The effect of mangrove restoration on avian assemblages of a coastal lagoon in southern Mexico

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Background. Mangrove forests provide many ecosystem services, including the provision of habitat that supports avian biodiversity. However, hurricanes can knock down trees, alter hydrologic connectivity, and affect avian habitat. In 1995, Hurricanes Opal and Roxanne destroyed approximately 1,700 ha of mangrove forest in Laguna de Términos, Mexico. Since then, hydrological restoration has been implemented to protect the mangrove forest and its biodiversity. **Methods.** Since avian communities are often considered biological indicators of ecosystem quality, avian diversity and species relative abundance were evaluated as indicators of mangrove restoration success by comparing undisturbed mangrove patches with those affected by the hurricanes. Using bird surveys, similarity analyses, and generalized linear models, we evaluated the effects of water quality variables and forest structure on the relative abundance and diversity of the avian community in disturbed, restored, and undisturbed mangrove patches. **Results.** Higher bird species richness and relative abundances were found in disturbed and restored sites compared to the undisturbed site. After restoration, values of frequency of flooding, water temperature, tree density, and the number of tree species were more similar to that of the undisturbed site than to the values of the disturbed one. Such variables influenced the relative abundance of bird guilds in the different habitat conditions. Furthermore, some insectivorous bird species, such as the Yellow Warbler and Tropical Kingbird, were found to be similarly abundant in both undisturbed and restored sites, but absent or very low in occurrence at the disturbed site. **Conclusions.** Collectively, our results strongly suggest that hydrologic restoration helps to enhance niche availability for different bird guilds, including water and canopy bird species. Our work can help inform management strategies that benefit avian communities in mangrove forests and wetland systems.

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2 **Mexico**

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19 **Abstract**

20 **Background.** Mangrove forests provide many ecosystem services, including the provision of

21 habitat that supports avian biodiversity. However, hurricanes can knock down trees, alter

22 hydrologic connectivity, and affect avian habitat. In 1995, Hurricanes Opal and Roxanne

23 destroyed approximately 1,700 ha of mangrove forest in Laguna de Términos, Mexico. Since

24 then, hydrological restoration has been implemented to protect the mangrove forest and its

25 biodiversity.

26 **Methods.** Since avian communities are often considered biological indicators of ecosystem

27 quality, avian diversity and species abundance were evaluated as indicators of mangrove

28 restoration success by comparing undisturbed mangrove patches with those affected by the

29 hurricanes. Using bird surveys, similarity analyses, and generalized linear models, we evaluated

30 the effects of water quality variables and forest structure on the abundance and diversity of the

31 avian community in disturbed, restored, and undisturbed mangrove patches.

32   **Results.** Higher bird species richness and abundances were found in disturbed and restored sites

33   compared to the undisturbed site. At the restored site, frequency of flooding, water temperature,

34   tree density, and the number of tree species were, more similar to the undisturbed site than to the

35   disturbed site. Such variables influenced the abundance of bird guilds in the different habitat

36   conditions. Furthermore, some insectivorous bird species, such as the Yellow Warbler and

37   Tropical Kingbird, were found to be similarly abundant in both undisturbed and restored sites,

38   but absent or very low in occurrence at the disturbed site.

39   **Conclusions.** Collectively, our results strongly suggest that hydrologic restoration helps to

40   enhance niche availability for different bird guilds, including water and canopy bird species. Our

41   work can help inform management strategies that benefit avian communities in mangrove forests

42   and wetland systems.

44   **Introduction**

45   Mangrove forests provide valuable ecosystem services. These highly productive ecosystems can

46   prevent erosion, trap sediments, and provide wind protection for coastal communities (Warren-

47   Rhodes et al., 2011). Mangrove forests also support important nursery habitats for a variety of

48   organisms including pelagic and marine vertebrates and invertebrates, mammals, and birds

49   (Nagelkerken et al., 2008; Lee et al., 2014; Serafy et al. 2015). In Mexico, mangroves provide

50   important habitats for specialist species such as the Mangrove Cuckoo (*Coccizus minor*), the

51   Mangrove Finch (*Camarhynchus heliobates*), the Mangrove Hummingbird (*Amazilia buocardi*),

52   and the Mangrove Warbler (*Setophaga petechia bryanti*) (Polidoro et al., 2010; Andrade et al.,

53   2012; Gardner et al., 2012; Buelow & Sheaves, 2015). Mangrove forests can also improve water

54   quality (Wang et al., 2010), and provide economically important products. Nevertheless, it is

55   estimated that about 35% of the global mangrove cover has been lost, mainly due to forest

56   clearance for fish farming, urbanization, habitat fragmentation, and fuel and timber production

57   (Valiela, Bowen & York, 2001; Alongi, 2008; Donato et al., 2011).

58   In Mexico, four mangrove species are distributed along the Gulf of Mexico coast: red

59   (*Rhizophora mangle*), black (*Avicennia germinans*), white (*Laguncularia racemosa*), and button

60   (*Conocarpus erectus*) mangroves, covering approximately 742,000 hectares (ha) (Giri et al.,

61   2011). The estimated value of mangroves due to fisheries, carbon sequestration, forestry coastal

62   protection, erosion control, water treatment and other environmental, recreational and traditional

63   uses is about \$80,000 to \$194,000 USD per ha^{-1}yr^{-1} (Salem & Mercer, 2012; Costanza et al.,

64   2014). Such a value represents up to a total of \$59–143 billion USD for the Mexican mangroves.

65   Globally, Mexico ranks fourth in terms of total mangrove area (Giri et al., 2011); however, as in

66   other parts of the world, the rate of degradation of mangrove forests in Mexico has been high in

67   the past century. Mangrove cover has been reduced by approximately 10% of the original area in

68   the last 40 years, and about 2% (15,000 ha) of the area that remains has been classified as

69   disturbed (Valderrama et al., 2014). In most mangrove forests, there has

70   been a loss of connectivity and a decrease in heterogeneity, which has reduced faunal diversity,

71   including avian populations (Mohd-Azlan, Noske & Lawes, 2015; Hauser et al., 2017; Amir,

72   2018).

73   Because restoration can help mitigate climate change effects and the consequential biodiversity

74   loss (Nilsson & Aradottir, 2013), interest in the ecological restoration of coastal wetlands is

75   currently growing (Palmer, Hondula & Koch, 2014; Suding et al., 2015). The disturbance of

76   coastal wetlands is often accompanied by changes in hydrological patterns, including the

77   hydroperiod, which is defined as the amount of time, the frequency, and the level with which a

78   wetland is covered by water, a key factor determining success in wetland restoration (Turner &

79   Lewis, 1996; Zaldívar-Jiménez et al., 2010; Wortley, Hero & Howes, 2013). For instance,

80   sediment deposition in the tidal channels affects the amount of time and the frequency at which a

81   mangrove is flooded (Woodroffe et al., 2016). These kinds of changes affect the water quality

82   and the composition of plant and animal communities (Schaffelke, Mellors & Duke, 2005;

83   Krauss et al., 2006; Crase et al., 2013). Hence, the success of ecological restoration can be

84   assessed through a system of indicators that generate information about the recovery of wetland

85   functions. Such a system might include landscape features, biogeochemical processes (Cvetkovic

86   & Chow-Fraser, 2011; Zhang et al., 2012), ecosystem services, and the composition of biological

87   assemblages (e.g., vegetation, crustaceans, mollusk, and vertebrates) (Thornton & Johnstone,

88   2015; Salmo, Tibbetts & Duke, 2016). Therefore, species richness, abundance, and community

89   structure can be used to evaluate the biological outcomes of restoration efforts (Zhao et al.,

90   2016).

