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Abstract

The frequency and intensity of hurricanes are likely to increase in the Caribbean due to climate change, potentially threatening the long-term conservation of biodiversity in vulnerable island ecosystems. The effects of hurricanes were assessed for the understory forest birds of Cozumel Island during the first and second year after two consecutive hurricanes (Emily and Wilma) struck the island in July and October of 2005. Post-hurricane values were compared to pre-hurricane values for summer and winter bird assemblages. A total of 2,504 individuals of 45 species (29 resident and 16 migrants) were captured using mist nets. Strong negative effects of the hurricanes were detected during the first winter season, that is, 3 months following the second hurricane, with significantly lower mean values per site for the number of individuals, the number of species, and the percentages of migratory individuals and species. During the second winter (16 months after the hurricanes), parameter values of the bird assemblages were similar to pre-hurricane values. Response variables showed no effects of hurricanes in the case of summer bird assemblages (either 8 or 21 months after the hurricanes). Yet, when we carried out ordinations of the samples, taking into consideration the bird species and their relative abundances, we found that in both winter and summer seasons, bird assemblages for the three sampling periods (pre-hurricanes, first year and second year after the hurricanes) could be clearly distinguished. Management strategies for hurricane-prone areas are recommended, in particular for diverse insular ecosystems highly threatened by the synergistic effects of natural and anthropogenic disturbances.

Keywords

bird conservation, Caribbean, climate change, insular ecosystem, natural disturbance, Yucatan Peninsula

Introduction

Disturbances cause changes in the physical environment and the availability of resources, thus affecting biotic populations and communities as well as ecosystems. Natural disturbances, such as fires, landslides, and storms, are considered crucial for the maintenance of important ecological and evolutionary processes (Brawn, Robinson, & Thompson, 2001; Pickett & White, 1985). Anthropogenic disturbances, on the other hand, such as habitat loss/degradation, overexploitation, introduced species, and climate change, are considered great threats to biodiversity. In reality, however, species and ecosystems are subject to many disturbances simultaneously, with potentially complex interactions (e.g., synergism) between natural and anthropogenic disturbances (Groom, 2006; Hogan, Zimmerman, Thompson, Nych, & Uriarte, 2016).

Global climate change caused by human activities is of enormous relevance because of predictions that the frequency and intensity of natural disturbances may vary at rates faster than ecosystems have experienced historically.

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For example, it is now well established that as surface temperatures increase due to global warming, storms are becoming more intense, and as a consequence, highly destructive storms (i.e., hurricanes, cyclones, and typhoons; hereafter all referred to as hurricanes) are becoming more frequent (Sobel et al., 2016; Walsh et al., 2016). Under these conditions and with the added impact and interaction of other disturbances, species and ecosystems supposedly adapted to severe storms might face many changes in the next decades (Hass et al., 2012; Hogan et al., 2016). This is why a better understanding of the effects of such storms on species and ecosystems in hurricane-prone regions, particularly those affected simultaneously by anthropogenic disturbances, is urgently needed (Hogan et al., 2016).

A region strongly influenced by hurricanes is the Caribbean (Waide, 1991a; Walker, Lodge, Brokaw, & Waide, 1991). Much of the biodiversity in this region, including a high proportion of endemic species, occurs on islands. Insular ecosystems are particularly vulnerable to the cumulative effects of anthropogenic and natural disturbances (Goulding, Moss, & McAlpine, 2016), and many groups of island organisms are known to be more sensitive to anthropogenic disturbances in comparison to their mainland counterparts (Groom, 2006). Hurricane effects can be particularly strong on small islands with flat topography, such as Cozumel Island off the Yucatan Peninsula in the Mexican Caribbean. Within Mexico, the Yucatan Peninsula in general and Cozumel Island in particular are recognized as avian biodiversity hot spots with a high proportion of endemic species and of great importance for migrating species (Arizmendi & Márquez-Valdemar, 2000; Cortés-Ramírez, Gordillo-Martínez, & Navarro-Sigüenza, 2012; Macouzet, 1997; Navarro-Sigüenza et al., 2014; Stattersfield et al., 1998). Only one study exists on the effects of hurricanes on birds in the Mexican Caribbean showing a reduction in the abundance of common insectivorous and generalist bird species and a scarcity of frugivorous and nectarivorous species (Lynch, 1991); however, none exists for Cozumel Island. Yet, hurricanes in synergy with anthropogenic threats, in particular the introduction of invasive species, are thought to play a role in the decline of the highly endangered endemic Cozumel Curassow (*Crax rubragris-comi*; Martínez-Morales, Cruz, & Cuarón, 2009) and the believed-extinct endemic Cozumel Thrasher (*Toxostoma guttatum*; Correa-Sandoval & McKinnon, 2011).

Effects of hurricanes on birds have been reported for several sites worldwide, and these natural disturbances are recognized as an important force structuring avian communities in hurricane-prone areas (e.g., Brown, Sherry, & Harris, 2011; Freeman, Pias, & Vinson, 2008; Lee et al., 2008; McNair, 2008; Rittenhouse et al., 2010). Negative effects of hurricanes on animals, including bird

populations and communities, have been previously reviewed (Waide, 1991a; Wiley & Wunderle, 1993) and three general categories can be recognized: (a) direct mortality of individuals (difficult to document and mostly reported for waterbirds, see Wiley & Wunderle, 1993), (b) decrease in populations and changes in behavior due to indirect effects (e.g., food shortage; Dobbs et al., 2009), and (c) changes in community structure or composition (e.g., Rittenhouse et al., 2010). Still, hurricane-related changes in bird species and communities may be highly context-dependent, with no effects in some cases (e.g., Lain, Zenzal, Moore, Barrow, & Diehl, 2017) and even positive effects in others (e.g., some marine species; Ancona, Drummond, Rodríguez, & Zúñiga-Vega, 2017; Nicoll et al., 2017). In addition, relatively little is known about the temporal recovery patterns of population and community parameters after severe hurricanes (Yaukey, 2012).

Finally, while it is well established that the frequency of intense hurricanes has increased in the past decades, and that this trend will likely continue (Sobel et al., 2016; Walsh et al., 2016), there are very few studies on the effects of repeated hurricanes occurring over a short time period and those that exist report somewhat contrasting results. For example, one study focusing on corals reported that three major hurricanes in a period of 5 years caused unusually severe coral loss as well as declines in the associated fish community, with limited recovery after 4 years (Cheal, MacNeil, Emslie, & Sweatman, 2017). Another study, focusing on migratory songbirds, found that while two intense hurricanes occurring over a 3-year period strongly affected coastal forest habitat, there were no consequent effects on birds (Lain et al., 2017). On the other hand, a study assessing the effects of two consecutive typhoons in two types of forest found changes in the vegetation structure of one habitat and a consequent increase in the similarity of bird communities between habitats (Lee et al., 2008).

