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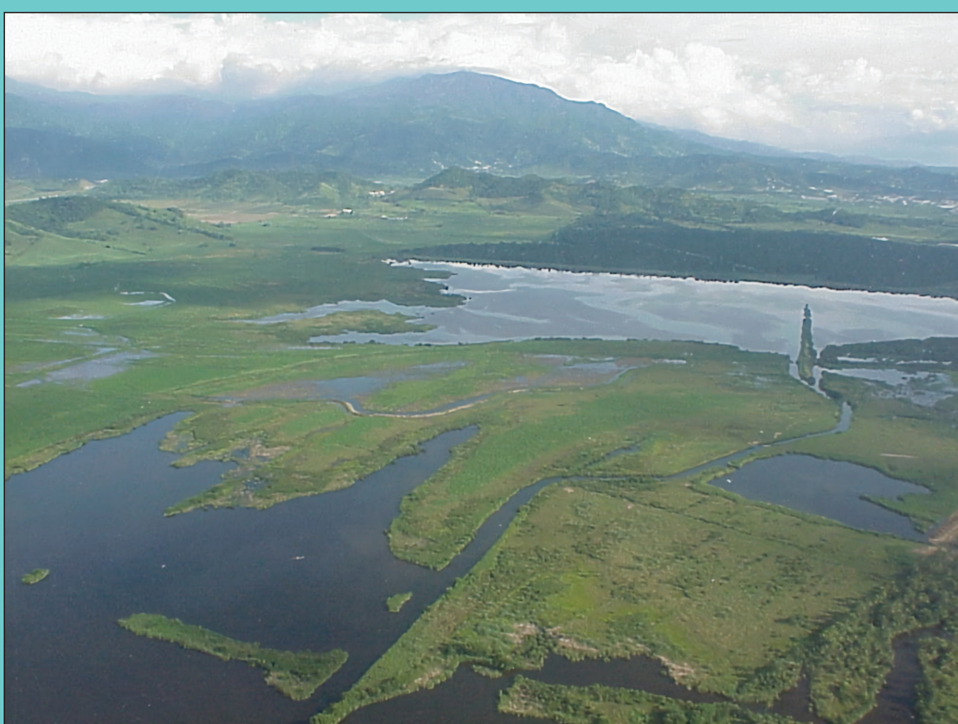

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Cover Photograph: Aerial view of the Mandri lagoons and associated wetlands at the Humacao Nature Reserve, Puerto Rico. Restoration site is located on the left portion of the photograph. Photograph courtesy David Ramos, taken during field surveys conducted by the Puerto Rico Department of Natural and Enviromental Resources.

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Avian Community Responses to Management of Vegetation and Water Levels in Restored Wetlands at the Humacao Nature Reserve, Puerto Rico

Francisco J. Vilella[1,*], José A. Cruz-Burgos[2], Richard M. Kaminski[3], Henry R. Murkin[4], J. Brian Davis[5], Spencer L. Weitzel[5], and Fernando Vizcarra[5]

Abstract - Coastal wetlands of the Caribbean have been greatly reduced in area and quality, and information on wildlife responses to management is lacking. We applied wetland management practices (disking, control of water levels) in a site historically disturbed by *Saccharum* spp. (sugarcane) cultivation at the Humacao Nature Reserve, southeastern Puerto Rico, and evaluated avian community response. We conducted weekly bird surveys and nest searches on disked and non-disked plots within recently constructed impoundments. The avian community shifted from 16 upland dominated species pre-restoration, to 67 wetland-dependent species at the end of our study (2001–2002). Ordination analysis indicated avian guild use of plots varied with environmental variables. Bird species diversity was not influenced by treatment, month, or salinity levels but was influenced by water depth and vegetation cover. Bird abundance was influenced by water depth, but not by treatment, month, salinity or vegetation cover. Furthermore, water depths of 0.10–0.20 m and salinity of ≤15 ppt promoted habitat conditions suitable for a diverse wetland avian community. We located 268 nests of 8 wetland bird species and observed adults with young of various other waterbirds, including species of conservation concern such as *Dendrocygna arborea* (West Indian Whistling Duck) and *Porzana flaviventer* (Yellow-breasted Crake). Bird community responses suggest that management practices (i.e., soil disturbance and control of water levels) can improve wetland biodiversity in abandoned sugarcane fields of Puerto Rico. Moreover, these practices may benefit wetland biodiversity in other Caribbean islands with a similar history of land use and habitat degradation.

Introduction

Wetlands are important repositories of global biodiversity and provide many essential ecosystem services (Hansson et al. 2005, Mitsch and Gosselink 2007). Birds are key vertebrate indicators of wetland conditions and provide a valuable economic resource via ecosystem services such as ecotourism and hunting (Green

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and Elmberg 2014, Woodward and Wui 2001). Wetland losses have contributed to global declines in populations of waterbird species. Global loss of wetlands augments the importance of remaining habitats for waterbirds, particularly in oceanic islands (Laurance et al. 2012). Importantly, wetland restoration has improved habitat conditions, promoting diverse waterbird communities and essential resources in many parts of the world (Murkin and Caldwell 2000, O'Neal et al. 2008).

The Caribbean islands are a priority biodiversity hotspot due to high rates of endemism and habitat loss (Brooks et al. 2006). Caribbean ecosystems have been subjected to anthropogenic impacts for centuries (Lugo and Brown 1988), which have dramatically changed the wetlands of many Caribbean islands. For example, conversion of forested wetlands to wet savannas in Cuba has been attributed to long-term agriculture and use of fire to clear vegetation (Blanco-Rodríguez et al. 2014).

In Puerto Rico, palustrine emergent and forested wetlands of the coastal plain have been greatly impacted in quality and area by deforestation and *Saccharum* spp. (sugarcane) agriculture (Adams and Hefner 1996). These activities reduced *Pterocarpus officinalis* Jacq. (Dragonsblood Tree) swamps to a small number of relict fragments and resulted in loss of ~50% of mangrove forests. While mangroves have recovered in extent and habitat conditions due to legal protection and changes in land use (Martinuzzi et al. 2009), threats to coastal palustrine wetlands remain including agriculture, draining, dredging, siltation, eutrophication, road construction, tourism, and urban encroachment (Adams and Hefner 1996, del Mar López et al. 2001).

The coastal wetlands of Puerto Rico provide wintering and stopover habitat for migratory waterbirds, including *Anas discors* (Blue-winged Teal), *Anas crecca* (Green-winged Teal), *Aythya affinis* (Eyton) (Lesser Scaup), and species of shorebirds (e.g., *Calidris* spp.) (Raffaele et al. 1998). Furthermore, harvest of several resident waterfowl species of Puerto Rico including *Anas bahamensis* (White-cheeked Pintail), *Dendrocygna arborea* (West Indian Whistling Duck), *Oxyura jamaicensis* (Ruddy Duck), and *Nomonyx dominicus* (Masked Duck) is currently prohibited because of historical declines from extensive habitat loss and unregulated hunting (García et al. 2005). Therefore, improving habitat availability and quality for resident and migratory waterbirds in Puerto Rico is an important conservation priority (García et al. 2005, Vilella and Gray 1997). However, available information on avian community response to restoration practices has been mostly limited to temperate wetlands (e.g., Murkin and Caldwell 2000) and is generally lacking for tropical wetlands, including in the Caribbean. Furthermore, no manipulative experiments have been conducted to examine response of wetland wildlife to habitat restoration in the Caribbean islands. We hypothesized that environmental disturbance from soil manipulation and flooding would induce responses by the avian community in coastal wetlands degraded by previous agricultural activities. Herein, we report responses of avian assemblages to the restoration of degraded emergent wetlands in a coastal ecosystem of Puerto Rico.

