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SUSANA AGUILAR MUGICA

PADRÕES ESPAÇO-TEMPORAIS DE AVES AQUÁTICAS: EFEITO DA
CONFIGURAÇÃO DA PAISAGEM E DAS MUDANÇAS CLIMÁTICAS EM CUBA

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2020



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CONFIGURAÇÃO DA PAISAGEM E DAS MUDANÇAS CLIMÁTICAS EM
CUBA

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RESUMO

Cuba é a maior ilha do Caribe, possuindo as áreas úmidas mais extensas da região. Das ~ 370 espécies de aves cubanas, 40% são dependentes de zonas úmidas e a maioria é migratória. O conhecimento do uso destas áreas por aves é crítico para a conservação regional, principalmente no que refere-se à estrutura da paisagem. Além disso, as aves dependentes das áreas úmidas são consideradas altamente ameaçadas pelos efeitos das mudanças climáticas. No Capítulo 1, nós caracterizamos assembléias de aves aquáticas da costa sul cubana, relatamos suas variações espaço-temporais e sugerimos estratégias de conservação. Realizamos amostragens em seis zonas úmidas entre 2011-2013. Identificamos diferenças na composição das aves aquáticas entre locais e estações, mas não entre anos. Não foram encontradas diferenças na variabilidade espacial ou temporal da abundância entre locais, estações ou anos. Doze espécies apresentaram abundância superior a 1% da população global. Este estudo destaca a importância global da costa sul cubana para a conservação das aves aquáticas, particularmente durante a migração no outono. Com estes resultados propomos a criação de novas áreas de conservação. No Capítulo 2, testamos o efeito da configuração da paisagem na estrutura das comunidades de aves aquáticas em áreas úmidas costeiras em um gradiente de conservação no sudoeste de Cuba. Foram realizados levantamentos de aves aquáticas em 14 pontos na costa durante o outono de 2016. A estrutura da paisagem foi descrita por 11 índices em três escalas espaciais. Nossos resultados mostram que na escala de 6 km a área de mangue influenciou negativamente a abundância de aves, enquanto que, na escala de 2 km, a porcentagem coberto por lagoas teve um efeito positivo. Também na escala de 2 km, a porcentagem de cobertura por manguezais e lagoas influenciou positivamente a composição de espécies. A porcentagem de área com uso antrópico não influencia nenhuma variável da comunidade de aves. Nossos resultados mostram que detectar os efeitos de escala dos recursos de paisagem é muito importante para um manejo eficaz das aves aquáticas. No Capítulo 3, previmos distribuições atuais e futuras do flamingo *Phoenicopterus ruber* e da garça-vermelha *Egretta rufescens* usando modelos de distribuição de espécies. Para cada espécie, previmos dois cenários de emissões em 2050 e 2070, em Cuba. As variáveis bioclimáticas que mais contribuíram para modelar a distribuição do flamingo foram a variação média diária e sazonalidade da temperatura. A variação média diária da temperatura também contribuiu mais para a modelagem garça-vermelha, seguida pela precipitação no quarto mais quente. Nossos resultados mostram que a distribuição atual do flamingo deve reduzir 38% no cenário pessimista de 2070, enquanto a área de distribuição da garça-vermelha deverá aumentar em 44%. Nossas descobertas sugerem que a modelagem da distribuição de espécies pode informar sobre o manejo futuro do flamingo e da garça-vermelha. É necessária uma estratégia de conservação para proteger o flamingo sob um clima em mudança. Os resultados desta tese não apenas destacam a boa saúde de zonas úmidas cubanas, mas incentivam seu manejo no nível da paisagem e a previsão dos efeitos de mudanças climáticas.

Palavras-chave: Cenários climáticos futuros, Comunidade de aves aquáticas, Estrutura da paisagem, Variação sazonal, Zonas úmidas costeiras

ABSTRACT

Cuba is the largest Caribbean island, presenting the most extensive wetlands in the region. From all ~370 bird species in this country, 40% are wetland-dependent and most are migratory. Understanding how birds use Cuba's wetlands and how landscape structure affects waterbird distribution is critical for regional conservation. Also, wetland-dependent birds are considered to be endangered by climate change effects. In chapter 1, we characterized waterbird assemblages in Cuban south coastal wetlands, reported spatio-temporal variations in waterbirds and suggested conservation strategies. We conducted surveys across six wetlands (2011-2013). Differences in waterbird composition were identified among sites and seasons but not among years. No differences were found in spatial or temporal variability in abundance among sites, seasons or years. Twelve species were at abundance levels exceeding 1% of their estimated global population. This study highlights the global importance of Cuban south coast to waterbird conservation. Based on our results, we encourage the creation of conservation areas. In chapter 2, we aimed to investigate the effect of landscape configuration on the structure of waterbird communities in coastal wetlands in a conservation gradient in southwestern Cuba. We conducted waterbird surveys across 14 points on southwest coast during fall migration of 2016. Landscape structure was described using 11 indices at three spatial scales. Our results show that, in 6km, the mean patch area of mangrove had a negative influence in waterbird abundance, while at 2km the percentage of landscape covered by lagoons have a positive effect. Instead, a higher percentage of landscape covered by mangroves and lagoons had a positive effect in waterbird composition in 2 km. The percentage of anthropogenic land use does not influence any response variable. Our study shows that detecting the scale of effect of important landscape resources is very important for the effective management of waterbird. In chapter 3, we predicted current and future distributions of American Flamingo *Phoenicopterus ruber* and Reddish Egret *Egretta rufescens*, two resident species in Cuba, using species distribution models with Maxent software. For each species, we predicted two emissions scenarios in 2050 and 2070, in Cuba. Bioclimatic variables that contributed the most to modeling the potential distribution of American Flamingo were mean diurnal temperature range (mean of monthly (max temp - min temp)) and temperature seasonality. Mean diurnal range also contributed most to the modeling of Reddish Egret followed by precipitation of warmest quarter. Our results show that the current distribution of American Flamingo is predicted to reduce 38% under a changing future climate, in the pessimistic scenario of 2070, while the current distribution size of Reddish Egret is predicted to increase in 44%. Our findings suggest that species distribution modeling can inform the current and future management of the American Flamingo and Reddish Egret throughout Cuba. A conservation strategy is needed to conserve American Flamingo under a changing climate. The results of this thesis not only highlights the good health of Cuban wetlands, but encourage their management at the landscape level and the prediction of the possible effects of future climate changes.

Keywords: Coastal wetlands, Future climate scenarios, Landscape structure, Seasonal variation, Waterbird community

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GENERAL INTRODUCTION

Waterbirds have been recognized as indicators of wetland health given that their presence provides information on this ecosystem functioning (Becker 2003). Waterbirds depend on wetlands for survival because these areas are used during all stages of their annual life cycle (Mugica et al. 2006). Specifically, coastal wetlands are areas of great importance as they harbor fragile ecosystems, which are very sensitive to climate change (Erwin 2009).

Cuba is the largest Caribbean island which contains the most extensive wetlands in the region (CNAP 2013). The Cuban archipelago covers 109,886 km² and comprises 4,196 islands and cays. The main island of Cuba has an extension of 1,250 km from East to West and is bordered by four group of cays: Sabana Camagüey Archipelago, Canarreos Archipelago, Jardines de la Reina Archipelago and Los Colorados Archipelago. Cuba is divided into three biogeographic regions: east, central and west (Vales et al. 1998).

In Cuba, 369 bird species have been recorded (Garrido and Kirckconnell 2010), of which 150 are wetland-dependent. These waterbirds are grouped into 8 orders and 27 families, being Anatidae, Scolopacidae and Laridae the richest ones (Acosta and Mugica 2006). Among all species, 123 are migratory, 27 winter residents, 10 summer residents, 16 transients, 43 accidentals and 27 maintain bimodal populations (Garrido and Kirckconnell 2010). Given its biogeographic position, Cuba receives an important flow of migratory birds from North America (Frederick et al. 1996). For these reasons, studies of waterbirds in Cuba are important not only at the local, but also at the regional level.

Studies on waterbirds in Cuba focus mostly on ecological aspects related to population dynamics, morphology, feeding or reproduction (Denis et al. 1999; Denis et al. 2004; Denis

et al. 2006), with ducks and herons being the most studied groups. In recent years, a scientific advance has been carried out in Cuba through research addressing the dynamics of waterbird populations, such as those in anthropic wetlands (rice fields) in the Sur del Jíbaro, Sancti Spiritus (Mugica et al. 2001; Acosta et al. 2002; Mugica et al. 2003), Havana Bay, (González 2007), La Havana artificial lagoon (Silvera, 2005) and in natural wetlands in Ciénaga de Zapata (LLanes 1993, Parada 2000), Río Máximo (Perera 2004), Ciénaga de Birama (Molina 2007), Playa la Tinaja (Acosta et al. 1992) and Ciénaga de Lanier (Forneiro 2000). In general, these studies comprised few and small wetlands, and none included the three biogeographic regions of the island and covered a long-term temporal scale to allow for a robust sampling of different periods of the waterbirds' life cycle.

Wetland and waterbirds conservation

Biodiversity conservation strategies are more efficient when relying upon studies and managements at large spatial and temporal scales (Poiani et al. 2000). The spatial and temporal scales are of particular interest for wetland conservation since these areas are used by high mobile organisms such as waterbirds (Wen et al. 2016). These species normally use multiple wetlands on their daily and annual activities, even though this aspect is often ignored in species conservation planning (Haig et al. 1998). The coastal wetlands in Cuba have different degrees of degradation, fragmentation and habitat loss due to the anthropic actions (Iturralde and Serrano 2015). In this sense, the study of landscape patterns is essential for conservation biology in anthropic regions (Bennet 2004).

In recent years, multiple investigations related to spatial patterns in organisms and specifically birds have been carried out, focusing on the effect of patches and heterogeneity,

habitat connectivity and the influence of the spatial context in this group (Boscolo et al. 2009; Brandolin and Blendinger 2016; Herbert et al. 2018). However, this approach has not been studied in the Cuban context.

Landscape studies are often conducted at a single spatial scale for the studied species (Trzcinski et al. 1999; Holland and Fahrig 2000). However, it is likely that different species respond to their environments at different spatial scales (Lyra-Jorge et al. 2010; Jackson and Fahrig 2015). Usually little is known about the scales at which a species responds to structural characteristics of its environment. Furthermore, even though there have been several studies on the spatial scale in waterbirds (Perez-Garcia et al. 2014, Webb et al. 2010; Beatty et al. 2014), this has been little evaluated in coastal wetlands. Understanding issues associated with scale is essential in landscape ecology (Turner and Gardner 2015).

In addition to habitat loss and fragmentation, wetland-dependent birds are considered to be at particularly high risk for negative climate change effects (Steen and Powell 2012). Global climate warming is projected to be between 0.3 and 4.8°C by 2100 (IPCC 2013), with significant consequences for global biodiversity (Thomas et al. 2004). Much of the capacity to mitigate against species losses will lie in our ability to anticipate the effects of climate change (Heller and Zavaleta 2009). Climate change is identified as one of the greatest threats to biodiversity in Cuba (CITMA 2016). However, there are few studies that explore possible changes in the distribution of wildlife species in future climate scenarios.

In this context, species distribution modeling (SDMs) is widely used to address issues in biogeography, global climate change, and conservation biology (Engler et al. 2004; Guisan et al. 2006). SDMs utilize species presence data and associated ecological variables, e.g. physical and environmental conditions, to map areas of suitable habitat for the species in question (Guisan and Thuiller 2005). Improving the efficiency of the SDMs, i.e. identifying

areas with the highest conservation value, establishment of protected areas, implementation of suitable conservation measures and determining the potential impacts of predicted future climate change on species' range shift, is a critical point for conservation biology (Carvalho et al. 2010; Bosso et al. 2013). Also, several studies have use SDMs to evaluated the effect of climate change specifically in waterbirds (Hu et al. 2010; Steen and Powell 2012; Hu and Liu 2014).

Considering the information gaps and the importance of the topics discussed above for bird conservation in Cuba, the general objectives of this thesis are to i) characterize waterbird assemblages in Cuban south coastal wetlands, report spatio-temporal variations in waterbird diversity and suggest conservation strategies, ii) test the effects of landscape structure on waterbird communities in coastal wetlands within a conservation gradient in southwestern Cuba and evaluate the relative contribution of the configuration of lagoons, mangrove, rice field and anthropogenic land to waterbirds diversity, and iii) evaluate the effect of climate change in two key waterbird species in Cuba through SDMs.

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**CAPÍTULO I. Spatio-temporal patterns of waterbird assemblages in
Cuba's south coast wetlands: conservation implication**

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Abstract Cuba is the largest Caribbean island, supporting the most extensive wetlands in the region. Of the ~370 bird species in this country, approximately 40% are wetland-dependent and most are migratory. Knowledge of bird use of Cuba's wetlands is critical for regional conservation. This study characterized waterbird assemblages in Cuban south coastal wetlands, reports spatio-temporal variations in waterbird diversity and suggests conservation strategies. We conducted 543 surveys across six wetlands (2011-2013). We recorded 110 species. Blue-winged Teal (*Spatula discors*) and Least Sandpiper (*Calidris minutilla*) were the dominant species. The site with the highest richness and waterbird abundance was Humedal Sur de Los Palacios. Differences in waterbird composition were identified among sites and seasons but not among years. No differences were found in spatial or temporal variability in abundance among sites, seasons or years. Assemblage composition was not spatially dependent on the location of wetlands. Twelve species were at abundance levels exceeding 1 % of their estimated global population. This study highlights the global importance of the Cuban south coast to waterbird conservation, particularly during fall migration and the uniqueness of Humedal Sur de Los Palacios. We encourage creation of new Ramsar sites, an Important Bird Area and a new protected area.

Keywords Diversity. Community structure. Migration. Multivariate analysis. Seasonal variation. Waterbird composition

1. Introduction

Wetlands are important conservation sites due to their high biodiversity (Malik and Joshi 2013) and the ecosystem services they provide (Green and Elmberg 2013; Sutton-Grier and Sandifer 2018). However, the rapid degradation of these ecosystems globally (Perillo et al. 2005; Davidson 2014) produces an urgent need for ecological studies to support conservation actions (Lee 2017). Coastal wetlands provide suitable habitats and food resources for a variety of birds (Ali et al. 2016), including stopover sites for migratory waterbirds (Bamford et al. 2008; Webb et al. 2010). Because of their high mobility, waterbirds respond quickly to habitat changes (Romano et al. 2005; Cumming et al. 2012; Henry and Cumming 2017), thus they are considered good bio-indicators of habitat quality (Bhat et al. 2009; Bai et al. 2015) and they provide information on the health of wetland ecosystems (Amat and Green 2010; Ogden et al. 2014).

Studies of bird community structure and function are important for grounding ecological theory and conservation practice (Chettri et al. 2001; Hurlbert 2004). Conserving bird diversity requires an understanding of bird–environment relationships year-round (Newton 1998; Russell et al. 2014) and a management of both breeding and wintering habitats of migratory birds (Rappole et al. 2003; Kirby et al. 2008). Consequently, a knowledge of the processes occurring in winter, as well as the annual and seasonal variations in waterbird diversity, are necessary to understand the function and biodiversity values of wetlands (Saygili et al. 2011). The worldwide conservation crisis emphasizes the need for a large scale, long term and multiple species approach in recent research. This approach is of particular interest for the conservation of wetlands that host highly mobile organisms such as

waterbirds. The population dynamics of these species depend on multiple wetlands; this aspect, however, is often ignored in conservation planning (Haig et al. 1998; Wen et al. 2016).

Cuba is the largest Caribbean island (48 % of the region's emerged land area) and it contains the most extensive wetlands in the region (1,366,844.89 ha) covering 12.4 % of the country's surface (CNAP 2013). Given its biogeographical position, Cuba receives a significant flow of migratory birds, as shown by recaptures of individuals banded in North America (Frederick et al. 1996; Blanco et al. 2014). Two of the six migratory American Flyways for migratory birds extend across Cuba: the Mississippi and Atlantic Flyways (González et al. 2006).

Of the 369 bird species reported for Cuba (Garrido and Kirckconnell 2010), 150 are wetland-dependent and these are mostly migratory species (82 %) (Acosta et al. 2011). In Cuba, several studies have been conducted on waterbird dynamics in both natural (Acosta et al. 1992; González et al. 2016b) and anthropogenic wetlands (Mugica et al. 2001; Acosta et al. 2002; Mugica et al. 2003; González and Jiménez 2011). To date, most studies have been conducted in a single wetland site; none have covered an extensive area of the island, or included several years or several periods of avian annual life cycles.

Historically, Cuban biodiversity has been better studied on the north coast than on the south coast (Rodríguez et al. 2014). However, the south coast is lower and swampier, with more wetland areas, and it contains the largest wetlands in Cuba and the insular Caribbean region, including Zapata Swamp. Many wetlands on the south coast have been recognized as Important Bird Areas (Aguilar 2010) and Ramsar sites (CNAP 2013). Nonetheless, only general information has until now been available on the diversity and dynamics of waterbirds assemblages on the Cuban south coast (Mugica et al. 2014). Here we provide baseline

information on waterbird assemblages in a three-year study of the six natural wetlands of this region. Our study is of paramount importance for wetland conservation planning and for highlighting the Cuban south coast's value at the national and international level. Our specific aims are to (i) characterize the waterbird assemblages in natural wetlands on the Cuban south coast; (ii) test the effect of spatial and temporal (annual and seasonal: spring migration, summer and fall migration) variation on waterbird diversity in the region, and (iii) develop recommendations for wetland management to improve waterbirds conservation.

2. Materials and Methods

2.1 Study Area

We carried out the study in six natural wetlands along the southern Cuban coast. About 942 km of the coast were surveyed (from 83°42'W, 22°11'N to 77°02'W, 20°25'N) from Pinar del Río province to Granma province (Table 1, Fig. 1). In a general way, this stretch of coast comprises a strip of wetlands with similar landscapes. They are characterized by swampy lowland plains, including coastal lagoons, salt marshes, mudflats and estuaries. They are covered mainly by mangrove ecosystems (with the exception of Canales del Hanábana, the only freshwater wetland included in our study), swamp grasslands and swamp forests, flooded or temporarily flooded, with different degrees of salinity. Their differences are mainly in the size, configuration, water salinity and diversity of coastal habitats. Specific descriptions of each wetland are shown in Supplementary material 1. We selected these sites because they contain the largest number and variety of wetland habitats in the region. All the study sites are national protected areas except Humedal Sur de Los Palacios (Table 1). The

climate on Cuba's southern coast is subtropical humid, with two clearly defined seasons, dry season (winter) from November to April, and the rainy season (summer) from May to October. The average annual temperature is 24 °C.

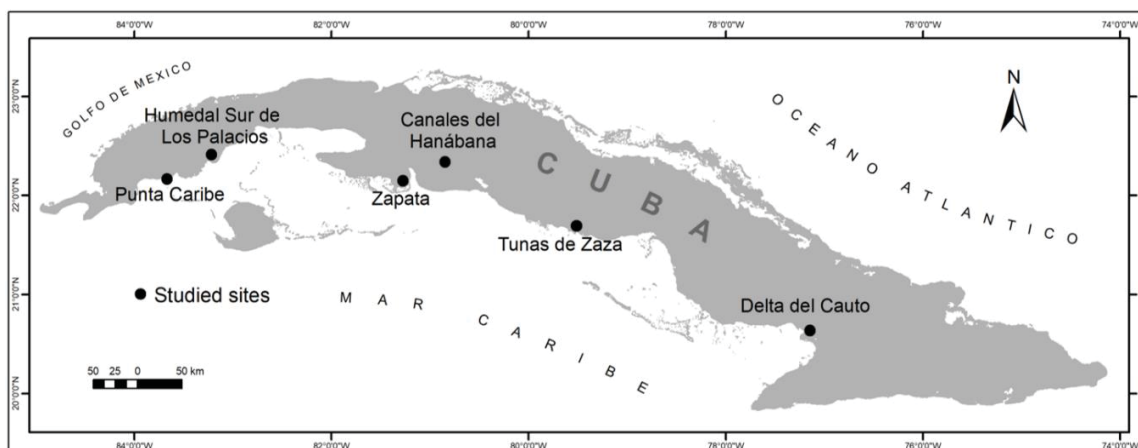


Fig. 1 Location of wetland study sites on the Cuban south coast

Table 1 Natural wetland study sites (2011 to 2013) on the Cuban south coast

Code	Study sites	¹ Protection designation	Province	Habitats	Sampled area size (ha)	Latitude and Longitude
S1	Punta Caribe	FR	Pinar del Río	Mudflats, temporary salty lagoons, mangrove	300	83°37'44''W 22°11'55''N
S2	Humedal Sur de Los Palacios	IBA	Pinar del Río	Salty lagoons, mangrove, mudflats. Near rice paddies	140	83°12'01''W 22°20'49''N
S3	Zapata	NP, IBA BR, RS	Matanzas	Largest wetland in the Caribbean. Shallow salty lagoons, mangroves, swampy grasslands	480	81°13'21''W 22°09'23''N
S4	Canales del Hanábana	FR, IBA BR, RS	Matanzas	Basin of the Hanábana river. Fresh water deep and shallow channels, fresh water flooded grasslands	500	81°02'12''W 22°21'29''N
S5	Tunas de Zaza	FR, IBA	Sancti Spiritus	Mudflats, temporary salty lagoons, mangrove. Near rice paddies	200	79°32'14''W 21°39'25''N
S6	Delta del Cauto	FR, IBA, RS	Tunas-Granma	Second largest wetland in the Caribbean. Mudflats, salty, freshwater and brackish lagoons, mangrove, estuarine habitats associated with Cauto River. Near rice paddies	560	77°09'08''W 20°35'30''N

¹Protection designation:

Protected Areas: NP. National Park, FR. Faunal Refuge (CNAP 2013)

International designation (does not confer protection): BR. Biosphere Reserve, RS. Ramsar Site (CNAP 2013), IBA. Important Bird Area (Aguilar 2010)

2.2 Waterbird Surveys

We conducted bird surveys at each wetland site in three seasons and during three consecutive years, from May 2011 to November 2013. The seasons sampled were: spring migration (February and March), summer season (May and June) and fall migration (October and November), except in 2011 when a spring migration survey was not conducted. This approach recorded the most important migration movements in the annual cycle as well as resident birds. Bird counts were carried out during three alternative days (one day out of a three-day period), always simultaneously by observers located in each of the six wetland sites, in the second half of each month, to standardize and collect comparable data. Occasionally, counts were not conducted during poor weather conditions or if a boat was not available.

In each wetland site, we chose between five and eight sampling locations (in lagoons and salt marshes), depending on site characteristics (e.g. size, accessibility, habitat heterogeneity). Sampling locations, where counts were conducted, were the most prominent waterbird feeding or resting areas in each wetland site. Therefore, they were not selected randomly. We conducted fixed point counts (Bibby et al. 2000) at each sampling location. During the counts, all individuals of each species seen or heard in a period of time (30 minutes) were recorded without prefixing a radius and always in the first four hours after sunrise. A GPS was used to record geographical coordinates. In total, we conducted 543 waterbird surveys during this study.

Each species was identified and classified according to its occurrence (common, rare, very rare and vagrant) (Garrido and Kirkconnell 2010) and status (bimodal, summer migrant,

permanent resident and winter migrant) (Navarro and Reyes 2017). Bimodal species are those characterized by both resident and winter migratory populations. Observations were made using 10 x 50 binoculars and 20 x 60 spotting scopes. Bird taxonomy follows the American Ornithological Society (AOS) checklist (Chesser et al. 2018). Species conservation status was noted according to the Red Lists of González et al. (2012) and IUCN (2017). We recorded only aquatic birds and species that depend on wetlands to meet their daily needs. As our survey method was diurnal, results may be biased low for secretive birds, (e.g., gallinules) and nocturnal birds (e.g., night-herons; whistling ducks).