91   Because of their diverse roles within the trophic webs, bird communities are key elements for

92   describing the energetics of ecosystems (Wenny et al., 2011; Adame et al., 2015; McFadden,

93   Kauffman & Bhomia, 2016), and are considered useful indicators of ecosystem health

94   (Canterbury et al., 2000; Bryce, Hughes & Kaufmann, 2002; Catterall et al., 2012). For instance,

95   monitoring of pollutants such as DDT and organochlorines, and the effects of variations in

96   hydroperiod in the Everglades were carried out using water and wading bird species (Frederick et

97   al., 2009; Lavoie et al., 2010; Lantz, Gawlik & Cook, 2011; Boyle, Dorn & Cook, 2012).

98   Moreover, bird diversity has been used as an indicator of temporal changes in mangrove health

99   (Behrouzi-Rad, 2014), and to assess the impacts of climate change and coastal development

100   (Ogden et al., 2014). While avian community monitoring can be a useful tool for evaluating the

101   health of wetland ecosystems, its use for assessment of ecological restoration has been rarely

102   employed (Weller, 1995; Cui et al., 2009; Gyurácz, Bánhidi & Csuka, 2011; Li et al., 2011;

103   Catterall et al., 2012; Zou et al., 2014).

104   Laguna de Términos is a coastal lagoon located in Mexico along the southwestern coast of the

105   Gulf of Mexico. It is the second biggest coastal lagoon in Mexico, supporting approximately

106   259,000 ha of mangrove forest (33% of all mangrove forest in Mexico) and 262 bird species,

107   among other vertebrate taxa (Villalobos-Zapata & Mendoza-Vega, 2010). As a result, Laguna de

108   Términos has been recognized as a Ramsar wetland of international importance (Chape,

109   Spalding & Jenkinst, 2008). However, due to fisheries, oil-extraction activities, illegal timber

110   exploitation, and urbanization, nearly 26% of the mangrove habitat in this lagoon is considered

111   degraded (Zaldívar-Jiménez et al., 2017). Additionally, in 1995, the lagoon was affected by

112   Hurricanes Opal (category 4) and Roxana (category 3), which destroyed 1,700 ha of mangrove

113   (Pérez-Ceballos et al., 2013). Fallen trees blocked some creeks (hereafter tidal channels), mainly

114   the secondary ones. The silting of channels altered the hydroperiod patterns and biogeochemical

115   conditions, leading to the mortality of adult trees and inhibiting the natural regeneration of the

116   mangrove. Moreover, this condition has led to a constantly increasing area of dead trees around

117   the points affected by the hurricanes. In order to increase the resilience of these mangrove

118   forests, protect their biological diversity, educate others, and contribute to the sustainable

119   development of the adjacent local communities, from October 2010 to November 2012,

120   restoration activities were implemented. In brief, restoration activities included an environmental

121   and social diagnosis, as well as the formulation of a management plan before the restoration

122   implementation. The primary restoration activity was the desilting and unblocking of the main

123   and secondary tidal channels. Where needed, new secondary channels were dug based on the

124   microtopography analysis of each site selected for restoration. Desilting, unblocking, and

125   channel digging were carried out by local women and men only by hand.

126   The objective of this study was to use the changes on the avian abundance and diversity as

127   indicators of the restoration success of a mangrove site. We specifically asked: 1) whether the

128   avian community structure differs between not obviously affected mangrove patches and those

129   affected by the hurricanes; 2) whether hydroperiod and water quality influence the diversity or

130   the abundance of birds; and 3) which species could be used as indicator species of post-

131   restoration recovery? The sampling was carried out on a landscape mosaic with different strata:

132   undisturbed patches, patches without restoration, and patches three years after restoration. The

133   water quality variation among the study sites, along with the avian community diversity and

134   abundance of species, were evaluated as indicators of mangrove restoration success.

135

136   **Materials & Methods**

137   **Study area**

138   Laguna de Términos is a coastal wetland located in Campeche, Mexico. It covers about 150 km^2

139   and is connected to the Gulf of Mexico by two inlets at the east and west sides of Isla del

140   Carmen, a calcareous sandbar that supports 5,900 ha of mangrove, of which around 26% are

141   disturbed. The annual average rainfall and temperature are approximately 1,420 mm and 27 °C

142   respectively (David & Kjerfve, 1998). The study area is an estuary known as Bahamitas, located

143   on the east of Isla del Carmen (637787.52E, 2066226.35N, and 633872.60E, 2064181.96N UTM

144   Q15, Fig. 1). The hydrological restoration was implemented from October 2010 to November

145   2012 through desilting and unblocking of natural tidal channels. Where needed, new secondary

146   channels were created to induce natural regeneration of the vegetation, and to enhance the water

147   quality (oxygenation and salinity) of 1,300 ha of disturbed mangrove through water exchange

148   (Zaldívar-Jiménez et al., 2017). The creation of new tidal channels relied on the modeling of

149   hydrological flow-paths after analysis of a digital elevation model created from the obtained

150   microtopography data. All the work was undertaken by hand using shovels, and involved local

151   inhabitants (10 people ha^{-1}), who were trained through workshops on habitat restoration and

152   environmental education, as well as being advised on social and community organization for

153   sustainable development through bird watching and catch-and-release fishing (Zaldívar-Jiménez

154   et al., 2017).

155

Sampling sites and forest structure

157   Based on the digital analysis of a Worldview 2013 image and subsequent field surveys, three
158   different patches for sampling were identified and selected according to their condition of
159   degradation: i) First were undisturbed sites with well-established adult trees and no significant
160   human activities. Here, at least 80% of the trees were alive and there was no evident alteration of
161   the hydrological connectivity due to the effects of hurricanes. ii) Second were disturbed sites
162   with all the trees dead, except for some few individuals at the edges, and no seedling
163   establishment or with no more than 10% of scrub mangroves alive. iii) Third were restored sites
164   that showed similar conditions to the degraded site prior to restoration activities implemented
165   during 2010 and 2012 to allow water to flow in and out through the topography of the wetland.
166   After restoration (three years), this site already showed the establishment of seedlings and some
167   saplings, and no more than 50% of the scrub mangroves were dead.
168   For each sampling site, two 10 m x 10 m random sampling plots were surveyed to determine the
169   forest structure and the number of live trees. On the same plots, measures of diameter at breast
170   height (DBH), canopy height, and basal area were collected to determine the forest cover. Tree
171   density was estimated by counts of all trees with DBH > 2.5cm (Schaeffer-Novelli, Vale &
172   Cintrón, 2015). These data were used to investigate the effects of the vegetation structure on bird
173   abundance in each sampling site (McElhinny et al., 2005; Azhar et al., 2013).

174

Hydrologic and water quality parameters

176   To assess the relationship of bird abundance with the water quality parameters, 11 sampling
177   points were established every 100 m within each survey site to measure the water depth, as well
178   as the temperature and salinity of surficial water of the tidal channels. Water depth was measured
179   using a ruler at the center of the tidal channels. Temperature and salinity were recorded using a
180   parametric probe, YSI-30 (YSI Incorporated, USA). The pH and oxidation reduction potential
181   (ORP) were recorded using a portable tester, HI916 (Hanna Instruments, Inc., USA). All these
182   data were recorded twice monthly. The hydroperiod patterns among the sampling sites were also
183   compared by contrasting the tidal range (the level of the flooding in cm), the flooding duration
184   (the time in hours that a site stand flooded), and the flooding frequency (the number of times per

185   month that a place floods). These measures were recorded during the entire sampling period

186   every 60 minutes using a HOBO U20-001-01-Ti logger placed at each sampling site.