Field-Site Description

The Humacao Nature Reserve (HNR) is located in the southeastern coastal plain of Puerto Rico (18°10'N, 65°46'W). Annual average rainfall is 190 cm and annual average temperature is 25 °C (Villella and Gray 1997). Sugarcane cultivation, which eliminated the original coastal wetlands during the early 1900s, continued until 1979 when Hurricane David and Tropical Storm Frederick flooded the area. As a result, estuarine lagoons and herbaceous marshes developed (Fig. 1). Habitat types within the HNR include: (1) coastal lagoons; (2) emergent wetlands characterized by dense stands of *Typha domingensis* Persoon (Southern Cattail), sedges, grasses, and vines distributed along a moisture gradient; (3) mangrove forest including the 4 species present in the Caribbean (*Rhyzophora mangle* L. [Red Mangrove], *Avicennia germinans* L. [Black Mangrove], *Laguncularia racemosa* L. [White Mangrove]), and *Conocarpus erectus* L. (Buttonwood Mangrove); (4) Pterocarpus swamp forest; (5) secondary coastal forest; and (6) beach scrub.

When sugarcane production ceased at HNR, unmanaged cattle grazing became common in areas where native vegetation replaced sugarcane. In areas where soil

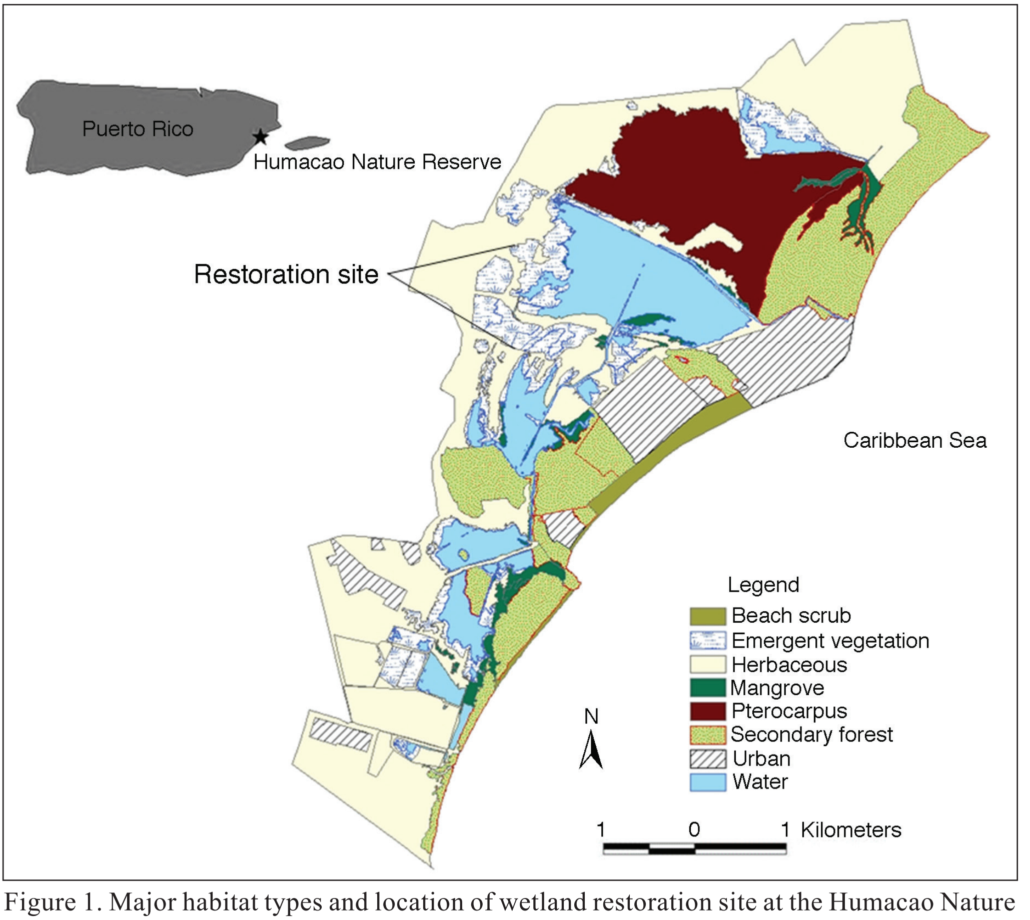

Figure 1. Major habitat types and location of wetland restoration site at the Humacao Nature Reserve, PR, 2001–2002.

was too wet to support cattle, dense stands of spiny vines *Mimosa casta* L. (Graceful Mimosa), *Brachiaria mutica* Forssk. (Para Grass), and *Centrosema pubescens* Benth. (Centro) impeded access by waterbirds. These plant species are typical of disturbed and abandoned agricultural fields in the Caribbean islands and provide little or no value to wetland wildlife (Acevedo-Rodríguez 2005).

Prior to our study, the bird community using emergent wetlands at the HNR was characterized by few species and guilds (Vilella and Gray 1997). Further, water depths (≥2.5 m) of estuarine lagoons increased rapidly from shore to center, limiting use to larger, open water species such as *Pelecanus occidentalis* (Brown Pelican) and *Fregata magnificens* (Magnificent Frigatebird). Following recommendations in the ecological assessment and management plan of the HNR (Vilella and Gray 1997), the Puerto Rico Department of Natural and Environmental Resources (DNER) constructed 3 impoundments. Impoundments were constructed in clay-dominated soils and equipped with water-control structures. Cattle were removed 1 year prior to our study. We labeled the impoundments as north (10.19 ha), east (14.69 ha), and west (20.63 ha). Because of uneven topography, area flooded in the east and west impoundments was 9.34 ha and 10.68 ha, respectively. The north impoundment was entirely flooded.

Methods

Experimental design

We used a randomized complete block design and designated impoundments as blocks to account for variability in soil composition, differences in water sources used to flood impoundments, and existing vegetation among impoundments (Cruz-Burgos 2005). During May 2000, we randomly located 0.5-ha square plots in the north (n = 6), east (n = 7), and west (n = 9) impoundments. We randomly assigned soil and vegetation disturbance (disking) to half of the study plots. Given uneven flooding in the impoundments, we randomly located 3 smaller plots (10 m x 15 m) adjacent to each 0.5-ha disked plot within each impoundment amid continuous stands of vegetation in 2001. We used disking as treatment because the soil had not been disked since 1979 when sugarcane production ceased, and we wanted to stimulate plant germination from the seed bank as is typical of moist-soil wetland management (Fredrickson and Taylor 1982, Hagy and Kaminski 2012). Prescribed timeline for flooding and disking of impoundments was drawdown in late June 2001, followed by disking during late July to early August 2001. Impoundments were flooded during early September 2001. Reserve staff began flooding impoundments about 1–2 weeks after disking, when plants had begun to emerge in disked plots.

Water sources used to flood impoundments included the Antón Ruiz River for the north impoundment, a nearby lagoon for the east impoundment, and runoff and pumping from a nearby lagoon for the west impoundment. We used a YSI® meter (YSI, Yellow Springs, OH, USA) to monitor water salinity and recorded mean water depths in each impoundment. Water depth in the impoundments was maintained at 0.2–0.3 m for the duration of our experiment.