The main objective of the present study was to assess the combined effects that two major hurricanes occurring in the same year (Emily and Wilma, from now on referred to as “the hurricanes”) had on the understory forest birds of Cozumel Island and how community parameter values recovered over time. In particular, we aimed to estimate bird abundance, number of species, and community structure and composition, for both the summer and winter bird assemblages, and to compare pre-hurricane values to those obtained for two winter and two summer seasons following the hurricanes. Our study provides the first quantitative data on hurricane effects on Cozumel’s forest understory avifauna and its recovery over time. These data represent valuable input information for the development of context-specific management plans for Cozumel’s vulnerable ecosystems.

Methods

Study Area

The study was carried out on Cozumel Island, located 17.5 km off the northeastern coast of the Yucatan Peninsula in the Mexican state of Quintana Roo ($20^{\circ}16'–20^{\circ}36' N$, $86^{\circ}44'–87^{\circ}02' W$; Figure 1). In 2016, Cozumel Island was included in UNESCO's World Network of Biosphere Reserves. Cozumel has an approximate area of 480 km², of which approximately 65% is covered by semideciduous tropical forest. This forest has a canopy height that varies between 8 and 20 m. The island has a moderately warm and humid climate, with average temperatures of 25.5°C. Mean annual precipitation is 1,505 mm, but rainfall is highly seasonal (Instituto Nacional de Estadística y Geografía, 1994). The forests of Cozumel constitute important habitat for a very diverse vertebrate fauna, including numerous endemic taxa and many migratory bird species (Cortés-Ramírez et al., 2012; Cuarón et al., 2009; Perdomo Velázquez, 2006). More detailed information about the study site can be found elsewhere (Cuarón, 2009).

The hurricane season in this region occurs from June to November. On average, Cozumel is affected by a major hurricane (Categories 3–5 in the Saffir–Simpson scale) once every 10 years (Martínez-Morales et al., 2009), but in 2005, Cozumel was hit directly by two hurricanes: Emily and Wilma. In the two decades prior to the 2005 hurricanes, Cozumel was affected by two major hurricanes: “Gilbert” (Category 5) in 1988 and “Roxanne” (Category 3) in 1995. No other hurricane has affected Cozumel since 2005.

Hurricane “Emily” (Category 4) hit the island on July 18, 2005 with winds of 215 km/h, causing strong defoliation of the forest vegetation (Figure 2). Three months later (October 21, 2005), before the vegetation had had time to recover, the island was struck by hurricane “Wilma” (Category 5) during approximately 36 hours, with winds of 240 km/h and wind gusts of up to 295 km/h (Perdomo Velázquez, 2006). After Wilma, the semideciduous forests of Cozumel suffered extensive tree damage and mortality (including total defoliation, loss of branches, snapped trunks, and uprooted trees) and forest flooding (H. P.-V. and A. D. C., personal observations; Figure 2), which are common effects of hurricanes in

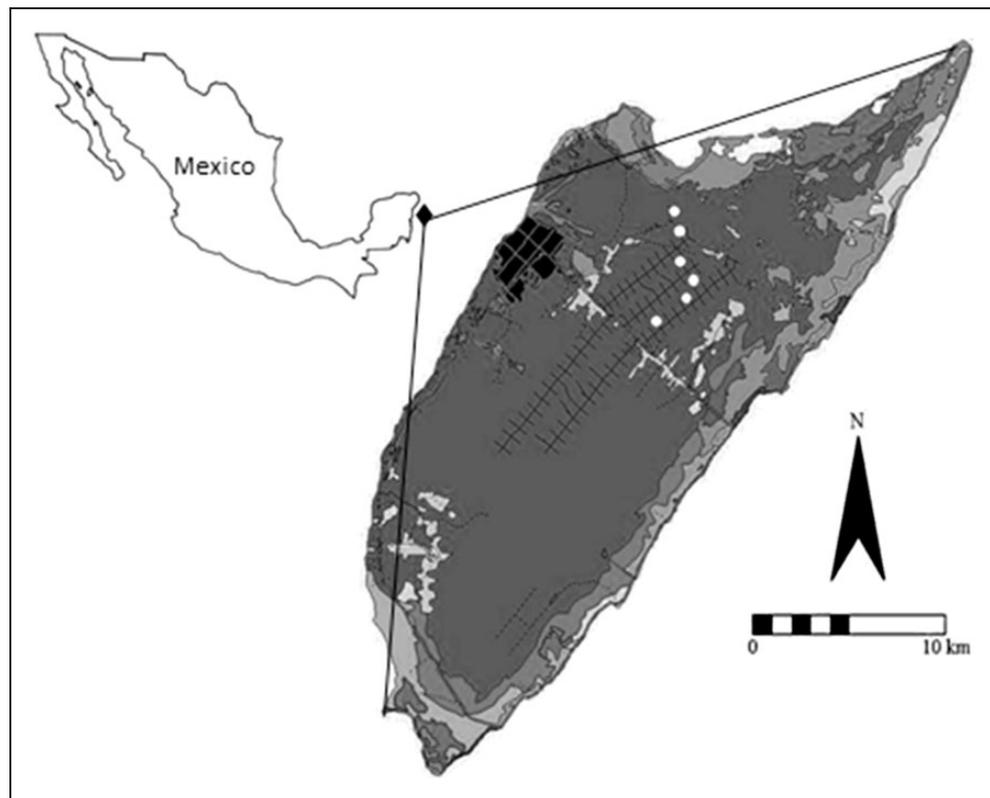


Figure 1. Location of Cozumel Island off the Yucatan Peninsula in southeastern Mexico. The six sites used for sampling understory forest birds in the semideciduous tropical forest (dark gray) are shown as white circles. Lighter shades of gray represent deciduous forest, mangrove forest, and coastal dunes. The main urban settlement (San Miguel) is shown in black.



Figure 2. The semideciduous forest of Cozumel Island and representative understory bird species. The forest in 2004, before the hurricanes (a), in 2005 after hurricane Emily (b), and in 2005 after hurricane Wilma (c). Some endemic bird species or subspecies of Cozumel include the Cozumel Black Catbird (d), the Northern Cardinal (e), and the Yellow-faced Grassquit. A common migratory species is the Hooded Warbler (see Appendix A for scientific names). All photos by H. P.-V.

forest ecosystems (reviewed by Lugo, 2008). Forest damage was more severe near open areas, such as adjacent to roads (H. P.-V. and A. D. C., personal observations). In a nearby mainland site at El Edén Ecological Reserve, 25% of mature forest trees were dead and 13% damaged, after Wilma; however, defoliated trees had produced new leaves by December 2005 (Goode & Allen, 2008).

