 June 2015]). Live Oak (Quercus virginiana), Sabal Palm (Sabal palmetto), Slash Pine (Pinus elliottii), and Loblolly Pine (Pinus taeda) typically dominate the forested sites on the island. Wax Myrtle (Morella cerifera), Bitter Panicgrass (Panicum amarum), other grass species, shrubs, and trees characterize the sand dune habitats on the island. The island has a maximum elevation of 6.11 m above sea level and an average of 1.43 m above sea level. Historically, there were 31 known non-marine herpetofaunal species on Kiawah: 24 reptiles and seven amphibians (Gibbons and Harrison 1981).

We sampled four sites in each of three development areas (high, moderate, and low density) for a total of 12 sites on the entire island (Table 1; Fig. 1). Of the four sites within each development area, we sampled two forested sites and two sand dune sites (Table 1: Fig. 1). We categorized the west end of the island as the high development area, the east end of the island as the low development area, and center of the island as the moderate development area. We categorized development areas in this way because the island was developed step-wise from west to east starting in the 1970s and the east end of the island has an additional security checkpoint that limits the number of tourists and has additional building standards. We later quantified development areas using remote sensing and GIS techniques (see below). Study sites ranged in area from 1.3-8.5 ha, and were located in various sized fragments (Table 1; Fig. 1). Forest and sand dune sites were coupled, with each forest site located inland from each sand dune site (Fig. 1). Mean distance between coupled forest and sand dune sites was 1,065 m. Mean distance between adjacent forest sites was 2,364 m and between adjacent sand dune sites was 1,817 m. The distances between sites and separation of sites by roads, marsh, and developed areas probably prevented many species from moving between sites. However, some of the snakes and lizards we captured can have large home ranges (Clark 1967; Macartney et al. 1988) that could overlap between two adjacent sites, particularly sites that were not separated by major barriers (e.g., some of the adjacent sand dune sites).

Characterization of human development and land use.—Accurate data on land use are essential for the analysis of environmental processes and implementation of effective management plans (Anderson et al. 1976).

Site Number	Site Name	Habitat	Development Category	Methodology Used	Site Size (ha)	Fragment Size (ha)
1	Can Sam's	Forest	High	VES only	85	27.3
2	Cap Sam's	Sand Dune	High	VES only	8.1	9.3
3	Townhall	Forest	High	Traps and VES	2.7	4.0
4	West Beach	Sand Dune	High	Traps and VES	2.2	7.3
5	River Course	Forest	Moderate	VES only	1.7	5.1
6	Sanctuary	Sand Dune	Moderate	VES only	1.5	1.3
7	Vanderhorst	Forest	Moderate	Traps and VES	2.2	6.1
8	Surfsong	Sand Dune	Moderate	Traps and VES	1.4	8.9
9	The Preserve	Forest	Low	VES only	3.4	7.3
10	Beach Club	Sand Dune	Low	VES only	1.9	6.3
11	Cougar Island	Forest	Low	Traps and VES	4.8	88.0
12	Ocean Course	Sand Dune	Low	Traps and VES	1.6	4.2

TABLE 1. Study sites on Kiawah Island, South Carolina, USA used to estimate the effect of habitat and development on herpetofaunal biodiversity.

To accurately investigate the effects of human development on the herpetofauna of Kiawah, we used remote sensing and GIS tools to characterize and quantify land-use and human development on the Island.

We acquired imagery of Kiawah Island from 1994, 1999, 2006, 2009 and 2011 from the South Carolina Department of Natural Resources (SCDNR) in the form of Digital Orthophoto Quarter Quandrangles (DOQQs) with 1 m cell size. We acquired additional aerial photographic imagery (0.5 m cell size) for the year 2006 from the Federal Emergency Management Agency. We used ENVI 4.8 (Excelis Visual Information Solutions, Boulder, Colorado, USA) for processing and analyzing all imagery. We stacked imagery to create a multitemporal, multi-band raster image of the island. From the stacked image, we defined six regions of interest that included marsh, planted grass/golf course, forest, water, houses and concrete, and sand. We chose these regions because they are related to developmental density and may have an impact on herpetofauna. We then used supervised maximum likelihood classification to analyze and quantify the regions of interest on the entirety of the We converted the analysis of the island, island. categorized into the six regions, to a polygon shapefile and exported to ArcMap 10.0 (ESRI, Redland, California, USA). In ArcMap, we integrated the



FIGURE 2. Schematic of a drift fence array used to study community composition on Kiawah Island, South Carolina, USA. Solid black line represents drift fence. Filled circles represent large pitfall traps. Open circles represent small pitfall traps, and rectangle represents funnel trap.