2.3 Data Analysis

We estimated total abundance of each species per sampling plot, in each season, as well as maximum abundance (registered in any one-day observation). Density (bird/ha) was calculated for each species, per site, in each season. To derive the density, we used the sampled area size (hectares) for each wetland site, shown in Table 1. The sampled area size was obtained as the total area covered by all lagoons and salt marches sampled in the wetland site. We obtained the estimated extension of lagoons and salt marshes sampled from a Cuban wetland shapefile layer (CNAP 2013) using a geographic information system software QGIS 2.18.14.

Frequency of waterbird species was given as the number of samplings where the bird was recorded/total number of samplings ($N = 543$). Relative abundance was determined separately for each status category by dividing total maximum abundance for each species across the three seasons by the total abundance of all species included in the corresponding status category; the outcome was multiplied by 100. The Alpha diversity index, such as

species richness, Shannon diversity index (Magurran 1988) and Pielou evenness index (Pielou 1969) were also calculated for the six study sites. Total abundance and density were summarized for the six sites in each season. Waterbird abundance per month for each season, in the six wetlands, was calculated for 2012 and 2013 separately (monthly samplings for 2011 were not included in this latter calculation because these were incomplete).

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to test the effect of wetland site, season and year (2012 and 2013) on waterbird composition. We also tested the differences among wetland sites and years (2011 to 2013) considering only the fall migration season because most species presented their highest abundance and densities in this season. Bird abundance was previously transformed with $\log(x + 1)$ to ensure normality. Significance testing of the Bray–Curtis similarity measures (Legendre and Legendre 1998) and *post hoc* comparisons ($P < 0.05$) were made using 999 permutations.

Non-metric multidimensional scaling (NMDS; Kruskal 1964) ordination was carried out to analyze the degree of similarity in waterbird assemblage structure among the six wetlands sites (data $\log(x + 1)$ transformed). The analysis was based in the Bray–Curtis metric of dissimilarity. We used two-dimensional joint plots to compare spatial patterns and species composition similarities of the waterbird communities among sites. A stress value of < 0.3 is deemed adequate. Data entities that are closer together in the plot reflect waterbird communities that are more similar than those further apart (McCune and Grace 2002). A multivariate test for abundance homogeneity of group dispersions (permutation dispersion) (BETADISPER; Anderson 2006; Anderson et al. 2006) was conducted among sites, seasons and years, using Jaccard distance method.

The Mantel test was performed to detect whether assemblage composition of waterbirds and presence/ absence of waterbird species were linked to site spatial positions in the region (correlation between an Euclidean distance matrix and the Bray–Curtis dissimilarity matrix) (Legendre and Legendre 1998). The test was carried out in each month evaluated (16 months) for both assemblage composition and presense/absence. To calculate the linear distance separating the populations sampled, a matrix was constructed with the coordinates in decimal degrees of latitude and longitude at each site. All statistical analyses were conducted in R software environment version 3.4.4 (R Core Team 2018) using *vegan* (version 2.5-1) (Oksanen et al. 2018) and *MASS* packages (Venables and Ripley 2002).

The conservation importance of the Cuban south coastal wetlands for waterbird populations was assessed by comparing the observed abundance for each species with global flyway population estimates (Wetland International 2018). A species' population was determined to be globally important to conservation if it regularly met or exceeded the 1% global population threshold set by Criterion 6 of the Ramsar Convention (Ramsar Convention Secretariat 2010).

3. Results

3.1 Composition of the waterbird assemblage

We recorded a total of 110 species and 367,941 individuals at six Cuban south coastal wetlands, representing 72 genera and 23 families (Supplementary material 2). The most species-rich families were Scolopacidae (22 species), Anatidae (19 species), Laridae (15

species) and Ardeidae (12 species). The order best represented was Charadriiformes with 48 species. Most species (71 %; 79 species) were considered common birds, while the others were rare (20 species), very rare (7 species) or accidental (5 species). The Blue-winged Teal *Spatula discors* was the most abundant species followed by Least Sandpiper *Calidris minutilla*, American Flamingo *Phoenicopterus ruber*, American Coot *Fulica americana* and Glossy Ibis *Plegadis falcinellus*.

The most frequently observed birds were six species of egrets and herons (Great Blue Heron *Ardea herodias*, Great Egret *Ardea alba*, Snowy Egret *Egretta thula*, Little Blue Heron *Egretta caerulea*, Green Heron *Butorides virescens* and Tricolored Heron *Egretta tricolor*), with 70 to 85 % of occurrences, followed by White Ibis *Eudocimus albus*, Black-necked Stilt *Himantopus mexicanus* and American Flamingo, with 75.7 %, 66.1 % and 64.1 % respectively (see Supplementary material 2). Of the species detected, four are categorized as threatened; West Indian Whistling-Duck *Dendrocygna arborea*, Masked Duck *Nomonyx dominicus*, Snowy Plover *Charadrius nivosus* and Piping Plover *Charadrius melodus*. Piping Plover was recorded for the first time on the southern coast of Cuba (Humedal Sur de Los Palacios) with 19 individuals.

Among the wetland birds observed, 78.2 % (86 species) were winter migrants, 31 of which were bimodal, 18.2 % (20 species) were permanent residents and 3.6 % (4 species) were summer migrants. These results highlight the importance of the region for North American birds during the winter. The results showed that 45 % of bimodal birds were observed during fall migration, 38 % during spring migration and 17 % during the summer season. Although some species were characterized by resident and migratory populations, it is evident that Cuba supports important numbers of birds during fall migration, since 66 % of the species presented their highest abundance and densities in this season.

In the bimodal group, the American Coot had the highest values of relative abundance (22.65) with very high migratory populations. The species with the second highest relative abundance was the Glossy Ibis (16.21), with the highest abundance and density during the two migratory seasons, also reflecting a strong migratory component. The two bimodal species with the largest populations during summer, and apparently the least influenced by migratory populations from North America, were Killdeer *Charadrius vociferus* and American Avocet *Recurvirostra americana*. The species with highest relative abundance within the winter migrant category were Blue-winged Teal (69), Least Sandpiper (11.76) and Short-billed Dowitcher *Limnodromus griseus* (5.39).

3.2 Spatial and temporal patterns in waterbird assemblages

The site with highest species richness and greatest waterbird abundance in all seasons, primarily during fall migration, was Humedal Sur de Los Palacios, followed by Delta del Cauto (Fig. 2). However, Humedal Sur de Los Palacios had the highest values of species richness. These estimates resulted in having a low index of Shannon diversity (H'), as well as low evenness (J), indicating a greater dominance of specific species in the waterbird assemblage composition (Table 2). In contrast, Canales del Hanábana showed the highest diversity and equitability indices.

Fall migration season showed the highest values of total abundance and density at each of the sites evaluated, while the lowest values (Table 2; Fig. 2) were recorded in the summer season. Given that the months corresponding to fall migration (October and November), were characterized by the highest numbers of waterbirds at all sites during our study (Fig. 3), this

season is likely the most important time for the conservation of waterbirds on the south coast of Cuba.

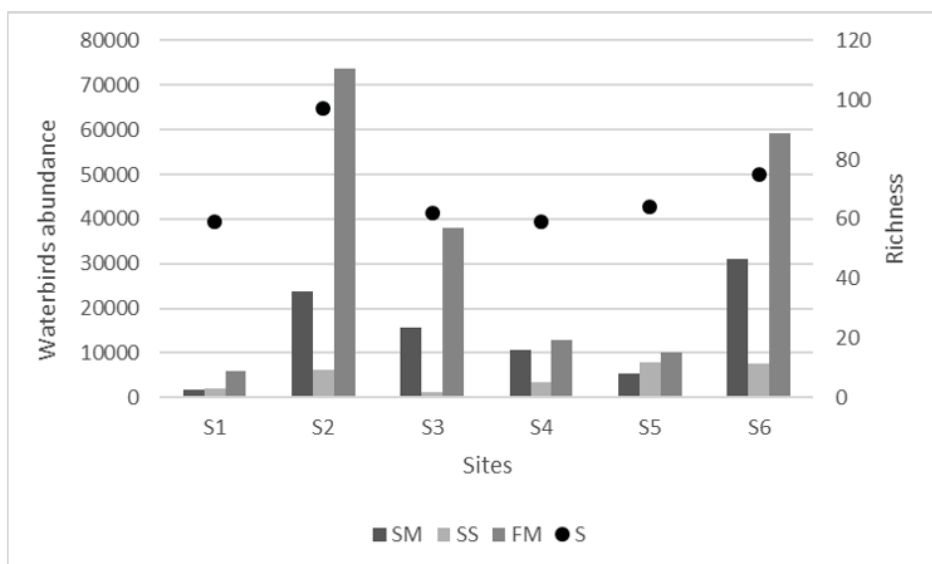


Fig. 2 Spatio-temporal variation in waterbird abundance (bars), per seasons (SM: Spring Migration, SS: Summer Season, FM: Fall Migration) and richness: S (points), in each site during 2012 and 2013, in the Cuban south coastal wetlands. Codes for the sampled sites (S1 to S6) are presented in Table 1

Table 2 Density of waterbirds per sites, in Cuban south coastal wetlands, per season (SM: Spring Migration, SS: Summer Season, FM: Fall Migration). Diversity indices of waterbirds per sites, H': Shannon-Weaver index, J: Pielou index

Code	Sites	Total density			Diversity indices	
		SM	SS	FM	H'	J
S1	Punta Caribe	5.71	6.43	20.14	2.69	0.66
S2	Humedal Sur de Los Palacios	170.22	44.11	525.84	1.89	0.41
S3	Zapata	66.53	7.46	153.42	1.41	0.34
S4	Canales del Hanábana	21.47	7.07	25.83	3.06	0.75
S5	Tunas de Zaza	9.10	15.96	16.01	2.81	0.67
S6	Delta del Cauto	62.30	15.05	118.17	2.31	0.53

Waterbird composition was significantly different (PERMANOVA, $P < 0.05$) among sites ($F_{5,244} = 31.93$, $P = 0.001$, Fig. 4), and seasons ($F_{2,244} = 11.11$, $P = 0.001$, Fig. 3). However, there were no differences in the assemblage compositions of waterbirds ($P > 0.05$) among years ($F_{1,244} = 1.79$, $P = 0.053$). Considering only the fall migration season, assemblage composition, was significantly different among sites ($F_{5,135} = 15.27$, $P = 0.050$), but there was not a significant difference in waterbird assemblage composition among the three years for this season ($F_{2,135} = 2.19$, $P = 0.117$). This result indicates that all sites do not have the same importance during fall migration and these conditions are relatively stable over time.

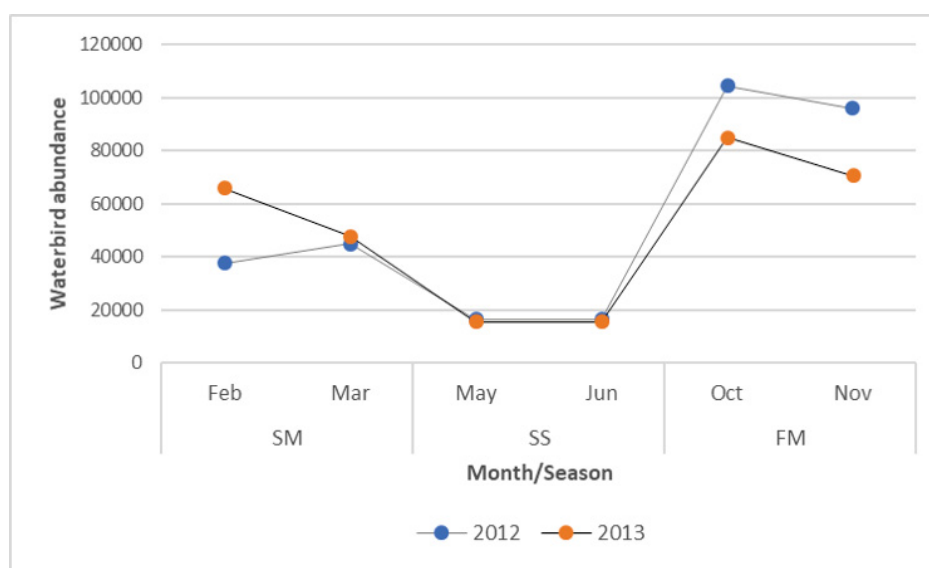


Fig. 3 Total maximum waterbird abundance per month, in each season (SM: Spring Migration, SS: Summer Season, FM: Fall Migration) in 2012 and 2013, in six Cuban south coastal wetlands

When we assessed the spatial pattern and species composition similarities of waterbird communities among sites, we identified the following sites as those with the greatest similarity in assemblage composition: Humedal Sur de Los Palacios (S2) and Delta del Cauto

(S6), followed by Punta Caribe (S1) and Zapata (S3). The site most dissimilar in its assemblage composition was Canales del Hanábana (S4) (Fig. 4).

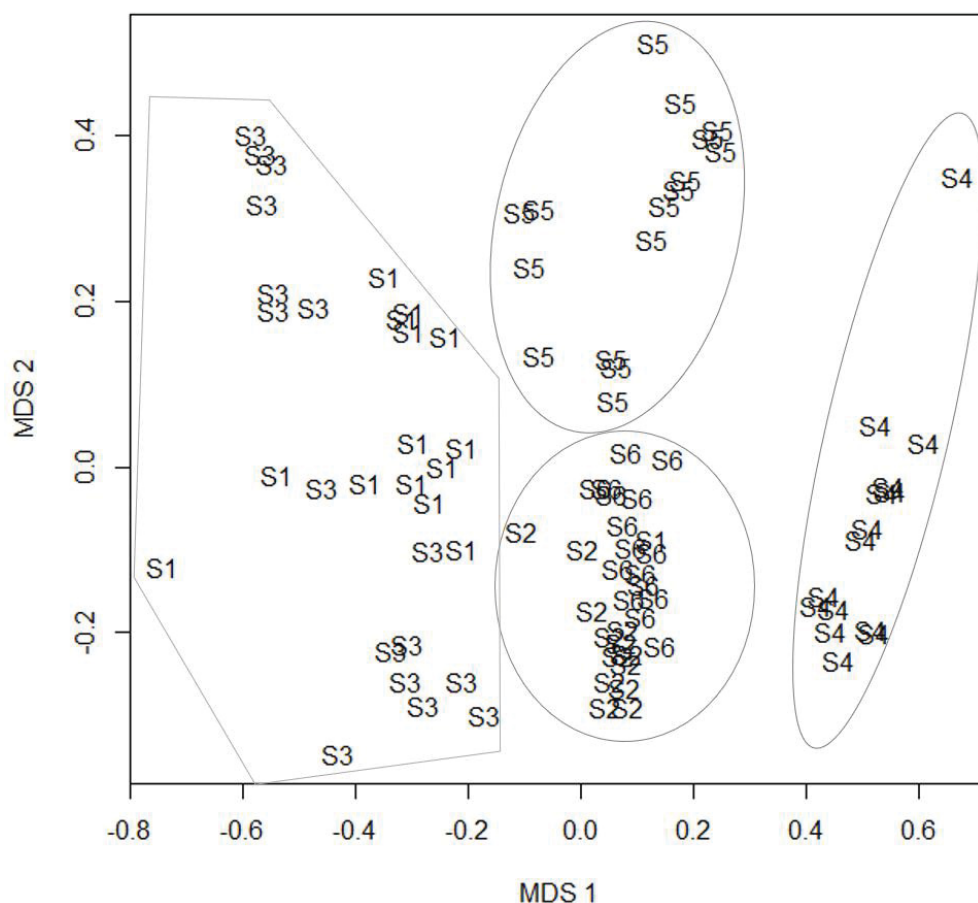


Fig. 4 Two-dimensional non-metric multidimensional scaling (NMDS) plot (stress = 0.16) of waterbird composition (abundance data $\log(x + 1)$ transformed) in six Cuban south coastal wetlands ($N = 92$), based on the Bray–Curtis metric of dissimilarity (years 2011–2013). Codes for the sampled sites (S1 to S6) are presented in Table 1

The Betadisper test revealed no differences ($P > 0.05$) in spatial or temporal variability in abundances of waterbirds among sites, seasons or years. Therefore, waterbird abundances were not more variable among the six wetlands ($F_{5,86}=1.76$, $P = 0.11$, Fig. 5). Also, there

were no differences in the temporal variability of the sites among the three seasons ($F_{2,89} = 2.59$, $P = 0.084$, Fig. 6a) and among the three years ($F_{2,89} = 0.07$, $P = 0.934$, Fig. 6b).

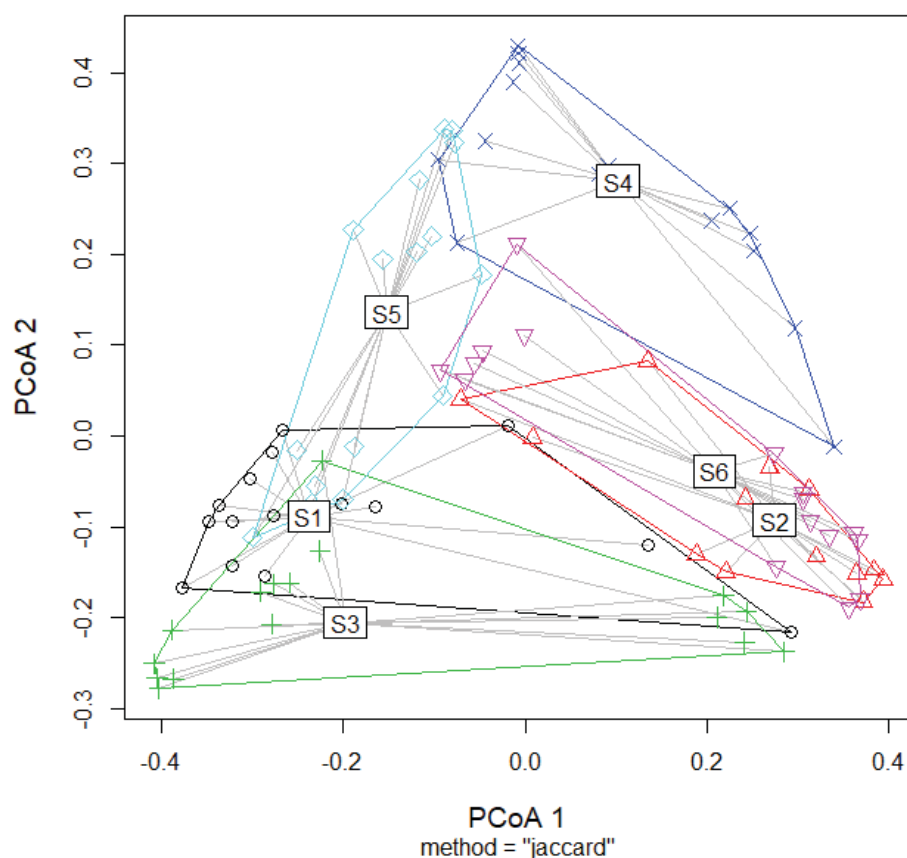


Fig. 5 Multivariate dispersion of waterbird abundance among six Cuban south coastal wetlands (2011 to 2013) based on the Jaccard index method (Betadisper plot). Codes for the sampled sites (S1 to S6) are presented in Table 1

Mantel test results indicated no spatial correlation for any of the months sampled (16 months) among the six wetlands, both for waterbird abundance and presence/absence ($P > 0.05$; P values varied between 0.51 and 0.99). Mantel r values for the 16 months varied between - 0.06 and - 0.66 (Supplementary material 3). Therefore, neither waterbird

assemblage composition nor presence/absence of waterbird species was found to be linked to a site's spatial position on the south coast of Cuba.

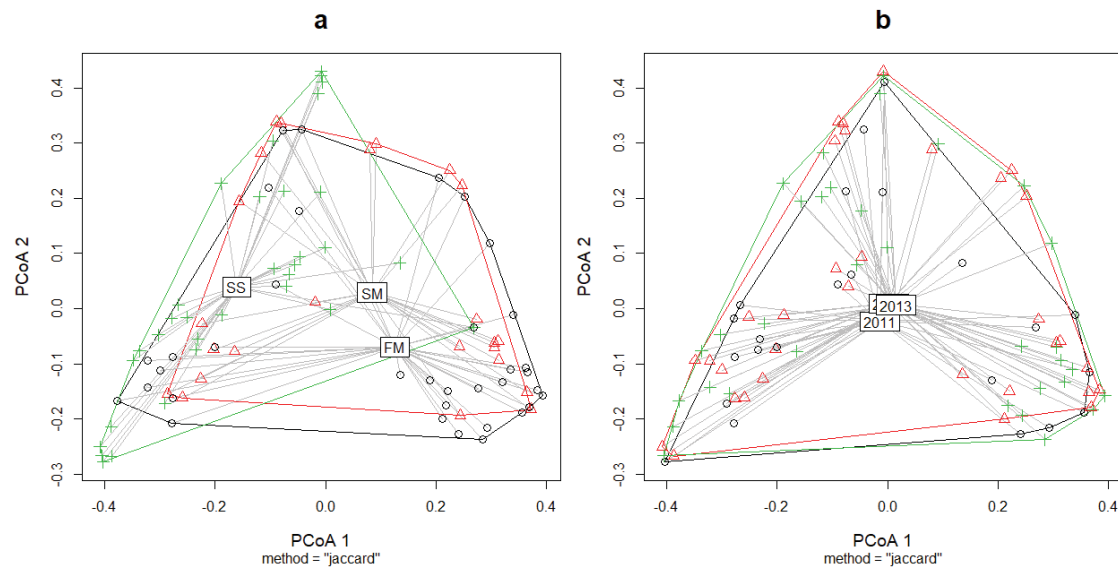


Fig. 6 Multivariate dispersion of waterbird abundance in each season (SM: Spring Migration, SS: Summer Season, FM: Fall Migration) (Fig. 6a) and years (Fig. 6b) among six Cuban south coastal wetlands (2011 to 2013) based on the Jaccard index method (Betadisper plots)

3.3 Conservation assessment

Twelve waterbird species in the Cuban south coastal region, were found at abundance levels exceeding the 1 % criterion of the world's population in more than one site (Table 3). The American Flamingo was recorded with > 1% of the world's population in the most wetlands (5 sites), followed by the Roseate Spoonbill *Platalea ajaja* with four sites. Notably, the Glossy Ibis, American Flamingo and Roseate Spoonbill exceeded the 1 % criterion at remarkably high abundance (i.e. 35, 25 and 17 times greater), respectively. This observation demonstrates the great importance of Cuba's south coastal wetlands for the conservation of

these species. All six wetlands surveyed supported at least two species that met the 1 % criterion for recognition as an internationally important site. Delta del Cauto had the most species (6) that met this criterion, followed by Humedal Sur de Los Palacios (5 species).

