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Abstract Habitat fragmentation represents one of the most important threats to biodiversity. Fragmentation of aquatic ecosystems is pervasive, fundamentally altering aquatic community structure and ecosystem function on a worldwide scale. Because of the many ecological changes associated with hydrologic fragmentation of coastal wetlands, there may be cascading effects on non-aquatic organisms. Here we explored if anthropogenic fragmentation of tidal creek wetlands on Abaco Island, The Bahamas, affected bird communities. By comparing fragmented and unfragmented sections of nine separate tidal creeks, we tested whether fragmentation of coastal wetlands (due to roads)

affected the richness, abundance, and composition of wetland bird assemblages. Although bird communities significantly differed among tidal creeks (irrespective of fragmentation status), and water salinity was positively correlated with species richness and abundance of wetland-associated birds, we found no significant differences in bird communities between fragmented and unfragmented sections of wetlands. Our findings suggest fragmented portions of tidal creek wetlands support avian communities relatively similar to their unfragmented counterparts, despite a range of differences in environmental features. These results indicate that other ecological factors (i.e., salinity) may be more important than fragmentation *per se* in affecting bird utilization of wetland habitats in The Bahamas.

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Introduction

Coastal wetlands provide important foraging and nesting areas for migratory and resident wildlife, especially birds (Maccarone and Parsons 1994; Erwin et al. 2004; Stolen et al. 2007). Yet, coastal wetlands continue to be modified extensively (Bildstein et al. 1991), and such alterations may critically affect their suitability for various wetland species. One particularly widespread form of wetland alteration is hydrologic fragmentation, e.g., by dams, levees, and irrigation canals. For example, over half of the world's major river drainages have dams (Nilsson et al. 2005), and in the United States alone, 2.6 million impoundments account for 20 % of existing standing inland water (Smith et al. 2002). Even in the extensive marshlands of the southeastern United States, fragmentation has directly affected at least 84,000 ha (20 %) of coastal estuaries (Montague et al. 1987).

Coastal wetlands in the Caribbean are frequently fragmented, typically by the construction of roads across a section of the wetland. This results in reduced hydrologic exchange, as well as limited movement of organisms and materials between oceanic and inland sections of the ecosystem (e.g., Layman et al. 2004, 2007). This reduced hydrologic connectivity can have significant effects on many aspects of aquatic community structure and ecosystem function (Layman et al. 2007; Valentine-Rose et al. 2007; Araújo et al. 2014). While effects of fragmentation for Caribbean fish assemblages are relatively well studied (e.g., fragmentation causes extirpations and reduces population sizes of remaining species), many questions remain regarding the impacts of hydrologic alteration on other taxa, such as birds (Latta 2012).

Effects of habitat fragmentation on upland bird communities have been an important area of ecological research for decades (Turner 1996; Coppedge et al. 2001). This research has shown strong, and generally deleterious, effects of fragmentation on bird abundance and species richness (Stouffer and Bierregaard 1995; Uezu and Metzger 2011). Despite the pervasive fragmentation of coastal aquatic ecosystems, we know relatively little about how hydrologic

fragmentation might affect the rich and abundant bird communities that utilize them (Latta 2012). In this study, we examined a series of tidal creeks and characterized bird assemblages in fragmented and unfragmented sections of tidal creek wetlands in The Bahamas to examine possible effects of fragmentation on wetland birds. We additionally examined a number of potentially important environmental factors that could underlie patterns of variation in bird communities (e.g., salinity, water depth, surrounding habitat type).

Methods

We examined wetland systems on Abaco Island, The Bahamas, locally known as tidal creeks (Fig. 1). A relatively narrow creek mouth typically characterizes most tidal creek systems, which forms the primary conduit for tidal exchange (semi-diurnal tidal regime, ~0.8 m tidal amplitude). Creeks typically broaden moving landward from the mouth, grading into expanses of shallow (<1 m at low tide) wetlands with red mangrove (*Rhizophora mangle*) as the primary emergent vegetation. These wetlands often are surrounded by one of two upland plant communities, dry evergreen forest (typically known as coppice), or a sub-tropical, pine woodland known as pineland.

In The Bahamas, hydrologic fragmentation results from the construction of roads that lack adequate flow conveyance structures (e.g., a bridge), thereby substantially reducing tidal exchange between marine and landward sections of tidal creeks. Typical ecological changes following fragmentation are more extreme physico-chemical conditions, and reduced colonization rates of floral and faunal species (Layman et al. 2007). These changes ultimately result in altered aquatic species assemblages in fragmented systems (Layman et al. 2004; Valentine-Rose et al. 2007), and fundamental shifts in ecosystem function (Layman et al. 2007; Allgeier et al. 2010). Nevertheless, fragmented creeks often still have abundant red mangroves and support populations of tolerant fishes and invertebrates (Layman et al. 2007).