187

188   **Birds survey**

189   To estimate species richness and abundance, monthly bird surveys (December 2014 to June

190   2015) were conducted by boat. This period of time was selected because it allows finding both

191   migrant birds in winter and residents species in spring and early summer. Counting points (n =

192   11 for each sampling site) were used to record bird species and count individuals per species

193   within each sampling site. We carried out a systematic sampling with a randomly selected start

194   point at each sampling area. Then, the next ten counting points were separated 100 m from each

195   other. Because a count at a particular point can be affected by whether the neighboring points are

196   above or below their averages (Pendleton, 1995), we tested for independence of our counting

197   points through a Pearson's test of conditional independence. Additionally, we used the function

198   Moran included in the R package ape (Paradis, Claude & Strimmer, 2004) to treat the abundance

199   data across counting points with a Moran's index test to ensure that they were not spatially

200   biased. As recommended for field methods in bird surveys (Gregory, Gibbons & Donald, 2004),

201   we used a minimum of four visits to each counting point (four in winter and four in spring). To

202   avoid double count, a single observer counted individual birds at standard intervals of time (10

203   min). To help deal with varying detectability of different species, observations were made for

204   two consecutive days (Bibby et al., 1992; Gregory, Gibbons & Donald, 2004; Schmidt, McIntyre

205   & MacCluskie, 2013). To deal with species mimicry, besides song and call recognition, birds

206   were identified by a trained observer that sought field marks using 10 x 42 binoculars. We

207   recorded all species and individuals seen or heard within the first 20 m radius at each counting

208   point. All species and individuals observed on the vegetation, water, or flying within the

209   observation radius (up to 15 m above) were counted. We did not account for passing or transient

210   birds flying on the sampling areas that did not stop there to feed or rest. The sampling effort was

211   equivalent to approximately 77 hours of surveying over the three sampling sites. All bird species

212   observed outside the sampling radius were also recorded but not included in further analyses of

213   species abundance. The reliability of our sampling design concerning species detectability,

214   temporal, and size representativeness was assessed by the implementation of an evaluation

215   framework for ecological research (Battisti, Dodaro & Franco, 2014).

216

Statistical analyses

218 The data on hydroperiod and environmental variables were explored for normality through

219 Shapiro-Wilk tests, which are ratios of two estimates of the variance in a normal distribution

220 calculated from a set of observations (Royston, 1995). Data that met the assumptions of

221 normality and independence were analyzed using a one-way analysis of variance (ANOVA) to

222 compare the means between the data from all sampling sites. When significant differences were

223 found, ANOVA results were further examined through an honestly-significant-difference

224 Tukey's test, a multiple comparisons procedure to find the differences between all levels of a

225 factor once the hypothesis of equality from the ANOVA test is rejected. When the data did not

226 meet the assumption of normality, we used Kruskal-Wallis one-way analysis of variance by

227 ranks, a non-parametric alternative to ANOVA for multiple comparisons. To contrast the levels

228 of a factor from this analysis, we used the function posthoc.kruskal.nemenyi.test from the R

229 package PMCMR, a post-hoc alternative to performing multiple comparisons for non-

230 parametrics (Pohlert, 2014).

231 Species richness and abundance for each sampling site were calculated based on the number of

232 recorded individuals per species. Diversity was estimated using the inverse of Simpson's Index

233 $(1\Sigma(n/N)^2)$ which indicates greater diversity as the resulting value approaches 1, while the

234 dominance (the extent to which a taxon is more numerous than others) was assessed through the

235 Berger-Parker Index ($d = N_{max}/N_T$), in which the lower the value of d results in a more even

236 dominance in the sample (for details on the formulae see Ingram (2008)). To reduce biases

237 caused by non-detected species, the expected species richness was calculated using the Jack1

238 estimator, which is adequate to estimate actual species richness when the number of sampling

239 units is small (< 20 samples or individuals) or when the samples are not the same size. It uses the

240 total number of observed species in a set of samples, the total number of unique species in each

241 sample, and the number of samples for the calculations (Smith & van Belle, 1984; Gotelli &

242 Colwell, 2011). Abundance and evenness (how equal the bird community is numerically) among

243 sampling sites were compared through rank-abundance curves. The curves were constructed as

244 implemented in the R package BiodiversityR (Kindt & Coe, 2005). From the pooled data, the

245 total number of individuals was calculated to obtain their abundance (y-axis) and then ranked

246 from the most to the least abundant species (x-axis). Then, the same procedure was implemented

247   for each sampling location (Kindt & Coe, 2005). Key bird species to particular sampling sites

248   were identified on the basis of their abundance through a one-way Simper test carried out in

249   PRIMER 7 (Anderson, Gorley & Clarke, 2008). The Simper test estimated the contribution of

250   each species abundance to the total dissimilarity among the sampling sites using Bray-Curtis

251   distances, which helps find discriminating features within habitats that explain differences in

252   community composition (Clarke, 1993). Additionally, we estimated the indicator species index

253   value (IndVal) to find the value of particular species to each sampling site as indicators of their

254   condition. The IndVal uses both the relative abundance (instead of the absolute abundance), and

255   the relative frequency of each species to estimate its value as a percentage (Roberts, 2016). We

256   also investigated the relationship between species abundance and environmental variables by

257   means of redundancy (RDA) and multivariate analyses through generalized linear models (glms).

258   The RDA was selected because there was a linear response of the abundance of birds to the

259   measured environmental variables. For both the RDA and the glms, the birds' abundances were

260   used as the dependent variable, and habitat levels, environmental characteristics, and forest

261   structure were explanatory variables. The RDA test was carried out as implemented in

262   BiodiversityR while the glms were fitted through the R package mvabund (Wang et al., 2012).

263   The mvabund functions help test for interactions through multiple testing to predict abundance

264   between sites or treatments. The primary function of mvabund (manyglm) fits a glm to each

265   species in the dataset using a common group of environmental variables. This approach uses a

266   resampling-based hypothesis testing to infer which environmental variables relate to multivariate

267   abundances at community or taxon-specific levels (Wang et al., 2012). The independence of the

268   abundance estimates across sampling sites, as well as the quadratic mean-variance and log

269   linearity in the dataset, were checked through the functions plot and meanvar.plot, as

270   implemented in the same package before fitting the models. Several glms were fitted to tests for

271   variable effects. The data set included the mangrove degradation condition as a categorical

272   variable within the environmental matrix. We performed the same analysis but with the data

273   grouped by functional groups according to the birds primary source of food: insectivores,

274   nectarivores, scavengers, macroinvertivores (polychaetes, mollusks, crustaceans), frugivores,

275   omnivores, and meat eaters (fishes, small reptilians, amphibians, and mammals). Because of the

276   difficultly of measuring this directly in the field, this group classification was sourced from

277   literature on local species (Mackinnon, 2013; Fagan & Komar, 2016), and from specialized web

278   sources (https://www.allaboutbirds.org). Models were ranked according to the Akaike's

279   information criterion (AIC) (Burnham & Anderson, 2002; Burnham, Anderson & Huyvaert,

280   2011). All tests were set to be significant at 0.05 level, if not indicated otherwise.

281

282   **Results**

283   Pearson's test of conditional independence showed that although the sampling points in each site

284   were closely located, they were independent ($\chi^2 = 26.166$, df = 20, $p = 0.1604$). Similarly, no

285   evidence of spatial autocorrelation of the abundance was detected across sampling points

286   (Moran's Index value = 0.0074, $p = 0.3335$).

287

288   **Water quality parameters and forest structure**

289   The frequency of flooding was approximately two and three times greater at the restored and

290   undisturbed sites, respectively, than at the disturbed one (ANOVA test $F_{2,18} = 12.47$, $p = 0.003$,

291   Fig. S1). However, there were no significant differences among treatments in tidal range or

292   flooding duration (ANOVA test $F_{2,18} = 2.259$, $p = 0.133$; $F_{2,18} = 2.416$, $p = 0.118$, respectively).

293   Environmental variables such as salinity concentration, water depth, pH, and temperature were

294   found to be statistically different among sites (Table 1). The mangrove structure also showed

295   significant differences between sites in terms of the number of tree species, basal area, and tree

296   density (Table 1). However, due to the size of the remaining live trees in the disturbed and

297   restored sites, no statistical differences in the heights of trees between sampled sites were

298   observed (Fig. S2). Finally, the ORP values were not statistically different between treatments.

299   However, the ongoing water exchange due to the greater frequency of flooding in the

300   undisturbed and restored areas might indicate higher oxygen concentration in the water (all ORP

301   values were positive).