polygon shapefile of Kiawah Island with polygon shapefiles of roads, lakes, and buildings, which we previously digitized. We did this to correct for the obstruction of overhanging vegetation because the analysis was done using aerial imagery. We cleaned the final map using dissolve commands to group all similar land uses into the proper classes (Fig. 1). Following the integration of shapefiles for roads, lakes, and houses, we were able to identify seven prevalent land use classes on the island. These categories were marsh, water, forest, planted grass/golf course, sand, concrete/pavement, and buildings. We quantified the area of these categories for the whole island and for specific development areas (Table 2; Fig. 1). Additionally, we quantified the actual levels of development by comparing current built land (pavement/cement and built land/buildings) to the total area of buildable land (pavement/cement, built land/buildings, and forest). Results of these analyses showed that 32% of the buildable land in the high area has been constructed on, compared to 27% in the moderate area, and 20% in the low area. Thus, our initial classification of sites based on a known history of Kiawah Island matched the quantitative data derived from the GIS method.

Sampling methods.—From April to December 2011 we used passive and active capture techniques to increase our ability of encountering a wide variety of herpetofaunal species. Passive capture methods included drift fence arrays with pit and funnel traps, which allowed for a more complete sampling of herpetofaunal diversity (Todd et al. 2007). We installed drift fence arrays at three forest sites and three sand dune sites, one in each development area (Table 1). We installed four sections of drift fence at each site; each section consisted of 30 m by 1 m black construction siltation control fence (77 g fabric) with 1.2 m wood stakes, erected in transects installed at least 20 cm into the ground. When possible, we placed two sections of fence in N-S orientation, and

	Wh	ole Island	High l	High Development		Medium Development		Low Development	
Land Use Type	Area	% of Area	Area	% of Area	Area	% of Area	Area	% of Area	
Water	456	13.6	46	7.7	152	12.5	258	17.0	
Golf Course	149	4.5	27	4.5	92	7.5	30	2	
Built Land/Buildings	270	8.1	79	13.2	129	10.6	63	4.1	
Forest	981	29.4	207	34.7	455	37.3	318	20.9	
Marsh	1101	33.0	126	21.1	300	24.6	675	44.4	
Sand	302	9.1	94	15.7	50	4.1	158	10.4	
Pavement/Cement	78	2.3	18	3.1	42	3.4	18	1.2	
Total	3337	100	597	100	1220	100	1520	100	

TABLE 2. Land use type by area (ha) and percentage for the whole island and for each type of development area on Kiawah Island, South Carolina, USA.

two sections in E-W orientation. We always spaced sections of fence a minimum of 20 m apart. We placed pitfall traps along each section of fence and this consisted of five 18.9 L (small) plastic buckets and two 37.8 L (large) plastic trashcans per fence. We placed three small pit traps on one side of each fence, and two small pit traps on the opposite side, all spaced evenly apart (Fig. 2). We placed one large pitfall trap on each end of each section of fence (Fig. 2). We also placed one large, two-way funnel trap (Burgdorf et al. 2005) in the center of each piece of fence, on the side with two small pitfall traps (Fig. 2). We used additional fabric to direct animals from the wall of the fence to the funnels of the trap. We placed 24 pieces of fence (four/site), 120 small pitfalls (five/fence), 48 large pitfalls (two/fence), and 24 funnel traps (one/fence). We opened traps for a 24-h period then checked and closed for at least four days before reopening. We opened every trap for a total of 22 trap nights (88,704 pit trap hours; 12,672 funnel trap hours). We released all captured animals (following data collection) on the opposite side of the fence.

For active sampling we used two types of visual encounter surveys (VES) along transects and timeconstrained searches (TCS). We sampled four 100 m transects at each site with drift fences, these transects were parallel to each piece of fence and separated from the fence by 5 m. We sampled four additional transect lines in each of the six sites where no drift fence arrays were installed. We marked transect paths to facilitate consistent, season-long sampling. We walked each transect at a standard pace (approximately 1.5-4.8 km per hour) visually searching for reptiles and amphibians by turning natural cover objects, and inspecting vegetation and leaf litter. We took an average of 15.8 min to complete transects (dunes = 12.14 min; forest = 19.50 min) and they covered 13,200 m over the course of the project. We conducted TCS at each of the 12 sites using the same searching methods, but the TCS lasted 30 min and began from random points within each site for a total of 66 search hours over the course of the project. We performed one VES transect or TCS at each site prior to the opening of traps, alternating methods each visit.

Sampling artificial cover objects is a common method for surveying and capturing reptiles and amphibians (Hampton 2007). We used 60 cover objects to sample reptiles and amphibians at the six sites where drift fence arrays were located. We placed 10 pieces of treated plywood (122 cm \times 48 cm \times 1.3 cm) 10 m apart in a single transect at each site. We placed the cover boards a minimum of 5 m from any permanent or semipermanent water and we did not remove vegetation prior to the placement of the boards. We checked cover objects after the VES or TCS was complete, but before pitfall traps were opened. Additionally, we counted opportunistic sightings (i.e., encounters of reptiles or amphibians that fell outside of any sampling methodology) towards the total number of species on the island, but we did not use opportunistic sightings for any statistical analyses.