Table 3 Waterbird species that meet Ramsar 1% criterion (Wetlands International 2018) in Cuban south coastal wetlands from 2011 to 2013. Total waterbirds abundance at Cuban south coastal wetlands and maximum abundance of specific sites. Maximum abundance > 1% of the estimated global flyway population are shown in bold. Codes for the sampled sites (S1 to S6) are presented in Table 1

Species	1% of world population	Abundance in Cuban south coastal	Sites /Abundance (Maximum)					
			S1	S2	S3	S4	S5	S6
West Indian Whistling Duck <i>Dendrocygna arborea</i>	140	534	47	26	10	374	31	46
White-cheeked Pintail <i>Anas bahamensis</i>	750	1732	0	341	0	1370	0	21
Blue-winged Teal <i>Spatula discors</i>	89500	113056	3250	53588	22272	3923	50	29973
American Flamingo <i>Phoenicopterus ruber</i>	400	10277	538	657	1082	0	2390	5610
Wilson's Plover <i>Charadrius wilsonia</i>	100	652	134	325	11	0	26	156
Least Sandpiper <i>Calidris minutilla</i>	7000	12073	150	1964	248	317	585	8809
Short-billed Dowitcher <i>Limnodromus griseus</i>	1100	5989	61	4471	387	348	150	572
Laughing Gull <i>Leucophaeus atricilla</i>	550	769	83	165	5	0	150	366
Caspian Tern <i>Hydroprogne caspia</i>	190	541	34	115	272	2	110	8
Reddish Egret <i>Egretta rufescens</i>	60	370	48	28	54	2	68	170
Glossy Ibis <i>Plegadis falcinellus</i>	210	7531	0	901	0	503	122	6005
Roseate Spoonbill <i>Platalea ajaja</i>	45	790	33	232	144	1	210	170
Number of species per site with more than 1% of world population	12		2	5	3	3	3	6

4. Discussion

This is the most comprehensive study on waterbird assemblages in Cuban natural wetlands to date, consisting of a 3-year assessment of an extensive area of wetlands using standardized methods. We identified spatio-temporal patterns of waterbird assemblages characterized in three seasons of the avian annual cycle, along a quarter of Cuba's coastline and in areas

representing 40 % of Cuban wetlands. Documentation of the wide occurrence and abundance of migrants and species important for conservation affirms the national and international importance of wetlands of the Cuban south coast as habitat for waterbirds. Two families, Scolopacidae and Anatidae, consisting primarily of migratory species, were the most-highly represented families, highlighting the strong migratory component of the bird assemblage of this region (Mugica et al. 2006a). Species richness recorded for the southern coast of Cuba represents 68 % of the waterbird species reported for Cuba (Acosta et al. 2011), indicating that the region provides habitat for most of these species in the country.

Our results for Blue-winged Teal, consistent with other studies in Cuba, report this species as the most abundant of the Cuban anatids (Rodríguez 2004; Acosta and Mugica 2006; Blanco et al. 2014). The abundance of Least Sandpipers also coincides with reports from other studies that identify this species as the most common in its genus to occur in Cuban wetlands (Blanco 2006). Both species are winter migrants and species that exceed 1% of the world's population in Cuba's south coastal wetlands (Table 3). Additionally, several other studies report a high frequency of egrets and herons in Cuban wetlands (González et al. 2016a; 2018).

The fact that the Glossy Ibis is one of the most abundant species of the Cuban south coast, at a level exceeding 35 times the estimate for 1% of the world's population, indicates the global importance of these wetlands to this species. The Glossy Ibis was formerly considered uncommon in Cuba (Garrido and Kirkonnell 2010); however, in the 1980s its populations began to increase sharply in close relationship with rice fields (Acosta and Mugica 2013). This species feeds on rice during the winter (Acosta et al. 1996). The reduction in use of pesticides in Cuba (Mugica et al 2006a) and the increased use of these sites for breeding were presumably the biggest factors in the dramatic increase in the Glossy Ibis

populations. Specifically, the largest nesting colony (5,000 individuals) of this species reported in Cuba is found in Delta del Cauto (Denis et al. 2005; Mugica et al. 2006b; Acosta and Mugica 2013).

The American Flamingo was one of the most frequent and abundant species in our study, with numbers in Cuban south coastal wetlands exceeding by 25 times the estimate of 1% of the world's population. It is distributed mainly in the Caribbean (Blanco et al. 2002), and the Cuban population is one of the most important in the region (Ottenwalder 1991), producing at least 50% of annual recruitment (Morales 1996). Delta del Cauto supports the second largest nesting sites in the Cuban archipelago with 20,000-30,000 reported nests (Denis et al. 2005). During this study, we discovered several juveniles banded in Yucatan, Mexico (HTTZ, HTTV, HTTD, HSBP bands) which documents movement in the Caribbean and use of Cuban wetlands during the first years of life (data in accordance with Blanco et al. 2002 and Galvez et al. 2016). Lack of published studies on flamingo population dynamics in a wide region of Cuba emphasizes the important contribution of our study to the understanding of spatio-temporal patterns of this species.

Several factors have been associated with waterbird abundance and richness, such as wetland size (Cintra et al. 2007; Sebastian-González and Green 2014), food resources and landscape configuration (Amezaga et al. 2002; Taft and Haig 2006; Pérez-García et al. 2014). Our finding that the south coastal wetlands with the highest species richness and waterbird abundance occurs at Humedal Sur de Los Palacios, followed by Delta del Cauto, may be attributable to their landscape structure, proximity to rice fields, large size of water bodies, stable (perennial) lagoons of various depths, as well as heterogeneity (mix of wetland types). These two areas were the most similar in species composition (Fig. 4) and we recorded the largest number of birds exceeding 1% of the world population (Table 3) at these locations.

In contrast, Humedal Sur de Los Palacios showed lower equitability, which indicates large concentrations of individuals of the same species. Both sites are near to two of the major rice paddies in Cuba (Mugica et al. 2006a). Rice cultivation in proximity to refuge areas in the coastal wetlands allows birds to use both ecosystems. Waterbirds use the rice fields mainly for resting and feeding; in this way they acquire their daily nutritional needs with relatively low energetic cost (Stafford et al. 2010; King et al. 2010; Toral et al. 2011). Multiple studies have been carried out on the ecology of bird communities in rice fields of the southern coast of Cuba (Mugica et al. 2001; Acosta et al. 2002; Acosta and Mugica 2013), however, the functional connectivity with the coastal wetlands of this region has not been well explored. Connectivity of complementary wetlands within a mosaic can be a management strategy to reduce disturbance and provide the resources required by diverse waterbird assemblages (Kelly et al. 2008; Ma et al. 2010).

Canales del Hanábana can be considered a unique site, with a species composition dissimilar to the other wetland sites; it is also the most diverse site of the six sampled (Fig. 4). This was an expected result, given the wetland's specific characteristics. First, it contains exclusively fresh water (CNAP 2015), so some species with preference for this habitat type (e.g., Anatidae, Rallidae, Podicipedidae) are better represented. The aquatic vegetation is very beneficial to wetland birds as it provides food, resting places, shelter and nesting habitat for many birds (Mugica et al. 2006b). In addition, it is the farthest site from the coastline of the six wetlands studied, therefore its use by marine species (e.g., Laridae, Fregatidae and Scolopacidae) is limited. Canales del Hanábana is a protected Faunal Refuge, representing an extensive, unique freshwater habitat within the Cuban national protected areas system (CNAP 2013); hence, its importance to conservation of this ecosystem and the bird community.

Fall migration is characterized by the highest waterbird abundances and densities along the south coast, consistent with other studies of bird dynamics in other Cuban wetlands (Acosta et al. 1992; González et al. 2016b). According to González et al. (2006), bird richness and abundance during fall migration is greater than in the winter season. Fall migration is an essential period for waterbird conservation in Cuba for several reasons. First, many migratory birds arriving in Cuba are transients, and use the archipelago as a stopover site to restore energy and continue their movement to other Caribbean islands or South America (Mugica et al. 2006b). Also, because migration routes reflect avian ecological requirements, waterbirds, for example, require access to coastal and/or inland wetland habitats (CMS 2014). Generally, fall migrants to Cuba, come from North America, covering a journey of several thousand kilometres between their breeding and non-breeding grounds (Peter 2001). The birds arrive with minimum fat reserves, and this vulnerable state is an additional reason why protection of these sites is very important. When birds return to their North American breeding sites in the spring, we find waterbird composition differs with abundances lower than during fall migration. From this observation we suggest that many birds, that use Cuba as a stopover in fall migration, do not make the same use during return in spring migration.

The homogeneity in waterbird abundances among seasons (Fig. 6a) and years (Fig. 6b) indicates community stability over time in our study region. Additionally, species composition also remained constant over the years. This suggests that both resident and migratory bird populations make consistent use of southern Cuba coastal wetlands annually, despite the high mobility and abundance variability of these species (Guevara et al. 2012; Tomankova et al. 2013). This result indicates that the protected status and management of the wetlands, designated as protected areas, may be at an adequate level to support important

waterbirds populations. Longer term monitoring is needed to confirm this conclusion, however.

We hypothesized that wetlands in the western region of Cuba are most important in terms of richness and abundance of migratory species, given their spatial location, closer to the Mississippi Flyway (Mugica et al. 2014), as well as wetlands of the eastern region that is traversed by birds following the Atlantic Flyway (Garrido and Kirkconnell 2010). However, we did not find any relationship between waterbird assemblage composition nor presence/absence of waterbird species based on a site's location in the western, central or eastern region of the island, in any of the sampled months. Waterbirds are highly mobile species that easily disperse in search of resources (Wen et al. 2016), and it appears that the distance among the studied wetlands does not represent an obstacle for their dispersion.

4.1 Conservation implications

Our study provides quantitative evidence that the southern coast of Cuba, as a whole, is of global importance for waterbird conservation, as many of the 350 migrant species that breed in North America and winter in the Caribbean and South America are in rapid decline (Birdlife International 2018). Also, each wetland individually can be considered of global importance (Table 3), according to Ramsar criteria (Ramsar Convention Secretariat 2010). Based on data from this study, proposals for three new Ramsar sites (Humedal Sur de Los Palacios, Punta Caribe and Tunas de Zaza) and a new Important Bird Area (IBA, Punta Caribe), according to Birdlife International criteria (2018), can be made. Additionally, the current IBA status of four sites (Humedal Sur de Los Palacios, Zapata, Tunas de Zaza and Delta del Cauto), is reaffirmed ten years after their original identification (Aguilar 2010), as

well as the status of two Ramsar sites (Zapata and Delta del Cauto), established in 2002 (CNAP 2009).

Even though our results indicate stability in waterbird populations in the southern coast of Cuba, we recommend the new designations of global importance for four sites, which are currently protected areas, because international designations strengthen protection at the national level and commit governments and citizens to prioritize these lands for conservation. International conservation status and recognition may protect these sites in the long-term, as economic demands for infrastructure development, tourism, agriculture and maritime transport could threaten these wetlands at a national scale. Additionally, these sites require long-term monitoring and management and global recognition may provide greater national and international visibility thus increasing priority for conservation funding.

We identified Humedal Sur de Los Palacios as the most important site for conservation among the wetlands studied as it has the highest species richness and abundance of waterbirds. Among the main threats to this site is illegal hunting of waterbirds for food or sport, which could affect populations in the near future. However, to date, no legal protection is provided for this wetland, which constitutes a large gap in the Cuban national system of protected areas.

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7. Supplementary materials

Supplementary material 1 Description of six wetland sites under study (2011 to 2013) on the Cuban south coast

S1. Punta Caribe:

Punta Caribe is a Faunal Refuge of recent creation (CNAP 2013). It is located on the southern coast of Pinar del Rio province, in western Cuba. It is a small wetland with predominance of intertidal mudflats, temporary lagoons and mangrove ecosystems. The area includes 2.5 km of the Guamá river basin, with an exuberant mangrove forest, reaching up to 6 m in height. Mangrove and swamp grass are the predominant plant formations in the area (Novo 2010). The wetland has a small extension of swamp forest and about 10 km² covered by temporary lagoons and salt marshes. It is the smallest wetlands sampled.

S2. Humedal Sur de los Palacios:

Humedal Sur de Los Palacios is an unprotected wetland, located on the south coast of the Pinar del Rio province, in western Cuba. It was recognized as an Important Bird Area (IBA) (Aguilar 2010). It is formed by an elongated coastal strip of mangrove forest (main plant formation), natural coastal wetlands, coastal salty lagoons, marshes, swamp grass and intertidal mudflats. These natural coastal lagoons are among the largest on the southern west coast of Cuba (Basal 2014). There are approximately 30 km² of lagoons and salt marshes in this wetland, where Maspoton and Media Casa lagoons are the most remarkable. The area is surrounded by extensive rice fields in the north side, that are among the most important in the country.

S3. Zapata:

Ciénaga de Zapata is a National Park, located within a Biosphere Reserve, a Ramsar site (CNAP 2013) and an IBA (Aguilar 2010). It is located in southern Matanzas province, in western Cuba. This area is considered the largest and best-preserved wetland in the insular Caribbean, with the largest area of marshes in Cuba and considerable extensions of forests (mangrove and semideciduous). It contains the largest and most complex karst drainage system in Cuba, Zapata Basin, that produces a unique hydrological phenomenon such as the swamp spring vegetation complex and a surface drainage system characterized by the existence of several rivers, lagoons, marshes, ditches and channels (Rodríguez et al. 1993). Las Salinas is a well-known system at Ciénaga de Zapata including coastal shallow lagoons, surrounded by mangroves. The main plant formations are mangroves, flooded savannahs and swamp grassland. Lagoons and salt marshes cover about 47 km² in this wetland.

S4. Canales del Hanábana:

Canales del Hanábana is a Faunal Refuge, also located in southern Matanzas province, in western Cuba. It is part of a Biosphere Reserve, a Ramsar site (CNAP 2013) and IBA (Aguilar 2010). The area contains a large system of fresh water channels of 5.7 km² and lagoons, combined with fresh water flooded grassland areas. The hydrographic network is fed by the Hanábana river, considered as the most important in the area. It is the only Cuban protected area that is completely covered by fresh water ecosystems. Swamp grasslands predominate in 87% of the area, with swamp forests and freshwater vegetation in a lesser extent. Swamp grasslands are composed of herbaceous plants that remain flooded most of the year. The swamp forest is characterized has an arboreal stratum of 5-15 m height. These

forests grow on peaty soils, temporarily flooded and have the highest floristic species richness in the area (CNAP 2015). The site is surrounded by rice fields in the north.

S5. Tunas de Zaza:

Tunas de Zaza is a Faunal Refuge (CNAP 2013), and an IBA (Aguilar 2010). It is located in the Zaza river delta, in Sancti Spiritus province southern coast, central Cuba. It comprises a set of natural coastal wetlands, important salty lagoons such as El Basto and La Limeta, and huge intertidal mudflats. The presence of the Zaza river, provides an important lagoon system, connecting the lagoons, estuaries and the sea. Mangrove is the most abundant plant formation in the area and occurs throughout the lower coastline, the lagoon systems and at the river mouths of the Tayabacoa and Zaza rivers. They have an arboreal stratum of 5-15 m in height and can occupy several kilometers in width. Other plant formations covering this wetland, in a lesser extent, are the evergreen microphyll forest, sandy vegetation complex, coastal scrub and savanna with *Copernicia* palms (ENPFF 2009). About 25 km² of lagoons and salt marshes are estimated in the protected area. In the eastern limits of the area, it's found the largest rice paddies of the country.

S6. Delta del Cauto:

Delta del Cauto is a Faunal Refuge, a Ramsar site (CNAP 2013) and an IBA (Aguilar 2010). It is located in Las Tunas and Granma provinces in south-eastern Cuba. It is the most extensive, complex and best-preserved deltaic system of Cuba and the Caribbean and the second wetland in extension, being the final result of the largest Cuban fluvial system, the Cauto river. This river is the main source of fresh water in this wetland, connecting innumerable lagoons, estuaries and the sea, and resulting the formation of an estuarine system.

Towards the interior, it has a system of sweet and salty lagoons of great extension, such as Birama, Hoja de Maíz and Leonero (the latter permanently sweet). Further to the coast, there are extensive salting ponds, shallow lagoons with saline-hypersaline functioning or temporarily sweet (Denis et al. 2005). Lagoons and salt marshes cover a large area in the wetland, about 142 km². The predominant habitats are mangroves, swamp grasslands and savannahs (Guanal with *Copernicia giga* palm). Mangroves forest are considered the most vigorous in the country (approximately 30 m high). Other plant formations covering a less extension include swamp forest and aquatic vegetation in fresh water.

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Supplementary material 2 Waterbird assemblage from six Cuban south coastal sites: S1 . Punta Caribe, S2. Humedal Sur de Los Palacios, S3. Zapata, S4. Canales del Hanábana, S5. Tunas de Zaza, S6. Delta del Cauto. Total abundance and density (birds/ha) of waterbirds for each season (SM. Spring Migration, SS. Summer Season, FM. Fall Migration). Maximum abundance (Max Abun), registered in any one-day observation. Frequency of waterbirds (Fr) (number of sampling plots where the bird was seen/total number of sampling plots: N = 543). Relative abundance (Rel Abun) (sum of the maximum abundance of each species in the three seasons/total abundance of all species included in the correspondent status category)

Family/Species ('Threatened category)	Sites						Total abundance						Total density						Rel Abun	
																				Fr %
	S1	S2	S3	S4	S5	S6	2Stat us	3Occ urrence	SM	SS	FM	SM	SS	FM	Max Abun					
Anatidae																				
Black-bellied Whistling-Duck <i>Dendrocygna autumnalis</i>			x				WM	VR	0	0	4	0.00	0.00	0.01	3	0.37	0.00			
West Indian Whistling-Duck <i>Dendrocygna arborea</i> (IU*, IU**)	x	x	x	x	x		PR	C	334	344	464	0.77	0.70	1.08	200	24.68	3.25			
Fulvous Whistling-Duck <i>Dendrocygna bicolor</i>		x	x	x	x		B	C	3584	1605	2886	9.12	3.51	6.78	1400	26.89	8.83			
Snow Goose <i>Anser caerulescens</i>	x				x		WM	A	26	0	0	0.16	0.00	0.00	21	1.10	0.01			
Wood Duck <i>Aix sponsa</i>		x		x			B	C	23	7	84	0.13	0.01	0.30	45	6.63	0.12			
Green-winged Teal <i>Anas crecca</i>	x						WM	R	225	0	500	1.61	0.00	3.58	500	2.58	0.38			
Redhead <i>Aythya americana</i>	x						WM	R	8	0	0	0.06	0.00	0.00	8	0.55	0.00			
Mallard <i>Anas platyrhynchos</i>	x			x			WM	VR	0	0	3	0.00	0.00	0.01	4	0.74	0.00			
White-cheeked Pintail <i>Anas bahamensis</i>	x		x	x	x		PR	C	1345	144	1689	4.44	1.01	4.92	500	25.41	9.05			
Northern Pintail <i>Anas acuta</i>		x	x		x		WM	C	95	0	25	0.57	0.00	0.17	600	6.26	0.06			
Blue-winged Teal <i>Spatula discors</i>	x	x	x	x	x		WM	C	17939	108	113056	71.93	0.60	507.90	30026	42.36	69.36			
Cinnamon Teal <i>Spatula cyanoptera</i>		x			x		WM	A	17	0	2522	0.12	0.00	5.16	2500	2.03	1.34			
Northern Shoveler <i>Spatula clypeata</i>	x	x	x	x			WM	C	889	51	2658	5.51	0.25	6.15	2300	14.92	1.90			
American Wigeon <i>Mareca americana</i>		x	x		x		WM	C	232	0	578	1.30	0.00	1.25	545	9.02	0.43			
Ring-necked Duck <i>Aythya collaris</i>			x	x			WM	C	10	0	97	0.02	0.00	0.19	40	2.76	0.06			
Lesser Scaup <i>Aythya affinis</i>			x	x	x		WM	C	57	0	122	0.12	0.00	0.25	78	4.97	0.09			

Red-breasted Merganser <i>Mergus serrator</i>	x	x	x	WM	C	4	0	5	0.02	0.00	0.04	2	2.58	0.00
Ruddy Duck <i>Oxyura jamaicensis</i>	x		x	B	C	8	0	45	0.05	0.00	0.09	14	1.47	0.06
Masked Duck <i>Nomonyx dominicus</i> (VU*, LC**)			x	PR	R	4	0	0	0.01	0.00	0.00	2	0.37	0.01
Phoenicopteridae														
American Flamingo <i>Phoenicopterus ruber</i>	x	x	x	x	PR	C	8003	4182	7390	17.63	10.06	19.13	2850	55.76
Podicipedidae														
Least Grebe <i>Tachybaptus dominicus</i>	x	x	x	x	PR	C	10	4	4	0.05	0.01	0.03	4	0.05
Pied-billed Grebe <i>Podilymbus podiceps</i>	x	x		x	B	C	23	9	28	0.08	0.06	0.09	20	0.07
Rallidae														
Black Rail <i>Laterallus jamaicensis</i>	x		x		WM	R	4	1	1	0.01	0.00	0.00	3	0.00
Mangrove Rail <i>Rallus longirostris</i>	x	x	x	x	PR	C	50	48	35	0.27	0.18	0.17	11	0.38
King Rail <i>Rallus elegans</i>	x				B	C	1	0	2	0.01	0.00	0.01	2	0.00
Yellow-breasted Crane <i>Hapalocrex flaviventer</i>	x				PR	R	1	0	1	0.01	0.00	0.01	1	0.01
Purple Gallinule <i>Porphyrio martinicus</i>	x	x		x	B	C	356	181	695	0.72	0.41	1.42	320	1.35
Common Moorhen <i>Gallinula chloropus</i>	x	x	x	x	B	C	344	73	248	0.75	0.16	0.51	89	0.73
American Coot <i>Fulca americana</i>	x	x	x	x	B	C	7412	13	13290	15.48	0.05	27.78	12968	22.65
Aramidae														
Limpkin <i>Aramus guarauna</i>	x		x	x	PR	C	30	68	54	0.07	0.14	0.12	23	0.43
Recurvirostridae														
Black-necked Stilt <i>Himantopus mexicanus</i>	x	x	x	x	B	C	1604	991	2373	6.91	3.08	10.22	1102	5.43
American Avocet <i>Recurvirostra americana</i>	x	x	x	x	B	R	63	4	200	0.38	0.01	1.32	130	0.29
Haematopodidae														
American Oystercatcher <i>Haematopus palliatus</i>	x		x		B	R	4	0	1	0.03	0.00	0.01	2	0.01
Charadriidae														

Black-bellied Plover <i>Pluvialis squatarola</i>	x	x	x	x	WM	C	1474	101	448	9.74	0.21	2.37	750	24.13	1.07
American Golden-Plover <i>Pluvialis dominica</i>		x	x		WM	R	69	0	30	0.49	0.00	0.21	40	3.13	0.05
Snowy Plover <i>Charadrius nivosus (VU*, NT**)</i>		x			PR	R	19	0	22	0.14	0.00	0.16	17	1.84	0.12
Wilson's Plover <i>Charadrius wilsonia</i>	x	x	x	x	SM	C	534	242	283	2.80	0.61	1.11	300	34.07	0.82
Semipalmated Plover <i>Charadrius semipalmatus</i>	x	x	x	x	WM	C	82	37	251	0.30	0.08	0.67	90	9.39	0.20
Piping Plover <i>Charadrius melodus (VU*, NT**)</i>		x			WM	R	13	0	6	0.09	0.00	0.04	10	1.29	0.01
Killdeer <i>Charadrius vociferus</i>	x	x	x	x	B	C	150	171	120	0.59	0.41	0.38	67	28.73	0.48
Jacaniidae															
Northern Jacana <i>Jacana spinosa</i>		x		x	PR	C	114	108	127	0.24	0.23	0.26	39	19.34	0.99
Scolopacidae															
Whimbrel <i>Numenius phaeopus</i>				x	WM	VR	24	15	13	0.05	0.03	0.03	22	2.58	0.03
Long-billed Curlew <i>Numenius americanus</i>	x		x		WM	VR	0	0	2	0.00	0.00	0.01	2	0.18	0.00
Marbled Godwit <i>Limosa fedoa</i>				x	WM	VR	8	4	0	0.02	0.01	0.00	5	0.92	0.01
Ruddy Turnstone <i>Arenaria interpres</i>	x	x	x	x	WM	C	130	58	248	0.42	0.14	0.87	70	20.99	0.23
Stilt Sandpiper <i>Calidris himantopus</i>	x	x	x	x	WM	C	7	4	40	0.01	0.01	0.11	30	2.76	0.03
Sanderling <i>Calidris alba</i>	x	x		x	WM	C	150	60	452	0.70	0.12	1.11	350	7.18	0.35
Dunlin <i>Calidris alpina</i>		x	x		WM	R	55	0	65	0.37	0.00	0.46	65	1.66	0.06
Least Sandpiper <i>Calidris minutilla</i>	x	x	x	x	WM	C	11118	1024	10089	28.55	2.80	30.52	8000	44.38	11.76
White-rumped Sandpiper <i>Calidris fuscicollis</i>	x	x	x	x	WM	R	135	116	841	0.38	0.24	1.80	800	2.95	0.58
Pectoral Sandpiper <i>Calidris melanotos</i>		x			WM	R	0	0	1	0.00	0.00	0.01	1	0.18	0.00
Semipalmated Sandpiper <i>Calidris pusilla</i>	x	x		x	WM	C	27	18	154	0.18	0.04	0.38	500	7.73	0.11
Western Sandpiper <i>Calidris mauri</i>	x	x	x	x	WM	C	1024	200	2289	3.41	0.42	5.31	640	16.94	1.86
Short-billed Dowitcher <i>Limnodromus griseus</i>	x	x	x	x	WM	C	4214	327	5655	23.76	2.20	34.41	5000	28.36	5.39
Long-billed Dowitcher <i>Limnodromus scolopaceus</i>	x	x	x	x	WM	R	287	70	1161	0.81	0.15	4.38	500	8.66	0.80