Field sampling

We conducted weekly bird surveys during February and March 2001, and October 2001 to March 2002. Surveys began at sunrise with 1 observer walking the same approximate route both years to scan the impoundments completely, locating or flushing birds, while 3 separate observers recorded birds from a truck bed on the nearby levee. The individual walking the impoundment relayed information (i.e., plot number, bird species, number of individuals) via radio to observers on the truck. Counts were completed for the entire impoundments, including experimental plots. Use of multiple observers allowed us to record information while visually following flushed birds and therefore avoid double counting (Kaminski and Prince 1981, Murkin et al. 1997). We randomly selected the order of impoundments for surveys and sampled all impoundments on every count. Surveys usually required ~3 hours to complete.

Like many avian species in the Neotropics, several Caribbean waterbirds nest throughout the year (Raffaele et al. 1998). Systematic nest searches of the entire impoundments were conducted by teams of 3 observers spaced at regular intervals during 2001 and 2002. We georeferenced nest locations using a portable GPS. Due to time constraints, our nest searches during 2001 were conducted opportunistically. However, in 2002 we conducted weekly systematic nest searches to determine nest stage and nest fate. We estimated survival using the Mayfield (1975) method for all nests located between October 2001 and March 2002 and calculated nest-exposure days from the first day a nest was located until hatching or failure. We considered nests that were disturbed and eggs that were broken or lost before the estimated hatching date as evidence of depredation. We considered a nest to be successful if ≥1 chick hatched.

We used a grid system to randomly locate 3 sampling sites per plot in which we collected vegetation, water depth, and salinity data monthly beginning in February 2001 (Petersen 1985). We clipped plants at ground level within a 0.5-m^2 square inside plots to estimate species-specific above-ground standing crop (van der Valk 1989). We averaged subsample data from each experimental unit (i.e., disked and non-disked plots) to provide a single datum per plot (Gray et al. 1999). We used species-specific above-ground biomass to calculate plant species diversity per plot using the Shannon–Weaver (H') index (Ludwig and Reynolds 1988, Gray et al. 1999). We estimated vegetation cover using a density board located 10 m in each cardinal direction from the center or each sampling site and then averaged percentages to provide a single datum per site (Higgins et al. 1994, Nudds 1977).

Statistical analyses

We estimated bird community metrics for disked and non-disked plots. We used species-specific abundance to calculate bird species diversity (H') and defined richness as the number of species per plot. We estimated bird abundance of all species as the sum of the total number of birds/species counted per plot. Subsequently, we divided each plot sum by the number of surveys performed per month on each impoundment (Ludwig and Reynolds 1988, Nummi and Holopainen 2014).

Community metrics were calculated using package 'vegan' in program R (Oksanen et al. 2018, R Core Team 2017). Metrics included relative abundance (all species), species richness, and species-specific abundance. We created a time-series graph of weekly total avian abundance to visualize numerical dynamics during the study, seasonally, and following applied management practices.

Further, we used package 'vegan' in R to conduct a non-metric multidimensional scaling (NMDS) ordination to examine bird species associations with physical (salinity, water depth) and habitat (plant species diversity, vegetation cover) attributes. For this analysis, we used only bird species known to use wetlands as part of their life history and classified species by foraging guilds. Therefore, we excluded accidental species observed during surveys (e.g., doves, owls).

We analyzed bird species diversity, richness, and abundance using mixed models with random and repeated statements (Little et al. 1996, SAS 1999). Treatment and month were used as fixed main effects. We tested interactions of month by treatment and included salinity, water depth, and vegetation cover as covariates. Differences among significant main effects and interactions were tested using least-square means statements. We designated $\alpha = 0.05$.

Results

Community metrics and ordination

Over the course of the study (February 2001–June 2002), we detected a total of 67 bird species within the HNR impoundments, of which 28 were migratory species (Table 1). Mean species richness per survey was 6.11 ± 0.77 for disked and 3.76 ± 1.07 for non-disked plots. The most abundant bird observed in the impoundments was *Ardea alba* L. (Great Egret, $n = 7226$). Overall, the bird community was dominated by wading birds, including Great Egret (25.2%), *Egretta thula* (Snowy Egret; 13.7%), *Egretta tricolor* (Tricolored Heron; 7.7%), and *Himantopus mexicanus* (Black-necked Stilt; 5.5%). These 4 species accounted for over 52% of the relative abundance in the HNR impoundments. Great Egret and Tricolored Heron were the most frequently observed species in disked plots (94% of surveys), while *Gallinula galeata* (Common Gallinule) and *Butorides virescens* (Green Heron) were the most frequently observed species in non-disked plots (75% of surveys).

Increases in avian abundance throughout the study coincided with management of the HNR impoundments (Fig. 2). The greatest increases in total bird abundance were recorded in 2001 during mid-March–early-April and mid-May–late June. During 2002, abundance began increasing in mid-March, peaking in early May and again in early June. The period of least total bird abundance occurred during late November 2001 (Fig. 2).

Ordination results indicated plant species diversity was negatively associated with water depth, and plant horizontal cover (vertical obstruction) was negatively associated with salinity (Fig. 3). The NMDS ordination yielded an optimal solution in 2 dimensions, with a stress value of 0.22 indicating a moderate degree of fit between the observed and estimated dissimilarity matrices. As expected, diving birds were associated with deeper water and lower plant diversity, whereas granivores

Table 1. Bird species detected during 2001–2002 in the impoundments (impound.) of the Humacao Nature Reserve, PR. Scientific names follow Chesser et al. (2018). N = north, E = east, W = west impoundments.[Table continued on following page.]

Family	Scientific name	Common name	Impound.
Pelecanidae	*Pelecanus occidentalis* L.	Brown Pelican	N, E, W
Fregatidae	*Fregata magnificens* Mathews	Magnificent Frigatebird	E
Laridae	*Larus atricilla* L.	Laughing Gull	E, W
	Gelochelidon nilotica (Gmelin)	Gull-billed Tern	W
Ardeidae	*Ardea alba* L.	Great Egret	N, E, W
	Ardea herodias L.	Great Blue Heron	N, E, W
	Bubulcus ibis (L.)	Cattle Egret	N, E, W
	Butorides virescens (L.)	Green Heron	N, E, W
	Egretta thula (Molina)	Snowy Egret	N, E, W
	Egretta tricolor (P.L.S. Müller)	Tricolored Heron	N, E, W
	Egretta caerulea (L.)	Little Blue Heron	N, E, W
	Nyctanassa violaceus (L.)	Yellow-crowned Night Heron	N, E, W
	Nycticorax nycticorax (L.)	Black-crowned Night Heron	N, E, W
	Ixobrychus exilis (Gmelin)	Least Bittern	N, E, W
Threskiornithidae	*Plegadis falcinellus* (L.)	Glossy Ibis	E
Scolopacidae	*Tringa melanoleuca* (Gmelin)	Greater Yellowlegs	N, E, W
	Tringa flavipes (Gmelin)	Lesser Yellowlegs	N, E, W
	Tringa solitaria (Wilson)	Solitary Sandpiper	N, E, W
	Calidris melanotos Vieillot	Pectoral Sandpiper	N, E, W
	Calidris minutilla Vieillot	Least Sandpiper	N, E, W
	Calidris mauri (Cabanis)	Western Sandpiper	E, W
	Calidris himantopus (Bonaparte)	Stilt Sandpiper	W
	Actitis macularia (L.)	Spotted Sandpiper	N, E, W
	Limnodromus griseus (Gmelin)	Short-billed Dowitcher	E, W
Charadriidae	*Charadrius vociferus* L.	Killdeer	E, W
	Charadrius semipalmatus Bonaparte	Semipalmated Plover	E, W
	Gallinago delicata Ord	Wilson's Snipe	N, E, W
Haematopodidae	*Himantopus mexicanus* (P.L.S. Müller)	Black-necked Stilt	N, E, W
Rallidae	*Gallinula galeata* (Lichtenstein)	Common Gallinule	N, E, W
	Porphyrio martinicus L.	American Purple Gallinule	N, E, W
	Fulica caribaea Ridgway	Caribbean Coot	N, E, W
	Porzana carolina (L.)	Sora	N, E, W
	Porzana flaviventer (Boddaert)	Yellow-breasted Crake	N, E, W
Podicipedidae	*Podilymbus podicipes* (L.)	Pied-billed Grebe	N, E, W
Anatidae	*Anas bahamensis* L.	White-cheeked Pintail	N, E, W
	Anas discors L.	Blue-winged Teal	N, E, W
	Anas crecca L.	Green-winged Teal	E, W
	Anas americana Gmelin	American Wigeon	E
	Anas sp.	Mallard hybrid	E
	Oxyura jamaicensis (Gmelin)	Ruddy Duck	E, W
	Nomonyx dominica (L.)	Masked Duck	W
	Dendrocygna arborea (L.)	West Indian Whistling Duck	E, W
Pandionidae	*Pandion haliaetus* (L.)	Osprey	E, W
Accipitridae	*Circus cyaneus* (L.)	Northern Harrier	W
Falconidae	*Falco columbarius* L.	Merlin	W
Strigidae	*Asio flammeus* (Pontoppidan)	Short-eared Owl	E, W
Trochilidae	*Anthracothorax viridis* (Audebert & Vieillot)	Green Mango	E