Cozumel has a rich avifauna. Including rare and occasional records, the complete avifauna of Cozumel may encompass as many as 250 species (Lepage, 2013). Of these species, at least 49 can be found in the tropical forest understory: 31 resident species (including 4 endemic species and 14 endemic subspecies) and 18 migratory species (Macouzet, 1997; Perdomo Velázquez, 2006; Figure 2).

Bird Sampling

Two times before the hurricanes and four times afterward, understory forest birds were captured using mist nets (12 m in length, 2 m height, and 32 mm mesh size) in

six sites (>500 m apart) within the area covered by semi-deciduous tropical forest (Figure 1). In each site, mist nets were placed along three parallel 72 m long transects (3×72 m); distance between adjacent lines at each site varied between 13 and 29 m. This setup of nests was a sampling design that was used for a study that aimed to assess the effects of roads on bird movement, which was being carried out at the time the hurricanes struck the study site (see Perdomo Velázquez, 2006). During each of the six sampling periods, each site was sampled over 4 consecutive days. The first half of the three transects (3×36 m) were sampled simultaneously using a total of nine nets, during 2 days. Then, the nine nets were moved to the second half of the three transects for 2 more days of sampling. Nets were opened at sunrise and remained open for 6 hours, being checked every half an hour. Sampling effort per site was 216 net hours in each sampling period. All individuals were marked with numbered aluminium bands and released unharmed. For bird scientific names and migratory status, we used Avibase (Lepage, 2013) and Berlanga et al. (2015).

Prior to the hurricanes, we captured birds in two sampling periods: Summer 2004 (S-04; June 30–August 8) and Winter 2005 (W-05; January 17–February 20), which constituted our pre-hurricanes base information, for summer and winter seasons, respectively. Four additional sampling periods were conducted in the 2 years following the hurricanes: Winter 2006 (W-06; January 6–February 10, ca. 3 months after hurricane Wilma), Summer 2006 (S-06; June 17–July 28, ca. 8 months after Wilma), Winter 2007 (W-07; February 22–March 26, ca. 16 months after Wilma), and Summer 2007 (S-07; July 9–August 17, ca. 21 months after Wilma). In W-07, only three of the sites were sampled (but each with the same sampling effort of 216 net hours). In S-07, the last sampling day for one of the sites was missed due to a hurricane alert; this particular site was excluded from most statistical analyses (see later).

Data Analyses

We first estimated sample coverage for each sampling period using the function *iNEXT* in the package “iNEXT” (Hsieh, Ma, & Chao, 2016) in R version 3.2.3 (R Core Team, 2015). For a general description of the bird assemblages in each of the six sampling periods, we pooled all new captures registered in a given sampling period (i.e., excluding individuals recaptured during that period) and constructed rank-abundance (dominance–diversity) curves based on the relative abundances (\log_{10} of proportions). These graphs constitute a useful graphical alternative to diversity indexes, and unlike the latter, they provide information on several biologically relevant aspects of species diversity when comparing samples (Feinsinger, 2001). We calculated 95% confidence intervals for statistical comparisons of the curves’ slope estimates. Slope values are indicative of assemblage equitability or dominance (Feinsinger, 2001).

For all other data analyses, the “site” was the sample unit, but only sites with complete sampling effort during a given period (i.e., 216 net hours) were included. Thus, we had the following sample sizes for each of the sampling periods: S-04, $N = 6$; S-06, $N = 6$; S-07, $N = 5$; W-05, $N = 6$; W-06, $N = 6$; and W-07, $N = 3$. To determine the effects of the hurricanes on bird abundance and number of species, we used generalized linear mixed-effects models using the R package “lme4” (Bates, Maechler, Bolker, & Walker, 2015). We fitted two fixed factors: “hurricane” with three levels (pre-hurricanes, post-hurricanes 2006, and post-hurricanes 2007) and “season” with two levels (summer and winter). We fitted “site” as a random-effect factor. Due to overdispersion when using a Poisson error structure, we used the negative binomial distribution for modelling these count response variables (Crawley, 2007). After fitting the full model, the significance of the interaction term (“hurricane \times season”) was

tested through a deletion test, that is, by comparing the change in deviance when fitting the full model versus the model without the interaction term (Crawley, 2007). After this, we carried out treatment contrasts among years within seasons, that is, we made the following six comparisons: S-04 versus S-06, S-04 versus S-07, S-06 versus S-07, W-05 versus W-06, W-05 versus W-07, and W-06 versus W-07. To control for multiple comparisons and keep an experiment-wise significance level of .05, we used the sequential Dunn–Sidak method to calculate the α' value for each of the significance tests (Sokal & Rohlf, 1995). We acknowledge that the level of significance is an arbitrary value and that its correction for multiple comparisons is a controversial issue. Thus by providing exact p values as well as the corrected level of significance for each pairwise comparison, we encourage readers to reach their independent interpretation of our statistical results.

We also analyzed the percentage of migratory individuals, and the percentage of migratory species, but only for the winter season, which is when migrants are present. In this case, we fitted only one fixed factor (“hurricane”) and one random-effect factor (“site”). When using a binomial error structure for the response variables, we encountered overdispersion; we thus transformed the response variables with the angular transformation (Sokal & Rohlf, 1995) to achieve normality and carried out linear mixed effects models using the R package “nlme” (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2015). Multiple comparisons were carried out as described earlier.

To determine changes in community composition and structure, we carried out an ordination through non-metric multidimensional scaling (NMDS) of all samples (32 site/period combinations). Because winter and summer communities are naturally very different (due to the presence of migrants during winter), and our purpose was not to show an obvious seasonal pattern, but rather search for the effects of hurricanes, we then carried out two additional NMDSs, separately for each season. Distance matrices used for the NMDSs were built using abundance data and the Bray–Curtis distance index. Finally, for the summer and winter ordinations, also using Bray–Curtis distance indices, we performed analyses of similarity (ANOSIM) to test for statistical differences among sampling periods. NMDSs and ANOSIMs were carried out, using the functions *metaMDS* and *anosim*, respectively, in the R package “vegan” (Oksanen et al., 2015).