302

303   **Species diversity and abundance**

304   Fifty-three avian species were recorded in the surveys across the sampling sites (Table S1). One

305   of them, the Reddish Egret (*Egretta rufescens*) is near threatened while the rest are of least

306   concern according to the IUCN (2016). Regionally, five species are under special protection, and

307   one, the Yellow-crowned Night-heron (*Nyctanassa violacea*), is a threatened species

308   (SEMARNAT, 2010). For almost half of the recorded species (49%), the populations are

309   trending to increase while 24.5% show a decreasing trend (IUCN, 2016).

310   The total bird species richness was higher in the disturbed and restored than in the undisturbed

311   site, and, for all sampling sites, the observed species richness was lower than expected (Table 2).

312   This result is consistent with our empirical knowledge of the bird community found in the

313   vicinity of our sampling sites. For instance, species such as the migrant Lesser Scaup (*Aythya*

314   *affinis*), the Northern Pintail (*Anas acuta*), and the American Wigeon (*Anas americana*), as well

315   as the resident mangrove inhabitants, the Muscovy Duck (*Cairina moschata*) and the White-

316   fronted Parrot (*Amazona albifrons*) (both with important population declines in Mexico), were

317   expected but not observed. Diversity indexes showed that there is a clear dominance of few

318   species belonging to the families Ardeidae and Threskiornithidae, especially in the restored site.

319   Even though our sampling effort captured most of the species richness in the study area, the

320   species saturation curve did not reach a flat shape at the end of the surveys (Fig. S3).

321   Accordingly, an increased sampling effort might be necessary to show the true richness of the

322   study area. When pooled data were analyzed, the most abundant species were the Least

323   Sandpiper (*Calidris minutilla*), the Mangrove Warbler, the Black-bellied Whistling Duck

324   (*Dendrocigna autumnalis*), the Green Heron (*Butorides virescens*), the White Ibis (*Eudocimus*

325   *albus*), and the Great-tailed Grackle (*Quiscalus mexicanus*). Because birds detected in flight

326   were only about 10% of all counts and because there were no statistical differences in the

327   abundance between the whole set of data vs. the data that excluded birds detected in flight

328   (Wilcoxon's test with continuity correction, W = 1505.5, $p = 0.7716$), for further analyses, we

329   used the full dataset. Species abundance and evenness were similar for undisturbed and disturbed

330   sites. Although the restored site showed higher bird abundance, this was also the location with

331   the least evenness in species distribution. For instance, higher numbers of species such as the

332   Least Sandpiper and the White Ibis, which depend on mangrove habitats with open or semi-open

333   forest structure, were observed in the restored mangrove patches, while the Mangrove Warbler,

334   the Tropical Kingbird (*Tyrannus melancholicus*), and the American White Pelican (*Pelecanus*

335   *erythrorhynchos*) were the least abundant at this site (Fig. 2).

336   The RDA model was statistically significant (Pseudo- $F_{8,24} = 2.57$, $p = 0.030$), but only a small

337   part of the variation in species abundance within sampling sites was explained by environmental

338   variables since the proportion of unconstrained variance was larger than that of the constrained

339 (0.53 and 0.46, respectively, after 500 permutations for all eigenvalues). When only the first

340 eigenvalue was analyzed, no significant influence of the environmental variables on birds

341 abundance was observed (Fig. S4); however, a trend in some variables such as water

342 temperature, salinity, and tree density to influence the number of birds across sampling sites was

343 detected (Pseudo-$F_{1,24}$ = 17.97, p = 0.055). To explore the effects of environmental variables on

344 the abundance of birds further, five glms were fitted: one with only environmental variables and

345 not accounting for habitat condition and others that included habitat condition and multiple

346 interactions between environmental variables; however, none of these reached convergence.

347 Thus, the analysis was restricted to additive models between habitat condition and environmental

348 variables. Because pH and water depth showed high correlation with salinity (Spearman's rank

349 correlation Rho = 0.486, p = 0.001; Rho = -0.595, p = 0.001, respectively), these two variables

350 were dropped from the models. According to the AIC scores, the best models showed significant

351 effects of the environmental variables and forest structure on the abundance of bird species

352 (Table S2). Habitat condition, i. e., the condition of the mangrove as disturbed, restored or

353 undisturbed, showed more substantial effects on the number of detected birds as well as on the

354 distribution of the bird guilds across sites (Fig. 3). Additionally, vegetation cover, as well as the

355 number of tree species, also significantly positively influenced the birds' abundance (Table 3A).

356 When the same models were fitted to each single species, neither environmental variables nor the

357 habitat condition showed significant effects on the estimated abundances (*Padj* = 0.730 – 0.900

358 for all species and all variables). The multivariate analysis by functional group showed that only

359 detectability significantly influenced the abundance of bird guilds, while the other variables did

360 not show significant effects on the abundance of any of the analyzed functional groups (Table

361 3B). Similar to the univariate results by species, no significant result was observed when

362 functional groups were analyzed separately (*Padj* = 0.172 – 0.932 for all groups and all

363 variables).

364

365 **Key species in mangrove forests**

366 According to the similar percentage analysis, wader bird species, such as the Least Sandpiper,

367 the White Ibis, and the Great Egret (*Ardea alba*) are more associated with the disturbed site.

368 Insectivores such as the Yellow Warbler and the Tropical Kingbird, along with the Green Heron,

369 were more associated with the undisturbed habitat condition. The species associated with the

370   restored site were the Least Sandpiper, the insectivorous Yellow Warbler, and the Green Heron

371   (Table 4). Even though the estimated IndVal value suggested that three bird species might be

372   considered indicators of the different habitat conditions, these results were not significant (Table

373   5).

374

375   **Discussion**

376   The restored tidal channels allowed more frequent water exchange between the Bahamitas

377   estuary and the Laguna de Términos, which increased the frequency of flooding. This, in turn,

378   improved the mangrove soil quality by decreasing the salinity and enabled the natural

379   regeneration of the forest cover. Such changes positively impacted the abundance of

380   insectivorous birds. When comparing the undisturbed and restored sites with the disturbed areas,

381   in the latter, larger duration of flooding favors anaerobic conditions, hindering the oxidation and

382   enabling the rising of soil sulfides concentration (Reddy & Delaune, 2008), which affects the

383   ecophysiological functioning of individual plants and is toxic to aquatic fauna (Lamers et al.,

384   2013). On the other hand, the lack of connectivity with the main lagoon and the absence of

385   mangrove vegetation, as well as the low water exchange and higher rate of evaporation are

386   factors causing higher pH and salinity conditions (Tam et al., 2009, Molnar et al., 2014). These

387   conditions are also likely inhibiting the establishment and growth of seedlings and plants. This

388   effect has been observed in other areas of Laguna de Términos (Agraz-Hernández et al., 2015).

389   By contrast, the undisturbed site showed more frequent water exchange and dense vegetation

390   cover, leading to slower evaporation rate and lower salinity, as posited by Lee et al. (2008).

391   Although there were not yet statistical dissimilarities between the disturbed and the restored

392   sites, only three years after restoration, the opening and desilting of tidal channels brought down

393   the porewater salinity values (Fig. 4) and other components of water quality in the restored site,

394   being overall more similar to the undisturbed site than to the disturbed one, which probably

395   helped to increase the tree canopy cover, litterfall production and tree growth (Kathiresan &

396   Bingham, 2001; Kathiresan, 2002; Polidoro et al., 2010; Kamali & Hashim, 2011). This effect in

397   mangroves has been demonstrated in other sites of the coast of Campeche, where higher rates of

398   litterfall production are associated with lower water salinity (Chan-Keb et al., 2018). Besides the

399   fishing and mud-foraging species characteristic of estuarine areas (Kobza et al., 2004), higher

400 litterfall productivity, in turn, broadens the spectrum of resources by increasing niches for

401 insectivorous birds' prey species in the restored sites.