and insectivores were associated with shallower water and greater plant diversity. Guilds of waders, shorebirds, and surface feeders (including dabbling ducks) exhibited no apparent association with measured environmental conditions in the ordination. Within guilds, however, birds showed significant variation in their association with environmental variables. For example, *Nycticorax nycticorax*

Table 1, continued.

Family	Scientific name	Common name	Impound.
Cuculidae	*Crotophaga ani* L.	Smooth-billed Ani	N, E, W
Alcedinidae	*Megaceryle alcyon* L.	Belted Kingfisher	N, E, W
Tyrannidae	*Tyrannus dominicensis* (Gmelin)	Gray Kingbird	N, E, W
Emberizidae	*Quiscalus niger* (Boddaert)	Greater Antillean Grackle	E, W
	Dolichonyx oryzivorus (L.)	Bobolink	N, E
	Seiurus motacilla (Vieillot)	Louisiana Waterthrush	E, W
	Geothlypis trichas (L.)	Common Yellowthroat	N, E, W
	Setophaga discolor (Vieillot)	Prairie Warbler	N, E,
	Setophaga coronata (L.)	Yellow-rumped Warbler	E, W
	Coereba flaveola (L.)	Bananaquit	E
	Tiaris olivacea (L.)	Yellow-faced Grassquit	E, W
	Tiaris bicolor (L.)	Black-faced Grassquit	N, E, W
Passeridae	*Passer domesticus* (L.)	House Sparrow	E
Ploceidae	*Euplectes orix* (L.)	Red Bishop	N, E, W
Estrildidae	*Estrilda melpoda* (Vieillot)	Orange-cheeked Waxbill	N, E, W
	Lonchura punctulata (L.)	Nutmeg Mannikin	E
	Amandava amandava (L.)	Red Avadavat	E
Columbidae	*Zenaida aurita* (Temmnick)	Zenaida Dove	N, E, W
	Zenaida asiatica (L.)	White-winged Dove	E
	Columbina passerina (L.)	Common Ground Dove	E, W

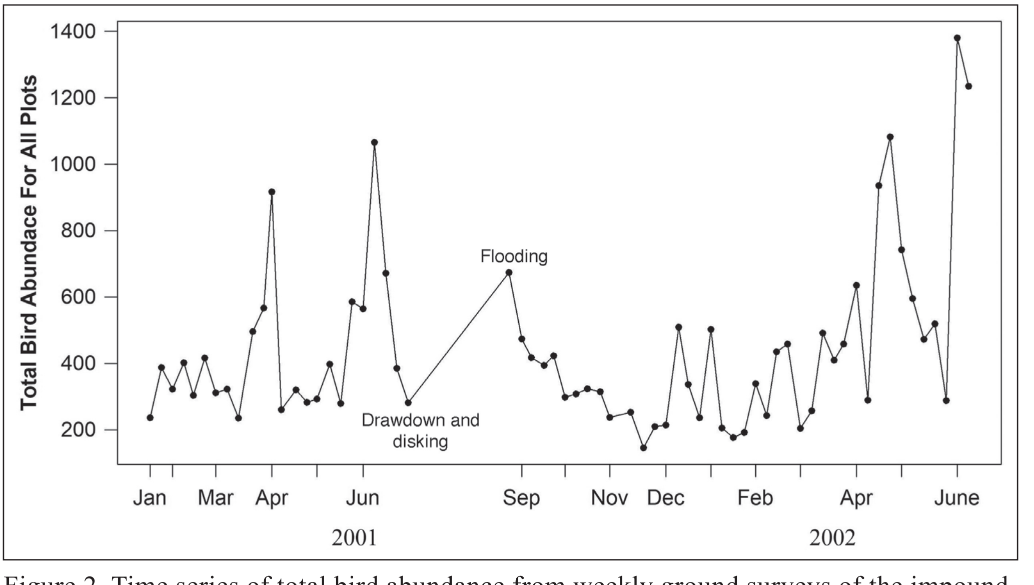

Figure 2. Time series of total bird abundance from weekly ground surveys of the impoundments at Humacao Nature Reserve, PR, January 2001–June 2002.

(Black-crowned Night-Heron, a wader) was associated with deeper water, lesser salinity, greater plant cover, and lesser plant diversity. Conversely, Snowy Egret (also a wader) was associated with shallower water, greater salinity, lesser plant cover, and greater plant diversity (Fig. 3). All environmental variables in the ordination analysis (water depth, water salinity, plant cover, plant diversity) significantly affected avian community dissimilarity ($P < 0.01$).

Bird species diversity and richness

Mixed-model analyses indicated no interaction of month by treatment ($F_{7,\,135}$ = 1.21, P = 0.30) and no month ($F_{7,\,140}$ = 0.83, P = 0.56) or treatment ($F_{1,\,29.9}$ = 1.12, P = 0.29) main effects on bird species diversity. However, bird species diversity was influenced by covariates water depth ($F_{1,\,138}$ = 10.80, P = 0.01) and vegetation cover ($F_{1,\,190}$ = 16.60, $P < 0.01$) but not salinity ($F_{1,\,151}$ = 1.64, P = 0.20). Covariate coefficients indicated bird species diversity would decrease by 1.75 units for each 1-m increase in water depth and 0.01 units for each 1% increase in vegetation cover (Table 2). Generally, bird species diversity fluctuated with increasing water depth (Fig. 4).