Results

A total of 2,504 individuals of 45 species were captured between 2004 and 2007, with a total effort of 7,074 net hours (Appendix A). Of all species captured, 29 were resident species and 16 were long-distance latitudinal

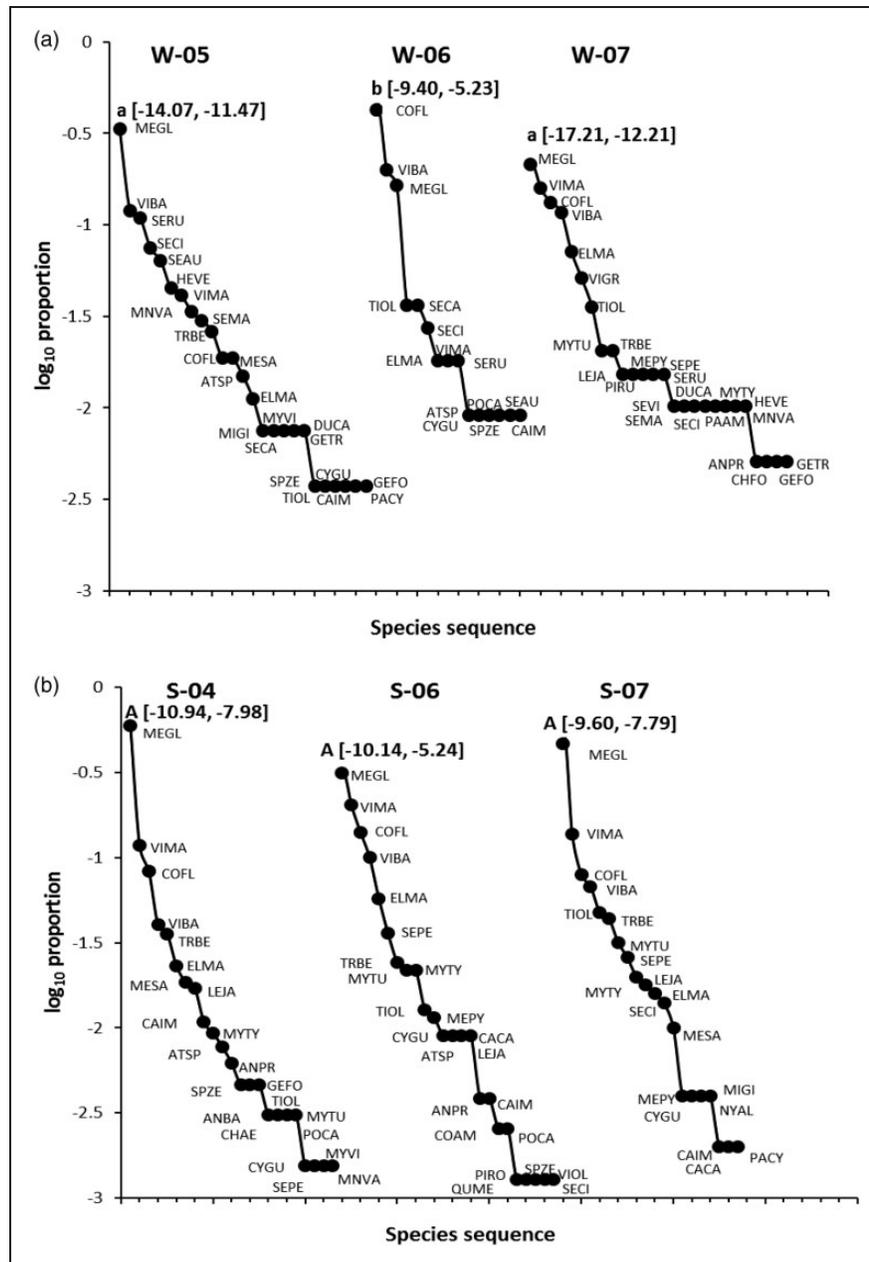


Figure 3. Rank-abundance curves for winter (a) and summer (b) sampling periods. Pre-hurricanes data correspond to the winter of 2005 (W-05) and the summer of 2004 (S-04); post-hurricanes curves are for the first year after the hurricanes (W-06 and S-06) and the second year after the hurricanes (W-07 and S-07). Each circle in a curve represents a bird species which is identified by an abbreviation; see Appendix A for full species names corresponding to each abbreviation. Different letters above curves indicate statistically significant differences for slope estimates and are followed by the 95% interval for these estimates. For clarity, curves are displaced along the x-axis rather than superimposed.

migrants. The resident birds included 13 endemic taxa: 3 at the species level and 10 at the subspecies level. In the winter sampling periods, we recorded a total of 37 species (22 resident species and 15 migratory species; Table S1). In the summers, we recorded 33 species (28 resident and 5 migratory; Table S2).

Sample coverage for all sample periods had values ≥ 0.95 , indicating near sampling completeness in all

cases. When comparing the pooled bird assemblages in each of the six sampling periods, we found a strong effect of the hurricanes only for the first winter after the hurricanes (Figure 3). In the winter sampling periods, we recorded 25 and 26 species in the year before the hurricanes (W-05) and the second year after the hurricanes (W-07), respectively, but only 15 species in the first winter after the hurricanes (W-06). Further, during W-06, the bird

assemblage was significantly less equitable when compared to the other two winter periods, as evidenced by a steeper slope of the rank-abundance curve (Figure 3(a)). For summer sampling periods, all curves showed similar equitability patterns and similar number of bird species were recorded during S-04, S-06, and S-07 (23, 24, and 20 species, respectively; Figure 3(b)). Finally, the rank-abundance curves also showed that the four most abundant species were the same in summer (and in the same order) regardless of the year, whereas in winter the dominant species' identity and order showed some variation depending on the sampling period (Figure 3).

The generalized linear models we carried out to assess the effects of hurricanes, season, and their interaction, on the mean number of individuals and mean number of species captured per site, showed the same general result as described in the previous paragraph: A strong effect of the hurricanes was evidenced only during the first winter (Figure 4, Appendix B). For both response variables, the "hurricane \times season" interaction was highly significant, corroborating that the effects of the hurricanes were different for winter versus summer bird assemblages (tests for the significance in the change of deviance between the full model and the model without the interaction term: individuals, $\chi^2 = 26.73$, $df = 2$, $p < .0001$; species, $\chi^2 = 28.31$, $df = 2$, $p < .0001$). For the winter bird assemblage, the mean number of individuals and species captured per site showed a dramatic decrease in W-06: from 44.5 ± 12.2 individuals (mean \pm standard deviation) and 12.7 ± 2.1 species in the winter before the hurricanes, to 18.3 ± 10.8 individuals and 5.3 ± 2.9 species 3 months after the second hurricane. However, both variables recovered their pre-hurricane values during W-07, that is, 16 months after the second hurricane (65.3 ± 8.4 individuals, 16.0 ± 2.0 species; Figure 4). For the summer bird assemblages, no statistical differences were found among the three periods, but the observed trends were somewhat different to those observed for the winter assemblages (Figure 4). In particular, during the first summer (S-06, 8 months after the second hurricane), we observed a trend of increase in the mean numbers of individuals (from 107.8 ± 27.0 to 130.3 ± 28.7) and species (from 11.8 ± 2.0 to 15.0 ± 2.0) captured per site. One year later, in S-07 (21 months after the second hurricane), the assemblage had returned to the pre-hurricane values (90.4 ± 37.2 individuals, 11.2 ± 1.8 species; Figure 4).