We selected nine tidal creek systems (Fig. 1), each bisected by a road, for this study. Each tidal creek had a distinct fragmented (landward) section and unfragmented (the side that retained a connection with the ocean) section, and surveys were conducted in each.

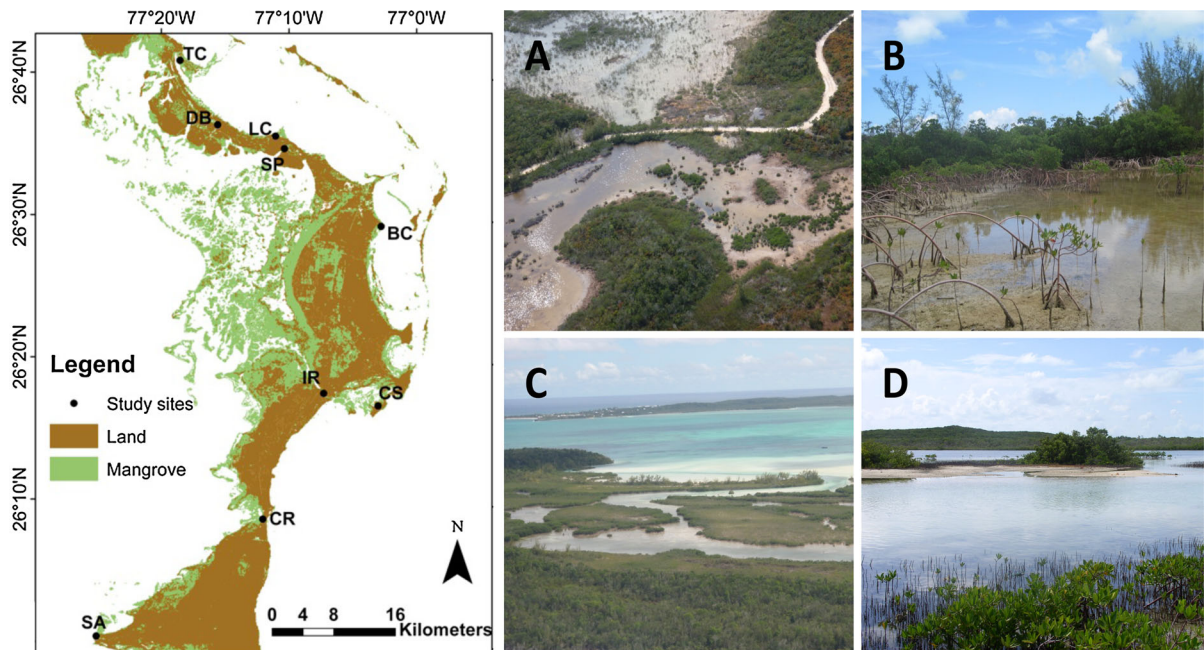


Fig. 1 Map of survey sites on Abaco Island, Bahamas and photos depicting Broad Creek fragmentation. *Left panel:* Treasure Cay (TC), Double Blocked Creek (DB), Loggerhead Creek (LC), Stinky Pond (SP), Broad Creek (BC), Indian River (IR), Cherokee Sound (CS), Crossing Rocks (CR), Sandy Point

(SA). *Right panels:* aerial photograph of Broad Creek showing the bisecting hydrological barrier, a road (a), the fragmented section of Broad Creek (b), an aerial photo of the unfragmented section of Broad Creek (c), and the unfragmented portion of Broad Creek (d)

Birds were surveyed June–August 2010, with each site visited once per week for twelve consecutive weeks in accordance with presumed peak nesting for many aquatic birds in the northern Bahamas (Kushland and Steinkamp 2007). Point-count surveys with unlimited radius were conducted on each visit for 10 min (Johnson 2008). All birds seen or heard were recorded during each survey. Bird surveys were conducted within 45 min of sunrise or sunset to capture periods of high bird activity.