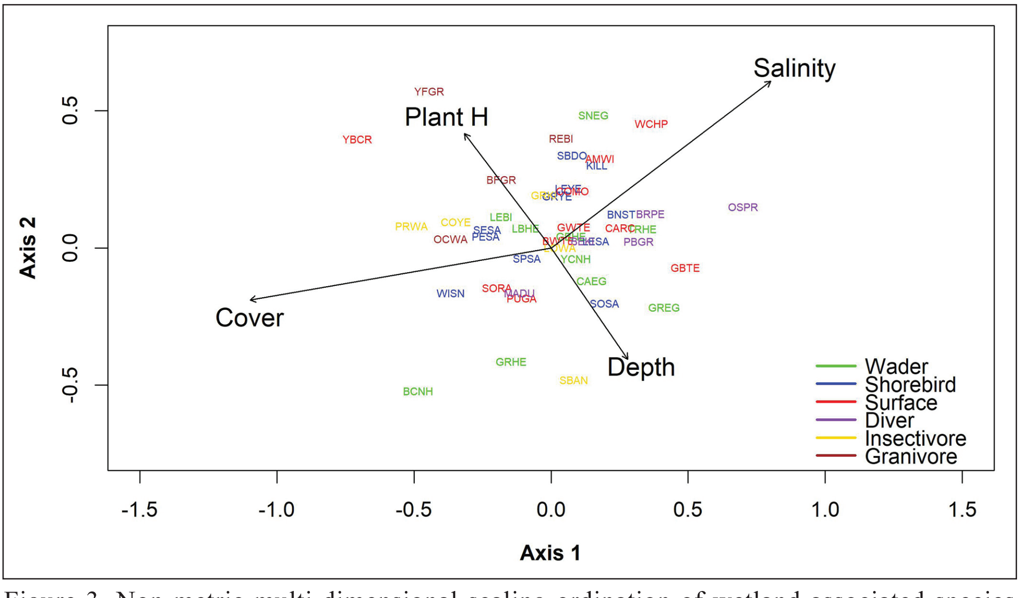

Figure 3. Non-metric multi-dimensional scaling ordination of wetland associated species and environmental characteristics in the impoundments of the Humacao Nature Reserve, PR, 2001–2002. Bird species alpha codes follow Chesser at al. (2018).

Table 2. Covariate coefficients (0 ± SE) of salinity, water depth, and vegetation cover with respect to bird species diversity, richness, and abundance in restored wetlands of the Humacao Nature Reserve, Puerto Rico, 2001–2002. * indicates not significant ($P > 0.05$).

Covariates	Species diversity	Species richness	Bird abundance
Salinity	-0.02* ± 0.02	-0.04* ± 0.09	0.26* ± 0.21
Water depth	-1.75 ± 0.55	-9.27 ± 2.96	-12.07 ± 6.12
Vegetation cover	-0.01 ± 0.003	-0.04 ± 0.01	-0.06* ± 0.05

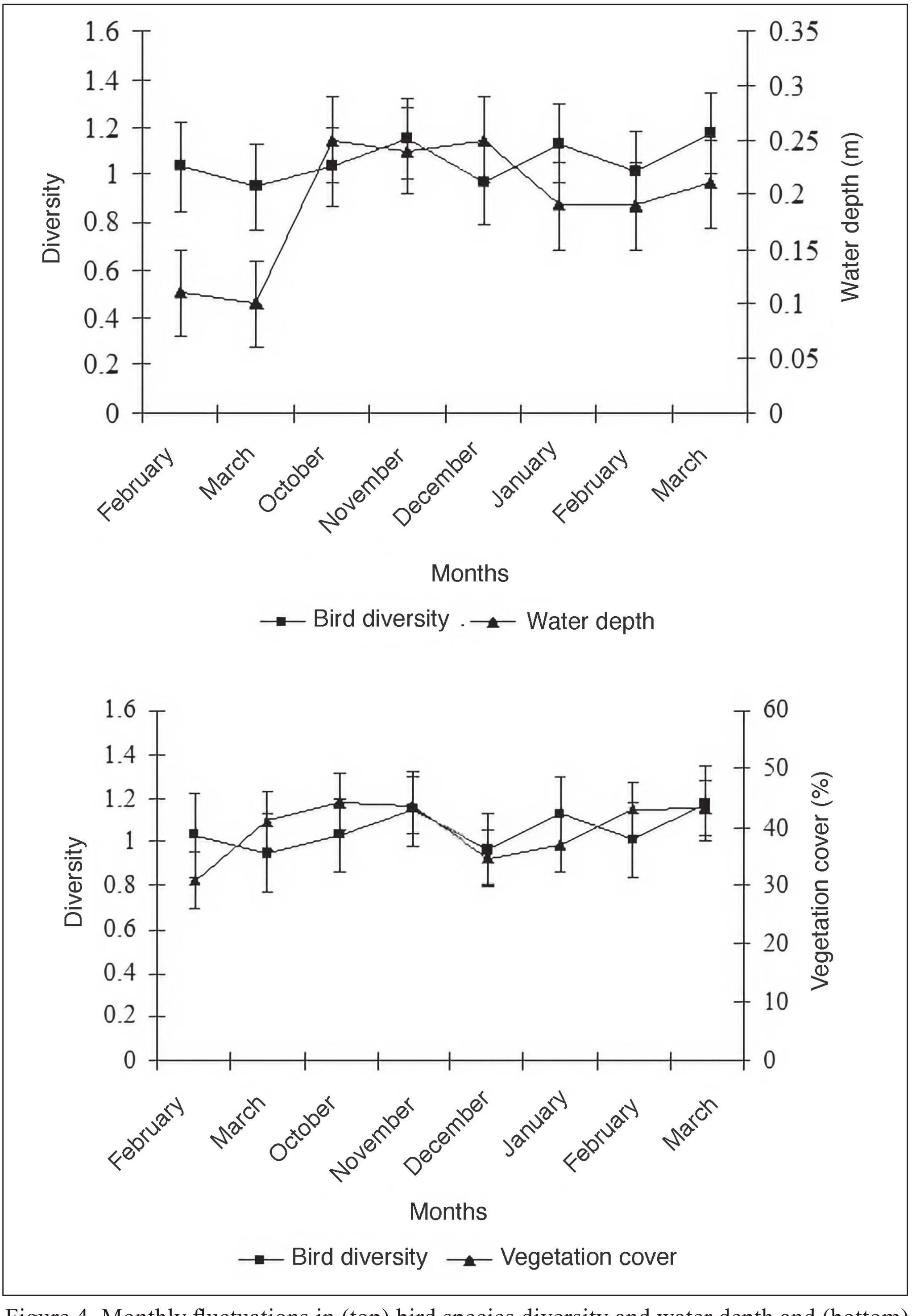

Figure 4. Monthly fluctuations in (top) bird species diversity and water depth and (bottom) bird species diversity and vegetation cover in 3 impoundments of the Humacao Nature Reserve, PR, February 2001–March 2002.

Similarly, there was no interaction of month by treatment ($F_{7, 127} = 0.83$, $P = 0.57$) and no treatment ($F_{1, 28.4} = 2.95$, $P = 0.10$) or month ($F_{7, 132} = 1.20$, $P = 0.30$) main effects on bird species richness. Overall, mean species richness was 6.11 ± 0.77 for disked plots and 3.76 ± 1.07 for non-disked plots. Further, bird species richness was influenced by covariates water depth ($F_{1, 168} = 9.79$, $P < 0.01$) and vegetation cover ($F_{1, 176} = 5.05$, $P = 0.02$) but not salinity ($F_{1, 168} = 0.19$, $P = 0.66$). Covariate coefficients revealed richness would decrease by 9.27 species with each 1-m increase in water depth and 0.04 species for each 1% increase in cover (Table 2). Therefore, overall bird species richness decreased with increasing water depth and vegetation cover. For example, during October 2001, vegetation cover increased to ~44% and water depth increased to ~0.25 while bird species richness decreased to ~5 species per plot (Fig. 5).