Data collection.---We attempted to capture all species of reptiles and amphibians we encountered; however, some individuals escaped prior to capture. We identified escaped individuals to species only when the identity was not ambiguous. We also recorded encounters by Michael Dorcas, J. Whitfield Gibbons and their students, who have been studying Diamondback Terrapins (Malaclemys terrapin) on Kiawah for the last several years and who often encounter herpetofaunal species on the island. We identified captured animals to species and marked them (lizards, snakes, and amphibians were scale or toe-clipped; turtles were notched with a file) and then released them. We clipped toes with sterilized surgical scissors, excising a single toe or combination of toes from each animal, never removing more than one toe per foot (Davis and Ovaska 2001). We marked Eastern Glass Lizards (Ophisaurus ventralis) with passive integrated transponder (PIT) tags. We clipped scales on snakes using surgical scissors (Fitch 1987). We uniquely marked individuals of all reptile species except for Green Anoles (Anolis carolinensis) and Sixlined Racerunners (Cnemidophorus sexlineatus). We mass-marked (the same toe was excised on every individual of the species) all amphibians, Green Anoles, and Six-Lined Racerunners. We completed all data

collection in the field within 1 h of capture and then released captured individual. We only recorded the abundance of individuals we encountered but did not capture, if we could uniquely identify them (i.e., we only encountered one Southern Leopard Frog, *Lithobates sphenocephalus*, at the low development site).

We quantified six site-specific landscape features for each site using ArcMap 10.0 (ESRI 2010) because these landscape features are thought be important in structuring herpetofaunal communities (Cushman 2006). We measured site perimeter, area, and distance to water (mean of the three nearest water bodies, including the ocean) using DOQQs from the South Carolina Department of Natural Resources (SCDNR) in ArcMap. Additionally, we measured the fragment area and perimeter within which each site was contained using the same technique. We analyzed elevation in ArcMap using the United States Geological Survey (USGS) enhanced 10 m resolution Digital Elevation Model (DEM). The USGS 10 m DEM is derived from hypsography (contour and spot elevations) and hydrography (lakes, shorelines, marsh) and is the most accurate data available. Absolute accuracy of the DEM is considered to have a maximum error of 1 to 3 m (Wells and Blackwell 1999). Based on previous studies of Kiawah, the DEM's of the region are accurate enough to differentiate between high marsh and low marsh areas (Batts 2007; Pendleton 2007). We collected four vegetation variables at each site because these variables are known to influence herpetofaunal communities (Jellinek et al 2004). We identified plants to estimate plant species richness. We measured canopy cover at 10 randomly located points within each site by having an observer (KMH) look vertically upwards at each point then determining the proportion of points where the sky is obscured (Vales and Bunnell 1988). We measured ground cover (live plants growing at ground level) at each site using 10 randomly placed 1-m² circular quadrats and estimated the percentage cover of live plants within the quadrat. We measured leaf litter cover in the same way with 10 different quadrat locations, and measured the amount of ground in the quadrat covered by leaf litter.

Statistical analysis.—We compared species richness, abundance, diversity, and evenness among development areas (low, medium, high) and habitats (forest, sand dune) using two statistical methods. First, we computed individual-based rarefaction and extrapolation curves and associated unconditional 95% confidence limits (Colwell et al. 2012). We extrapolated curves to 1000 individuals. This method assumes that some species in the assemblage were not sampled and thus extrapolates the true number of species (Colwell et al. 2012). The extrapolated confidence intervals become very wide at 2–3 times the reference sample abundance, which can be

problematic when some sites have much smaller abundances (Colwell et al. 2012). We interpreted nonoverlapping 95% confidence intervals as evidence of significantly different species richness, which is a conservative approach (Colwell et al. 2012). We computed sampling completeness for richness by dividing the measured richness by the asymptotic richness estimate computed by extrapolation. We also computed Chao1 richness, ACE richness (Abundancebased Coverage Estimator), exponential Shannon diversity and inverse Simpson diversity indices. All of these metrics belong to the family of Hill numbers, which means they provide a measure biodiversity in terms of the number of species (Gotelli and Chao 2013). Chao1 and ACE have a Hill number of 0 and are therefore estimates of richness that do not account for abundance; they estimate the total number of species in a sample. ACE is less biased than Chao1, but Chao1 is more precise (Reese et al. 2014). Exponential Shannon diversity has a Hill number of 1 and therefore it estimates richness by weighting each species as proportional to its abundance (Gotelli and Chao 2013). The exponential Shannon diversity index has been interpreted as estimating the number of species that one might typically encounter at a given site (Gotelli and Chao 2013). The inverse Simpson diversity index has a Hill number of 2 and therefore it estimates richness with a large weight on the most abundant species. The inverse Simpson diversity index estimates the number of common or abundant species at a given site (Gotelli and Chao 2013). We performed these computations in EstimateS (Version 9.10, R. K. Colwell, http://purl. oclc.org/estimates [accessed September 2014]). Pielou's evenness quantifies how close abundances of species are within a community and we computed evenness using the Shannon index (Pielou 1966).