For the winter bird assemblages, we also analyzed the effects of the hurricanes on the mean percentage of migratory individuals and species per site. Contrasts of means between sampling periods showed significantly lower percentages of migratory birds ($10.6 \pm 12.9\%$ of the individuals and $20.9 \pm 26.6\%$ of the species), compared to the much higher pre-hurricanes values ($38.7 \pm 15.4\%$ migratory individuals and $47.8 \pm 10.2\%$ migratory species;

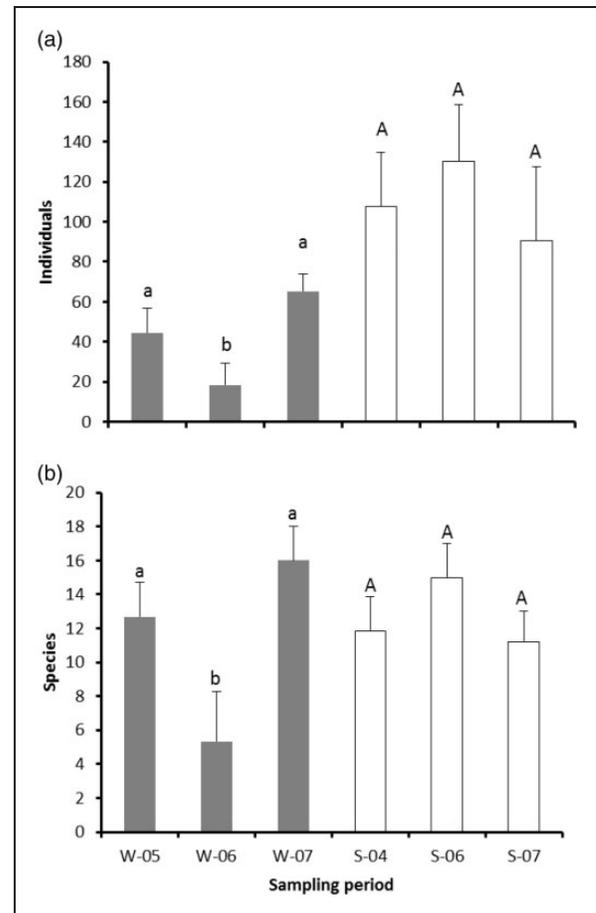


Figure 4. Mean number of individuals (a) and species (b) captured per site during winter sampling periods (W, gray bars) and summer sampling periods (S, white bars), before the hurricanes (W-05 and S-04), the first year after the hurricanes (W-06, S-06), and the second year after the hurricanes (W-07, S-07). Error bars indicate $+1$ standard deviation of the mean (for W-07 $N = 3$ and for S-07 $N = 5$, for the rest $N = 6$). Different letters above bars indicate statistically significant differences within seasons (lower case letters for winter comparisons; upper case letters for summer comparisons).

Figure 5). By the second winter after the hurricanes (W-07), the percentage of migratory birds had somewhat recovered ($16.5 \pm 6.1\%$ of the individuals, $35.2 \pm 7.8\%$ of the species) but was still lower (though not statistically significant) than pre-hurricanes values (Figure 5).

In terms of changes in community composition and structure, the ordination of all 32 samples (all site/period combinations) revealed a clear separation between the summer and winter samples (two-dimensional NMDS, stress = 0.17, $r^2 = 0.98$), and a much wider scatter of the latter (Figure 6(a)). When performing the NMDSs followed by ANOSIM, separately for winter and summer seasons, the different sampling periods could be clearly distinguished in both cases (winter: two-dimensional NMDS, stress = 0.15, $r^2 = 0.98$; ANOSIM, $R = 0.80$,

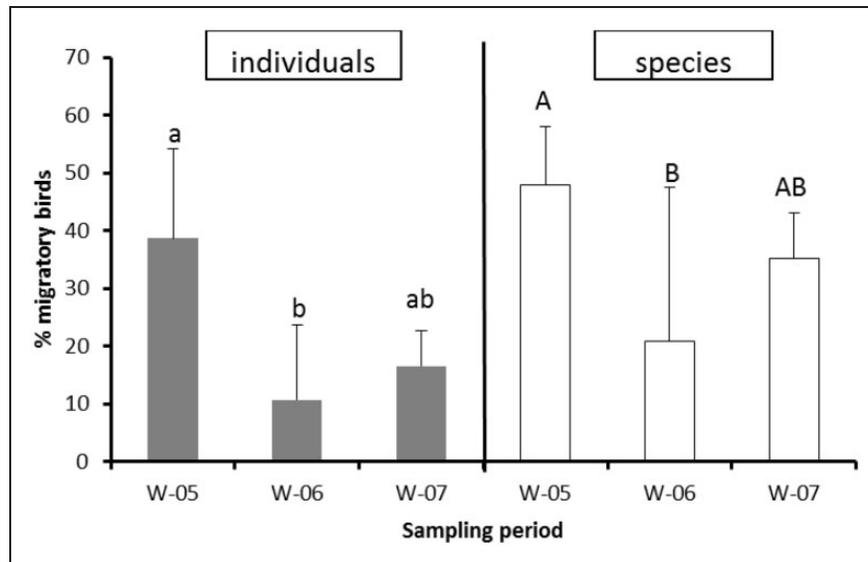


Figure 5. Mean percentage of migratory individuals (gray bars) and migratory species (white bars), captured per site during winter sampling periods before the hurricanes (W-05) and the first and second year after the hurricanes (W-06 and W-07, respectively). Error bars indicate ± 1 standard deviation of the mean. Different letters above bars indicate statistically significant differences (lower case letters for individuals; upper case letters for species). Sample sizes are six sites for W-05 and W-06 and three sites for W-07.

$p < .001$; Figure 6(b); summer: two-dimensional NMDS, stress = 0.15, $r^2 = 0.98$; ANOSIM, $R = 0.55$, $p < .001$; Figure 6(c)).