We measured several environmental factors at each site, selected based on their possible influence on avian habitat quality (Lefebvre and Poulin 1997; Collazo et al. 2002; Stolen et al. 2007). We measured average water depth as the average of 40 randomly located measures within each site. Salinity was measured at each site using a YSI 85 (Yellow Springs, OH). Distance to the mouth of the tidal creek (i.e., distance from ocean) was calculated as the distance from the center of survey area in the tidal creek to the mouth of the creek using Google Earth. Percent mangrove and percent upland forest (pineland and

coppice) of the surrounding habitat were estimated as the percentage of area along the perimeter of the wetland covered by mangrove or upland forest habitat using The Nature Conservancy habitat layers in ArcGIS v 9 (ERSI 2008).

Data analyses were conducted separately for three groups: (1) all birds (2) wetland-associated species and (3) wading birds only. The second group included species for which at least part of their natural history is tied to wetland habitats through feeding or nesting ecology (Table S1). The third group includes species belonging to the family Ardeidae; these birds feed primarily at the margins and in shallows of wetland environments and, therefore, may be especially susceptible to changes in wetlands induced by fragmentation (Koebel 1995; Miranda and Collazo 1997).

To test if bird communities differed between fragmented and unfragmented sections of tidal creeks, we used a two-factor Analysis of Variance (ANOVA) using JMP software (version 11). Fragmentation regime (fragmented or unfragmented) and tidal creek identity were included in the model. Tidal creek was

treated as a blocking variable. Separate models were conducted for species richness of (1) all birds, (2) wetland-associated birds, and (3) wading birds. Similar statistical models (to the species richness analysis) were conducted to test the effects of fragmentation on the total number of sightings (total number of birds observed throughout the summer) of (1) all birds, (2) wetland-associated birds, and (3) wading birds. All data met assumptions of normality and homogeneity of variance ($P > 0.05$). We conducted a power analysis to confirm that we had adequate statistical power to detect moderate differences in bird community response variables between fragmented and unfragmented environments. Using the average standard deviation observed for species abundances and species richness, we found that we had reasonable statistical power (~ 0.91) to detect differences of 10 individual sightings and 3 species between fragmented and unfragmented sites.

An Analysis of Similarity (ANOSIM) was performed to test whether the bird community structure differed among fragmented and unfragmented sections of tidal creeks (PRIMER © v 6, Clarke 1993). This analysis was restricted to species contributing at least 1 % of total bird sightings and was based on a Bray-Curtis similarity matrix of square-root transformed data of bird sightings.

We also examined whether ecological variation could explain differences in bird communities. The variables of interest were: salinity, average water depth, percent mangrove cover, percent upland forest cover, and distance to ocean (Table S2). The explanatory power of each was investigated with Stepwise Linear Regression ($P < 0.05$ to enter and >0.10 to leave, JMP 11). A separate model was run for the three bird groups (all birds, wetland-associated birds, and wading birds) for species richness and total number of sightings.

Results

We recorded a total of 461 individual bird sightings, representing 37 bird taxa (Table S1). The five bird taxa most sighted were *Agelaius phoeniceus*, red-winged blackbird (23 % of total bird sightings), *Tyrannus dominicensis*, gray kingbird (13.8 %), *Larus atricilla*, laughing gull, *Chordeiles gundlachi*, Antillean night-hawk (both 11.4 %) and Hirundinidae, swallow (7.6 %). Fifteen taxa classified as wetland-associated

Table 1 Effects of fragmentation on bird species richness and number of bird sightings across nine study sites. η_p^2 = partial eta squared, the proportion of variation explained by each model term

Source	Df	MS	F	P	η_p^2
Total bird sightings					
Fragmentation	1	18.0	0.40	0.546	0.05
Tidal Creek	8	66.6	1.47	0.299	0.60
Error	8	45.3			
Wetland bird sightings					
Fragmentation	1	16.1	0.86	0.380	0.11
Tidal Creek	8	69.4	3.74	0.040	0.79
Error	8	18.6			
Wading bird sightings					
Fragmentation	1	0.1	0.01	0.922	<0.01
Tidal Creek	8	5.6	1.04	0.481	0.51
Error	8	5.4			
Total species richness					
Fragmentation	1	0.5	0.33	0.580	0.04
Tidal Creek	8	5.8	3.83	0.038	0.79
Error	8	1.5			
Wetland species richness					
Fragmentation	1	0.5	0.36	0.563	0.04
Tidal Creek	8	4.9	3.59	0.045	0.78
Error	8	1.4			
Wading bird richness					
Fragmentation	1	0.5	0.80	0.397	0.09
Tidal Creek	8	1.8	2.82	0.082	0.74
Error	8	0.6			

species represented 185 individual sightings, and seven wading bird taxa (Ardeidae) were represented by 45 sightings.