We also used separate two-way ANOVAs to further test the hypotheses that habitat and development have significant effects on 1) species richness, 2) abundance, 3) diversity indexes, and 4) evenness. For these analyses we used observed values as opposed to the estimates described above. We checked the normality of the residuals from each ANOVA using Lilliefors normality test in the nortest package in R 3.0.2 (R Core Team 2013) and for homogeneity of group variances for each factor (habitat and development) using Fligner-Killeen tests in R 3.0.2 (R Core Team 2013). We \log_{10} transformed abundance and did not transform other response variables; this resulted in the assumptions of the ANOVAs being met. We set statistical significance at $\alpha = 0.05$. We also report effect sizes (η^2), which can be interpreted as the proportion of the response's variation explained by each factor.

Finally, we used partial least squares (PLS) analysis with the NIPALS algorithm to examine the multivariate relationship between site characteristics (site area, site

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TABLE 3. The abundances of herpetofaunal species present on Kiawah Island, South Carolina, USA that were quantified in the three development areas and the two habitat types. Numbers in parentheses represent individuals caught in pitfall and snake traps only. An asterisk (*) indicates species observed opportunistically (abundances were not recorded), ^ indicates species observed by Gibbons and Harrison (1981) but not observed during our surveys, and # indicates species that were reported by others working on the island (Michael Dorcas, J. Whitfield Gibbons, and members of their laboratories). **Bold** indicated species not observed by Gibbons and Harrison (1981). The sum of abundances for each species across the development areas equals the sum across the habitat types (e.g. the total abundance of American Alligators was two observations).

		Development	Habitat		
Herpetofaunal Species	High	Moderate	Low	Forest	Dune
American Alligator, Alligator mississippiensis		1 (0)	1 (0)	2 (0)	
Lizards					
Eastern Glass Lizard, Ophisaurus ventralis	2 (0)		2(1)	4(1)	
Green Anole, Anolis carolinensis	8 (1)	17 (4)	6 (3)	28 (8)	3 (0)
Southeastern Five-lined Skink, Plestiodon inexpectatus	7 (7)	10 (8)	3 (3)	19 (17)	1(1)
Broad-headed Skink, Plestiodon laticeps	26 (24)	15 (13)	28 (25)	69 (62)	
Little Brown Skink, Scincella lateralis	17 (11)	1 (0)	2(1)	20 (12)	
Six-lined Racerunner, Aspidoscelis sexlineata	3 (1)	5 (2)	6(1)	3 (1)	11 (4)
Mediterranean House Gecko, <i>Hemidactylus turcicus*</i>					
Amphibians					
Southern Toad Anaxyrus terrestris	29 (29)	5 (3)	123 (112)	157 (144)	
Eastern Narrow-Mouth Toad Gastrophryne carolinensis		0 (0)	101 (100)	101(100)	
Squirrel Treefrog Hyla squirella			300 (0)	300 (0)	
Eastern Spadefoot Scanhiopus holbrookii		2 (2)	5 (5)	7(7)	
Southern Leopard Frog Lithobates sphenocenhalus	12(12)	= (=)	1(0)	13 (12)	
Green Treefrog, Hyla cinerea*; Slimy Salamander, Plethodon glutin	nosus^		1 (0)	10 (12)	
Turtles					
Eastern Mud Turtle, Kinosternon subrubrum			5 (0)	5 (0)	
Eastern Box Turtle, Terrapene carolina		3 (0)		3 (0)	
Slider Turtle, Trachemys scripta*					
Snakes					
Scarletsnake. Cemophora coccinea	1(1)	1(1)		1(1)	1(1)
Southern Black Racer. Coluber constrictor priapus	1 (1)	2 (0)	1 (0)	4(1)	
Coachwhip, Coluber f, flagellum	2(1)	2(1)	(-)		4 (2)
Eastern Ratsnake. Pantherophis alleghaniensis	× /	~ /	2 (0)	2 (0)	~ /
Southeastern Crowned Snake, <i>Tantilla coronata</i>	17 (15)	6 (6)		22 (20)	1(1)
Eastern Gartersnake, Thamnophis s. sirtalis	13 (11)	1 (0)	1(1)	15 (12)	
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Banded Watersnake, Nerodia fasciata fasciata*; Eastern Kingsnake, Lampropeltis getula; Rough Greensnake, Opheodrys aestivus*; Red Cornsnake, Pantherophis guttatus*; Eastern Ribbon Snake, Thamnophis sauritus^; Copperhead, Agkistrodon contortrix[#]; Cottonmouth, Agkistrodon piscivorus[#]; Eastern Diamondback Rattlesnake, Crotalus adamanteus[#]; Timber Rattlesnake, Crotalus horridus[#]