Discussion

Our study provides the first quantitative assessment of the combined effects of two hurricanes on the highly diverse, yet vulnerable, forest bird community of Cozumel Island as well as its recovery over a period of almost 2 years. The biodiversity of this island faces many threats, of which increased frequency of hurricanes is only one. As in other sites with an intense tourism activity along the Mexican Caribbean coast, Cozumel's natural ecosystems suffer great negative impacts from tourism-related land-used changes (Correa-Sandoval & McKinnon, 2011). It also suffers from threats that commonly affect island biotas, most prominently introduced invasive species such as the boa (*Boa imperator*), feral dogs, and cats as well as house mice and rats (Cuarón, 2009; Cuarón et al., 2009; Martínez-Morales et al., 2009). Unfortunately, hurricane-induced forest disturbance may have greater negative effects on avian populations and communities when coupled with anthropogenic disturbances due to synergistic relationships (Martínez-Morales et al., 2009; Rittenhouse et al., 2010).

In general, we found that after the occurrence of two major hurricanes in a 3-month period, the number of bird species and individuals captured in the forest understory of Cozumel Island showed strong declines in the short term (3 months after the second hurricane) but recovered

quickly thereafter (8 months after the second hurricane). We also found that pre- and post-hurricanes bird assemblages were still different in terms of species composition and the relative abundance of species, 21 months after the hurricanes. All our sampling periods had very high sample coverage (≥ 0.95), thus assuring that our comparisons between periods are robust. Nonetheless, our study only has 1 year of baseline data before the hurricanes occurred, and since we are unable to determine if these data are representative of a "typical year," some caution should be taken when interpreting the results presented here as effects unequivocally caused by the hurricanes.

Three months after hurricane Wilma (W-06), we found significant decreases in the number of birds captured. A similar decline in forest birds within a comparable time frame was observed in the U.S. Virgin Islands, 4 months after hurricane Hugo (Askins & Ewert, 1991), and also in the Yucatan Peninsula 5 to 6 months after hurricane Gilbert (Lynch, 1991). We attribute the declines in our study to both direct and indirect effects of the hurricanes. During W-06, dead birds were commonly seen (H. P.-V., personal observation) and the body condition of some species also decreased significantly (Perdomo Velázquez, 2006). Both common and rare species suffered declines in the number of captures. For example, one resident endemic subspecies, the Cozumel Black Catbird (*Melanoptila glabrirostris cozumelae*; Figure 2), which was the most abundant bird before the hurricanes, suffered an 80% reduction in captures (Table S1). However, the Bananaquit (*Coereba flaveola*), which was not common in the winter before the

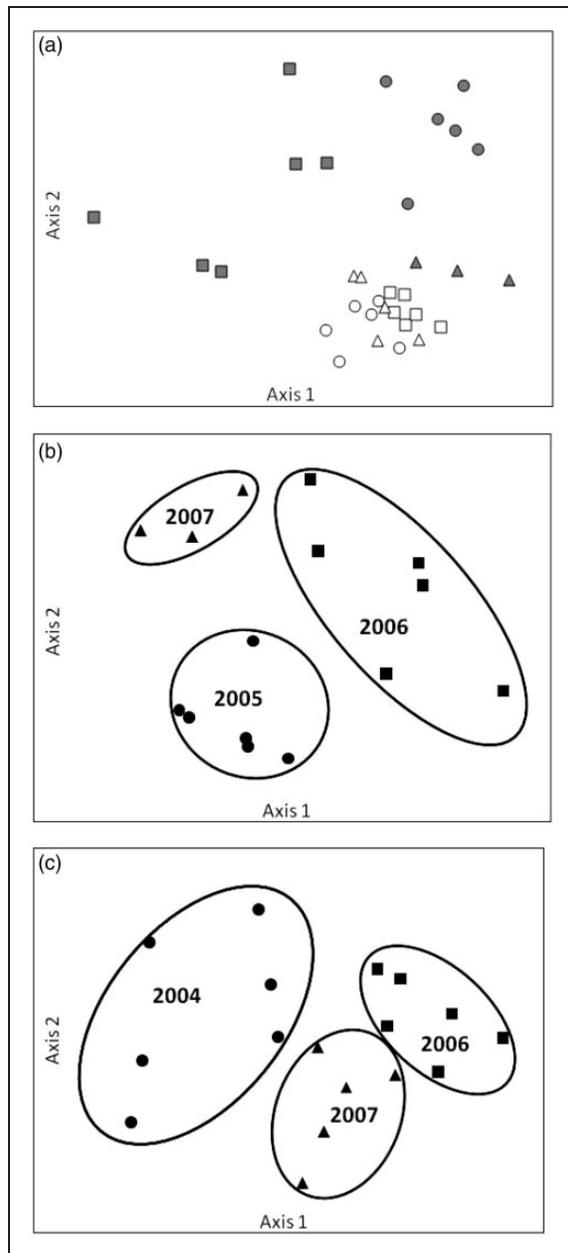


Figure 6. Two-dimensional ordinations (NMDS) of all site/period combinations (a), and separately for winter (b) and summer samples (c). Pre-hurricanes samples are represented by circles (2004 for summer and 2005 for winter), samples from the first year after the hurricanes (2006) are represented by squares, and samples from the second year after the hurricanes (2007) are represented by triangles. In (a), winter samples are represented by gray symbols and summer samples are represented by white symbols. The same six sites were sampled in each of the six periods, except Summer 2007 and Winter 2007 when only five and three of the six sites, respectively, were sampled fully.

hurricanes, was the most abundant bird species during the first winter after the hurricanes (Figure 3). A similar increase was reported for Bananaquits in Puerto Rico, one month after hurricane Georges (Tossas, 2006).

Interestingly, the Bananaquit was one of the species showing strongest declines in the U.S. Virgin Islands after hurricane Hugo (Askins & Ewert, 1991).

Despite the strong declines observed 3 months after the hurricanes, we found that the number of individuals and species recovered relatively fast. Eight months after the hurricanes, the summer bird assemblage (S-06) showed statistically similar mean values for these parameters (with even a trend of increase; Figure 4), when compared to those observed in the summer before the hurricanes. Similarly, both the winter and summer assemblages of the second year after the hurricanes (16 and 21 months after the hurricanes, respectively) had parameter values comparable to their respective pre-hurricanes assemblages. Other studies have also reported fast recovery times (≤ 1 year) for bird assemblages affected by hurricanes, which have been attributed to the capacity of species to modify their foraging behavior, exhibit diet plasticity, or move to other food patches (Freeman et al., 2008; Waide, 1991b; Wauer & Wunderle, 1992). However, some studies also report longer term effects of hurricanes on bird assemblages. For example, 13 years after hurricane Hugo destroyed 90% of a mature mangrove forest in the U.S. Virgin Islands, the abundance of landbirds was still 25% lower than the pre-hurricane value (McNair, 2008). As pointed out by Wiley and Wunderle (1993), recovery of forest bird assemblages is highly dependent on the extent and degree of damage that the vegetation suffered and on how fast its recovery is.