402 Both the disturbed and restored sites showed higher bird abundance and species richness than the

403 undisturbed one. This is similar to the findings reported in structurally complex habitats and

404 island setting, which are found to be more diverse if their habitats show heterogeneity (Acevedo

405 & Aide, 2008; Jones, Marsden & Linsley, 2003), even if they are disturbed, as were two of our

406 study sites. The results from the models highlight the fact that more heterogeneous habitats such

407 as the restored site and, to some extent, the disturbed one result in more species-rich places,

408 allowing for the existence of more structured bird communities than in the more homogenous

409 undisturbed site (Báldi, 2008). This effect is present because high-quality undisturbed mangrove

410 patches surround the disturbed and restored mangrove sites, increasing their heterogeneity.

411 Additionally, while canopy species such as insectivorous birds might use bushes and dead trees

412 from the restored and disturbed sites to feed or rest, bird species that prefer open and semi-open

413 habitats (sandpipers, avocets, cormorants, etc.) are not present in the densely vegetated

414 undisturbed mangrove. They take advantage of the open areas at the disturbed site, which are

415 adequate foraging niches for waders because of the long-lasting floods there. Accordingly, the

416 high abundance of these species could be indicative of sites with impacts affecting the

417 hydroperiod or the vegetation cover. Because of mangrove forests being structurally

418 homogenous when compared to other forest habitats (Mohd-Azlan, Noske & Lawes, 2015), the

419 number of bird species recorded was not as high as expected when surveys include another type

420 of tropical forests. This outcome might also be due to habitat preferences of the different bird

421 species recorded, or could be the effect of short-term monitoring (Canterbury et al., 2000).

422 However, the effects of the sampling duration and size might be negligible, since the

423 heterogeneity of the forest structure traits, such as cover and composition, results in a more

424 complex assemblage of bird communities at the landscape level (Kroll et al., 2014). Hence, the

425 avian community structure might be more influenced by the heterogeneity, diversity and

426 phenology of the mangrove forest than by the size of the sampled sites (Mohd-Azlan, Noske &

427 Lawes, 2012). Moreover, Chacin et al. (2015) demonstrated that hydrological fragmentation does

428 not always negatively affect avian abundance since the loss of hydrological connectivity might

429 result in prey concentration, facilitating forage activities for some species of fishing birds. We

430 agree with this hypothesis but only if tidal patterns allow a cyclic interruption-reconnection of

431   the main and secondary tidal channels to allow flooding and drainage of the mangrove sites. The

432   results of the multivariate analysis supported this idea. Moreover, it demonstrated that bird

433   abundance was more influenced by habitat condition (i. e. hydroperiod and forest structure) than

434   by the measured water parameters. Although there were no clear biological effects of the

435   measured water parameters on the abundance of the birds in our study area, they surely

436   determine resource availability because of their effect on the primary producers, and hence on

437   the presence of the benthonic, fish and crustacean communities (Holguin, Vazquez & Bashan,

438   2001; Sandilyan & Kathiresan, 2015), on which many bird species feed.

439   As the characteristics of the habitat influence the distribution of wading species, the sites with

440   less canopy cover provide better foraging areas for waders (Bancroft, Gawlik & Rutchey, 2002;

441   Curado et al., 2013). Additionally, the selection of open and semi-open areas likely reduces the

442   predation risk and increases the foraging efficiency of wading species (Pomeroy, 2006; Chacin et

443   al., 2015). Notwithstanding, while tall and broad canopy vegetation might negatively affect the

444   foraging efficiency of water birds, it might become more beneficial for the insectivores (Tavares

445   & Siciliano, 2013). Thus, the presence of wading and diving, together with canopy and

446   undergrowth species using the edges of primary habitat and the emerging vegetation within the

447   restored site, may have influenced the proportions of bird abundance and richness in the study

448   area.

449   Because our sampling sites are located within a landscape matrix of disturbed and undisturbed

450   patches, the geographical distribution of the study locations likely influenced the number of

451   species found in each sampling site. For example, recordings of birds common to undisturbed

452   sites, such as the Mangrove Warbler, were relatively frequent in the restored and disturbed sites

453   because this species uses features of the disturbed areas as rest spots or merely in the movement

454   between undisturbed patches, as other species do (Mohd-Azlan, Noske & Lawes, 2015). This

455   behavior might prevent the identification of particular species from each sampling location just

456   on the basis of observation. Thus, estimates of abundance might be a better indicator. For

457   instance, the abundance of the Mangrove Warbler was higher in both undisturbed and restored

458   areas, although we recorded this species in all studied sites. Additionally, based on the species-

459   by-species abundance, we obtained evidence of non-random use of the restored site as foraging

460   habitats for this and other insectivores (Table 4).

461 The regrowth of vegetation cover induced by the restoration activities, demonstrated by the

462 increase in the height (0–55 cm) of the mangrove scrub and increased recruitment (0–79

463 individualsha^{-1}) (see Echeverría-Ávila et al., 2019), improved the availability of resources and,

464 hence, the presence and the abundance of insectivorous birds such as the Mangrove Warbler and

465 the Tropical Kingbird. A very close relative of the former, the Yellow Warbler (*Setophaga*

466 *petechia*), has been considered a key species because of its sensitivity to changes in

467 environmental conditions and specific habitat needs (Lowther et al., 1999), and because its

468 populations may change according to the habitat management practices and food availability

469 (Salgado-Ortiz, Marra & Robertson, 2009). Since the higher abundance of the Mangrove

470 Warbler was apparently related to the undisturbed areas, it demonstrates its importance as an

471 indicator of habitat with negligible impacts, or of habitats showing signs of recovery. Also, the

472 open and semi-open areas in the restored site contributed to the higher availability of resources

473 for different bird guilds (Ortega-Alvarez & Lindig-Cisneros, 2012; Buelow & Sheaves, 2015).

474 These areas were more attractive to birds which usually flock in large groups and forage on the

475 ground, mud or inundated areas, leading to higher abundances than in the densely-vegetated

476 undisturbed site. Even though the IndVal was non-significant, both approaches used to identify

477 key species suggested that insectivores better represented the undisturbed site. According to the

478 Simper analysis, the species that best represents the restored mangrove is a meat-eater (the Green

479 Heron), whereas the IndVal suggested that an omnivore (the Blue-winged Teal [Anas discors])

480 could be an indicator for this site. This lack of coincidence might relate to differing information

481 used by each approach. While Simper uses only the information regarding abundance, IndVal

482 uses the relative abundance and also incorporates the relative frequency of occurrence.

483 Additionally, the presence of species such as ibises and wood storks is considered evidence of

484 success after the implementation of restoration activities (Ortega-Alvarez & Lindig-Cisneros,

485 2012; Zhao et al., 2016). This is because they depend mostly on communities of vertebrates and

486 invertebrates that are sensitive to changes in water and soil quality, induced among other factors,

487 by the alteration of the hydroperiod (Ogden et al., 2014). Accordingly, the presence and

488 abundance of the insectivorous and wading bird species similar to those found in the study area

489 are important elements by which to evaluate and monitor the effectiveness of habitat restoration

490 projects in mangrove ecosystems.

491

492 **Implications for Conservation**

493 There is no doubt that natural phenomena, such as hurricanes, contribute to habitat heterogeneity.

494 However, severe climatic events may alter the microtopography and hydrological connectivity

495 and make difficult post-hurricane natural regeneration. Such is especially the case in habitats that

496 depend on recurrent flooding and drainage (hydroperiods) such as mangroves. By altering the

497 hydroperiod, dead mangrove areas may increase in size through time. The loss of the vegetation

498 cover and the alteration of the environmental conditions may, in turn, lead to biotic

499 homogenization (Martínez-Ruíz & Renton, 2017). After degradation due to loss of hydrological

500 connectivity occurs in mangroves, restoration of water flow through deblocking of main and

501 secondary tidal channels increases the habitat heterogeneity, allowing the resettlement of

502 ecosystem services and strengthening the ecological relationships and structure of the biotic

503 communities living there. It may also improve the hydro-edaphic factors, such as nutrients, water

504 level, and porewater salinity (McKee et al., 2002), from which the micro and macrobenthos, as

505 well as fisheries and birds, are dependent.