perimeter, mean site elevation, fragment perimeter, fragment area, distance to water, canopy cover, ground cover, leaf litter cover, and plant species richness) and herpetofaunal species richness and abundance within each habitat type. One advantage of PLS is that it is robust to having many predictors and few observations (Carrascal et al. 2009); we had 10 predictors and six sites within each habitat. Prior to the PLS analysis, we centered and scaled all data. We considered site characteristic variables as important predictors of herpetofaunal richness or abundance if the variable had a variable importance in projection (VIP) score ≥ 0.8 and a coefficient that was large relative to other coefficients in the model (Wold 1994). We generated correlation loading biplots of the first two factors to help visualize the sites in multivariate space and to better show the relationship between site characteristics and

herpetofaunal richness and abundance. We used leaveon-out cross-validation to avoid over-fitting the PLS models.

RESULTS

We encountered 29 of the 31 historical non-marine herpetofaunal species on the island with all sampling methods and opportunistic sightings (Table 3). We did not observe the Slimy Salamander (*Plethodon glutinosus*) and the Eastern Ribbon Snake (*Thamnophis sauritus*) during our surveys. We found the Mediterranean House Gecko (*Hemidactylus turcicus*, a non-native introduction) and the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*); both species are new records for Kiawah Island. Thus, our findings show that herpetofaunal species diversity on Kiawah Island

Sam	ple	Measured Abundance	Measured Richness	Estimated Richness (95% CI)	Sampling Completeness for Richness	Chao1 (95% CI)	ACE
	Low	587	16	20 (13-26)	0.80	19 (16–33)	19
Development Area	Moderate	71	14	16 (12–20)	0.88	15 (14–24)	15
Tirou	High	138	13	15 (11–19)	0.87	14 (13–24)	14
	T (772	17	10 (17, 20)	0.04	10 (10, 10)	10
Habitat	Forest	112	17	18 (17-20)	0.94	18 (18–19)	18
	Dune	21	6	9 (2–16)	0.67	9 (6–30)	9

TABLE 4. Herpetofaunal species richness estimators and sampling completeness for development areas and habitats. Descriptions of each estimator can be found in the Methods.

has remained relatively stable over the last several decades, although species composition has changed.

We encountered 796 individuals of 20 herpetofaunal species (15 reptiles and five amphibians) representing 14 families with standardized methodology (VES, cover board and trap; Table 3). Amphibians dominated all of our encounters (73% of encounters and captures), with Southern Toads (*Anaxyrus terrestris*), Eastern Narrow-Mouth Toads (*Gastrophryne carolinensis*), and Squirrel Tree Frogs (*Hyla squirella*) accounting for 71% of all of



FIGURE 3. A). Abundance of all species at sites sampled within development areas on Kiawah Island, South Carolina, USA. B). Raw species richness of sites sampled within development areas.

our encounters with standardized methodology and Southern Toads and Eastern Narrow-Mouth Toads accounting for 60% of our trap captures (Table 3). Forests accounted for 775 individuals, which represented 97% of our total encounters and captures (Table 4). We encountered 13 families, four unique species [Eastern

Narrow-Mouth Toad, Squirrel Tree Frog, Eastern Ratsnake (*Pantherophis alleghaniensis*), and Eastern Mud Turtle (*Kinosternon subrubrum*)], and we had the most encounters of one distinctly sensitive species in the low development area [the Eastern Spadefoot Toad (*Scaphiophus holbrookii*), Table 3]. We encountered one unique species [Eastern Box Turtle (*Terrepine carolina*)], and nine herpetofaunal families, and the Eastern Spadefoot Toad in the moderate development area (Table 3). We encountered eight herpetofaunal families but no unique species in the high development area (Table 3).

We found that raw herpetofaunal species richness was highest in the low development area, followed by the moderate development area, and then the high development area (Fig. 3; Table 4). Likewise, we found more individuals in the low development area than the moderate or high development areas (Fig. 3; Table 4). However, we found no significant differences and very small effect sizes among development areas (Table 5) and the confidence intervals around species richness estimators (Table 4) and extrapolation curves (Fig. 4) broadly overlapped. Evenness was not significantly different among developmental areas even though development accounted for about 50% of the variation in evenness (Table 5). Likewise, diversity metrics did not significantly differ among developmental areas although development accounted for a moderate amount of variation in these metrics (about 35–45%, Table 5).