Common Snipe <i>Gallinago gallinago</i>	x	x	x	WM	C	330	0	479	0.67	0.00	0.98	200	7.37	0.43
Spotted Sandpiper <i>Actitis macularius</i>	x	x	x	WM	C	25	0	115	0.07	0.00	0.67	56	11.23	0.07
Solitary Sandpiper <i>Tringa solitaria</i>	x	x	x	WM	C	15	3	81	0.03	0.01	0.17	70	3.31	0.05
Lesser Yellowlegs <i>Tringa flavipes</i>	x	x	x	WM	C	439	151	395	1.51	0.61	1.60	101	35.36	0.52
Willet <i>Tringa semipalmata</i>	x	x	x	B	C	453	210	452	2.29	1.01	1.80	222	39.41	1.22
Greater Yellowlegs <i>Tringa melanoleuca</i>	x	x	x	WM	C	439	151	395	1.51	0.61	1.59	101	35.36	0.52
Red-necked Phalarope <i>Phalaropus lobatus</i>	x	x	x	WM	A	6	0	4	0.04	0.00	0.03	12	1.10	0.01
Red Phalarope <i>Phalaropus fulicaria</i>	x	x	x	WM	A	4	0	0	0.03	0.00	0.00	4	0.55	0.00
Laridae														
Black-legged Kittiwake <i>Rissa tridactyla</i>	x			WM	A	0	8	5	0.00	0.03	0.02	8	0.92	0.01
Bonaparte's Gull <i>Chroicocephalus philadelphia</i>	x			WM	VR	80	0	250	0.27	0.00	0.83	250	0.55	0.17
Laughing Gull <i>Leucophaeus atricilla</i>	x	x	x	B	C	322	457	745	1.46	1.41	2.43	150	56.72	1.67
Ring-billed Gull <i>Larus delawarensis</i>	x	x	x	WM	C	74	135	157	0.19	0.28	0.33	90	4.05	0.17
Herring Gull <i>Larus argentatus</i>	x	x	x	WM	C	52	0	7	0.37	0.00	0.02	52	1.66	0.03
Least Tern <i>Sterna antillarum</i>	x	x	x	SM	C	27	52	20	0.13	0.20	0.10	22	21.55	0.08
Bridled Tern <i>Onychoprion anaethetus</i>	x	x	x	SM	C	1	0	0	0.01	0.00	0.00	3	0.55	0.00
Gull-billed Tern <i>Gelochelidon nilotica</i>	x	x	x	WM	R	28	22	28	0.09	0.11	0.08	20	13.63	0.04
Caspian Tern <i>Hydroprogne caspia</i>	x	x	x	WM	C	372	85	501	1.11	0.52	1.65	272	30.76	0.51
Black Tern <i>Chlidonias niger</i>	x	x	x	WM	R	0	0	1	0.00	0.00	0.01	1	0.18	0.00
Common Tern <i>Sterna hirundo</i>	x	x	x	WM	R	3	10	13	0.02	0.02	0.03	23	3.13	0.01
Forster's Tern <i>Sterna forsteri</i>	x	x	x	WM	R	0	0	1	0.00	0.00	0.003	1	0.37	0.00
Royal Tern <i>Thalasseus maximus</i>	x	x	x	B	C	165	115	217	0.82	0.59	0.87	237	39.04	0.54
Sandwich Tern <i>Thalasseus sandvicensis</i>	x	x	x	SM	C	13	31	90	0.05	0.07	0.24	21	5.34	0.10
Black Skimmer <i>Rynchops niger</i>	x	x	x	WM	C	55	0	253	0.12	0.00	0.51	245	4.97	0.16

Ciconiidae																
Wood Stork <i>Mycteria americana</i>	x	x	x	x	x	PR	R	31	40	57	0.09	0.10	0.16	27	19.34	0.36
Fregatidae																
Magnificent Frigatebird <i>Fregata magnificens</i>	x	x	x	x	x	PR	C	49	43	46	0.22	0.20	0.22	16	27.81	0.39
Sulidae																
Brown Booby <i>Sula leucogaster</i>	x					PR	R	0	2	0	0.00	0.01	0.00	2	0.18	0.01
Phalacrocoracidae																
Neotropic Cormorant <i>Phalacrocorax brasilianus</i>	x	x	x	x	x	PR	C	891	1876	1295	1.83	3.89	2.65	1000	30.94	11.57
Double-crested Cormorant <i>Phalacrocorax auritus</i>	x	x	x	x	x	B	C	5367	4962	4490	32.56	26.33	26.71	3621	63.90	16.21
Anhingidae																
Anhinga <i>Anhinga anhinga</i>	x	x	x	x	x	PR	C	157	120	242	0.56	0.44	0.80	46	52.67	1.48
Pelecanidae																
American White Pelican <i>Pelecanus erythrorhynchos</i>	x	x	x	x		WM	C	339	479	551	1.79	3.21	3.52	403	26.52	0.72
Brown Pelican <i>Pelecanus occidentalis</i>	x	x	x	x	x	B	C	250	56	306	0.91	0.20	1.09	69	48.43	0.67
Ardeidae																
American Bittern <i>Botaurus lentiginosus</i>		x				WM	VR	0	4	1	0.00	0.01	0.002	2	0.92	0.00
Least Bittern <i>Ixobrychus exilis</i>	x	x		x		B	C	31	21	30	0.08	0.05	0.07	8	14.55	0.09
Great Blue Heron <i>Ardea herodias</i>	x	x	x	x	x	B	C	280	172	367	0.81	0.48	1.10	83	79.93	0.90
Great Egret <i>Ardea alba</i>	x	x	x	x	x	B	C	574	309	828	1.48	0.97	3.54	406	82.50	1.87
Snowy Egret <i>Egretta thula</i>	x	x	x	x	x	B	C	1638	1455	2637	5.25	4.64	9.98	659	84.16	6.27
Little Blue Heron <i>Egretta caerulea</i>	x	x	x	x	x	B	C	977	730	999	3.11	2.00	4.03	171	85.08	2.96
Tricolored Heron <i>Egretta tricolor</i>	x	x	x	x	x	B	C	305	416	656	1.04	1.16	2.45	156	73.11	1.51
Reddish Egret <i>Egretta rufescens</i>	x	x	x	x	x	B	C	184	205	333	0.49	0.5	0.88	164	46.41	0.79
Cattle Egret <i>Bubulcus ibis</i>	x	x	x	x	x	B	C	2274	1004	2041	5.60	2.63	8.68	902	37.38	5.82

Supplementary material 3 Mantel test to detect whether presence/ absence and waterbird composition was linked to the spatial position (coordinates in decimal degrees of latitude and longitude) of the six sites in the south coast of Cuba (correlation between a Euclidean distance matrix and the Bray–Curtis dissimilarity matrix). Test was conducted for each month evaluated (16 month) in three seasons (SM. Spring Migration, SS. Summer Season, FM. Fall Migration), from 2011 to 2013 ($P < 0.05$)

Year	Season	Month	Presence/absence		Waterbird composition	
			r	P	r	P
2011	SS	May	-0.487	0.982	-0.455	0.972
		June	-0.618	0.993	-0.599	0.990
	FM	October	-0.587	0.985	-0.585	0.997
		November	-0.668	0.993	-0.635	0.982
2012	SM	February	-0.065	0.482	-0.111	0.556
		March	-0.629	0.985	-0.501	0.925
	SS	May	-0.089	0.513	-0.118	0.532
		June	-0.417	0.942	-0.524	0.974
	FM	October	-0.454	0.932	-0.522	0.942
		November	-0.528	0.970	-0.581	0.983
2013	SM	February	-0.248	0.746	-0.25	0.721
		March	-0.358	0.872	-0.350	0.864
	SS	May	-0.358	0.872	-0.118	0.532
		June	-0.134	0.601	-0.203	0.665
	FM	October	-0.106	0.586	-0.211	0.675
		November	-0.459	0.922	-0.423	0.922

CAPÍTULO II. Effect of landscape structure on waterbirds community in a conservation gradient in southwestern wetlands coast of Cuba

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Abstract

Landscape structure can affect waterbird distribution across wetlands. While forest fragmentation effects have been extensively studied in birds, we still lack knowledge about how the loss of wetlands might impact waterbird populations. We investigated the effects of landscape configuration on waterbird communities in southwestern Cuba and evaluated the contribution of the configuration of lagoons, mangrove, rice fields and anthropogenic land use to waterbird diversity. Also, we identified the scale at which descriptors of waterbird community are most sensitive to landscape variables. We conducted surveys in 14 landscapes during fall migration season of 2016. Landscape structure was described with 11 landscape variables at three spatial scales. We used Generalised Linear Models to test the effects of landscape variables on waterbird community and Akaike's information criterion, for model selection. Our results show that, at the scale of 6 km, mangrove mean patch area had a negative influence on waterbird abundance, while percentage of landscape covered by lagoons had a positive effect at 2 km. However, a higher percentage of mangroves and lagoons had a positive effect in waterbird composition at 2 km. The percentage of mangroves had a negative effect on waterbird diversity at 4 km. The percentage of anthropogenic land use did not influence any response variable at the evaluated scales. Detecting the scales of effect of two important landscape resources is very important for the effective management of waterbird populations. These features contribute to the adequate planning of reserves on the coast of Cuba.

Key words. Coastal wetlands, Habitat fragmentation, Landscape structure, Multi-scale models, Scale of response, Spatial scale

1. Introduction

Landscape structure is potentially a crucial factor affecting the distribution of waterbirds in wetlands (Chan et al. 2007). Many landscape traits, such as type of surrounding habitat (Naugle et al. 2001; Riffell 2001), the amount of a nearby wetland (Fairbairn and Dinsmore 2001; Naugle et al. 2001; Taft and Haig 2006), and connectivity to other habitat patches (Haig et al. 1998; Guadagnin and Maltchik 2007), may affect the population density of certain species or the waterbird assemblage composition in wetland habitats. While effects of forest loss and fragmentation on terrestrial birds has been extensively studied, the impact of wetland loss on waterbird assemblages has not (Fairbairn and Dinsmore 2001; Riffell et al. 2001). On the other hand, the influence of landscape structure on waterbirds is an issue that has attracted increasing research interest in recent years.

Several studies relating landscape structure and waterbirds focus on artificial wetlands such as rice paddies (Chan et al. 2007; Elphick 2008; King et al. 2010) and artificial ponds (Fronemam et al. 2001; Pérez-García 2014; Hsu et al. 2019). Among studies testing the landscape configuration effects on waterbird community structure in natural wetlands (Perez-Garcia 2014; Brandolin and Blendinger 2016; Herbert et al. 2018), little focus has been given to coastal wetland habitats (Henry and Cumming 2017), especially in the Caribbean region. Nevertheless, these habitats are of great importance for waterbirds (Aguilar et al. 2019) and have undergone considerable degradation (Ma et al. 2010; Finlayson et al. 2019). The underlying drivers behind the loss of coastal wetland biodiversity include habitat change (such as drainage and infilling for agriculture or construction), climate change, pollution, the spread of invasive ‘alien’ species and overexploitation of resources (Ramsar Convention Secretariat 2011).

An important principle of landscape ecology is that the spatial distribution of environments can have major effects on a wide variety of ecological processes (Wiens 2002), thus determining species and community structure (Knutson et al. 1999; Froneman et al. 2001; Mazerolle et al. 2005; Thornton et al. 2011; Ekroos and Kuussaari 2012). In fact, the lack of knowledge about interactions between communities and landscape complexity are barriers for effective species conservation (Lindenmayer et al. 2008; Prugh et al. 2008; Ranganathan et al. 2010). Landscape patterns that favor population and community connectivity or ecological processes are key elements to conserve natural areas influenced by human impacts (Bennet 2004). For example, habitat cover and configuration must be considered in landscape planning and management for biodiversity conservation, because these are essential factors for many species survival (Williams et al. 2002; Lindenmayer et al. 2008), as shown in recent studies for waterbirds and wetland conservation (Kleyheeg et al. 2017; Xu et al. 2019; Zhang et al. 2019).

The relationship between biological responses and environmental variables also depends on the spatial extent (scale) at which they are measured (Wiens 1989; Bellamy et al. 2013; Jackson and Fahrig 2015). The ‘scale of effect’, i.e. scale that yields the strongest relationship (Boscolo et al. 2009; Jackson and Fahrig 2015), is usually not known for a given biological system. Consequently, researchers commonly measure landscape variables at multiple scales to characterize habitat features adequately and to identify their spatial configuration affecting the abundance of populations or their assembly (Moudry and Simova 2012; Shirk 2012; Wasserman et al. 2012; Sánchez et al. 2013). Therefore, to understand how anthropogenic environmental changes influence organisms it is crucial to evaluate the spatial scale at which organisms are mostly responding to changes (Ducci et al. 2015). The scale of effect has been evaluated in several research in waterbirds and wetlands landscape

(Chan et al. 2007; Elphick 2008, Perez-Garcia et al. 2014, Webb et al. 2010; Beatty et al. 2014), nevertheless, it has been little explored in coastal wetlands. Detecting the scale of effect of landscape features is very important to decide the landscape units that should be targeted for effective management (Pearce and Boyce 2006; Mander and Uuemaa 2010).

In Cuba, several anthropogenic actions have affected ecosystems negatively in coastal wetlands for a long time. More than 30% of Cuban mangroves have been affected by different types of land use (Menéndez et al. 2003). The southwestern coast of Cuba constitutes a continuous habitat of coastal wetlands characterized by swampy plain bordered by mangroves, with coastal lagoons, marshes and intertidal mudflats (Iturralde and Serrano 2015) which are preferred by waterbirds (Aguilar et al. 2019). This region includes the coastal strip with the highest degree of anthropic modification of coastal wetlands in Cuba (Vega et al. 1990; Moreno et al. 1998; Mitrani et al. 2000; Menéndez and Guzmán 2006) including legally hunting areas of six waterfowl species during the migratory season (Ministry of Agriculture 2015).

The southwestern coast of Cuba provides a suitable habitat for waterbirds and it is known empirically for waterbird concentrations, mainly in the migratory season. However, very few studies have been conducted in the region to foster waterbird conservation strategies. The most studied sites regarding waterbird assemblages are the Zapata Peninsula (González et al. 2016a), which is a national park, a biosphere reserve and a Ramsar site and Humedal Sur de los Palacios and their associated rice paddies (Acosta and Mugica 2013, Mugica et al. 2014; Aguilar et al. 2019). In the remaining study region, in southwestern coast of Cuba, there are few studies focusing on specific waterbirds species using these wetlands (Mugica et al. 2002; Mugica et al. 2005; Blanco et al. 2014; González et al. 2016b; González et al. 2018). Even though this region includes recently proposed protected areas, there are no studies at the

landscape level supporting such definitions and effective management, as well as important requirements by waterbird diversity.

In this study, we tested the effects of landscape structure on waterbird communities in coastal wetlands within a conservation gradient in southwestern Cuba and evaluated the relative contribution of spatial configuration of lagoons, mangrove, rice field and anthropogenic land use to waterbirds diversity. Our specific objectives were to (i) identify the scale at which different descriptors of waterbird community are most sensitive and (ii) identify the landscape factors that may influence richness, abundance, composition and diversity of waterbird communities. This information will be useful for waterbirds conservation planning and management actions in the study region.

2. Materials and Methods

2.1 Study Area

We sampled fourteen areas in southwestern coastal wetlands of Cuba, in Pinar del Río, Artemisa, Mayabeque and Matanzas provinces (Fig 1). These areas are located in a coastal region called Ciénaga Litoral del Sur (Núñez 1989), between Cabo Francés and Peninsula de Zapata (from 83 ° 58' W, 22 ° 06' N to 81 ° 15' W, 22 ° 07' N), along ~ 456 km and including wetlands habitats from 2 to 10 km wide of the coastline. This coastal strip is limited to the south by the Gulf of Batabanó (León 1996). The main plant formations are mangrove, swamp forest and swamp grasslands. It is a cumulative, biogenic plain on turbid swamp deposits (Mateo and Acevedo 1989; Menéndez and Guzmán 2006). The whole area is characterized by a low, swampy plain, which is waterlogged in almost all its extension, with coastal

lagoons, marshes and intertidal mudflats (Iturralde and Serrano 2015). Average temperatures range from 24.0 to 26.0 ° C and the average annual rainfall from 800 to 1000 mm (ICCACC 1989). Five protected areas are included in our study site, one is a Ramsar site and Biosphere Reserve (Zapata Peninsula; CNAP 2013) and two are Important Bird Areas (IBAs) (Zapata Peninsula and Humedal Sur de los Palacios; Aguilar 2010).

The study area is subject to different degrees of anthropic influence and degradation, and presents different patterns of land use. The highest degree of anthropic modification is within the southern coastal strip of Artemisa and Mayabeque provinces, between Playa Majana and Ensenada de Vizcaya (~ 129 km long) (Vega et al. 1990; Moreno et al. 1998; Mitrani et al. 2000, Iturralde and Serrano 2015). Mangroves in this area present one of the lowest ecosystem health indices in the Cuba western region (Menéndez and Guzmán 2006). Historically, these mangroves have been heavily impacted by timber extraction for railway construction and for charcoal production. In the 1950s, the establishment of a series of drainage channels led the mangroves and coastal swamps to dry out and farmers to deforest the swamps' landward margin. In order to counteract the effects of marine intrusion and groundwater salinization, a 50 km long retention wall (Southern Dike) was built in the 1980s; this, however, resulted in higher mangroves mortality due to flooding on its landward side, increased wave impact and reduced freshwater inputs on its seaward side (Menendez et al. 2006).

On the other hand, the western wetlands on the south coast of Pinar del Río province and on part of Artemisa province, from Cabo Francés to Playa Majana (~ 133 km), are less degraded. However, they are affected mainly by agricultural activity (rice cultivation), damming rivers and extreme weather events such as hurricanes (Menéndez and Guzmán 2006). The most preserved wetland in the study region is the Zapata National Park in

Matanzas province (CNAP 2013). Agriculture is also the main land use in the northern wetland strip of these provinces, except in Península de Zapata.

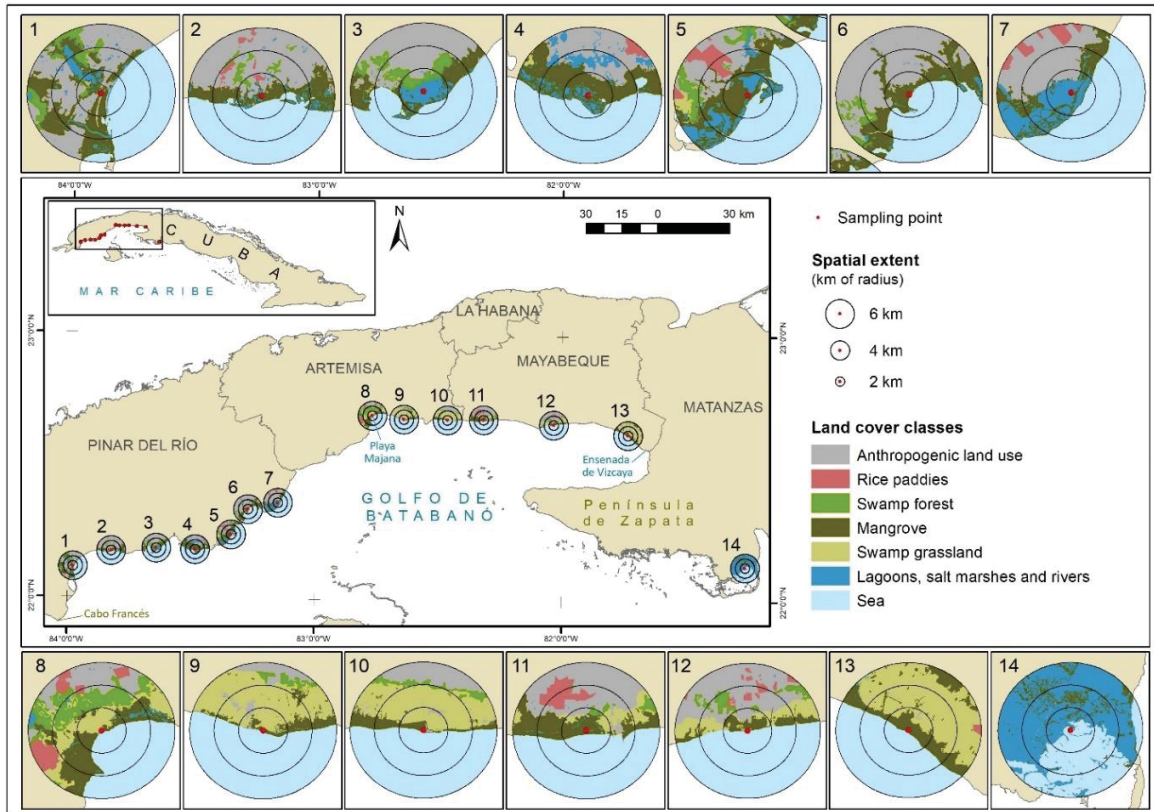


Fig. 1 Fourteen sampling areas in four provinces in the western south coast of Cuba. Individual maps for each sampling unit (1-14) show landscapes at three spatial extents (2, 4 and 6 km) and seven classes of land covers

2.2 Waterbird survey

We conducted waterbird surveys during 2016 fall migration season (October–November), at a central sampling point in each sampling area (Fig. 1). We selected fall migration because it is when most species have highest abundance and densities (Acosta et al. 1992; González et al. 2016b), so it is likely the most important time for the conservation of waterbirds on the

south coast of Cuba (Aguilar et al. 2019). Sampling points were separated by at least 12 km to avoid data autocorrelation and included three subsampling point counts within a radius of about 500 m at lagoons and salt marshes. We did fix point counts (Bibby et al. 2000) at each subsampling point by counting all individuals of each species seen or heard in 30-minute periods, always in the first four hours after sunrise. Bird counts were carried out during three alternate days (one day out of a three-day period). We used 10 x 50 binoculars and 20 x 60 spotting scopes to detect the birds and a GPS to record geographical coordinates of each sampling point. We recorded only aquatic birds and species dependent on wetlands to meet their daily needs. As our survey method was diurnal, results may be biased low for secretive birds (e.g. gallinules) and nocturnal birds (e.g. night-herons and whistling ducks). Bird taxonomy follows the American Ornithological Society (AOS) checklist (Chesser et al. 2018). Each species was identified and classified according to its occurrence (common, rare, very rare and vagrant; Garrido and Kirkconnell 2010) and status (bimodal, summer migrant, permanent resident and winter migrant; Navarro and Reyes 2017). Bimodal species are those characterized by both resident and winter migratory populations.

For further analyses for each sampling point, we considered species richness (number of species), waterbird abundance (number of individuals) and waterbird composition (matrix of abundances by species) by pooling results of the three subsampling counts. Additionally, to define abundance, we considered the maximum number of individuals of each species during the three days. Frequency of waterbird species was given as the number of samplings where the bird was recorded/total number of sampling points ($N = 14$). For each sampling point, we also calculated Shannon diversity index (Magurran 1988).