506 Long flooding periods limit the abundance of wading birds, especially the small species foraging

507 on the macrobenthos. Thus, identifying degraded areas and monitoring the hydroperiod, before

508 and after of hydrological restoration, will allow for better conservation strategies for the

509 mangroves and their avian communities. As the hydrological connectivity improves mangrove

510 heterogeneity by regenerating vegetation, avian communities can become more diverse,

511 acquiring a higher number of species from different functional groups. Thus, densely vegetated

512 mangroves, together with the restoration of patches unable to regenerate themselves, are essential

513 to maximizing the abundance of specialized bird guilds.

514 To realize the positive effects of restoration activities, it is necessary to create a link between the

515 restoration programs and the local communities through environmental and economic

516 development education. For instance, birdwatching and sport fishing (catch and release) can be

517 alternatives to socio-economic growth for the benefit of human coastal communities through the

518 development of a green touristic industry in restored places (Skelton & Allaway, 1996).

519 We expect that the restoration activities implemented will increase and maintain the habitat's

520 heterogeneity in the medium and the long term and will strengthen the resilience of the

521 mangrove forests.

522

523 **Conclusions**

524 The restoration activities in the estuaries of Laguna de Términos first helped the natural

525 regeneration of the mangrove forest through the water movement caused by the opening and

526 desilting of tidal channels, making tidal periodicity comparable to that of natural conditions

527 while also reducing water salinity. In addition, water exchange likely favored fish and crustacean

528 production and the appearance of mudflat and shallow water zones, which are attractive foraging

529 areas for different bird guilds. Consequently, habitat heterogeneity and the availability of

530 resources increased, and the avian community became more diverse, especially regarding the

531 abundance of insectivorous birds in the restored areas.

532

533 **Acknowledgements**

534 We thank Herminia Rejón Salazar and the 'Community of Mangrove Restorers' from Isla

535 Aguada for their support with the field work, Emma Guevara Carrió, Mario Alejandro Gómez

536 Ponce, Hernán Álvarez Guillén and Andrés Reda Deara for their assistance with logistics and

537 field data collection. To José Nava from CONANP-Laguna de Términos for the facilities to carry

538 out our surveys.

539

540

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Figure 1

Location of Bahamitas estuaries with different disturbance levels in Laguna de Términos, Campeche Mexico.

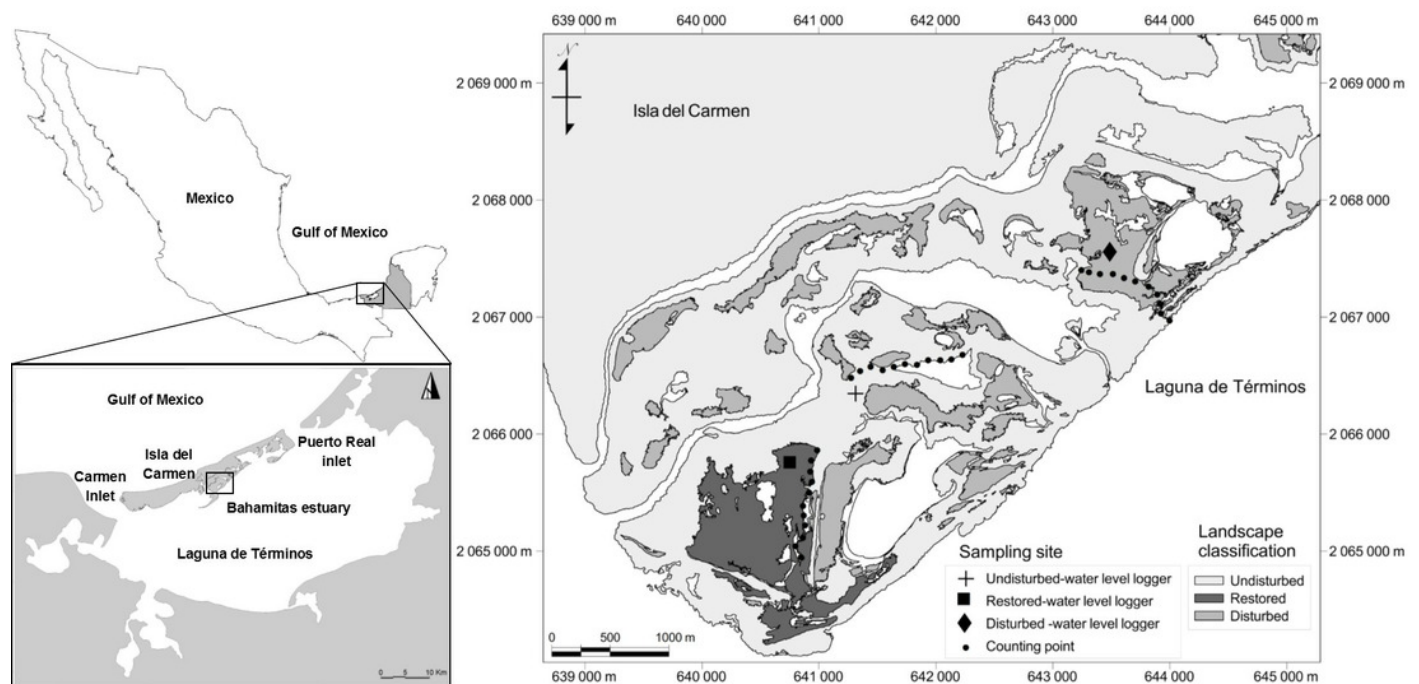



Figure 2

Ranking of the abundance of bird species by sampling site.

In the figure only the six most abundant bird species for each site are shown: Least Sandpiper (LS), Yellow Warbler (YW), White Ibis (WI), Green Heron (GH), Great Egret (GE), Tropical Kingbird (TK), Great-tailed Grackle (GG), Magnificent Frigatebird (MF), American White pelican (AWP), Black-bellied Whistling Duck (BWD), Green Kingfisher (GK), and Roseate Spoonbill (RS).