We found that raw herpetofaunal species richness was higher in every forest site (Fig. 3). Additionally, we found that raw abundance varied among sites, with forest sites having the more individuals than sand dunes except Captain Sam's. We found that herpetofaunal species richness and abundance were significantly higher in the forest than in the sand dune with relatively large effect

	Habitat					Development				Interaction				
Site variables	Forest	Sand Dune	$F_{1,6}$	Р	η^2	Low	Mod.	High	$F_{2,6}$	Р	η^2	$F_{2,6}$	Р	η^2
Richness	8.5 ± 3.1	2.5 ± 1.7	13.0	0.011*	0.49	5.8 ± 4.9	5.5 ± 3.5	5.3 ± 3.1	0.1	0.971	0.01	1.5	0.302	0.14
log ₁₀ Abundance	1.7 ± 0.7	$\begin{array}{c} 0.5 \pm \\ 0.2 \end{array}$	16.7	0.006*	0.51	1.4 ± 1.0	1.0 ± 0.5	$\begin{array}{c} 0.9 \pm \\ 0.7 \end{array}$	1.1	0.395	0.06	2.0	0.214	0.19
Exp. Shannon	4.3 ± 2.6	2.7 ± 1.5	1.8	0.223	0.15	1.8 ± 1.4	4.4 ± 1.6	4.4 ± 2.5	2.3	0.182	0.36	0.1	0.914	0.02
Inv. Simpson	3.7 ± 2.1	2.6 ± 1.4	1.4	0.284	0.01	1.5 ± 0.9	3.4 ± 1.2	4.1 ± 2.0	3.3	0.108	0.47	0.1	0.892	0.02
Evenness	0.4 ± 0.2	0.3 ± 0.2	2.0	0.212	0.11	0.1 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	4.6	0.062	0.50	0.5	0.655	0.05

TABLE 5. Means \pm standard deviation, *F*-statistics, *P*-values and effect sizes (η^2) from two-way ANOVAs testing the effects of habitat, development area, and their interaction on each biodiversity metric. An asterisk (*) denotes statistical significance at 0.05 level.

sizes (Table 5) and confidence intervals that did not overlap for estimated richness (Table 4, although Chao1



FIGURE 4. Rarefaction (solid) and extrapolation (dotted) curves with 95% confidence intervals (shaded envelopes) for development areas (Panel A) and habitats (Panel B) at the study site on Kiawah Island, South Carolina, USA. Solid circles represent the measured abundance and richness for each area.

upper 95% confidence interval for the sand dune sites does overlap with the forest sites) and did not overlap for the extrapolation curves (Fig. 4). We found that evenness and the diversity metrics were not significantly different among habitats with very small effect sizes (Table 5). We encountered 80–87% of the estimated true number of species in each development area and 67–94% in each

habitat (Table 4; Fig. 4), which is important because it indicates that our data met one of the main assumptions of extrapolation (Colwell et al. 2102).

Our partial least squares analysis of the forested sites extracted three factors that collectively explained 90% of the variance in site characteristics and 97% of the variance in species richness and abundance. Forested sites with greater plant species richness and larger mean elevation difference had greater herpetofaunal richness (Table 6; Fig. 5). Forested sites with larger site and fragment perimeters, larger mean elevation difference, greater canopy cover, and greater plant species richness had greater herpetofaunal abundance (Table 6; Fig. 5)

Our partial least squares analysis of the sand dune sites extracted four factors that collectively explained 91% of the variance in site characteristics and 93% of the variance in species richness and abundance. Sand dune sites with larger fragment perimeter, larger mean elevation difference, greater canopy cover, greater ground cover and fewer plant species had greater herpetofaunal richness (Table 6; Fig. 5). Sand dune sites farther from water, with larger mean elevation difference, more ground cover, and fewer plant species had greater herpetofaunal abundance (Table 6; Fig. 5).

DISCUSSION

Changes in herpetofaunal diversity.—We found 29 of the 31 historically recorded herpetofaunal species and two new species (Mediterranean House Gecko and the

		Forest		Sand Dune				
		Model Coefficients			Model Coefficients			
	VIP scores	Richness	Abundance	VIP scores	Richness	Abundance		
Site Perimeter	1.171*	-0.192	0.456*	0.579	0.068	-0.008		
Site Area	0.718	-0.106	0.029	0.511	0.027	0.045		
Fragment Perimeter	1.008*	0.124	0.280*	0.814*	0.293*	0.179		
Fragment Area	0.844*	0.177	0.110	0.787	0.184	0.164		
Distance to Water	0.662	0.158	-0.082	0.911*	0.036	0.292*		
Mean Elevation Difference	1.327*	0.226*	0.226*	0.856*	0.290*	0.268*		
Canopy Cover	1.028*	0.130	0.243*	1.241*	0.293*	0.199		
Leaf Litter Cover	0.958*	0.169	0.022	0.947*	0.028	0.203		
Ground Cover	0.554	-0.008	0.107	1.564*	0.271*	0.408*		
Plant Species Richness	1.380*	0.255*	0.238*	1.294*	-0.594*	-0.277*		

TABLE 6. Variable Importance in Projection (VIP) scores and model coefficients from partial least squares analysis of the relationship between site characteristics and richness/abundance for forest and sand dune habitats. An asterisk (*) denotes VIP scores and coefficients that were considered 'important' predictors of richness or abundance.