2.3 Landscape structure

We measured 11 landscape variables at three spatial scales in each landscape unit (2, 4 and 6 km radius buffers around the sampling points, Fig. 1). The total extension in each spatial scale was 1,257, 5,026 and 11,309 hectares, respectively. We selected these scales based on the current knowledge about the largest waterbird mobility (Cumming et al. 2012; Henry and Cumming 2017). To avoid spatial autocorrelation, we limited the extent of the higher scale to 6 km. We did not use smaller scales because in these extensions some land cover classes did not have enough variation in size when comparing sampling areas (e.g. mangroves).

Land cover data was obtained from the following shapefile layers: a) Vegetation of Cuba, from Landsat ETM 7 (Estrada et al. 2013); b) Forest Cover of Cuba, from Landsat ETM 7 (Geocuba 2012); c) soil use (IPF 2007) and d) two layers of road and land use in Cuba, from OpenStreetMap (2019) (www.openstreetmap.org). In order to update the information, we digitized and rectified eleven classes for this study, from these shapefile layers, through Google Maps (2019) images, supported by personal field experience. This update was made within the limits of the largest spatial extent (6 km of buffer), in each of the 14 sampled landscapes. The final map was obtained through the overlay of all different layers.

The eleven classes updated were aggregated to form seven classes: anthropogenic land use; rice paddies; swamp forest; mangrove; swamp grassland; lagoons, salt marshes and rivers and sea (Fig. 1). However, we analyzed only four classes (anthropogenic land use; rice paddies; mangrove; lagoons, salt marshes and rivers) because these are the main habitat types that are expected to be influencing the structure of the waterbird communities in the region, according to their ecological requirements and relevant to our hypotheses (Mugica et al.

2006). The anthropogenic land use included several types of land covers, such as villages, industries, bare soil, scrub and secondary forests, pastures, crops, canals and roads. Rice paddies were excluded from anthropogenic land use cover and were analyzed independently, due to its importance for waterbird communities mainly for feeding and resting (King et al. 2010; Toral et al. 2011). The average percentage of sea cover for the 14 landscape units was $43 \pm 7 \%$. Considering that there was few variation across units ($CV = 16 \%$), we assumed it should not have an effect on landscape metrics and the samples could be compared. We converted final shapefile maps in raster files (.tif and .img) with 2-m pixel sizes (resolution) for all landscapes (in total 42 landscapes: 14 for each of the three spatial scale). Data was processed using the geographical information system QGIS 12.14.18.

We quantified 11 landscape variables associated with the four land cover classes, inside each sampling unit at the three spatial extent, using FRAGSTATS v. 4.2 software (McGarigal et al. 2012). We selected indices of landscape composition and configuration that described shape, aggregation, size and quantity of the four different environments in the landscape. We chose these variables because they are expected to influence waterbird diversity due to habitat requirements of these species (Pérez-García et al. 2014; Brandolin and Blendinger 2016; Amira et al. 2018). Landscape variables, at each land cover class, are described in Table 1. Due to their multicollinearity, we used only five metrics as predictor variables in statistical analyses (see Data Analysis).

Table 1 Landscape variables describing the landscape structure of each sampling point for each land cover class. In bold, five non-collinear variables included in statistical analyses

Land cover class	Code	Variable	Unit	Description
Lagoons, salt marshes and rivers	AREMN-lag	Mean patch area	m ²	Mean area of all lagoons, salt marshes and rivers patches in the landscape
Lagoons, salt marshes and rivers	PLAND-lag	Percentage of landscape	%	Percentage of landscape covered by lagoons, salt marshes and rivers
Lagoons, salt marshes and rivers	LPI.lag	Largest patch index	%	Percentage of total landscape area comprised by the largest patch of lagoons, salt marshes and rivers
Lagoons, salt marshes and rivers	SHAPEMN.lag	Mean shape index	unit	Mean shape of all lagoons, salt marshes and rivers patches in the landscape
Lagoons, salt marshes and rivers	NP.lag	Number of patches	n	Number of lagoons, salt marshes and rivers patches
Mangrove	AREMN-mag	Mean patch area	m ²	Mean area of all mangrove's patches in the landscape
Mangrove	PLAND-mag	Percentage of landscape	%	Percentage of landscape covered by mangroves
Mangrove	PD.mang	Patch density	n/m ²	Number of mangrove's patches divided by total landscape area
Mangrove	ENNMN.mang	Mean of Euclidean nearest-neighbor distance	m	Mean of Euclidean nearest-neighbor distance among mangrove patches
Rice paddies	PLAND.rice	Percentage of landscape	%	Percentage of landscape covered by rice paddies
Anthropogenic land use	PLAND-ant	Percentage of landscape	%	Percentage of landscape covered by anthropogenic land use

2.4 Data Analysis

A Mantel test was performed to detect spatial autocorrelation between the linear distance (Euclidean distance matrix) of sampling points and waterbirds composition (Bray–Curtis dissimilarity matrix) in the study area (Legendre and Legendre 1998). To calculate the linear spatial distance, we build a matrix with coordinates in decimal degrees of latitude and longitude at each sampling point. The tests showed no significant spatial correlation ($r = 0.15$; $p = 0.156$). This analysis was made in R (R Core Team 2018) using vegan version 2.5-1 (Oksanen et al. 2018).

We tested the relationship between waterbird community's variables [species richness, waterbird abundance and Shannon diversity index] and landscape variables (Table 1) in three steps. First, we selected only landscape variables that were weakly correlated with any other using Pearson's correlation ($r < 0.6$, Table S1) and indicating no collinearity through variance inflation factor ($VIF < 3$; Kutner et al. 2004). As a result, we selected only five landscape variables as predictors for further analyses: mean patch area of lagoons, salt marshes and rivers percentage of landscape covered by lagoons, salt marshes and rivers, mean patch area of mangroves, percentage of landscape covered by mangroves and percentage of landscape covered by anthropogenic land use. Second, we selected the scale of effect using r^2 of linear regressions between waterbird community's variables (responses) and the five landscape variables (predictors) for each of the three spatial scales. Response variables were transformed to ensure normality (richness: root square-transformed; abundance and Shannon diversity index: log- transformed). Linear regression was made in R. The landscape variable at the spatial scale with the highest r^2 (Table S2) were further used in the next step of the analyses.

The third step was to build one generalized linear model (GLM) for each waterbird community variable to relate with landscape variables selected in the previous steps. All continuous predictors showed normal distributions, except AREMN-lag, which was log-transformed to achieve a normal distribution. In GLM, we used negative binomial error distribution (log link function) for richness and waterbird abundance data to control for overdispersion and Gaussian distribution for Shannon diversity index (Zuur et al. 2009). This procedure was made in R using MASS (Venables and Ripley 2002) and car packages (Fox and Weisberg 2011). We built single and multi-scale models based on the results of our second step of analyses (linear regressions). Single-scale models were those in which predictors variables belonged to the same spatial scale, while multi-scale refers to models containing landscape variables of distinct scales. We fitted a set of candidate models using the following combinations of predictor variables: a) each variable alone, (b) only variables of mangroves (AREMN-mang and PLAND-mang), c) only variables of lagoons, salt marshes and rivers (AREMN-lag and PLAND-lag, d) combination of two or three variables of mangroves and lagoons, salt marshes and rivers, g) all models including (PLAND-ant) as a covariate, and (d) an intercept-only model (null model) (88 candidate models in total, 22 models for each response variable; Table S3).

As we had multi-models to explain the response variables, we conducted a model selection procedure based on maximum likelihood, considering the Akaike's Information Criterion corrected for small number of observations (AICc; Burnham and Anderson 2002), using the R package AICcmodavg (Mazerolle 2010). Under this approach, the lower the AICc, the better the model fits the data. We also calculated the difference between AICc for a model i and the lowest observed AICc (i.e. $\Delta AICc$). The relative ranking of models based on $\Delta AICc$ values also provides an estimate of each model's relative explanatory value.

Models with $\Delta AICc < 2$ are equally plausible to explain the observed pattern as the best model (Burnham and Anderson 2002). We also calculated the Akaike's information criterion weight (w_i), which expresses the relative contribution of the model i to explain the observed pattern and the evidence ratios (ER) between the best and a second models (ratio of w of one model against the other, Burnham et al. 2011). When Akaike weights of the most plausible model was lower than 0.80, we used model averaging to draw inferences about the importance of predictors in the most plausible models. With this purpose, we calculated weighted averages of estimates for predictors across all the models using model probabilities as weight, the unconditional standard errors and 95 % unconditional confidence intervals (CI) of each predictor (Burnham and Anderson 2002). Predictors with CI that did not include the 0 value were considered as having an influence on the response variable. The final scale of effect was considered as the scale at which the predictors had an influence on the response variables.

We performed redundancy analyses (RDA) to test the relationships among waterbirds composition and the five landscape variables used in GLMs at each spatial scale (Legendre and Legendre 1998). A significance value for the overall RDA solution was determined by ANOVA (Analysis of Variance) for each spatial scale. Before the analysis, the five landscape variables were standardized, and waterbird composition data was $\log(x+1)$ transformed. This procedure was made in R using the vegan package (version 2.5-1; Oksanen et al. 2018). All statistical analyses were conducted in R software environment version 3.4.4 (R Core Team 2018).

3. Results

3.1 Characterization of the waterbird community structure

In total, we recorded 65 waterbird species during the study, belonging to 45 genera and 21 families (Table S4). Species richness per sampling plot ranged from 15 to 38. The most frequently represented families were Scolopacidae and Ardeidae, with 14 and nine species, respectively. A total of 24,432 waterbirds were observed. Most species (86.2 %, 56 species) were considered common birds, while the others were rare (eight species) and one species (Willson's Phalarope *Phalaropus tricolor*; nine individuals in Guanimar, Artemisa province) was classified as accidental. Among observed birds, 80 % (52 species) were migrants, 24 of which were bimodal and 20 % (13 species) were permanent residents. The most frequently observed birds were Double-crested Cormorant *Phalacrocorax auritus* (92.9 %), Laughing Gul *Leucophaeus atricilla* (78.9 %) and four species of egrets and herons (Great Blue Heron *Ardea herodias*, Great Egret *Ardea alba*, Snowy Egret *Egretta thula* and Little Blue Heron *Egretta caerulea*), with 78 to 85 % of occurrences (Table S4). Blue-winged Teal *Spatula discors* was the most abundant species followed by Double-crested Cormorant, American Flamingo *Phoenicopterus ruber*, Snowy Egret *Egretta thula* and Least Sandpiper *Calidris minutilla*.

3.2 Landscape configuration correlates with waterbirds community structure

3.2.1 AICc model selection

Species richness was not related to any variable, as shown by model selection uncertainty (best model, $w_i = 0.193$) (Table 2), with the null model being the best although showing low

probability in comparison to the second model ($ER = 1.16$). Considering all landscape variables, model-averaged estimates were low and with broad confidence intervals (Table 3).

Four models of waterbird abundance had the best fits ($\Delta AICc < 2$, Table 2). The first most plausible model had low probability ($w_i = 0.212$) and low strength of evidence in comparison with the two other best models ($ER = 1.25$ and 2.27 , respectively). Considering all these models, two variables had the strength of evidence to predict waterbird abundance: mean patch area of mangroves at 6 km spatial scale ($\beta_{AREMN.mang6} = -0.770 \pm 0.338$, $CI = -1.433, -0.107$) and percentage of landscape covered by lagoons, salt marshes and rivers at 2 km spatial scale ($\beta_{PLAND.lag2} = 0.814 \pm 0.107$, $CI = 0.078, 1.550$). These results indicate that waterbird abundance increases in areas with smaller mangrove patches, at 6 km spatial scale and larger percentage of lagoons, salt marshes and rivers at 2 km spatial scale.

Table 2 Model selection for landscape metrics in relation to richness, abundance, and Shannon diversity index (H') at spatial multiscale, on the southwestern coast of Cuba, in fall migration season of 2016. Models with $\Delta AICc < 4$ are omitted

Response variable	Models	K	AICc	$\Delta AICc$	w_i
Richness	~1	2	107.71	0	0.192
	scale(PLAND.lag2)	3	108.02	0.30	0.165
	scale(AREM.N.mang6)	3	108.13	0.41	0.156
	scale(PLAND.mang4)	3	109.42	1.70	0.082
	scale(PLAND.lag2)+scale(AREM.N.mang6)	4	109.77	2.05	0.069
	scale(log(AREM.N.lag6))	3	110.27	2.55	0.053
	scale(PLAND.ant4)	3	110.56	2.85	0.046
	scale(PLAND.mang4)+scale(PLAND.lag2)	4	110.97	3.25	0.037
	scale(log(AREM.N.lag6))+scale(AREM.N.mang6)	4	111.09	3.37	0.035
	scale(PLAND.lag2)+scale(AREM.N.mang6)+scale(PLAND.ant4)	5	111.14	3.42	0.034
Abundance	scale(PLAND.lag2)	3	237.54	0.00	0.212
	scale(log(AREM.N.lag2))	3	238.00	0.46	0.169
	scale(PLAND.mang2)+scale(AREM.N.mang6)+scale(PLAND.lag2)	5	239.19	1.65	0.093
	scale(PLAND.mang2)+scale(PLAND.lag2)	4	239.26	1.72	0.090
	~1	2	239.64	2.10	0.074
	scale(PLAND.lag2)+scale(AREM.N.mang6)	4	240.06	2.52	0.060
	scale(log(AREM.N.lag2))+scale(AREM.N.mang6)	4	240.23	2.69	0.055
	scale(AREM.N.mang6)	3	240.92	3.38	0.039
	scale(PLAND.lag2)+scale(AREM.N.mang6)+scale(PLAND.ant4)	5	240.94	3.40	0.039
	scale(PLAND.mang2)+scale(log(AREM.N.lag2))	4	241.10	3.55	0.036
	scale(PLAND.lag2)+scale(log(AREM.N.lag2))	4	241.14	3.59	0.035
H'	scale(PLAND.mang4)	3	16.92	0.00	0.510
	scale(PLAND.mang4)+scale(log(AREM.N.lag2))	4	20.37	3.45	0.091
	scale(PLAND.mang4)+scale(AREM.N.mang4)	4	20.58	3.66	0.082

K: number of parameters, AICc: second-order Akaike's information criteria, w_i : Akaike's weight

Table 3 Result of model averaging for landscape metrics related to richness, abundance and Shannon diversity index (H') at spatial multiscale on the southwestern coast of Cuba, in fall migration season of 2016. In bold are predictor variables with an influence in each response variable. For abbreviations of landscape variables see Table 1

Response variable	Predictor variables	Model-averaged estimate	Unconditional SE	95% Unconditional confidence interval
Richness	PLAND.mang4	-0.121	0.112	-0.34, 0.09
	AREMN.mang6	-0.200	0.112	-0.42, 0.02
	PLAND.lag2	0.160	0.099	-0.03, 0.35
	AREMN.lag4	0.073	0.115	-0.15, 0.29
	PLAND.ant4	0.150	0.123	-0.09, 0.39
Abundance	PLAND.mang2	0.603	0.450	-0.27, 1.48
	AREMN.mang6	-0.77	0.338	-1.43, -0.10
	PLAND.lag2	0.814	0.375	0.07, 1.55
	AREMN.lag2	0.688	0.385	-0.06, 1.44
	PLAND.ant4	0.458	0.376	-0.27, 1.19
H'	PLAND.mang4	-0.301	0.104	-0.50, -0.09
	AREMN.mang4	0.039	0.143	-0.24, 0.32
	PLAND.lag6	-0.014	0.124	-0.25, 0.22
	AREMN.lag2	-0.081	0.113	-0.30, 0.14
	PLAND.ant6	-0.178	0.115	-0.40, 0.04

The first model of waterbird Shannon diversity index showed a higher probability ($w_i = 0.510$) and strength of evidence in comparison to the second and third models ($ER = 5.60$ and 6.21 ; Table 2). The percentage of landscape covered by mangroves at 4 km spatial scale had a negative effect on the waterbird diversity ($\beta_{\text{PLAND.mang4}} = -0.301 \pm 0.104$, $CI = -0.506, -0.096$) (Table 3). Percentage of landscape covered by anthropogenic land use did not predict richness, abundance, waterbird composition and Shannon diversity.

3.2.2 RDA Analysis

RDA analysis for the correlation between landscape variables and waterbird composition were not significant at the spatial scale of 6 and 4 km ($F = 1.363$, $p = 0.113$; $F = 1.473$, $p = 0.059$; respectively). At the smaller spatial scale (2 km), RDA analyzed was significant ($F = 1.507$, $p = 0.044$), in which the landscape variable explained 48.5 % of the total waterbird community composition variation. Results showed that percentage and mean area covered by lagoons, salt marshes and rivers at 2 km (PLAND.lag2 and AREMN.lag2, respectively) had the highest positive correlation with the waterbird composition score of the first RDA axis (Fig. 2, Table 4). The second RDA axis was determined primarily by the positive correlation of percentage of landscape covered by mangroves at 2 km (PLAND.mang2). These results indicate that areas with larger percentage and patches of lagoons, salt marches and rivers, and larger percentage of mangroves at 2 km spatial scale influence the variation of waterbird community composition. Based on RDA results at 2 km, we found a separation of the species within the waterbird community (Fig. 2). In this way, shorebirds *Calidris*, the waterfowl Blue-winged Teal *Spatula discor* and the Reddish Egret *Egretta rufescens* (sp21, sp23, sp2 and sp53 respectively; Fig. 2) tended to be more abundant in areas with large percentage of lagoons, salt marshes and rivers (PLAND.lag2) and large patches of lagoons, salt marshes and rivers (AREMN.lag2).

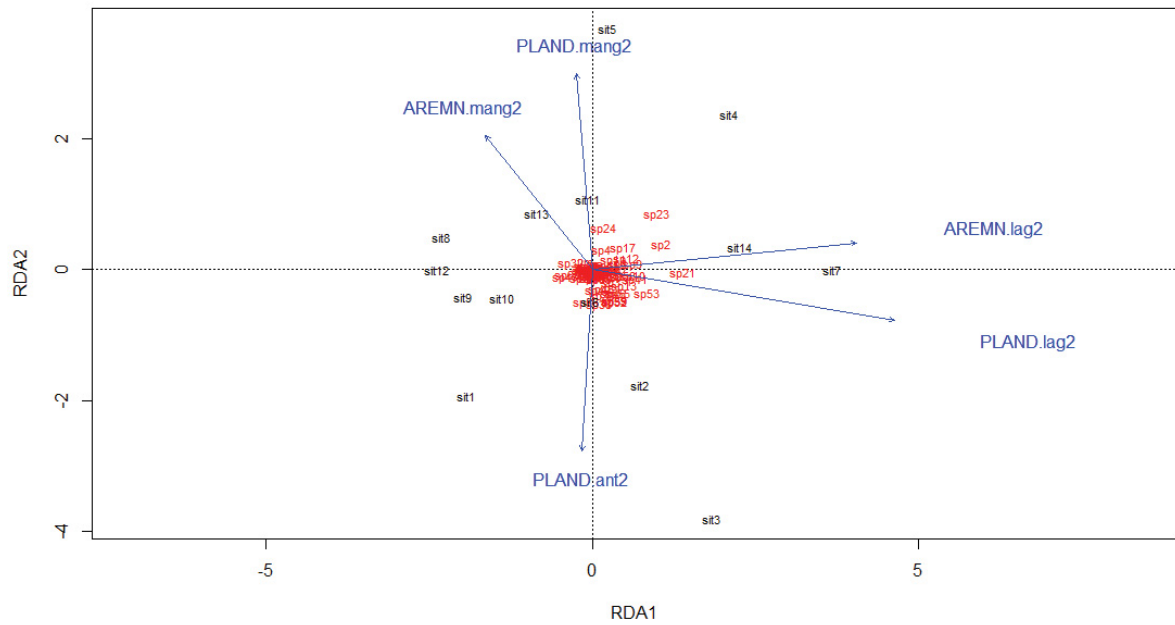


Fig. 2 Ordination biplot of the first two axes of RDA (RDA1 and RDA2) of waterbird composition constrained by landscape variables (in blue) at 2 km spatial scale, in western coast of Cuba, in 2016 fall migration season. Sampling areas are indicated in black and waterbird species in red. For abbreviations of landscape variables see Table 4

Table 4 Correlation between landscape variables at 2 km spatial scale and the first two RDA axes of waterbird composition scores

Code	Variables description	Waterbird composition	
		RDA1	RDA2
PLAND.mang2	Percentage of landscape covered by mangroves	-0.05	0.61
AREMN.mang2	Mean area of all mangrove's patches in the landscape	-0.33	0.42
PLAND.lag2	Percentage of landscape covered by lagoons, salt marshes and rivers	0.95	-0.16
AREMN.lag2	Mean area of all lagoons, salt marshes and rivers patches in the landscape	0.83	0.08
PLAND.ant2	Percentage of landscape covered by anthropogenic land use	-0.03	-0.57

4. Discussion

This study shows that the landscape context of coastal wetlands influence waterbird abundance, species composition and diversity. The effects of landscape variables varied according to the spatial scale and the sensitivity of the waterbird community descriptor. Our results show that variations in the scale at which the landscape structure of coastal wetland is measured is a key factor to predict abundance, waterbird composition and diversity.

The positive influence of percentage of landscape covered by lagoons, salt marshes and rivers on waterbird abundance emphasize the importance of this environmental factor in determining habitat use by these species (Froneman et al. 2001; Sebastian-Gonzalez et al. 2010; Chacon de la Cruz et al. 2017; Kleyheeg et al. 2017; Herbert et al. 2018). We found this relationship only at the smallest measured scale (2 km), suggesting that a greater abundance of birds is conditioned by a greater coverage of lagoons, salt marshes and rivers at a local level. We highlight that this study was conducted during the fall migration season, a period with the highest abundance and density of birds in wetlands in the southern coast of Cuba (Aguilar et al. 2019), and consequently an increased food demand. Waterbirds depend on wetlands (Ramsar 2010) for foraging, and lagoons, salt marshes and rivers offers a great diversity of trophic resources (seeds and aquatic plants, aquatic invertebrates and vertebrates, like fishes and frogs) (Ma et al. 2010). According to predictions of Miguel et al. (2015), the scale of effect is smaller for landscape variables that most strongly influence foraging success than for landscape variables that most strongly influence dispersal success. Landscape variables that most strongly affect foraging habitat should have smaller scales of effect because foraging success mainly depend on interactions between individuals and the environment within their home range (i.e. during daily movements).

On the other hand, the mean patch area of mangroves had a negative influence on waterbird abundance at a broader scale (6 km), meaning that smaller fragments of mangrove on a wider scale, along with higher percentage of lagoons, salt marches and rivers at local scale (2 km), will favor a higher number of individuals. Smaller fragments of mangrove, naturally, favor the existence of a larger open water coverage. Waterbirds congregate in large groups for feeding in fall migration, demanding larger lagoons, and therefore smaller mangrove fragments, surrounding lagoons and interspersed among them are an indication of

optimal environment conditions for these birds. Waterbird abundance was the only response variable related to a landscape variable within the larger scale of 6 km. This result could be explained because a high number of individuals will need to disperse and explore other habitats on a larger scale, or to use them as roosts for resting, as is the case of small fragments of mangroves. While the metrics related to open water have been widely used to measure the influence of landscape context on waterbird richness and abundance, few studies considered mangroves to measure landscape wetland configuration and their effect on waterbirds. Mangrove habitats' potential to support waterbirds is poorly understood globally (Sandilyan and Kathiresan 2015).