Despite the fast recovery that seems to occur often after hurricanes, in terms of bird abundance and species numbers, changes in community composition or structure may be observed for longer periods of time (e.g., Rittenhouse et al., 2010; Tejada-Cruz & Sutherland, 2005; Wunderle, 1995). In our study, we found that all our post-hurricanes bird assemblages were distinguishable from pre-hurricanes assemblages when species identities linked to their abundance ranks were taken into consideration (Figures 3 and 6), even 22 months after the hurricanes. After the hurricanes some species showed increases in their capture rates (e.g., *Vireo magister*, *Vireo bairdi*, *Setophaga petechia rufivertex*, *Elaenia martinica remota*, *Myiarchus tuberculifer*, and *Myiarchus tyrannulus*), while others suffered declines (e.g., *Leptotila jamaicensis gaumeri*, *Spindalis zena benedicti*, and the endemics *M. g. cozumelae* and *Troglodytes beani*). The species that showed higher captures rates after the hurricanes were mainly insectivorous or dietary generalists that tend to forage on leaves or sally for insects on open spaces or forest edges. These species seem to have benefitted from the change in the structure of the vegetation after both hurricanes. On the other hand, the most affected species were frugivorous. This result is consistent with the findings of previous studies in the Caribbean

which report stronger negative effects of hurricanes on frugivorous and nectarivorous species (Askins & Ewert, 1991; Lynch, 1991; Waide, 1991b; Wauer & Wunderle, 1992; Wunderle, Lodge & Waide, 1992; but see Tossas, 2006).

Another change in community structure and composition observed during the first winter after the hurricanes was the strong decline, not only of the absolute abundance but also the relative abundance of migratory birds, both species and individuals (Figure 5). Such a decrease was most likely due to migrating birds avoiding damaged areas as has been previously reported (Wauer & Wunderle, 1992; but see Lain et al., 2017). While our results on the effect of hurricanes for migratory species coincide with those reported by McNair (2008) for a mangrove forest, they differ from those of two studies in which no effect of hurricanes on the abundance of migratory birds was found (Lain et al., 2017; Lynch, 1991). One study focused on northward-moving spring migrants in the southern United States after having crossed the Gulf of Mexico (Lain et al., 2017), a very different scenario from our study. In that case, birds had little choice but to stop in the isolated coastal forest patches after a trans-Gulf journey, even when vegetation had been strongly affected by a hurricane. On the other hand, the study by Lynch (1991) was carried out in the Yucatan Peninsula and focused on overwintering migrants, a scenario similar to ours. Yet, Lynch (1991) found that overwintering migrants continued to contribute about the same proportion of individuals and species during the first winter after the passage of hurricane Gilbert. The difference of results between Lynch's and our study could be explained by two complementary hypotheses: (a) the damage caused by the hurricanes in Cozumel was higher due to a greater effect of two consecutive hurricanes occurring over a short period of time, causing migrant bird communities to show a stronger response; and (b) the fact that our study site is an island, where the effects of the hurricanes on resource abundance cannot be buffered by the proximity of less affected habitats, contrary to what happens in mainland settings. As the frequency of major hurricanes is unfortunately increasing, studies in the near future will likely be able to determine the degree to which organisms supposedly adapted and resilient to recurrent hurricane disturbance, such as migratory birds (Lain et al., 2017), are able to cope with such an increase. Island ecosystems in the Caribbean play a crucial role for many Neotropical-Nearctic migratory bird species; conjunct multinational efforts will be necessary to ensure that adequate habitat patches for migrants are maintained in as many islands as possible in order to provide alternative stop-over sites and secure migration routes.

Implications for Conservation

Natural disturbances, such as hurricanes, are unfortunately not the only threat to the integrity of Cozumel's forest bird community. The relatively recent, but fast growth of the human population in Cozumel has caused an increase in anthropogenic disturbances that can directly or indirectly affect forest birds. Among these disturbances, the decrease and fragmentation of the forest cover, and the introduction of species, are probably the most serious threats to Cozumel's biodiversity (Cuarón, 2009; Cuarón et al., 2009; Martínez-Morales et al., 2009). Also, competition with more aggressive bird species that are usually confined to urban areas but may invade the forest interior after disturbances, such as the Great-tailed Grackle (*Quiscalus mexicanus*; H. P.-V., personal observation), could constitute a threat in the future. In this regard, introduced exotic bird species may also represent an imminent threat for the native forest bird community due to competition for food and nest sites, particularly when these species are recognized as invasive, such as the Common Starling (*Sturnus vulgaris*), the House Sparrow (*Passer domesticus*), and the Eurasian Collared-Dove (*Streptopelia decaocto*), all of which are already present in Cozumel's urban areas.

During the next few decades, it is very likely that most Atlantic hurricane seasons will have above average activity, in terms of the frequency of intense hurricanes (Sobel et al., 2016; Walsh et al., 2016). Anthropogenic disturbances will also likely increase in number and magnitude. These two types of disturbances, and their synergistic effects, will negatively affect fragile island ecosystems, such as Cozumel, and their extinction-prone endemic species (e.g., McFadden et al., 2010). Some actions need to be taken to protect island biodiversity in areas where hurricanes occur frequently and are coupled with anthropogenic disturbances: (a) permanent biodiversity monitoring programs, in order to quantify the real effects of each driver on different taxa or guilds of organisms and thus be able to design specific management strategies to prevent or mitigate negative effects after a hurricane, (b) captive breeding and reintroduction of endemic native taxa, (c) establishment of effective and strategic protected areas, (d) enhancement of natural habitat connectivity in fragmented landscapes, (e) management of introduced invasive species and (f) involvement of the local community and authorities in the decisions and actions necessary to solve or mitigate the negative effects of human development. If the local communities do not fully understand the value and services provided by their natural environments and their components, long-term conservation becomes a difficult task.

Appendix A. List of Resident and Migratory Bird Species and the Total Number of Individuals Captured (Ind.) During 2004–2007 (7,074 net hours) in the Understory of the Semideciduous Forest of Cozumel Island.