Eastern Diamondback Rattlesnake), suggesting that species diversity has remained relatively stable on Kiawah Island over the last several decades. We suggest that Kiawah's development practices of low-density development, maintaining natural habitats on the edges of developed lots, along roadways, and in undeveloped lots prior to purchase, may facilitate the movement of herpetofauna among habitat patches and co-existence with humans.

Our results suggest that patches in low developed areas, like Cougar Island, have the ability to harbor a high number of native herpetofaunal species and individuals. However, continued development of Kiawah and the subsequent division of large habitat patches into small fragments may lead to a loss in amphibian species diversity and a herpetofaunal community dominated by a few, disturbance-tolerant species, similar to the composition of our high development area. It is important to note that our survey only sampled a small percentage of the total area of Kiawah Island (Fig. 1) and in particular focused on relatively natural areas (woodlots, dunes); these areas may not reflect herpetofaunal biodiversity in other areas of Kiawah (residential properties, golf courses). Additionally, we sampled for eight months and thus patterns we observed might not reflect variation across longer time scales.

The Mediterranean House Gecko is an introduced species that has become well established near human development throughout the southeastern US over the past few decades (Gibbons et al. 2009) and thus it is likely a new species that came to Kiawah with widespread human development. The Eastern Diamondback Rattlesnake is an elusive species with low population density in many parts of its range (Gibbons and Dorcas 2005) and it may have been present, but went undetected, during the original surveys in the 1970s and 1980s. We failed to encounter the Eastern Ribbon Snake and the Slimy Salamander. These apparent absences, or lack of encounters, could be the result of a

number of factors including low detectability, low population numbers on the island, or the fact that the sites we sampled did not contain populations of these species. For example, the species richness estimators suggest that we did not have complete sampling, which may indicate that we missed these species due to undersampling. Our failure to detect these species could also indicate that they are no longer on Kiawah; however, statistically establishing absence or extinction of species, especially rare or elusive species, can be extremely difficult and typically requires a much larger, multi-year search effort (Kery et al. 2002). The Eastern Ribbon Snake is a freshwater wetland species that consumes small fish and aquatic amphibians (Gibbons and Dorcas 2005). Many of the freshwater wetlands on Kiawah Island are golf course associated ponds where the shoreline vegetation has been reduced, Tilapia (Oreochromis niloticus) and Grass Carp (Ctenopharyngodon idella) have been stocked for aquatic vegetation control and pesticides and fertilizers are regularly applied nearby. All of these factors could imperil the Eastern Ribbon Snake by eliminating their habitat (Harding 1997) and food sources (Zambrano et al. 1998; Sparling et al. 2000; Martin et al. 2010). The Slimy Salamander was historically found in moist hardwood or Palmetto (Sabal palmetto) areas with heavy ground cover (J. Whitfield Gibbons, pers. comm.) and several of our sampling sites included these features. Additionally, drift fence arrays with associated pit and funnel traps are the most effective means of salamander capture (Todd et al. 2007). Thus, sampling bias in terms of location or gear type probably did not contribute to the lack of detection of the Slimy Salamander. Our results are consistent with the demonstrated negative effects of urbanization on salamander abundances (Price et al. 2012) and suggest that Slimy Salamanders have either been extirpated from Kiawah or have a severely reduced population size.

More generally, detectability of species is important for ecological studies because undetected species result



FIGURE 5. Partial least squares correlation loading biplots. A) Forested Sites, B) Sand Dune Sites. Site identities are numbered as in Table 1. X-variable abbreviations: SP = site perimeter, SA = site area, FP = fragment perimeter, FA = fragment area, E = mean elevation difference, DW = distance to water, LL = leaf litter cover, VC = vegetative canopy cover, VG= vegetative ground cover, VS = plant species richness. Y-variable abbreviations: N = abundance of herpetofauna, S = number of herpetofaunal species.