Several waterbirds, resident species (e.g. herons, egrets and ibis) usually use mangrove areas during the reproductive season for nesting, often in large colonies (Mugica et al. 2006). However, during our study season, which was not in the reproductive season, their dependence on mangrove areas are expected to be smaller. Alternatively, waterbirds may need smaller patches of mangroves, even if isolated from the feeding areas, mainly for resting and protection against predators. In addition, mangrove patches on a wider scale of 6 km may be a source of food for waterbirds feeding in interior lagoons, due to their high productivity (Mugica et al. 2006). Fallen mangrove leaves incorporate organic matter between their roots, increasing biomass into trophic chains. This helps lagoons, surrounded and interspersed with mangroves fragments, to have a constant and reliable source of food (e.g. fish and aquatic invertebrates) for these waterbirds (Mugica et al. 2006; Hagy and Kaminsky 2012). Smaller mangrove areas also allow more space for more open water, offering a greater amount and potentially greater diversity of feeding resources for waterbirds which may reduce interference competition (van Dijk et al. 2012). A balance between these two habitats is thus necessary for the survival of waterbirds in these tropical coastal wetlands.

The negative effect of percentage of landscape covered by mangroves on waterbird diversity index can also be explained by the role of mangroves as a habitat resource for waterbirds during the migratory period. However, in this case, this response variable was sensitive at a 4 km scale. This result makes sense because this index considers the number of species present in the area (species richness), and the relative number of individuals of each species (abundance) (Magurran 1988). As it is influenced by two variables with different sensitivity, the scale at which it has an effect could tend to be the mean between the scales of effect of both variables.

Waterbird richness was not influenced by any landscape metric at any spatial scale we evaluated, even though that contradicts previous studies in wetlands (Fairbairn and Dinsmore 2001; Webb et al. 2010). Waterbirds usually gather in close aggregations for foraging following abundant moving resources (e.g., fish populations), even though this behavior is not common when resources are stationary, and prey are not abundant, so they disperse to forage (Goodale et al. 2017). However, the same species may be present in both situations, so abundance may change in response to the moving prey abundance, but not the species richness. It seems that in many cases, just the presence of a few prey items in an area may attract a number of different waterbird species.

Waterbird composition was positively related to the percentage of landscape covered by lagoons and mangroves at the smaller spatial scale (2 km). This result may be given by different requirements of waterbird species in relation to these two resources. For example, areas with larger mangrove coverage may present less congregator species that use mangroves for resting and shelter, while in areas with more open water and reduced mangrove they will be more propitious for congregating species, such as waterfowls (Beatty et al. 2014; Herbert et al. 2018) and shorebirds (Webb et al. 2010). Some not congregating

species, as Reddish Egret, also need large open water to foraging displays (Del Hoyo et al. 1992).

The degree of anthropogenic land use did not influence species richness, abundance, waterbirds composition and waterbird diversity on any spatial scale. However, we emphasize some important considerations regarding this result. First, our sampling points presented only 0.04 to 40% of anthropic areas in the largest scale (6 km), such that half of them have less than 15% of impacted areas by humans. Second, anthropic areas in our study include environments which were probably not repelling waterbirds in the long-term. One of the most impacted areas in our study site include the South dike, built 40 years ago in south Artemisa province (Menendez et al. 2006), which initially caused the death of natural mangroves and their replacement by swamp grasslands. Since then, an alternative lagoon system has taken place, allowing several waterfowl species to congregate during the migratory period. Therefore, along the time, both vegetation and bird communities in restored wetlands became similar to those of natural wetlands (Galatowitsch and van der Valk 1996; VanRees-Siewert and Dinsmore 1996). On the other hand, in highly impacted sampling points, land is used mainly for crops (29 to 93%) and pastures, scrub and secondary forests (29 to 100%), a typical rural anthropic use. Also, these lands are located towards the northern end of the sampling points, farthest from the coast (Fig. 1).

Since anthropic use in the study region is mainly rural, with minor urbanization, industrialization or tourist development, we conclude it does not exert an important pressure on waterbird community, at the scales evaluated. However, we advocate that if anthropic impacts increase, degrading and reducing lagoons, salt marshes and rivers, which affect waterbird communities, as supported in this study, we predict negative consequences to the coastal fauna. In addition, the impact of human disturbances may be low because some

waterbird species are tolerant to human disturbance (Burton et al. 2002). Our results do not mean an increase in anthropic activity has no negative effect upon birds, but that the current human land use, considering spatial scales from 2 to 6 km in the south coast of Cuba, provides little impact. Several other studies showed that human activities directly or indirectly influence waterbird habitat selection and abundance in wetlands (Madsen and Fox 1995; Lepczyk et al. 2008; de Boer et al. 2011; Fox and Madsen 2017).

4.1 Conservation implications

Wetland management aiming preserving habitats for waterbirds must be based on specific knowledge of regional bird communities (Ma et al. 2010). We suggest that to protect waterbird diversity in coastal wetlands of western Cuba, especially during fall migration season, it is essential to implement management plans at the local and regional level for conserving and recovering a heterogeneous landscape at different spatial scales. As we showed here, larger open waters favor increasing waterbird abundance during migration congregation, while mangroves may provide resting and shelter. Thus, conservation strategies for nomadic wildlife, such as these waterbirds, require both classical models of conventional reserves and the establishment of protected areas networks (Margules and Pressey 2000). Waterbird requirements extrapolate local scales since they demand a complex of wetland landscape, then conservation value of individual wetlands cannot be measured in isolation from the wetlands mosaic in which they are inserted (Roshier et al. 2002).

The management of habitat resources for waterbird should consider the scale at which the different descriptors of the community are sensitive. We found a greater influence of landscape variables on waterbird community at 2 km, which is the spatial scale that should

receive a greater attention to habitat management. However, on the 4 and 6 km scales there was also some effect of the landscape configuration. In this way, the protection of patch mangrove at 6 km spatial scale is very important to keep waterbird abundance. We recommend that boundaries of protected areas should be based on the results of these scales of effect, both for new areas and for the re-analysis of the limits of existing reserves. Even if our study area includes non-protected areas, biodiversity protection laws, such as the Cuban coast law, for example, must be adequately implemented in order to protect lagoons and salt marshes and mangroves. The protected areas of the study region should follow similar management protocols for these coastal wetland habitats suitable for waterbird, respecting the suggested scales of effect. This work could be relevant, not only for waterbird management and conservation of waterbird in Cuba, but also at the Caribbean region.

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7. Supplementary materials

Table S1 Pairwise Pearson correlation coefficient among 11 landscape variables. In bold are predictors and values with correlation > 0.6. Abbreviation of landscape variables used as columns and rows are defined in Table 1

	PLAND.mang	AREMN.mang	PD.mang	ENNMN.mang	PLAND.lag	LPI.lag	AREMN.lag	SHAPEMN.lag	NP.lag	PLAND.ant	PLAND.rice
PLAND.mang	1										
AREMN.mang	0.43	1									
PD.mang	-0.17	-0.56	1								
ENNMN.mang	-0.48	0.01	-0.21	1							
PLAND.lag	-0.36	-0.29	0.72	0.20	1						
LPI.lag	-0.52	-0.21	0.38	0.48	0.89	1					
AREMN.lag	-0.48	-0.03	-0.13	0.68	0.52	0.83	1				
SHAPEMN.lag	-0.05	0.07	-0.28	0.36	0.24	0.50	0.67	1			
NP.lag	0.58	0.10	0.40	-0.44	0.30	0.05	-0.21	-0.17	1		
PLAND.ant	0.46	0.45	-0.38	-0.62	-0.47	-0.46	-0.38	0.04	0.19	1	
PLAND.rice	-0.25	0.14	-0.34	0.45	0.27	0.55	0.80	0.71	-0.32	0.26	1

Table S2 Results of linear regression (r^2) of response variables (richness, abundance and Shannon diversity index (H') in relation to five landscape metrics at three spatial scales in the southwestern coast of Cuba. In bold are predictor variables with the major r^2 of the three spatial scale from each response variable. For abbreviations of landscape variables see Table 1

Spatial scale	Response variable	Predictor variable	r^2
6 km	Richness (sqrt)	PLAND.mang6	0.055
		AREMN.mang6	0.182
		PLAND.lag6	0.087
		AREMN.lag6	0.052
		PLAND.ant6	0.001
4 km	Richness	PLAND.mang4	0.104
		AREMN.mang4	0.125
		PLAND.lag4	0.042
		AREMN.lag4	0.045
		PLAND.ant4	0.039
2 km	Richness	PLAND.mang2	0.063
		AREMN.mang2	0.043
		PLAND.lag2	0.227
		AREMN.lag2	0.051
		PLAND.ant2	0.018
6 km	Abundance	PLAND.mang6	0.001
		AREMN.mang6	0.119
		PLAND.lag6	0.188
		AREMN.lag6	0.127
		PLAND.ant6	0.005
4 km	Abundance	PLAND.mang4	0.001
		AREMN.mang4	0.051
		PLAND.lag4	0.193
		AREMN.lag4	0.003
		PLAND.ant4	0.062
2 km	Abundance	PLAND.mang2	0.004
		AREMN.mang2	0.061

		PLAND.lag2	0.371
		AREMN.lag2	0.203
		PLAND.ant2	0.006
6 km	H'	PLAND.mang6	0.305
		AREMN.mang6	0.003
		PLAND.lag6	0.017
		AREMN.lag6	0.014
		PLAND.ant6	0.238
4 km	H'	PLAND.mang4	0.430
		AREMN.mang4	0.063
		PLAND.lag4	0.009
		AREMN.lag4	0.034
		PLAND.ant4	0.149
2 km	H	PLAND.mang2	0.331
		AREMN.mang2	0.019
		PLAND.lag2	0.001
		AREMN.lag2	0.054
		PLAND.ant2	0.021

Table S3 Candidates models for each response variable. For abbreviations of landscape variables see Table 1

Response variable		Candidate models
Richness	1	scale(PLAND.lag2)+scale(log(AREM.N.lag6))
	2	scale(PLAND.lag2)+scale(log(AREM.N.lag6))+scale(PLAND.ant4)
	3	scale(PLAND.mang4)+scale(AREM.N.mang6)
	4	scale(PLAND.mang4)+scale(AREM.N.mang)+scale(PLAND.ant4)
	5	scale(PLAND.mang4)+scale(PLAND.lag2)
	6	scale(PLAND.mang4)+scale(log(AREM.N.lag6))
	7	scale(PLAND.lag2)+scale(AREM.N.mang6)
	8	scale(log(AREM.N.lag6))+scale(AREM.N.mang)
	9	scale(log(AREM.N.lag6))+scale(PLAND.lag2)+scale(AREM.N.mang6)
	10	scale(log(AREM.N.lag6))+scale(PLAND.lag2)+scale(PLAND.mang4)
	11	scale(PLAND.mang4)+scale(AREM.N.mang)+scale(log(AREM.N.lag6))
	12	scale(PLAND.mang4)+scale(AREM.N.mang6)+scale(PLAND.lag2)
	13	scale(PLAND.mang4)+scale(PLAND.lag2)+scale(PLAND.ant4)
	14	scale(PLAND.mang4)+scale(log(AREM.N.lag6))+scale(PLAND.ant4)
	15	scale(PLAND.lag2)+scale(AREM.N.mang6)+scale(PLAND.ant4)
	16	scale(log(AREM.N.lag6))+scale(AREM.N.mang)+scale(PLAND.ant4)
	17	scale(PLAND.mang4)
	18	scale(AREM.N.mang6)
	19	scale(PLAND.lag2)
	20	scale(log(AREM.N.lag6))
	21	scale(PLAND.ant4)
	22	~1
Abundance	1	scale(PLAND.lag2)+scale(log(AREM.N.lag2))
	2	scale(PLAND.lag2)+scale(log(AREM.N.lag2))+scale(PLAND.ant4)
	3	scale(PLAND.mang2)+scale(AREM.N.mang6)
	4	scale(PLAND.mang2)+scale(AREM.N.mang6)+scale(PLAND.ant4)
	5	scale(PLAND.mang2)+scale(PLAND.lag2)
	6	scale(PLAND.mang2)+scale(log(AREM.N.lag2))
	7	scale(PLAND.lag2)+scale(AREM.N.mang6)
	8	scale(log(AREM.N.lag2))+scale(AREM.N.mang)
	9	scale(log(AREM.N.lag2))+scale(PLAND.lag2)+scale(AREM.N.mang6)
	10	scale(log(AREM.N.lag2))+scale(PLAND.lag2)+scale(PLAND.mang2)
	11	scale(PLAND.mang2)+scale(AREM.N.mang6)+scale(log(AREM.N.lag2))
	12	scale(PLAND.mang2)+scale(AREM.N.mang6)+scale(PLAND.lag2)
	13	scale(PLAND.mang2)+scale(PLAND.lag2)+scale(PLAND.ant4)
	14	scale(PLAND.mang2)+scale(log(AREM.N.lag2))+scale(PLAND.ant4)
	15	scale(PLAND.lag2)+scale(AREM.N.mang6)+scale(PLAND.ant4)
	16	scale(log(AREM.N.lag2))+scale(AREM.N.mang6)+scale(PLAND.ant4)
	17	scale(PLAND.mang2)
	18	scale(AREM.N.mang6)
	19	scale(PLAND.lag2)
	20	scale(log(AREM.N.lag2))
	21	scale(PLAND.ant4)
	22	~1

	20	scale(log(AREMNI.lag2))
	21	scale(PLAND.ant6)
	22	~1
H'	1	scale(PLAND.lag6)+scale(log(AREMNI.lag2))
	2	scale(PLAND.lag6)+scale(log(AREMNI.lag2))+scale(PLAND.ant6)
	3	scale(PLAND.mang4)+scale(AREMNI.mang4)
	4	scale(PLAND.mang4)+scale(AREMNI.mang4)+scale(PLAND.ant6)
	5	scale(PLAND.mang4)+scale(PLAND.lag6)
	6	scale(PLAND.mang4)+scale(log(AREMNI.lag2))
	7	scale(PLAND.lag6)+scale(AREMNI.mang4)
	8	scale(log(AREMNI.lag2))+scale(AREMNI.mang4)
	9	scale(log(AREMNI.lag2))+scale(PLAND.lag6)+scale(AREMNI.mang4)
	10	scale(log(AREMNI.lag2))+scale(PLAND.lag)+scale(PLAND.mang4)
	11	scale(PLAND.mang4)+scale(AREMNI.mang4)+scale(log(AREMNI.lag2))
	12	scale(PLAND.mang4)+scale(AREMNI.mang4)+scale(PLAND.lag6)
	13	scale(PLAND.mang4)+scale(PLAND.lag6)+scale(PLAND.ant6)
	14	scale(PLAND.mang4)+scale(log(AREMNI.lag2))+scale(PLAND.ant6)
	15	scale(PLAND.lag6)+scale(AREMNI.mang4)+scale(PLAND.ant6)
	16	scale(log(AREMNI.lag2))+scale(AREMNI.mang4)+scale(PLAND.ant6)
	17	scale(PLAND.mang4)
	18	scale(AREMNI.mang4)
	19	scale(PLAND.lag6)
	20	scale(log(AREMNI.lag2))
	21	scale(PLAND.ant6)
	22	~1

Table S4 Waterbird assemblage in the southwestern coastal wetlands of Cuba. Total abundance of waterbirds (Total abund), maximum abundance (Max abund) registered in any one-day observation, frequency of waterbirds (Fr, number of sampling plots where the bird was seen/total number of sampling plots: N = 14)

Family/Scientific Name	English Common Name	Status ¹	Ocurrence ²	Total abund	Max abund	Fr %
Anatidae						
<i>Anas bahamensis</i>	White-cheeked Pintail	PR	C	9	9	7.14
<i>Spatula discors</i>	Blue-winged Teal	WM	C	8,355	3,850	64.29
<i>Spatula clypeata</i>	Northern Shoveler	WM	C	300	300	7.14
<i>Aythya affinis</i>	Lesser Scaup	WM	C	18	15	14.29
Phoenicopteridae						
<i>Phoenicopus ruber</i>	American Flamingo	PR	C	2,153	1,331	50.00
Podicipedidae						
<i>Podilymbus podiceps</i>	Pied-billed Grebe	B	C	35	28	28.57
Rallidae						
<i>Rallus longirostris</i>	Mangrove Rail	PR	C	4	2	21.43
<i>Gallinula chloropus</i>	Common Moorhen	B	C	94	65	28.57
<i>Fulica americana</i>	American Coot	B	C	666	585	21.43
Aramidae						
<i>Aramus guarauna</i>	Limpkin	PR	C	1	1	7.14
Recurvirostridae						
<i>Himantopus mexicanus</i>	Black-necked Stilt	B	C	191	104	28.57
<i>Recurvirostra americana</i>	American Avocet	B	R	63	63	7.14
Charadriidae						
<i>Pluvialis squatarola</i>	Black-bellied Plover	WM	C	153	67	71.43
<i>Pluvialis dominica</i>	American Golden-Plover	WM	R	3	2	14.29
<i>Charadrius nivosus</i>	Snowy Plover	PR	R	4	4	7.14
<i>Charadrius wilsonia</i>	Wilson's Plover	SM	C	101	54	42.86
<i>Charadrius semipalmatus</i>	Semipalmated Plover	WR	C	91	65	35.71
<i>Charadrius vociferus</i>	Killdeer	B	C	30	9	57.14
Jacaniidae						
<i>Jacana spinosa</i>	Northern Jacana	PR	C	5	5	7.14
Scolopacidae						
<i>Arenaria interpres</i>	Ruddy Turnstone	WM	C	34	20	28.57
<i>Calidris alba</i>	Sanderling	WM	C	34	28	21.43
<i>Calidris alpina</i>	Dunlin	WM	R	1	1	7.14
<i>Calidris minutilla</i>	Least Sandpiper,	WM	C	1,592	522	71.43
<i>Calidris pusilla</i>	Semipalmated Sandpiper	WM	C	17	9	21.43
<i>Calidris mauri</i>	Western Sandpiper	WM	C	8	6	14.29
<i>Limnodromus griseus</i>	Short-billed Dowitcher	WM	C	566	228	28.57

<i>Limnodromus scolopaceus</i>	Long-billed Dowitcher	WM	R	3	2	14.29
<i>Gallinago gallinago</i>	Common Snipe	WM	C	607	606	14.29
<i>Actitis macularius</i>	Spotted Sandpiper	WM	C	49	18	71.43
<i>Tringa flavipes</i>	Lesser Yellowlegs	WM	C	34	24	28.57
<i>Tringa semipalmata</i>	Willet	B	C	82	25	50.00
<i>Tringa melanoleuca</i>	Greater Yellowlegs	WM	C	54	14	42.86
<i>Phalaropus tricolor</i>	Willson's Phalarope	WM	A	9	9	7.14
Laridae						
<i>Leucophaeus atricilla</i>	Laughing Gul	B	C	374	120	78.57
<i>Sternula antillarum</i>	Least Tern	SM	C	2	2	7.14
<i>Gelochelidon nilotica</i>	Gull-billed Tern	WM	R	5	3	21.43
<i>Hydroprogne caspia</i>	Caspian Tern	WM	C	94	68	14.29
<i>Sterna hirundo</i>	Common Tern	WM	R	2	2	7.14
<i>Thalasseus maximus</i>	Royal Tern	B	C	303	156	64.29
<i>Thalasseus sandvicensis</i>	Sandwich Tern	B	C	303	20	64.29
Ciconiidae						
<i>Mycteria americana</i>	Wood Stork	PR	R	2	2	7.14
Fregatidae						
<i>Fregata magnificens</i>	Magnificent Frigatebird	PR	C	22	19	28.57
Phalacrocoracidae						
<i>Phalacrocorax brasilianus</i>	Neotropic Cormorant	PR	C	195	195	7.14
<i>Phalacrocorax auritus</i>	Double-crested Cormorant	B	C	2,518	1895	92.86
Anhingidae						
<i>Anhinga anhinga</i>	Anhinga	PR	C	56	36	42.86
Pelecanidae						
<i>Pelecanus erythrorhynchos</i>	American White Pelican	WM	C	1,148	627	35.71
<i>Pelecanus occidentalis</i>	Brown Pelican	B	C	102	71	50.00
Ardeidae						
<i>Ardea herodias</i>	Great Blue Heron	B	C	216	184	78.57
<i>Ardea alba</i>	Great Egret	B	C	886	575	78.57
<i>Egretta thula</i>	Snowy Egret	B	C	1,953	622	85.71
<i>Egretta caerulea</i>	Little Blue Heron	B	C	143	36	78.57
<i>Egretta tricolor</i>	Tricolored Heron	B	C	389	220	71.43
<i>Egretta rufescens</i>	Reddish Egret	B	C	73	44	42.86
<i>Butorides virescens</i>	Green Heron	B	C	21	4	71.43
<i>Nycticorax nycticorax</i>	Black-crowned Night-Heron	B	C	10	4	28.57
	Yellow-crowned Night-					
<i>Nyctanassa violacea</i>	Heron	B	C	32	12	50.00
Threskiornithidae						
<i>Eudocimus albus</i>	White Ibis	PR	C	348	244	64.29
<i>Plegadis falcinellus</i>	Glossy Ibis	B	C	10	10	7.14

<i>Ajaia ajaja</i>	Roseate Spoonbil	PR	C	40	25	35.71
Pandionidae						
<i>Pandion haliaetus</i>	Osprey	B	C	22	7	64.29
Accipitridae						
<i>Circus hudsonius</i>	Northern Harrier	WR	C	1	1	7.14
<i>Buteogallus gundlachii</i>	Cuban Black Hawk	PR	C	4	4	7.14
Alcedinidae						
<i>Ceryle alcyon</i>	Belted Kingfisher	WR	C	35	13	57.14
Falconidae						
<i>Falco sparverius</i>	American Kestrel	B	C	7	3	21.43
<i>Falco peregrinus</i>	Peregrine Falcon	WM	C	2	2	7.14

¹Status: B. Bimodal SM. Summer Migrant, PR. Permanent Resident, WM. Winter Migrant (Navarro and Reyes 2017)

²Occurrence: A. Accidental, C. Common, R. Rare, VR. Very Rare (Garrido and Kirkconnell 2010)

CAPÍTULO III. Potential effects of climate change on the distribution of waterbird in Cuba

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Abstract. — Wetland-dependent birds are considered to be at particularly high risk for negative climate change effects. Bioclimatic models are widely used tools for assessing potential responses of species to climate change. We predicted current and future distributions of American Flamingo *Phoenicopterus ruber* and Reddish Egret *Egretta rufescens*, two resident species in Cuba, using species distribution models in combination with climate data in Maxent software. For each species, we predicted four potential future distributions for two emissions scenarios in 2050 and 2070, in Cuba, combining three Global Circulation Models. Bioclimatic variables that contributed the most to modeling the potential distribution of American Flamingo were mean diurnal temperature range (mean of monthly (max temp - min temp)) and temperature seasonality. Mean diurnal range also contributed most to the modeling of Reddish Egret followed by precipitation of warmest quarter. Our results show that the current distribution of American Flamingo is predicted to be reduced by 38% under a changing future climate in the most pessimistic scenario of 2070, while the current distribution size of Reddish Egret is predicted to increase in 44%. The potential suitable habitat of American Flamingo in the most pessimistic scenario of 2070 would have 51% excluded from the National System of Protected Areas of Cuba. Our findings suggest that species distribution modeling can inform the current and future management of the American Flamingo and Reddish Egret throughout Cuba. A strong conservation strategy is needed to conserve American Flamingo populations under a changing climate.

Key words. American Flamingo, coastal wetlands, future climate scenarios, Maxent, Reddish Egret, species distribution modeling

1. Introduction

Waterbirds are one of the biological groups associated with coastal zones most vulnerable to the possible impacts of climate change (Planos et al. 2013). In Cuba, a country with a high ratio of coastline to overall surface area (5%, 5,746 km versus 109,886 km²), the national

report to the Convention on Biological Diversity and the National Environmental Strategy identify climate change as one of the greatest threats to biodiversity (CITMA 2014; CITMA 2016). In recent decades, earth's climate has undergone a dramatic change, including warming and more frequent extreme weather events, and there is strong evidence of imminent and profound transformations resulting from human activities (Solomon et al. 2007). Rapid climate change causes a clear fingerprint on global biodiversity (Gregory et al. 2009) and is a major issue for conservationists (Peterson et al. 2002; Thomas et al. 2004). Evidence is accumulating that climatic change has already altered the distributions of many species (Parmesan et al. 1999; Hickling et al. 2005; Guisan and Thuiller 2005; Tingley et al. 2009) and that more change is inevitable (Maclean et al. 2008; Anderson et al. 2009). In Cuba, several current actions have been carried out to address this issue (ODS 2019); however, there are few studies that explore wildlife distributions in future climate scenarios, and these have focused on reptiles and amphibians, resulting in the decrease of suitable habitats (Cobos 2016; Velazco 2017; Gonzales 2018).