There were no significant differences in the number of sightings among fragmented and unfragmented sections of the tidal creeks for any of the three bird groupings, although the number of sightings of wetland-associated birds differed among tidal creeks (Table 1; Fig. 2). Species richness did not differ between fragmented and unfragmented sections of tidal creeks for any of the three bird groupings (Table 1; Fig. 2). However, differences in species richness among tidal creeks were evident for all birds and wetland-associated birds, and suggestive for wading birds (Table 1). Overall avian community structure did not differ between the two fragmentation categories (ANOSIM global $R = 0.006$, $P = 0.54$).

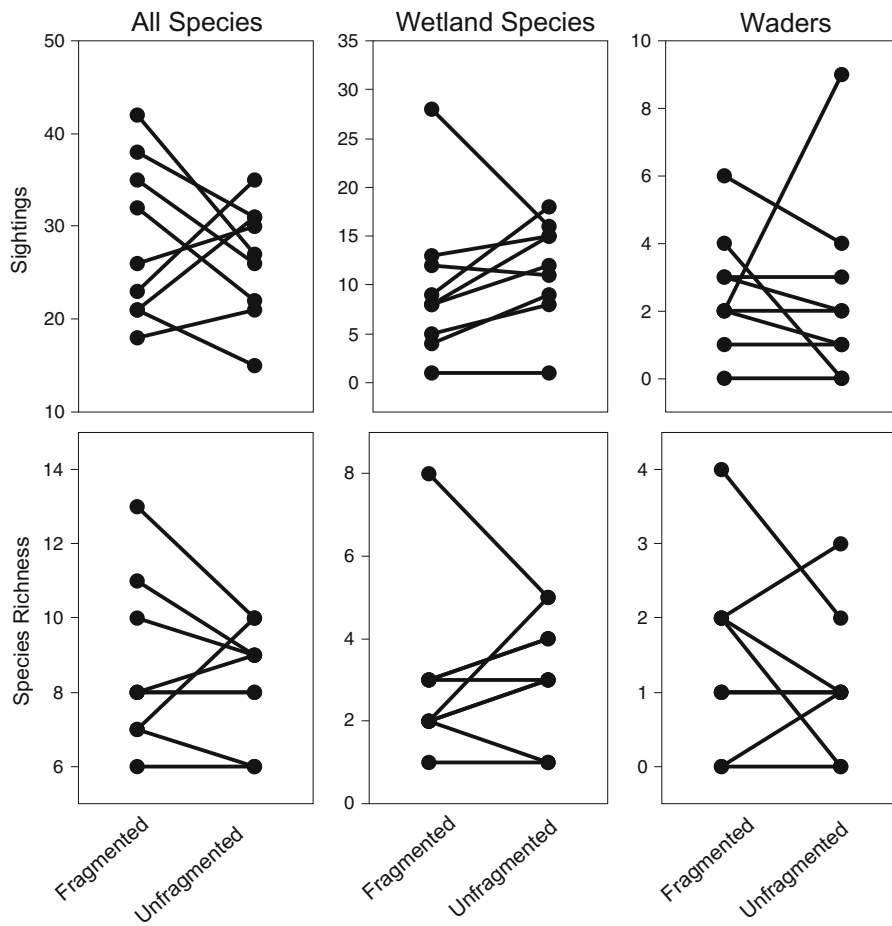


Fig. 2 Number of sightings and species richness of birds for unfragmented and fragmented sections of the nine tidal creeks examined in this study. Note that species richness data are

identical for several sites and lines overlap on the figure, all panels include data from 9 tidal creeks

Our analysis of the effects of environmental factors on bird community variation showed that none of the environmental factors included in our analysis significantly predicted total bird sightings or total species richness, or wading bird sightings or species richness (no terms remained in the model following stepwise regression). Nevertheless, the number of sightings and species richness of wetland-associated birds showed significant positive relationships with salinity (Table S3).

Discussion

Our results suggest that fragmented and unfragmented sections of tidal creeks in The Bahamas did not differ significantly in bird community composition. We did

not detect differences in the number of bird sightings, species richness, or community structure between fragmented and unfragmented sections of the tidal creeks studied. Below we discuss reasons why fragmented systems apparently still provide beneficial habitat and/or foraging areas for birds in The Bahamas and relate these findings to past studies of waterbirds in the Greater Caribbean region.