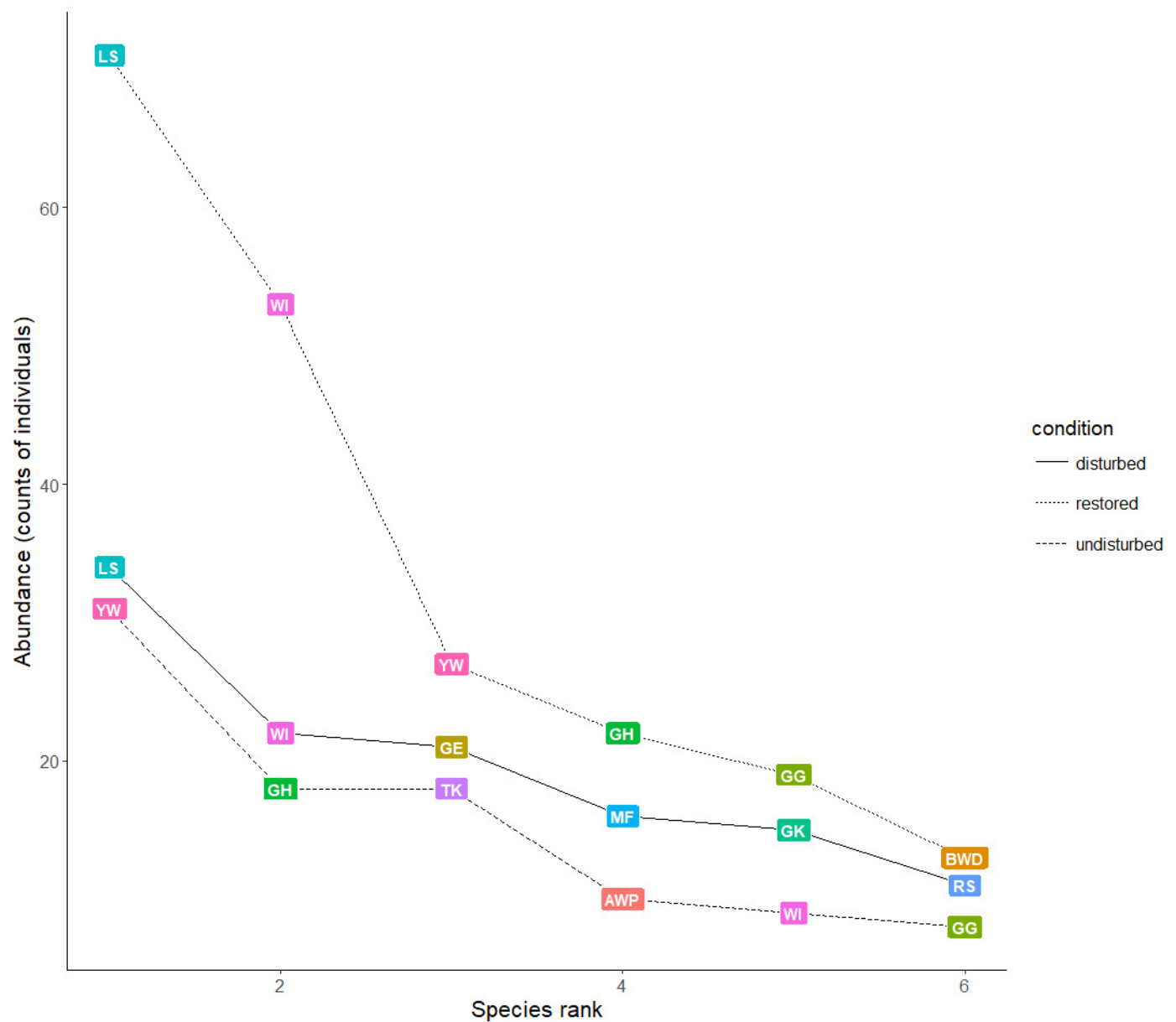



Figure 3

Abundance of bird functional groups by site.

In the restored site, the abundance of guilds such as macroinvertivores and insectivores increased as compared with the disturbed site.

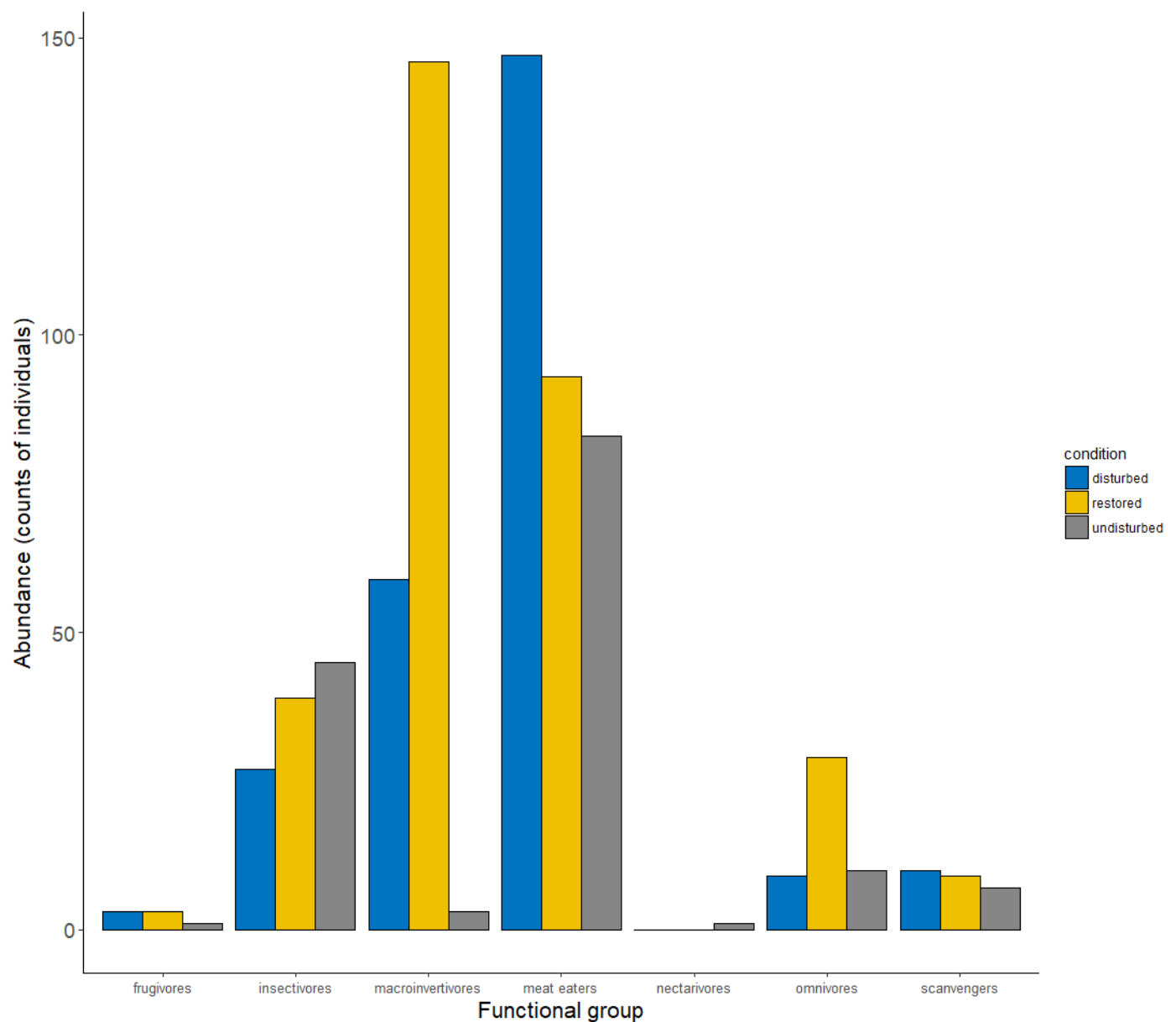
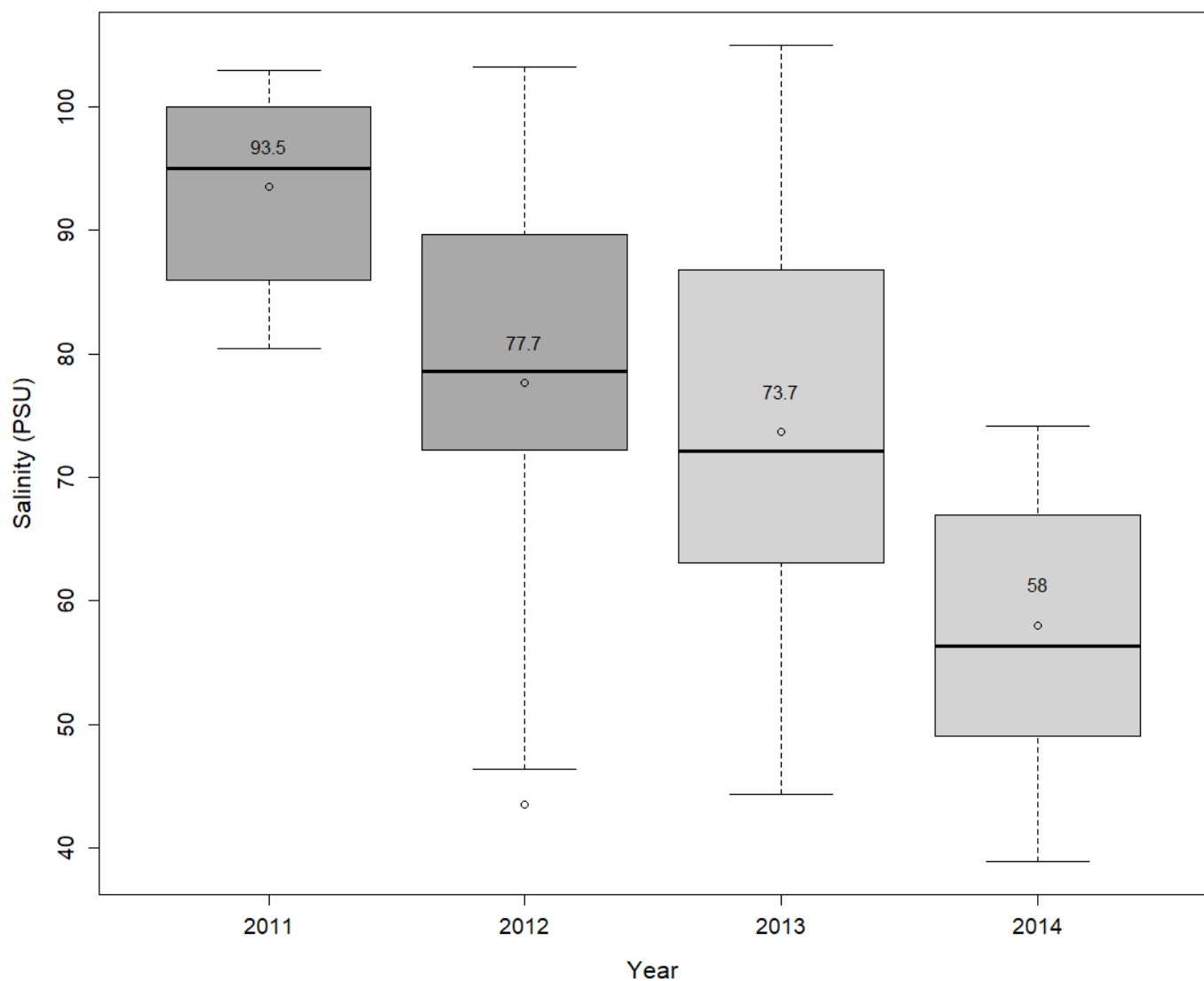