Besides avian distributions, climate change is affecting the timing of breeding and migration of birds around the world (Møller et al. 2010; Cox 2010). Also, it has been observed that many species have modified their seasonality, abundance and interspecific interactions (IPCC 2014). From a Caribbean perspective, only recently have a limited number of papers addressed climate change and birds, and these have focused primarily on influences of rainfall on habitat quality for overwintering migrants, thereby impacting spring departure schedules and breeding success through carryover effects (Sillett et al. 2000; Smith et al. 2010; Wilson et al. 2011; Studds and Marra 2011). Climate change is expected to affect migratory birds through changed weather and environmental conditions, such as temperatures, rainfall, sea level rises, and acidification and circulation of oceans (CMS

2014). The effects will be direct or indirect through changes in habitat availability, quality and food resources, with some of the indirect effects occurring naturally or brought about by human reaction to a changing climate (CMS 2014).

Climate forecasts indicate that the average global surface temperature is likely to increase between 0.3 and 4.8 ° C until 2100 (Stocker et al. 2013; IPCC 2013). With respect to rainfall, the contrast between wet and dry seasons will be accentuated, although there may be regional exceptions. In addition, the phenomena of precipitation and extreme temperatures in humid tropical regions will be more intense and frequent (Edenhofer et al. 2014; IPCC 2014). More specifically in the Caribbean basin, several global climatic models are consistent in predicting increased summer droughts over the next 50 years (Neelin et al. 2006). Recent rainfall declines in the Bahamas (Martin and Weech 2001), Puerto Rico (Heartsill-Scalley et al. 2007) and Jamaica (Studds and Marra 2007) are consistent with the predictions of these models. The expected effects of these summer droughts include phenological disruptions, declines in food availability, and an increase in fire frequency (Weaver and Gonzalez 2005). Models to help evaluate how Caribbean birds might respond to these combined threats are needed, as is empirical data about bird condition and population trends (Latta et al. 2012).

Cuba is moving towards climatic conditions similar to those projected by the IPCC under a scenario of intensified greenhouse gas effect. Particularly, there are expected increases in sea level, air temperatures, reductions in daily temperature ranges, and increased frequency of long and severe droughts (Iturralde and Serrano 2015). Increases in the total amounts of rainfall associated with major precipitation events in the wet season are also expected (Iturralde and Serrano 2015). Under different IPCC scenarios and levels of climate sensitivity, sea levels in Cuba are expected to rise 0.22–0.85m by 2100. Given its long and narrow configuration, these increases can have devastating consequences for biodiversity.

Cuba lies on one of the most active parts of the Atlantic/Caribbean hurricane region; hurricanes and cold fronts are amongst the main causes of destructive flooding along the whole coastline length (Pérez et al. 2009). Furthermore, warming is indubitable, according to evidence measured by the Cuban Meteorological Institute (Pérez et al. 2009). Since the middle of the last century, the median annual temperature has increased by almost 0.9°C, as well as there was an increase in temperature in waters around Cuba (Mitrani and Díaz 2008).

In this sense, species distribution models (SDMs) are fundamental bases for understanding the impact of climate change on them. In this way, their geographical distribution could be projected relating ecological factors with the presence of the species (Elith and Leathwick 2009; Soberón and Nakamura 2009). In the last 20 years, predictive SDMs had been generated using algorithms, based on incomplete distribution data (Elith et al. 2006; González et al. 2009; Peterson and Soberón 2012; Carmona et al. 2013).

Despite their limitations (Anderson 2012), SDMs synthesize the relationships between species and environmental variables that would be difficult to interpret and appreciate by other means (Fuller et al. 2012). On the other hand, a large number of SDMs articles have proven useful in multiple fields of biology (Mateo et al. 2011), including ecology, taxonomy and biogeography, as well as in species conservation programs, and assessment of climate change impact (Jeschke and Strayer 2008; Steen et al. 2012).

To predict the effects of climate change, and identify conservation strategies that might mitigate its undesirable consequences, it is essential to develop models linking species distributions to alternative scenarios of climate change (Lawler et al. 2006). In this paper we evaluate the effect of climate change on two waterbird species in Cuba, through SDMs.

Our specific aims are to i) predict the potential impact of climate change on the distribution of American Flamingo *Phoenicopterus ruber* (Family Phoenicopteridae) and Reddish Egret

Egretta rufescens (Family Ardeidae) in 2050 and 2070, ii) identify bioclimatic variables that most influence their distributions patterns, iii) identify the best climate suitable areas in future scenarios for each species and iv) assess the possible coverage of the National System of Protected Areas of Cuba for the conservation of these species in the future, in case of negative effect due to climate change. This research is a first reference for others studies about climate change effect on the distribution of waterbirds species in Cuba and the Caribbean.

2. Material and Methods

2.1 Study species

To assess the effect of climate change, we modeled the ecological niche of two species (American Flamingo and Reddish Egret) of Cuban waterbird community to predict their potential distribution areas in the future, specifically in Cuba. These two species, are part of the 12 waterbird species exceeding the 1 % of the world's population in Cuba, according with the first chapter of this thesis (Aguilar et al. 2019), wich demonstrates the great importance of Cuba's wetlands for the conservation of these species. These species were selected within this group because both are i) resident in Cuba, ii) had the most restricted distribution and iii) are habitat-specialists, coastal-dependent, inhabiting estuaries and saline lagoons. These characteristics could influence the vulnerability of these species to climatic changes. Instead, the other species are more habitat generalist and widely distributed.

The American Flamingo covers the northern shore of South America, most of Caribbean Sea shoreline, as well as islands in the Caribbean and Eastern Pacific (Fig. 1a). American Flamingo has been seen in southern United States, but they are more abundant in southern

latitudes (Fer 2006; Roynesdal 2007). Global estimates range from 260,000 to 330,000 adult individuals and an increasing population trend (Birdlife International 2019). Flamingos are long-lived colonial waterbirds, oftentimes numbering thousands of individuals. These birds tend to occupy large mud flats, at hyper-saline estuaries, where the loose mud can be easily formed into the mounds that they use as nests. These large mud flats are usually located near a food supply and a fresh water source supply is needed when they are breeding (Rooth 1965; Fer 2006). American Flamingo is not globally threatened (Birdlife International 2019).

The Reddish Egret occurs in Baja California and along the Pacific coast of Mexico, the southern coast of the United State USA, through the Caribbean islands and in the Central American coast to northern Colombia and Venezuela (Koczur et al. 2019) (Fig. 1b). Reddish Egrets are frequent in shallow coastal waters, salt-pans, open marine flats and shorelines. They breed in mangroves forest surrounded by shallow lagoons (Gonzales et al. 2016). The Reddish Egret is North America's rarest and least studied ardeid. Populations declined greatly in the 1800s due to feather hunting, and the species was nearly extirpated from the United States by 1900 (Koczur et al. 2019). Global population estimates range from 7,000 to 11,000 mature individuals. However, much is unknown regarding abundance and population trends in Mexico and throughout the Caribbean and it remains a species of conservation concern throughout its range (Koczur et al. 2019). This species is classified as Near Threatened because, despite its large range, it occupies a restricted habitat and is patchily distributed. For this reason, it is assumed to have a moderately small and declining global population (Birdlife International 2019).

2.2 Species occurrence data

We compiled 1444 and 1279 occurrence localities all over the distribution range for American Flamingo and Reddish Egret, respectively (Fig. 1). The data was obtained from primary literature, as well as from the on-line database GBIF (Global Biodiversity Information Facility, <http://data.gbif.org>) using package `rgbif` version 3.6.1 (Chamberlain et al. 2019) in R environment version 3.6.0 (R Core Team 2018). Spatial sampling biases were corrected by detecting duplicates data and possible georeferencing errors (e.g. occurrences in the sea or in latitudes or longitudes in sites not described for the species) using `raster` version 2.9-5 (Hijman 2019) and `maptools` packages version 0.9-5 (Bivand and Lewin-Koh 2019) in R. We also thinned data eliminating data within a radius of 10 km to avoid autocorrelation, using `spThin` package version 0.1.0. (Aiello-Lammens et al. 2019) in R. Finally, we used 110 and 185 records for modeling American Flamingo and Reddish Egret distributions, respectively.

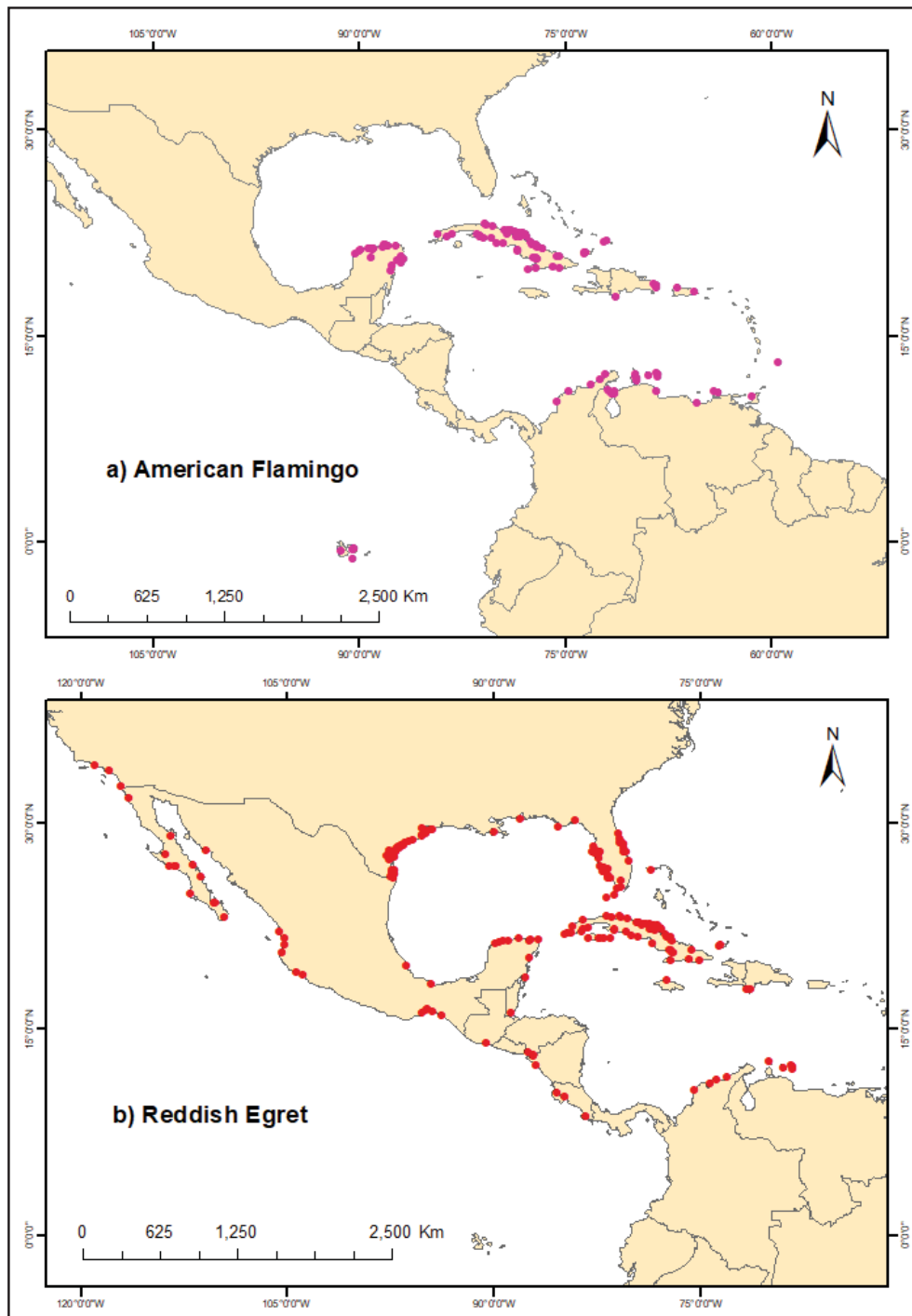


Fig. 1 Occurrences of American Flamingo (a) and Reddish Egret (b) compiled in this study

2.3 Environmental variables

Current and future climate data were obtained by 19 standard Bioclim variables (30 arc-sec resolutions; Table S1) from worldclim.org (Hijmans et al. 2005). Current climate data are derived from monthly precipitation and temperature (between 1950 and 2000) of meteorological stations all over the world.

Due to the high levels of correlations between environmental variables, we filtered our initial variable set based on the results of Pearson's correlation test and Jackknife analysis for Maxent modeling of American Flamingo and Reddish Egret (Fig S1). We correlated all pairwise combinations of climatic variables for each species (Table S2 and Table S3, respectively). We extracted climatic variables from occurrence localities of each species and 500 random background points, using *dismo* (Hijmans et al. 2017) and *raster* package (Hijman 2019) in R environment (R Core Team 2018). For highly correlated variable pairs ($r > 0.8$), we retained the variable that gave a higher value in the regularized gain to the Maxent model (Phillips et al. 2006). Consequently, six and seven bioclimatic variables were used in final distribution models of American Flamingo and Reddish Egret, respectively (Table 1).

Besides the bioclimatic layers, we considered a relevant non-climatic layer, the altitude, which is important to waterbird species living in low coastal areas. We got a global altitude layer (1 km resolution) from topography dataset of EarthEnv <https://www.earthenv.org/> (Amatulli et al. 2018).

Table 1 Bioclimatic variables used in the species distribution modeling for American Flamingo and Reddish Egret

Bioclimatic variables	Species	
	American Flamingo	Reddish Egret
bio2: Mean diurnal temperature range (mean of monthly (max temp - min temp))	x	x
bio4: Temperature seasonality (standard deviation *100)	x	-
bio8: Mean temperature of wettest quarter	-	x
bio10: Mean temperature of warmest quarter	x	x
bio14: Precipitation of driest month	x	x
bio15: Precipitation seasonality (coefficient of variation)	-	x
bio16: Precipitation of wettest quarter	x	-
bio17: Precipitation of driest quarter	-	x
bio18: Precipitation of warmest quarter	x	x

2.4 Bioclimatic variables of future climate projections

We used two future climate change scenarios, corresponding to the Representative Concentration Pathways, RCP 2.6 and 8.5 W/m² (IPCC 2014). The RCP 2.6 is an “optimistic scenario” which predicts low levels of concentration and emissions of greenhouse gas, with a maximum emission peak in 2040, and CO₂ concentration of 490 ppm, moderate population growth, GDP (Gross Domestic Product), carbon storage and capture technologies (IPCC 2014). At the other extreme, the RCP 8.5, a “pessimistic” scenario, predicts high emissions and concentrations of greenhouse gases, since it does not include the implementation of climate change mitigation policies, in addition to high population growth coupled with high energy demand, as well as a slow increase in GDP and low rates of technological changes and energy efficiency (Vuuren et al. 2011; Wayne 2013; Pachauri and Meyer 2014).

Data were derived from three general circulation models (GCM): BCC-CSM1-1 (Wu 2012), CCCM4 (Kim et al. 2003) and GISS-E2-R (Hansen et al. 2000). These models are considered the most advanced tools available to simulate the response of the global climate system based on the emission and concentration of greenhouse gases (IPCC 2013). The use of several GCMs allows simulate changes based on a set of anthropogenic forcing scenarios (IPCC 2013) and incorporate the variability observed between the different models (Araujo and New 2007; Varela et al. 2015). The selected bioclimatic variables were extracted under different climate change scenarios to make projections in years 2050 and 2070. Because no scenarios were available for the future development of altitude (Thuiller et al. 2006), this variable was assumed constant. All future predicted data was cropped and limited to project only in Cuba. To define climatic variation, we extracted the values of bioclimatic variables at each species occurrence locality under both, current and future scenarios, using spatial analysis functions with raster package version 2.9-5 (Hijman 2019) in R environment version 3.6.0 (R Core Team 2018).

2.5 Background points

We followed Anderson and Raza (2010) criteria to define the study area or calibration of the model. Proper area selection reduces the under or over-adjustment of models to occurrence localities and limits the use of background points to areas where the species may have actually accessed. In this way, more realistic models of the potential range of the species are generated (Barve et al. 2011).

For selecting these areas, 20 km radius buffers were created at each occurrence locality of the two species under study. This radio was selected taking into account the mobility of

these species (Cumming et al. 2012; Henry and Cumming 2017). Within these buffers, we randomly extracted 10,000 background points for model calibration. This procedure was made in R packages *dismo* version 1.1-4 (Hijmans et al. 2017) and *rgeo* version 0.4-3 (Bivand and Rundel 2019) according with Hijmans and Elith (2017).

2.6 Species distribution models

We build SDMs using Maxent version 3.3.3k (Phillips et al. 2006). Maxent is a machine learning method specifically designed for presence-only data and has been shown good predictive performance across various applications (Elith et al. 2006; Phillips et al. 2008; Doko et al. 2011; Virkkala et al. 2013; Bosso et al. 2013). Maxent uses environmental variables to predict environmental suitability for a particular species by assessing different combinations of variables and their interactions using the maximum entropy principle (Phillips et al. 2006). The complexity of Maxent models can be controlled through choice of feature classes and regularization parameters (Elith et al. 2011). This program is among the most used in the scientific literature of recent years (Heinamen and Numers 2009; Summer et al. 2012; Boria et al. 2014; Wang et al. 2018).

We mainly used default settings in this study (regularization multiplier = 1, maximum iterations = 500, convergence threshold = 10^{-5} , maximum number of background points = 10,000) and ran models with 30 bootstrap replicates. We assessed model performance using the average AUC, the area under the curve, from receiver operating characteristic curve (ROC) score by randomly assigning the occurrences records as training and test datasets (75 and 25 %, respectively). The ROC describes the correct presence identification rate

(sensitivity, in y) against the false rate (1-specificity, in x) (Peterson et al. 2008). Sensitivity is the probability of classifying as present when the species is really present and 1-specificity is the probability of classifying as present when the species is really absent (false positives) (Peterson et al. 2008). The AUC measures model ability to discriminate between locations where the species is present and where it is absent. AUC values vary between 0 and 1; values below 0.5 means that model predictive value is not higher than expected by chance and values higher than 0.7 are considered models with good precision (Phillips et al. 2008). We used logistic output format, which was easily interpretable with logistic suitability values ranging from 0 (lowest suitability) to 1 (highest suitability) (Phillips et al. 2008). The resulting model was projected to Cuban archipelago to identify areas of climatic suitability for American Flamingo and Reddish Egret.

2.7 Geospatial Analysis of the Impacts of Climate Change

We summarized the output logistic predictions from the three general circulation models under two emission scenarios of 2050 and 2070 by calculating the mean suitability within each grid-cell for each species. This is an ensemble-forecasting approach to reach a consensus scenario (Araujo and New 2007; Marmion et al. 2009). The resulting mean suitability maps was reclassified in binary maps (0 = not suitable area, 1 = suitable area), using the 10 percentile training presence logistic threshold (Maxent output) as a cutting value for each species. The suitable area of future and current models were then subtracted from each other, and areas of stability, contraction and expansion were calculated for each species.

We overlapped and clipped the vectorial map of potencial suitable area of American Flamingo in the most pessimistic scenario (RCP 8.5 W/m²) of 2070, with a layer of Cuban

National System of Protected Areas (SNAP; CNAP 2013), to estimate the protection percentage for this species in this extreme scenario.

We evaluated specifically the two most important sites for American Flamingo breeding in Cuba, Rio Maximo Faunal Refuge and Delta del Cauto Faunal Refuge, located in Camaguey and Granma provinces, respectively (Morales 1996; Denis et al. 2005). For these analyses, we considered the limits of these protected areas separately and showed models of its current range and future climatic scenarios. We used ArcGis 10.3 (ESRI 2011) for all post-geospatial processing and calculations.

3. Results

3.1 Model performance and environmental variables

American Flamingo model showed reasonable discrimination ($AUC_{\text{training}} = 0.876 \pm 0.016$; $AUC_{\text{test}} = 0.803 \pm 0.036$; Fig S2a), as well as Reddish Egret model ($AUC_{\text{training}} = 0.857 \pm 0.012$; $AUC_{\text{test}} = 0.811 \pm 0.028$; Fig. S2b). The standard deviation of AUCs, based on 30 bootstrap runs, was small for both species, suggesting little over-fitting of model predictions.

Model outputs clearly identified highly suitable habitat in coastal wetlands for American Flamingo and Reddish Egret, in coincidence with known occurrences and typical habitat descriptions for these species. Current models showed climatic suitability for American Flamingo in $\sim 11,231.2 \text{ km}^2$, being more restrictive than Reddish Egret which was $\sim 15,331.2 \text{ km}^2$, representing 10.2 and 14% of the Cuban archipelago surface, respectively (Fig 2 and 3).

For both species, the suitability current values are reached towards areas near the low coasts and adjacent islands (Fig. 2 and 3), mainly in five large groups of coastal wetlands (Sabana Camagüey Archipelago in north central coast, southwestern coast wetlands, Zapata Swamp, south and central coast wetlands and Delta del Cauto in southeast coast), to a greater or lesser extent depending on the species. However, there are also small patches with a likely occurrence in other coastal areas (Fig. 2 and 3).

Environmental variables that contributed the most to modeling the potential distribution of American Flamingo were mean diurnal temperature range (mean of monthly (max temp - min temp)), temperature seasonality and precipitation of wettest quarter. In contrast, mean temperature of warmest quarter, precipitation of driest month and precipitation of warmest quarter made only small contributions to model development (Table 2). In Reddish Egret distribution models, environmental variables that contributed the most were mean diurnal range (mean of monthly (max temp - min temp)) and precipitation of warmest quarter. On the other hand, precipitation of driest month, mean temperature of warmest quarter and precipitation seasonality made only small contributions to model development (Table 2).

Table 2 Contribution (%) of environmental variables to the Maxent SDMs of American Flamingo and Reddish Egret

Environmental variables	Species	
	American Flamingo	Reddish Egret
Altitude	67.2	79.1
bio2: Mean diurnal temperature range (mean of monthly (max temp - min temp))	10.1	7.5
bio4: Temperature seasonality (standard deviation *100)	6.2	-
bio8: Mean temperature of wettest quarter	-	2.6
bio10: Mean temperature of warmest quarter	2.2	2.1
bio14: Precipitation of driest month	4.3	1.2
bio15: Precipitation seasonality (coefficient of variation)	-	2.2
bio16: Precipitation of wettest quarter	5.3	-
bio17: Precipitation of driest quarter	-	1.8
bio18: Precipitation of warmest quarter	4.2	3.5

3.2 Potential effects of climate change

Climate change effects on the predicted distribution were discernible for both species (Fig. 2 and 3). As the time period increased (2000, 2050 and 2070) the strength of the effects from climate change increased for both species.

Our results predicted that American Flamingo would experience range contractions in future climates in Cuba. In the most optimistic scenario (RCP 2.6 W/m²) in 2050, American Flamingo distribution was predicted to be practically stable, with only a decrease of 10 % (1,123 km²) of its current size (Fig. 2). However, its current distribution would reduce by 27.8% (3,123 km²) according to the most pessimistic scenario (RCP 8.6 W/m²) in 2050, similarly to the contraction of 28.6% (3,213 km²) in 2070 in the most optimistic scenario.

Distribution size was predicted to decrease more on the most pessimistic scenario in 2070, reaching 38.3% (4,297 km²) of its current Cuban distribution (Fig. 2, Fig. 4a, Table S4).