Following fragmentation, tidal creeks are characterized by fundamentally different physico-chemical properties, including differences in salinity, temperature, and dissolved oxygen. While these alterations, drive major differences in the composition of the fish and invertebrate communities (Layman et al. 2004), they may not affect habitat suitability for birds. For instance, mangroves are abundant in both fragmented and unfragmented portions

of creeks (Valentine-Rose et al. 2007). Therefore, birds that utilize emergent vegetation to nest and roost (e.g., red-winged blackbirds; Forbes 2010) may be able to utilize wetlands irrespective of fragmentation status. Second, while fragmentation leads to a predictable decline in fish diversity, density of some fishes often increases in fragmented sites (Araújo et al. 2014). In particular, small fishes such as The Bahamas mosquitofish (*Gambusia hubbsi*) and sheepshead minnow (*Cyprinodon variegatus*) can be abundant in fragmented creeks (Layman et al. 2007). Given the broad and apparently flexible diets of many wetland-associated birds (Kent 1986; Miranda and Collazo 1997), increased densities of small prey fishes in fragmented creeks may compensate for the reduction or loss of larger forage fishes such as needlefish (*Stongylura notata*), yellowfin mojarra (*Gerres cirreus*), and snappers (*Lutjanus* spp.). In addition, many fragmented creeks often retain limited tidal exchange via culverts. In these partially connected sites, juvenile fish can still colonize fragmented portions on incoming tides. As water recedes during ebb tides and/or periods of low precipitation, fish become concentrated and provide a source of food that is readily available for birds.

While wetland bird communities did not appear to differ as a function of fragmentation, we found significant differences among tidal creeks. Upon further inspection of these results, we uncovered no associations between bird communities and geographic location of tidal creeks. This suggests that creek-level variation in environmental characteristics may drive observed variation in bird communities. Our stepwise regression analysis of the entire bird community and wader community did not reveal relationships between number of sightings or richness and the environmental characteristics we included in our models. However, we did detect a significant positive relationship between salinity and the number of bird sightings and species richness of wetland-associated bird species (Table S3). This finding suggests that salinity may be an important ecological driver, or indicator of habitat quality, for wetland bird communities on Abaco regardless of wetland fragmentation status. A potential reason for this might be availability of preferred food species, or that water clarity (salinity is typically positively correlated with turbidity in Abaco's tidal creeks) may increase prey detection ability and thus foraging efficiency. This is similar to other studies that have shown a positive relationship

between salinity and habitat quality for wading birds (Maccarone and Parsons 1994), e.g., the large numbers of shorebirds using hypersaline habitats in Puerto Rico (Collazo et al. 1995) and the preferential use of saline habitats by egrets in coastal Florida (Stolen et al. 2007).

While we did not find a significant effect of fragmentation on bird community composition, we do believe further study is warranted. First, examination of a greater number of tidal creek systems (on additional islands) would add confidence that fragmentation truly does not result in any consistent effect on summer bird communities in The Bahamas. Second, multi-year studies including different seasons (breeding and non-breeding) would greatly increase detection probabilities of bird community shifts (Latta 2012). For example, our study period encompassed the breeding season for many wetland-associated birds, but was on the tail end of the nesting season for some waders (Green et al. 2011). The Bahamas hosts a large and diverse migratory bird community during the winter months, including rare coastal species such as Piping Plovers (*Charadrius melodus*). Expanding survey efforts to include these distinct wintering communities is important to more fully explore any effects of fragmentation on bird communities and generate information that could inform coastal wetland management in the area. Indeed, visual inspection of our data yielded one suggestive trend that future studies could directly examine: fragmented sections of tidal creeks tended to exhibit reduced sightings of wetland-associated birds in many of the tidal creeks (Fig. 2). Although not significant, the results suggest variation among tidal creeks in the effect of fragmentation on wetland bird sightings. Future studies could investigate this suggestive pattern. Finally, studying communities across a gradient of hydrologic fragmentation might also be of interest. For our analysis we simply classified sites in a dichotomous way, that is, 'Fragmented' or 'Not Fragmented'. However, there is often much variation among tidal creeks in tidal flux, and this variation may affect bird communities.

Other studies have shown the high value of fragmented coastal ecosystems for aquatic birds (e.g., Collazo et al. 1995, 2002; Stolen et al. 2007; Vilella et al. 2011), and argue for the active management of these anthropogenically-altered ecosystems for migratory and resident aquatic birds. This perhaps underscores the primary point of the research reported here: hydrologic fragmentation, while largely deleterious for marine

organism diversity, may not strongly affect the habitat value for wetland birds. This study was another step in examining how ecosystem fragmentation may affect bird communities in wetland systems of The Bahamas, and we hope our study provides a baseline for future investigations of how anthropogenic habitat alteration affects bird utilization of these coastal ecosystems.

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