Bird abundance

Abundance was dominated by waders, followed by dabbling ducks and upland birds. Like diversity and richness, there was no interaction of month by treatment ($F_{7, 128} = 1.16$, P = 0.33) and no treatment ($F_{1, 29.2} = 2.15$, $P = 0.15$) or month ($F_{7, 133} = 0.70$, $P = 0.67$) main effects on bird abundance. Overall, the mean abundance was 5.19 ± 1.27 for disked and 4.98 ± 1.75 for non-disked plots. Covariate water depth ($F_{1, 161} = 6.89$, $P < 0.01$) influenced bird abundance but vegetation cover ($F_{1, 182} = 3.54$, $P = 0.06$) and salinity ($F_{1, 165} = 0.12$, $P = 0.73$) did not. Covariate coefficients indicated mean bird abundance of the HNR impoundments would decrease by 12.1 individuals for every 1-m increase in water depth (Table 2). We recorded the greatest mean relative bird abundance in March 2001 (7.5 ± 1.98 individuals/plot) when water depth was ~0.10 m (Fig. 6). From October to December 2001, water level remained near 0.25 m as mean bird abundance fluctuated between near 5 to down near 3 individuals. In 2002, mean water depth was 0.19 m while mean bird abundance increased from 3.9 ± 1.82 (January) to 5.7 ± 1.84 (February). Abundance decreased in March 2002 while water depth remained near 0.20 m (Fig. 6). These observed patterns in bird species richness and abundance matched the time-series graph of total bird abundance within the study area (Fig. 2).

Nesting response

We found 268 nests of 8 wetland bird species in the HNR impoundments (Table 3). The earliest nests were found during March 2001 surveys; by the end of the sampling period in July 2001, we found 46 nests in the east impoundment, 9 nests in the west impoundment, and none in the north impoundment. Of these, Black-necked Stilt (14 nests) and Common Gallinule (14 nests) were the most common nesting species (Table 3). We found a nest of *Porzana flaviventer* (Yellow-breasted Crake) in May 2001. This represented the first record of this rare species of Neotropical rail in Puerto Rico since 1925. By the end of the study, a total of 15 Yellow-breasted Crake nests were found in the HNR impoundments (Vilella et al. 2011).

During the second nesting season (October 2001–March 2002), we found the earliest nest in November 2001, and by the end of our sampling in July 2002, the

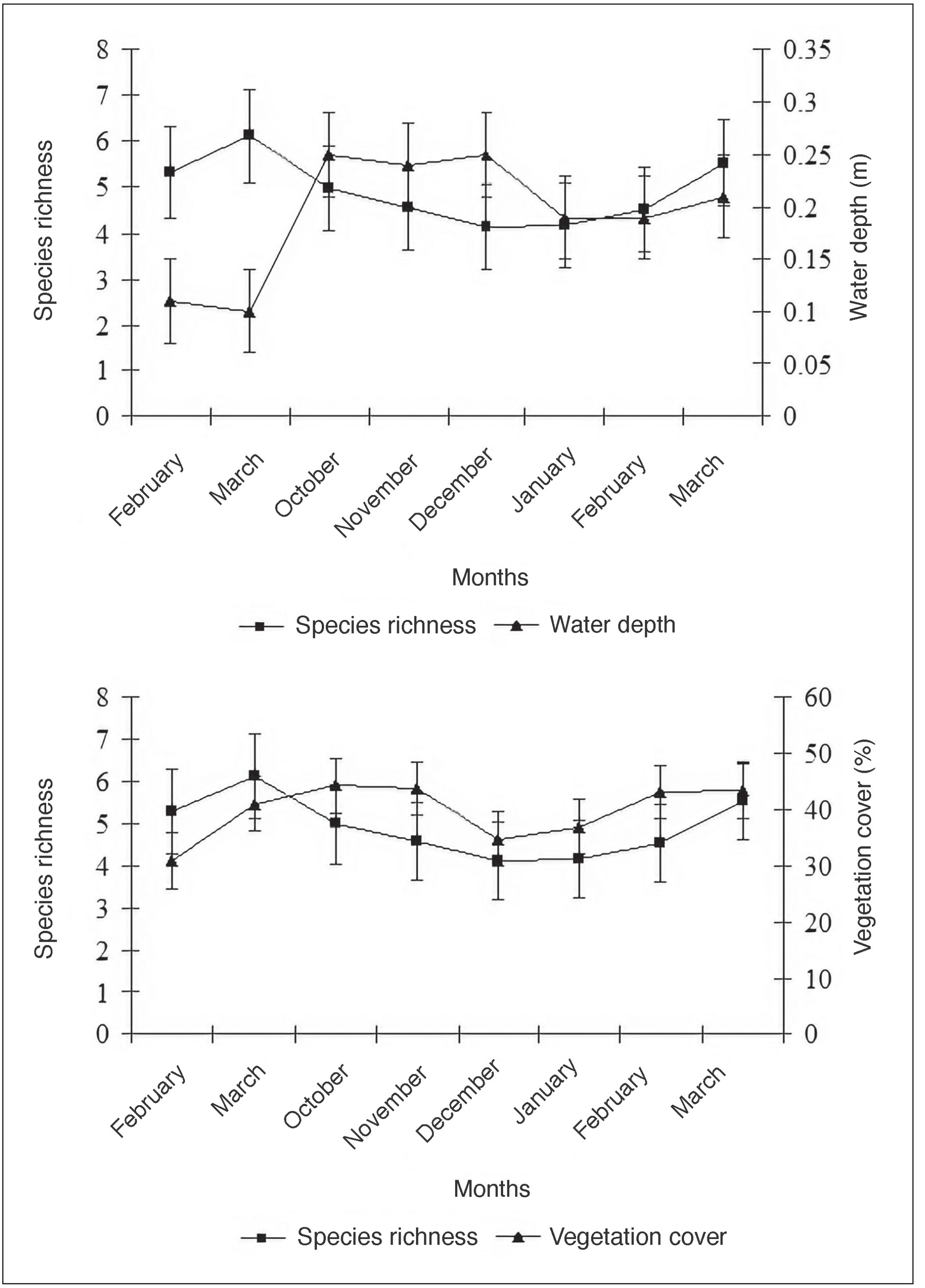

Figure 5. Monthly fluctuations in (top) bird species richness and water depth and (bottom) bird species richness and vegetation cover in 3 impoundments of the Humacao Nature Reserve, PR, February 2001–March 2002.

total included 205 nests in the east impoundment, 6 in the west impoundment, and 2 in the north impoundment. Contrary to the previous nesting season, the most abundant species were *Ixobrychus exilis* (Least Bittern; 79 nests), Common Gallinule (51 nests), *Podilymbus podiceps* (Pied-billed Grebe; 30 nests), and Black-necked Stilt (23 nests) (Table 3). Across all species, 54% of nests were successful. More than 50% of Yellow-breasted Crake, Ruddy Duck, Common Gallinule, *Fulica caribaea* (Caribbean Coot), and Pied-billed Grebe nests were successful. Further, 50% of Black-necked Stilt and White-cheeked Pintail nests were successful, while ~35% of Least Bittern nests were successful. Mayfield daily survival rate estimates varied from 0.95 to 1.00 (Table 3).