Figure 4

The observed changes in porewater salinity though time at the restored site from the beginning to the end of the hydrological restoration (2011-2012), and two years later.

The horizontal lines in the boxes are medians, the open circles are the means, and whiskers are the minimum and maximum values.

Comparison of the mean values of hydroperiod, water-quality parameters and forest structure between studied areas following restoration at the restored site.

Only statistically significant results are shown.

Variable	Disturbed	Restored	Undisturbed	Test	df	p	Post hoc
Flooding frequency (times/month)	2.71	9.00	14.42	$F = 12.47$	2.00	0.003	R-D = 0.038 U-D < 0.001
Flooding duration (h)	588.14	404.42	314.71	$F = 2.41$	2.00	0.118	-
Tidal range (m)	0.09	0.09	0.05	$F = 2.25$	2.00	0.133	-
Salinity (PSU)	34.93	34.12	33.28	$\chi^2 = 10.25$	2.00	0.005	U-D = 0.004
pH	8.15	8.11	8.02	$F = 12.32$	2.30	0.001	U-D < 0.001 U-R = 0.023
Redox potential	82.09	91.18	85.18	$\chi^2 = 3.42$	2.00	0.180	-
Temperature (°C)	28.02	29.94	28.87	$\chi^2 = 11.81$	2.00	0.002	R-D = 0.001
Depth (cm)	54.62	74.96	117.54	$F = 31.87$	2.00	< 0.001	U-D < 0.001 U-R < 0.001 R-D = 0.043
No. of tree species	1.09	1.36	1.90	$\chi^2 = 12.16$	2.00	0.002	U-D = 0.008
Tree density (trees/ha)	345	763	709	$\chi^2 = 6.45$	2.00	0.039	R-D = 0.035
Basal area (m²)	1.29	4.31	7.02	$\chi^2 = 15.39$	2.00	< 0.001	U-D < 0.001

1 Note: In Test column, F is for ANOVA and χ^2 is for Kruskal-Wallis rank sum test. In Post hoc
2 column, comparisons between pairs of sites (R = restored, D = degraded, U = undisturbed), were
3 tested for significance using either HDS Tukey's or Nemenyi's tests. A dash means that the test
4 was not carried out for that variable.

Avian community diversity indexes at the study locations.

Habitat	n	Observed richness	Mean ± SD	Expected richness	1-Simpson	Berger Parker
Undisturbed	11	28	5.27 ± 2.28	44.2	0.906	0.207
Restored	11	41	9.00 ± 3.38	46.3	0.893	0.230
Disturbed	11	41	9.36 ± 2.20	54.5	0.945	0.133

1   Note: n is the number of sampling points.

Results of the multivariate analysis (best fitted glm).

The greater the deviance, the stronger the effects of the environmental variables on the abundance of bird species (A) and the abundance of functional groups (B).

	A		B	
Site feature	Deviance	*P*	Deviance	*P*
Habitat condition	162.50	0.012	22.598	0.110
Water temperature	113.29	0.001	-	-
Redox	82.83	0.029	-	-
Water salinity	71.86	0.040	-	-
No. Tree species	83.02	0.003	8.623	0.388
Basal area	82.33	0.023	6.053	0.605
Tree density	76.50	0.035	6.719	0.490
Basal area : Tree density	45.00	0.157	-	-
Detectability	-	-	17.780	0.019

2 Note: Either dash is for variables not included in the models, or for models not reaching
3 convergence when including those variables.

Similarity analysis of species abundance among sites.

In **A)**, the comparison of Undisturbed (UN) vs Restored (RS) is shown, **B)** Undisturbed vs Disturbed (DS), and **C)** Restored vs Disturbed. Species are ordered by their contribution according to the dissimilarity:standard deviation ratio (D/SD).

A) Av. dissimilarity = 76.83

	Av.Abund UN	Av.Abund RS	Contribution (%)	D/SD
Yellow Warbler	1.45	1.14	6.11	1.21
Green Heron	0.89	1.08	7.35	1.12
White Ibis	0.84	0.56	5.84	1.04
Double-crested Cormorant	0.31	0.70	4.72	0.96
Tropical Kingbird	0.61	0.09	3.72	0.89
Great-tailed Grackle	0.26	0.88	6.32	0.65
Least Sandpiper	0.09	1.14	5.55	0.58

B) Av. dissimilarity = 80.93

	Av.Abund UN	Av.Abund DS	Contribution (%)	D/SD
Yellow Warbler	1.45	0.79	6.3	1.30
Green Heron	0.89	0.67	5.32	1.18
White Ibis	0.84	1.03	6.32	1.15
Great Egret	0.44	0.93	5.63	1.01
Tropical Kingbird	0.61	0.27	3.52	1.01
Least Sandpiper	0.09	1.19	6.68	0.95

C) Av. dissimilarity = 75.41

	Av.Abund RS	Av.Abund DS	Contribution (%)	D/SD
Green Heron	1.08	0.67	5.02	1.27
Yellow Warbler	1.14	0.79	4.43	1.18
White Ibis	0.56	1.03	4.90	1.08
Great Egret	0.62	0.93	4.84	1.08
Yellow-crowned Night-Heron	0.49	0.63	3.59	1.07
Least Sandpiper	1.14	1.19	8.23	1.05
Reddish Egret	0.53	0.53	3.24	1.02
Double-crested Cormorant	0.70	0.34	3.59	1.00

Indicator species index (IndVal) values for key species within each sampling site.

A percentage > 25% and a p-value ≤ 0.05 mean that the selected species are good indicators for a given habitat condition.

Species	Habitat condition	IndVal (%)	p
Tropical Kingbird	Undisturbed	39	0.068
Blue-winged Teal	Restored	29	0.057
Mangrove Swallow	Disturbed	27	0.951