Scientific name	Common name	Abbr.	Ind.
Resident species			
<i>Anthracothorax prevostii</i>	Green-breasted Mango	ANPR	8
<i>Antrostomus badius</i>	Yucatan Nightjar	ANBA	2
<i>Attila spadiceus cozumelae</i>	Cozumel Bright-rumped Attila	ATSP*	17
<i>Camptostoma imberbe</i>	Northern Beardless-Tyrannulet	CAIM	13
<i>Cardinalis cardinalis saturatus</i>	Northern Cardinal	CACA*	8
<i>Chloroceryle aenea</i>	American Pygmy Kingfisher	CHAE	2
<i>Chlorostilbon forficatus</i>	Cozumel Emerald	CHFO*	1
<i>Coccyzus americanus</i>	Yellow-billed Cuckoo	COAM	2
<i>Coereba flaveola</i>	Bananaquit	COFL	282
<i>Cyclarhis gujanensis insularis</i>	Rufous-browed Peppershrike	CYGU*	12
<i>Elaenia martinica remota</i>	Caribbean Elaenia	ELMA	87
<i>Leptotila jamaicensis</i>	Caribbean Dove	LEJA	31
<i>Melanerpes pygmaeus pygmaeus</i>	Yucatan Woodpecker	MEPY*	14
<i>Melanerpes santacruzi leei</i>	Velasquez's Woodpecker	MESA*	22
<i>Melanoptila glabrirostris cozumelae</i>	Cozumel Black Catbird	MEGL*	1017
<i>Mimus gilvus</i>	Tropical Mockingbird	MIGI	4
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	MYTU	39
<i>Myiarchus tyrannulus</i>	Brown-crested Flycatcher	MYTY	34
<i>Myiopagis viridicata</i>	Greenish Elaenia	MYVI	3
<i>Nyctidromus albicollis</i>	Pauraque	NYAL	2
<i>Piranga roseogularis cozumelae</i>	Rose-throated Tanager	PIRO*	1
<i>Polioptila caerulea cozumelae</i>	Blue-grey Gnatcatcher	POCA*	5
<i>Quiscalus mexicanus</i>	Great-tailed Grackle	QUME	1
<i>Setophaga petechia rufivertex</i>	Yellow Warbler	SEPE*	45
<i>Spindalis zena benedicti</i>	Western Spindalis	SPZE	6
<i>Tiaris olivacea intermedia</i>	Yellow-faced Grassquit	TIOL*	49
<i>Troglodytes beani</i>	Cozumel Wren	TRBE*	75
<i>Vireo bairdi</i>	Cozumel Vireo	VIBA*	215
<i>Vireo magister</i>	Yucatan Vireo	VIMA	348
Migratory Species			
<i>Dumetella carolinensis</i>	Grey Catbird	DUCA	4
<i>Geothlypis formosa</i>	Kentucky Warbler	GEFO	5
<i>Geothlypis trichas</i>	Common Yellowthroat	GETR	3
<i>Helmitheros vermivorum</i>	Worm-eating Warbler	HEVE	14
<i>Mniotilta varia</i>	Black-and-white Warbler	MNVA	12
<i>Passerina amoena</i>	Lazuli Bunting	PAAM	2
<i>Passerina cyanea</i>	Indigo Bunting	PACY	2
<i>Piranga rubra</i>	Summer Tanager	PIRU	3
<i>Seiurus aurocapilla</i>	Ovenbird	SEAU	18
<i>Setophaga caerulescens</i>	Black-throated Blue Warbler	SECA	6
<i>Setophaga citrina</i>	Hooded Warbler	SECI	33
<i>Setophaga magnolia</i>	Magnolia Warbler	SEMA	10
<i>Setophaga ruticilla</i>	American Redstart	SERU	34
<i>Setophaga virens</i>	Black-throated Green Warbler	SEVI	2

(continued)

Appendix A. Continued

Scientific name	Common name	Abbr.	Ind.
<i>Vireo griseus</i>	White-eyed Vireo	VIGR	10
<i>Vireo olivaceus</i>	Red-eyed Vireo	VIOL	1

Note. An asterisk (*) next to the name abbreviation (Abbr.) indicates endemic species or subspecies. For bird scientific names and migratory status we used Avibase (Lepage 2013) and Berlanga et al. (2015).

Appendix B. Statistical Results of the Linear Models for the Response Variables.

Response variable	Difference tested	Estimate of difference	Stand. error difference	Z value	p	α'
#individuals	W-05 vs. W-06	0.8867	0.1811	4.90	9.8×10^{-7}	.0102
#individuals	W-05 vs. W-07	0.3851	0.1976	1.95	.0513	.0170
#individuals	W-06 vs. W-07	1.2718	0.2105	6.04	1.5×10^{-9}	.0068
#individuals	S-04 vs. S-06	0.1920	0.1523	1.26	.2074	.0253
#individuals	S-04 vs. S-07	0.1790	0.1610	1.11	.2664	.05
#individuals	S-06 vs. S-07	0.3710	0.1633	2.27	.0231	.0127
#species	W-05 vs. W-06	0.8650	0.2006	4.31	1.6×10^{-5}	.0102
#species	W-05 vs. W-07	0.2336	0.1828	1.28	.2012	.0253
#species	W-06 vs. W-07	1.0986	0.2158	5.091	3.6×10^{-7}	.0068
#species	S-04 vs. S-06	0.2371	0.1605	1.48	.1388	.0170
#species	S-04 vs. S-07	0.0550	0.1792	0.31	.7588	.05
#species	S-06 vs. S-07	0.2921	0.1699	1.72	.0854	.0127
%migr.indiv	W-05 vs. W-06	24.673	6.630	3.721	.0002	.0170
%migr.indiv	W-05 vs. W-07	14.525	8.174	1.777	.0755	.0253
%migr.indiv	W-06 vs. W-07	10.149	8.174	1.242	.2142	.05
%migr.spp	W-05 vs. W-06	23.670	8.342	2.837	.0046	.0170
%migr.spp	W-05 vs. W-07	8.478	10.434	0.813	.4162	.05
%migr.spp	W-06 vs. W-07	15.192	10.434	1.456	.1454	.0253

Note. The following are the response variables: number of individuals (#individuals), number of species (#species), percentage of migratory individuals (%migr.indiv), and percentage of migratory species (%migr.spp). Multiple comparisons were carried out within the summer (S) and the winter (W) seasons, between sampling periods. Pre-hurricanes periods are represented by the 2004 and 2005 periods for summer (S-04) and winter (W-05), respectively. Post-hurricanes periods are represented by the 2006 and 2007 periods (06 and 07). The third, fourth, and fifth columns show absolute values. The probability p is compared to the adjusted significance level α' (sequential Dunn-Sidak adjustment method) in order to determine statistical significance; significant comparisons are shown in bold font.

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Supplementary Material

Supplementary material for this article is available online.

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