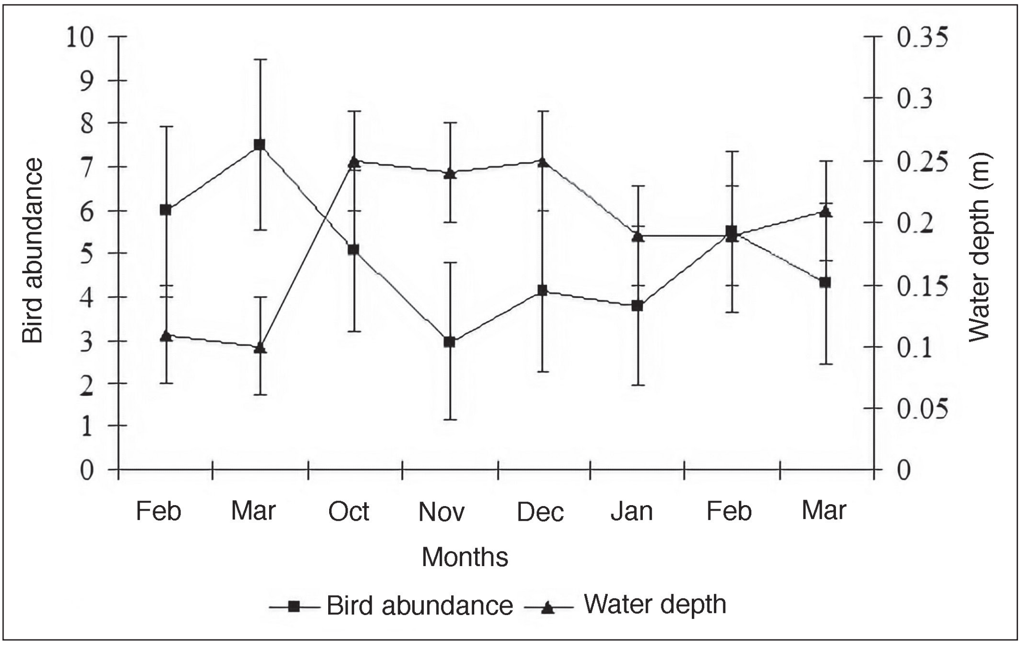

Figure 6. Bird abundance (*n* individuals/total species/plot) and water depth in 3 impoundments of Humacao Nature Reserve, PR, February 2001–March 2002.

Table 3. Nesting species and number of nests in restored wetlands at the Humacao Nature Reserve, PR, 2001–2002. Nests monitored for Mayfield (1975) survival estimates include only those located October 2001–March 2002. A nest was considered successful if ≥1 chick hatched.

	Nests found				
Bird species	2001	2002	Nests monitored	Successful	Daily survival rate
Himantopus mexicanus	14	23	22	11	0.96
Fulica caribaea	5	8	7	5	0.98
Gallinula galeata	14	51	48	35	0.98
Porzana flaviventer	1	14	14	9	0.95
Ixobrychus exilis	5	79	72	25	0.95
Podilymbus podiceps	7	30	21	13	0.97
Oxyura jamaicensis	1	4	4	4	1.00
Anas bahamensis	8	4	4	2	0.97

Discussion

We documented a rapid response by the avian community to newly available wetland habitats at HNR. Vilella and Gray (1997) reported the avian community of herbaceous marshes in this portion of the HNR before construction of the impoundments was dominated by upland seed-eating native species, such as *Tiaris bicolor* (Black-faced Grassquit), *Tiaris olivacea* (Yellow-faced Grassquit), and naturalized exotics like *Estrilda melpoda* (Orange-cheeked Waxbill). Following initial flooding in 2000, waterbirds quickly colonized the site and established a wetland-dependent avian community (Table 1). However, sustaining this initial diverse wetland avian community may be challenged by the ecological requirements of individual species (Paracuellos and Tellería 2004). Ordination analysis suggested bird species were arranged along environmental gradients. Although some guild-level trends were discernible from the ordination, an individual-species approach may be required to further interpret species' associations to the selected environmental variables. Our results suggest that continuing management practices (drawdown and disking) will be essential to sustain habitat quality and a diverse waterbird community in the restored wetlands.

Prior to restoration, wetlands at HNR were characterized by either overgrown stands of herbaceous vegetation or large expanses of deep, open water with little value for most waterbird species. These wetlands did not support the numbers of avian species and guilds found in the restored wetlands (Vilella and Gray 1997). Our results indicated bird abundances were greater, albeit not significantly so, in disked plots than in non-disked plots during flooding and drawdown periods. Brown and Smith (1998) suggested that lower avian species diversity and abundance in wetlands post-restoration could indicate that sites had yet to reach a successional stage capable of supporting a community typical of natural wetlands.

Following disking, plant germination may have been inhibited in areas of the impoundments where water depth exceeded tolerance limits of annuals requiring mudflats for germination. Plant cover increased almost twofold in untreated plots from October 2001 through March 2002, whereas it remained relatively constant during that same period in disked plots (Cruz-Burgos 2005). Increased plant cover in untreated plots suggests rapid vegetation growth under tropical conditions continued despite the absence of disturbance.

At the HNR impoundments, birds may have been initially attracted to available resources in disturbed (treatment) plots before moving to untreated areas. Fleming et al. (2015) reported that while managed wetlands yielded suitable feeding habitat for migrating and wintering waterfowl, management did not always result in expected waterbird responses. Nevertheless, continued application of these management prescriptions (control of water level and disking) during late July to early August may retard vegetation growth in these tropical coastal wetlands and allow waterbird access to habitats. Also, conducting manipulations during this period will insure activities are concluded before the rainy season (September to November) when tropical depressions, including hurricanes, move across Caribbean islands.

Dense vegetation may have decreased our ability to detect birds and thus influenced estimates of species diversity and richness, especially in non-disked plots. Species such as *Porzana carolina* (Sora), *Porphyrio martinicus* (Purple Gallinule), and Yellow-breasted Crake may have been missed during some surveys, likely due to dense stands of vegetation in some portions of the impoundments (Vilella et al. 2011). Habitat structure influences use of wetlands by waterbirds, affecting metrics such as abundance, species diversity. and richness (Murkin et al. 1997). While we did not test for vegetation:water ratios, overall avian diversity and abundance may have been influenced by the wetland habitat structure that ensued after restoration. Soil disturbance (disking) opened dense vegetation stands and when combined with shallow flooding (<0.25 m), provided areas where waterbirds could exploit prey compared to densely overgrown areas in the impoundments (Cruz-Burgos 2005).

Food availability also may influence bird use of wetlands (Gawlik 2002). The uneven topography of the HNR impoundments may have allowed foraging birds to access shallower areas where they could feed on invertebrates. Moreover, dense monotypic stands of vegetation in untreated plots may have decreased accessibility of invertebrates by waterbirds. High variability in available food resources favors opportunistic feeding by birds in prairie wetlands (Murkin and Caldwell 2000). Previous studies have recorded increased numbers and diversity of aquatic invertebrates when vegetation and water were well interspersed in emergent wetlands (Kaminski and Prince 1981). While we did not test different vegetation cover:water ratios, we believe overall avian diversity and abundance in our study may have been primarily influenced by the vegetation structure that developed post-restoration.

Bird abundance peaked on treatment plots in June 2001 and June 2002 during draining of impoundments. This pattern was related to increased abundance of egrets and herons feeding on fish moving from the Mandri lagoons into the restored wetlands during hydrological manipulations. When wetlands are gradually flooded or drained, conditions mimic natural seasonal events, often favoring the waterbird community (Murkin and Caldwell 2000, Taft et al. 2002). Many waterbirds rely on adaptive behaviors to exploit fluctuations in water levels in natural wetlands (Gawlik 2002). Further, wetlands can be managed for multiple waterbird guilds (Isola et al. 2000). Therefore, our results suggest managing coastal wetlands for a variety of waterbird guilds (i.e., waterfowl, shorebirds, wading birds) at HNR is feasible (Skagen and Knopf 1993).