in a downward bias in the estimate of species richness and diversity metrics (Iknayan et al. 2014; Broms et al. 2015). This can be especially problematic for species that exhibit seasonal or occasional bouts of activity or live a cryptic lifestyle (e.g. fossorial or aquatic species), which is the case for many species of reptiles and amphibians (Durso et al. 2011; Guzy et al. 2014). To help account for differential detection of species, one can estimate detection probabilities or fit occupancy models, both which help to correct for bias due to variable detection among species (Iknayan et al. 2014; Broms et al. 2015). Our study design did not explicitly include methods to account for differential detection across species and thus our estimates of richness, abundance, and diversity may be biased. However, both the Chao1 and ACE richness estimators correct for the bias due to rare species and thus comparing these to the measured richness suggest that, on average, 1-3 species went undetected at each site (Table 4). All of our estimates only use data from our traps and VES; these estimates did not use the observations from reliable expert sources that regularly work at Kiawah (Michael E. Dorcas and J.Whitfield Gibbons) that added an additional 10 species to the list of confirmed species. Thus, it is very likely that these 10 species were present at our sampling sites but went undetected due to low detectability of these species, limitations in sampling methods, or that our sampling sites did not overlap with the populations of these species.

Impact of development.---We did not find significant differences in richness or abundance among developmental areas on Kiawah Island. However, this finding did not mean that developmental areas were equally diverse; on the contrary, our data suggest that the low diversity area had lower diversity indexes and evenness as indicated by the relatively large effect sizes for development on these variables. This result appeared to be due to the high numbers of three amphibian species in the low development area. The high numbers and low site evenness were due to large numbers of metamorphosed froglets. Newly metamorphosed anurans are often present in tremendous numbers, especially close to breeding sites (Pechman et al. 1989). While our metrics for richness, abundance, and composition were encounters of species and individuals, large numbers of newly metamorphosed amphibians contributed negatively to the evenness, the exponential Shannon index and inverse Simpson index in the low development area.

Although we computed diversity indexes for the low development area that were less than the other areas, we found the most herpetofaunal families and the largest range of species with varying sensitivities to disturbance and fragmentation in the low development area. We encountered the most amphibian species in the low development area, which may be explained by their sensitivity to development (Delis et al. 1996; Pineda and Halffter 2004; Lannoo 2005; Bell and Donnelly 2006; Todd et al. 2009). We found the Eastern Ratsnake and the Eastern Mud Turtle exclusively in low development area, further highlighting the diversity of the low development area in spite of its relatively low diversity indexes.

Impact of habitat on biodiversity and community composition.—We found that forested sites had greater

herpetofaunal richness and abundance than sand dune sites. We found all amphibians, turtles, and alligators exclusively in the forests because they are dependent upon standing water and/or high moisture and would not survive in xeric dune habitats. We encountered more snakes and lizards in the forests than the sand dune and this may be explained by more complex habitat found in forests which would be expected to support more herpetofaunal species (Bell et al. 1991). Thus, we found most of the herpetofuana on Kiawah Island in forests. However, even though the dune habitat was less diverse it provided key habitat for at least two species (the Coachwhip and Six-lined Racerunner) that may not be able to persist in other habitats on barrier islands.

Site characteristics and herpetofaunal richness and abundance.---We found that elevation differences and vegetative variables (e.g., canopy cover, plant species richness. etc.) were important predictors of herpetofaunal species richness and abundance in both forested and sand dune habitats. Our results provide further support for the importance of environmental and vegetation variables in structuring herpetofaunal communities (Jellinek et al 2004). We could not explain why greater plant species richness was positively related to herpetofaunal richness and abundance in forested sites but negatively related in sand dune sites. We found that canopy cover and leaf litter cover were important predictors of richness and abundance, which is what we expected because these factors help maintain moisture and temperature which are important factors for many herpetofaunal species, especially amphibians (Shine 2005; Todd et al 2009). Additionally, greater leaf litter cover, ground cover and elevation differences may increase habitat complexity, which may explain why we found that these characteristics were positively related to herpetofaunal richness and abundance. Our finding that fragment perimeter was positively related to herpetofaunal richness in sand dunes and abundance in forests was at odds with previous studies of herpetofauna in fragmented habitat patches that show no relationship between fragment size and diversity (Burkey 1995; MacNally and Brown 2001; Jellinek et al. 2004). This suggests that management for larger fragment areas on barrier islands may be an important factor in maintaining herpetofaunal diversity.

Conclusion.—Even though Kiawah Island has been extensively developed over the past several decades, we found that its herpetofaunal richness has remained relatively stable. We found that the different levels of development on the island did not have dramatic effects on species richness or abundance but did have an impact community composition. In addition, we found that forested habitats were more diverse than sand dune habitats and each habitat type harbored unique species.

Collectively, our results indicate that a mixture of various levels of development and types of habitat with certain characteristics (e.g., plant species richness, canopy cover, etc.) may have the ability to maintain the greatest herpetofaunal diversity on barrier islands.

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