Nesting activity in the impoundments progressively increased during our study as birds colonized the newly restored wetland habitats (Table 3). The east impoundment appeared to provide the best nesting habitat compared to the north and west impoundments. For example, sparse stands of Southern Cattail in the east impoundment were successfully used as nesting sites by the Least Bittern (Fig. 7). Furthermore, the east impoundment had greater area of shallow water and vegetation cover that was less dense. Wetland vegetation cover is vital to bird species that nest over water (Murkin and Caldwell 2000). Conversely, dense stands of Para Grass dominated the north impoundment. This species of forage grass, native to Africa and parts of the Middle East, is widely naturalized throughout the

Caribbean islands and commonly colonizes coastal wetlands historically disturbed by agriculture (Hammerton 1981).

We found 3 groups of over-water nesters: (1) species with nests attached to emergent vegetation above the water (e.g., Least Bittern), (2) species with nests at the water surface but attached to emergent vegetation (e.g., Common Gallinule), and (3) species with floating nests or nests on floating mats of vegetation (e.g., Pied-billed Grebe). Hence, plant species diversity and the availability of flooded and unflooded habitats may have influenced increased use for reproduction by bird species with varying nest habitat requirements in the east impoundment (Murkin and Caldwell 2000). No other wetland at HNR had this diversity of species nesting simultaneously (Fig. 7).

Daily survival rate for White-cheeked Pintail nests was 0.97 (Table 3), suggesting restored wetlands provided effective nest cover for this Caribbean waterfowl species, which is listed as threatened in Puerto Rico and its satellite islands because of unregulated hunting, habitat loss, and degradation (García et al. 2005). Nests were found in dry areas of emergent vegetation surrounded by water and clumps

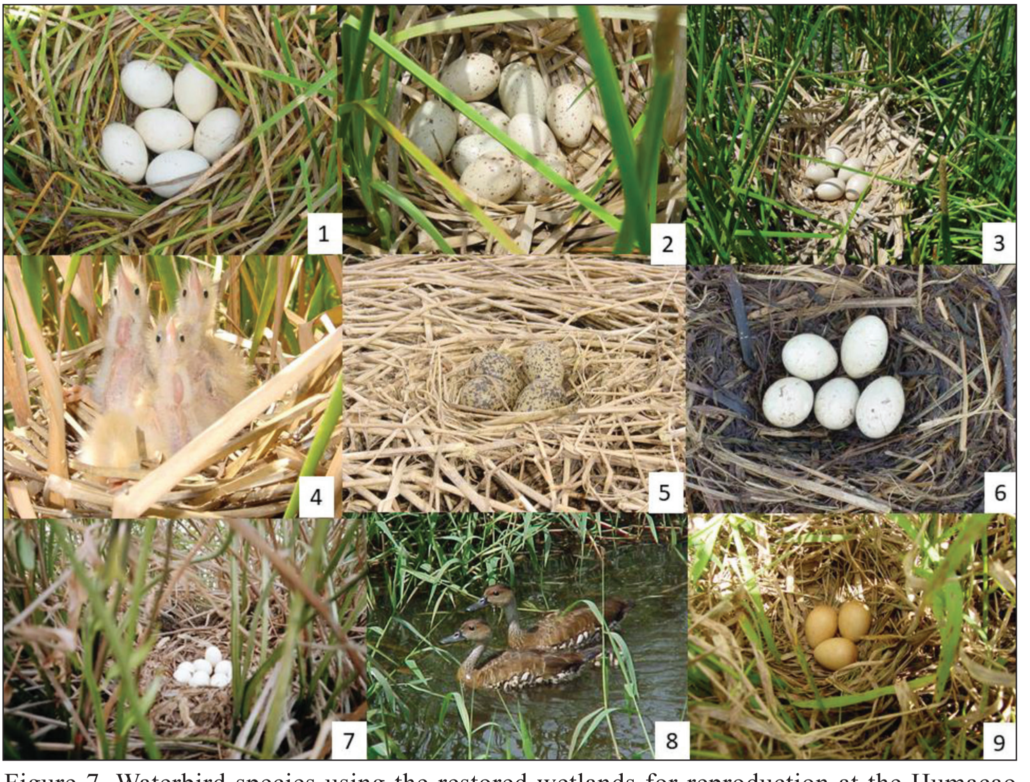

Figure 7. Waterbird species using the restored wetlands for reproduction at the Humacao Nature Reserve, PR, 2001–2002. From top left; (1) Ruddy Duck nest and eggs, (2) Common Gallinule nest and eggs, (3) Caribbean Coot nest and eggs, (4) Least Bittern nestlings, (5) Black-necked Stilt nest and eggs, (6) Pied-billed Grebe nest and eggs, (7) White-cheeked Pintail nest and eggs, (8) West Indian Whistling Duck pair with chick, and (9) Yellow-breasted Crake nest and eggs.

of *Megathyrsus maximus* (Jacq.) (Guinea Grass). During 2 field seasons, we found 12 White-cheeked Pintail nests in the restored wetlands, whereas a previous 5-year study throughout HNR assessing White-cheeked Pintail use of artificial nest structures located only 8 nests in natural cover (Ramos et al. 1995). Thus, providing suitable nesting habitat for waterbird species of concern in HNR wetlands may justify the need for further restoration. All waterfowl nests found during our study were over water or in vegetation growing in small, dry mounds surrounded by water, as opposed to the upland nesting habits of most North American dabbling ducks. Availability of brood-rearing habitat also is important by providing access to food and predator protection (Baldassarre 2014, Davis et al. 2017). At our study site in the HNR, wetlands with these characteristics were not available before restoration (Fig. 8). These results suggest lack of suitable nesting habitat may limit native waterbirds at HNR and other coastal wetlands of Puerto Rico (Davis et al. 2017).

The response of the avian community to our habitat-restoration efforts corroborated the degraded status of wetlands at HNR. Had the impoundments not been available, most bird species documented in our study would not have occurred at this site, given it was a grazing pasture prior to restoration (Fig. 8). Information on biodiversity responses to wetland management and restoration is virtually absent for the Caribbean islands. Available information on wetland restoration in the

Figure 8. Chronosequence of plant community response to wetland restoration at the Humacao Nature Reserve, PR, 2001–2002. Clockwise from top left illustrates the transition from grazing pastures (June 2000) to functioning wetlands (June 2002).

insular Caribbean is mostly limited to mangrove ecosystems and mostly focused on soil and plant responses, not wildlife (Ellison and Farnsworth 1996). However, positive responses of the bird community in the newly restored wetlands at HNR were almost immediate, emphasizing the value of these efforts.

Cardona and Rivera (1988) indicated habitat loss and degradation was primarily responsible for reduced waterbird populations in 64 coastal wetlands of Puerto Rico. The degraded status of emergent wetlands at HNR is typical of the coastal plain of Puerto Rico (Adams and Hefner 1996). Further, the potential of global climate change to affect the coastal plain via sea-level rise and changes to the frequency, intensity and timing of tropical storms, suggests additional restoration and waterbird monitoring efforts are warranted for the coastal wetlands of Puerto Rico (Michener et al. 1997).

Following the conclusion of our study, wetland management practices at the HNR impoundments were consistently maintained by DNER personnel for the following decade. Unfortunately, administrative constraints and loss of personnel precluded the continuation of management practices at the impoundments or restoration of additional sites at HNR as had been previously proposed (Vilella and Gray 1997). Nevertheless, our results provide evidence these restoration practices in coastal herbaceous marshes of Puerto Rico, and other Caribbean islands with similar historical land use (sugarcane cultivation), may benefit wetland biodiversity.

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