The potential suitable area for American Flamingo in the most pessimistic scenario (RCP 8.5 W/m²) for 2070 had 49% of protection covered by the National System of Protected Areas of Cuba, while under this system 51% of this suitable area would be unprotected (Fig. 5). We found a prediction of an alarming reduction of American Flamingo in 2070, specifically for Delta del Cauto Faunal Refuge (Fig. 6), while for Rio Máximo Faunal Refuge the reduction was much smaller (Fig. 7).

Reddish Egret was predicted to expand its distribution in Cuba in the future. In 2050, this species would have an expansion very similar for most optimistic (RCP 2.6 W/m²) and pessimistic (RCP 8.6 W/m²) future scenarios, 27.1% (4,158 km²) and 26.6 % (4,081 km²) of its current size, respectively. In 2070, the expansion would be greater, 35.5% (5,445 km²) for an optimist scenario and 44.3% (6,793 km²) for a pessimistic scenario, being notable the increase from one scenario to another (Fig. 3, Fig. 4b, Table S4).

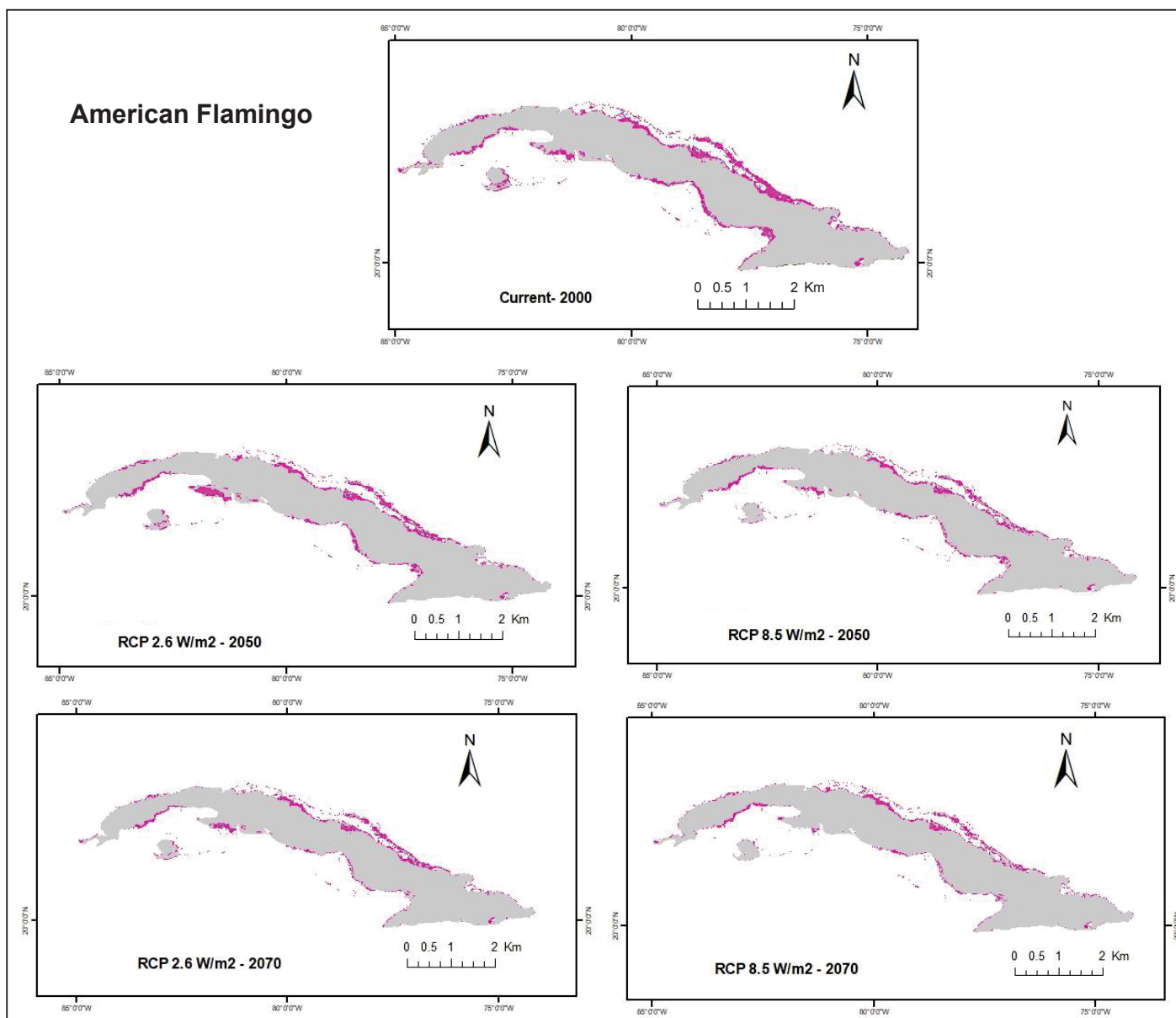


Fig. 2 Maps of binary suitable area from 10 percentile training presence logistic threshold (Maxent output) in current (2000) and future climate scenarios (RCP 2.6 W/m² and RCP 8.6 W/m²) for 2050 and 2070 for American Flamingo in Cuba. Maps were obtained using an ensemble-forecast approach across the three general circulation models BCC-CSM1-1, CCCM4 and GISS-E2-R. Gray = not suitable area, Pink = suitable area

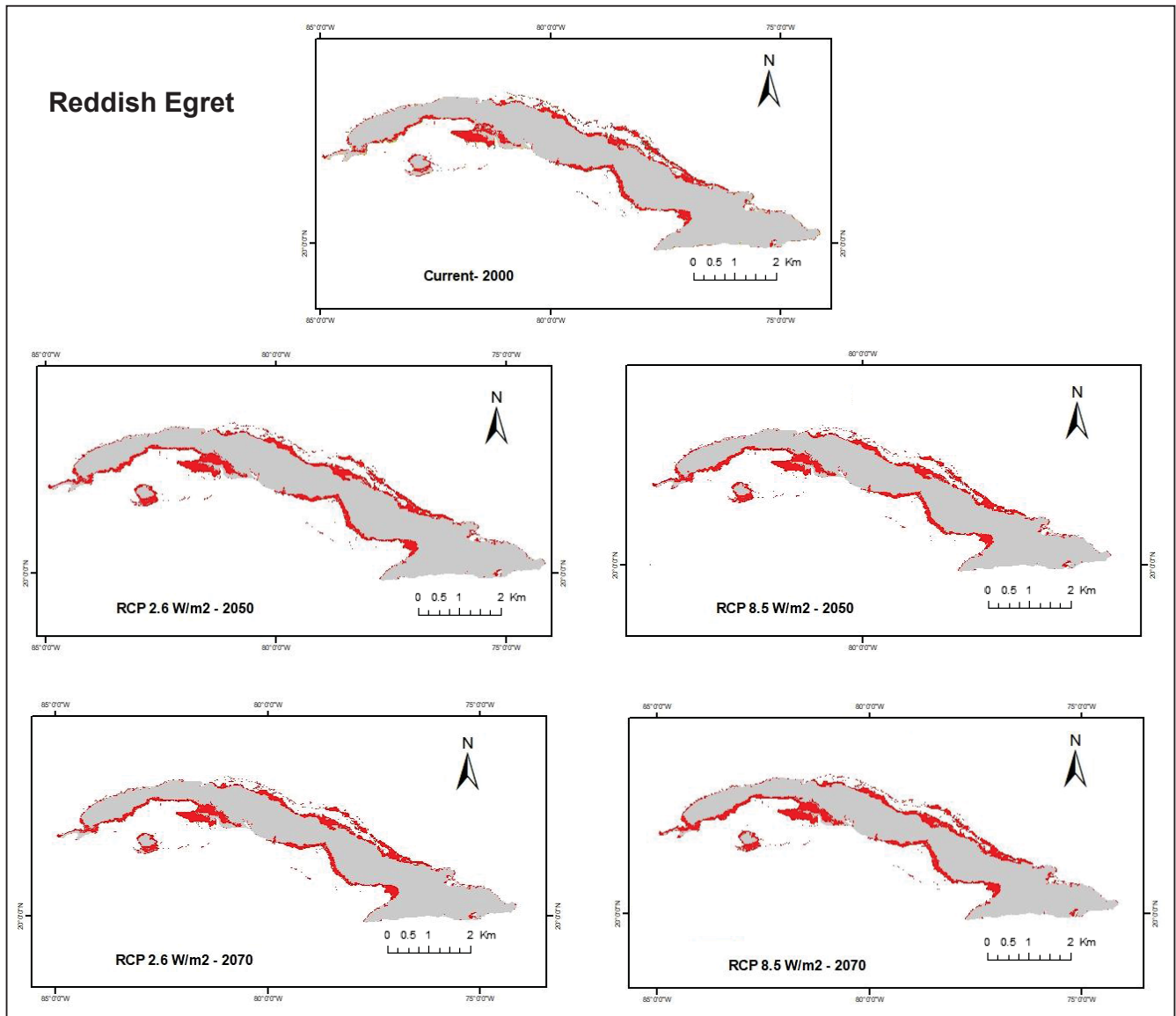


Fig. 3 Maps of binary suitable area from 10 percentile training presence logistic threshold (Maxent output) in current (2000) and future climate scenarios (RCP 2.6 W/m² and RCP 8.6 W/m²) for 2050 and 2070 for Reddish Egret in Cuba. Maps were obtained using an ensemble-forecast approach across the three general circulation models BCC-CSM1-1, CCCM4 and GISS-E2-R. Gray = not suitable area, Red = suitable area

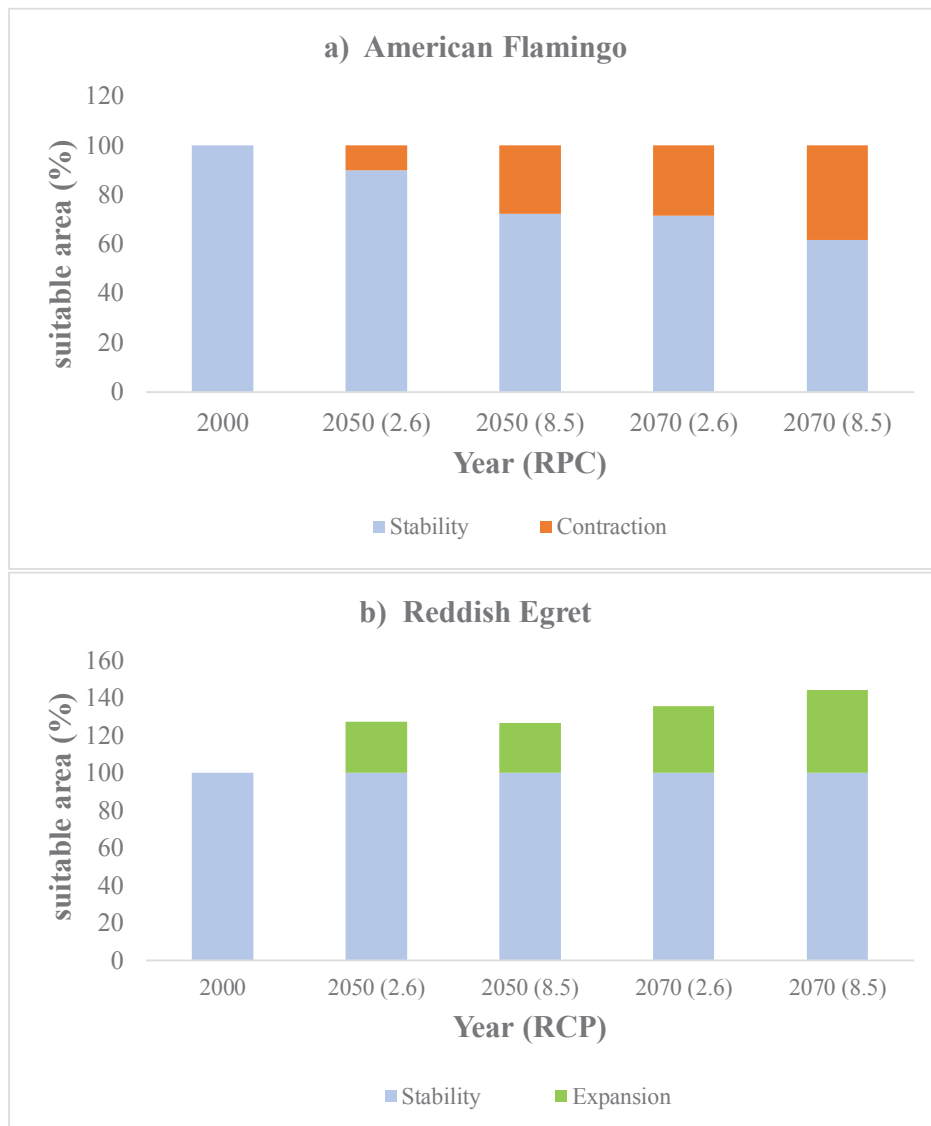


Fig. 4 Percentage of suitable area in current (2000) and future climate scenarios (RCP 2.6 W/m² and RCP 8.5 W/m²) for 2050 and 2070 for American Flamingo (a) and Reddish Egret (b) in Cuba. The predicted suitability is estimated based on the average 10 percentile training presence logistic threshold.

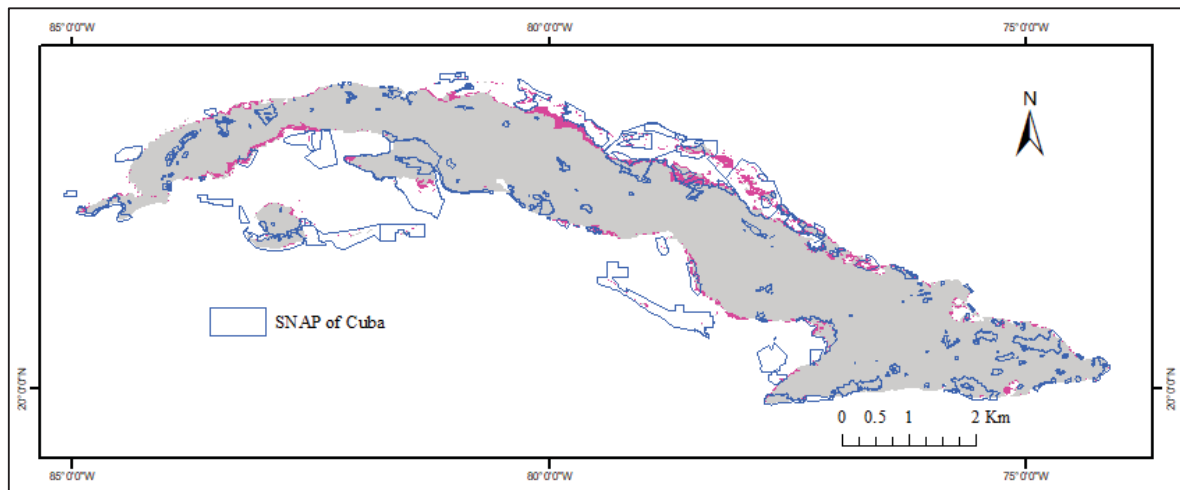


Fig. 5 National System of Protected Areas (SNAP) of Cuba and suitable area according to the most pessimistic future climate scenarios (RCP 8.5 W/m²) in 2070 for American Flamingo. Gray = not suitable area, Pink = suitable area

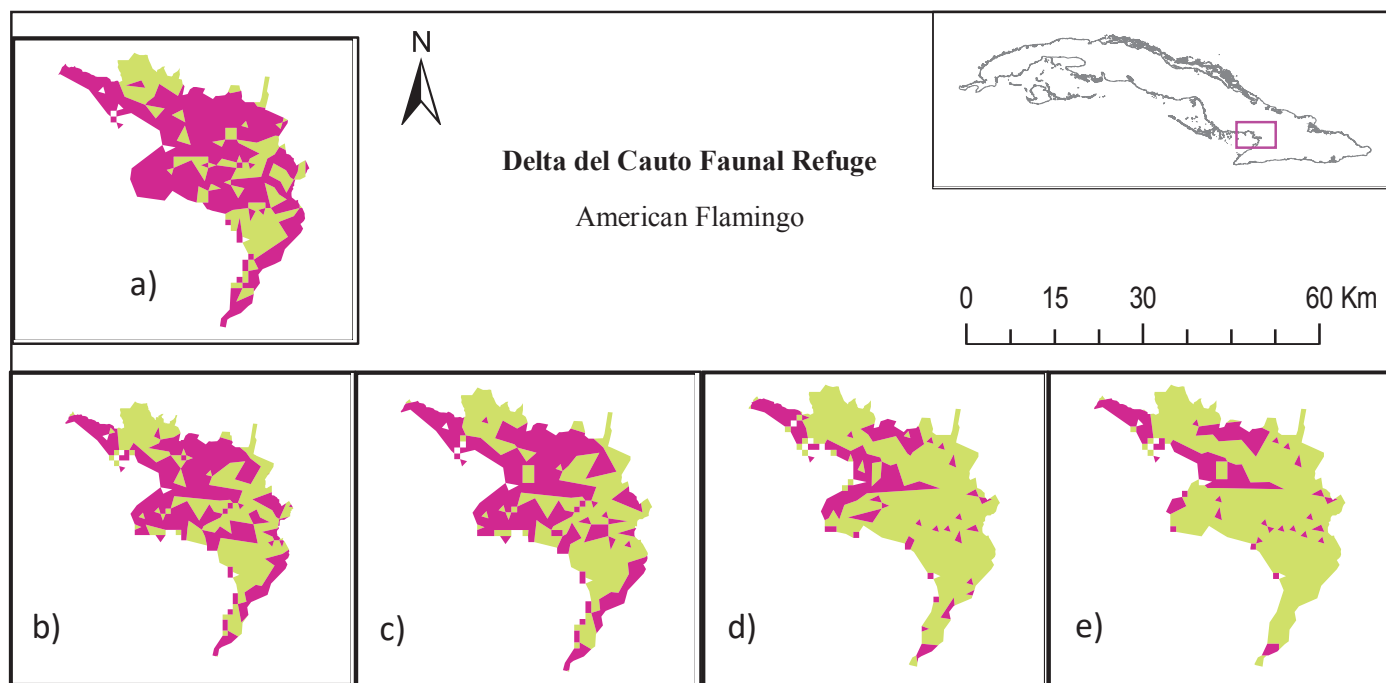


Fig. 6 Maps of binary suitable area from 10 percentile training presence logistic threshold (Maxent output) in a) current (2000) and future climate scenarios b) RCP 2.6 W/m² for 2050, c) RCP 8.5 W/m² for 2050, d) RCP 2.6 W/m² for 2070 and e) RCP 8.5 W/m² for 2070 for American Flamingo in Delta del Cauto Faunal Refuge, Cuba. Green = not suitable area, Pink = suitable area

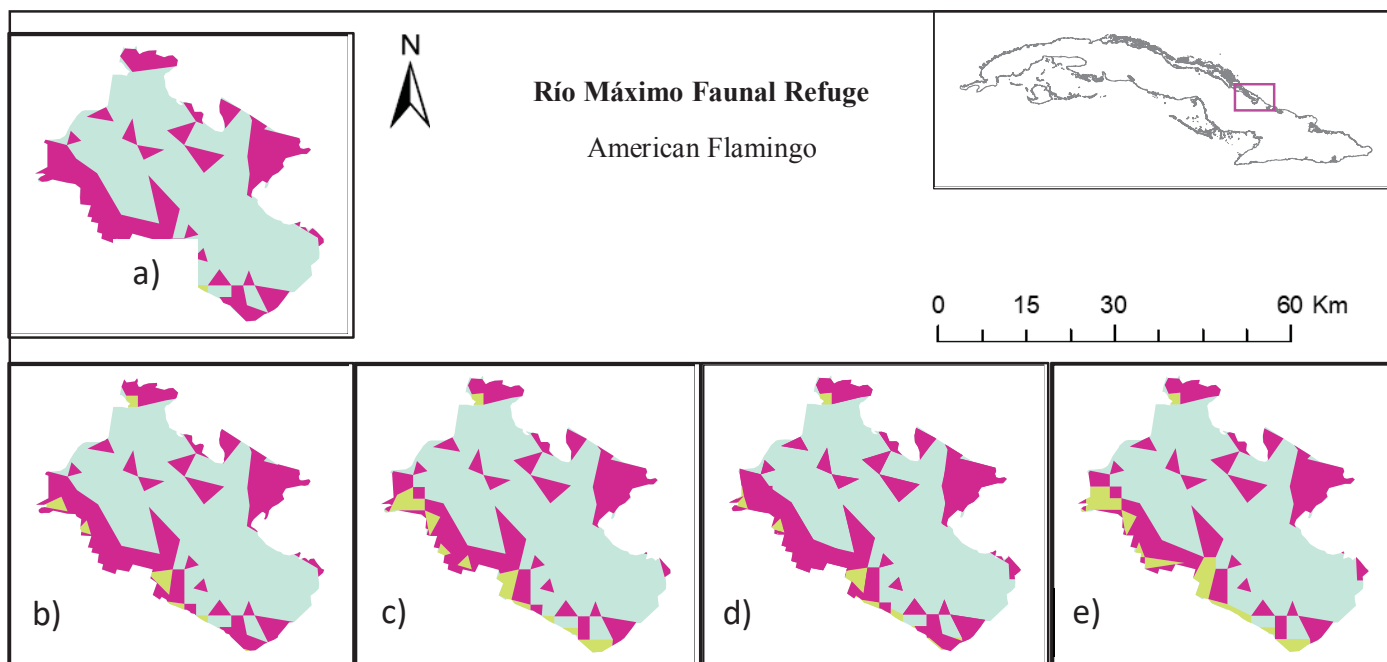


Fig. 7 Maps of binary suitable area from 10 percentile training presence logistic threshold (Maxent output) in a) current (2000) and future climate scenarios b) RCP 2.6 W/m² for 2050, c) RCP 8.5 W/m² for 2050, d) RCP 2.6 W/m² for 2070 and e) RCP 8.5 W/m² for 2070 for American Flamingo in Río Máximo Faunal Refuge, Cuba. Green = not suitable area, Pink = suitable area, Blue = sea

4. Discussion

Our models predicted that, by the end of this century, under future scenarios relative to current conditions, suitable habitat for two waterbird species will be changed in Cuba, either positively or negatively. This study represents the first research to predict the climate change effect on waterbirds species distribution in Cuba and the Caribbean.

4.1 American Flamingo

We demonstrated that the current suitable habitat of American Flamingo in Cuba would decrease considerably under the projected climate scenarios for 2050 and 2070. Species with

a small geographic range tends to be more vulnerable to climate change than more widely distributed species (Thomas et al. 2004; Jetz et al. 2007; Lu et al. 2012). Due to the current limited distribution to coastal zone, climate change may substantially affect this species by reducing its current suitable range. This situation is most likely to occur due to the high intensity of human activities and habitat fragmentation throughout most distribution range of American Flamingo, mainly in the north coast of Cuba with the tourism development and the construction of hotels and roads over the sea to connect different keys (Archipelago Sabana-Camaguey) (Rodríguez et al. 2014). Also is known that this species is very sensitive to human disturbance and this factor has been responsible for the disappearance of several nesting sites in the Caribbean in the last years (Del Hoyo et al. 1992).

Our predicted reduction of suitable habitats in American Flamingo is similar to other previous studies on the impacts of climate change on waterbirds species. For example, Larson (1995) extrapolated from a model relating current climate to future wetland density under a drier scenario, and suggested that suitable habitat for waterfowls would be reduced under those conditions. Steen and Powell (2012) predicted the range reduction of 64%, as average of the ensemble of five common waterbirds species, using SDMs in a drier future. The studies cited above correspond to species of orders Anseriformes, Pelecaniformes, Gruiformes, Chrdriiformes and Podicipediformes. So far, no other previous study has ever assessed the impact of climate change and modeled the distribution of any Phoenicopteriformes as we did here with flamingoes.

We found that the mean diurnal temperature range contributed the most to the American Flamingo distribution modeling, meaning that this species is more sensitive to the variation of this variable. One of the most important concerns with flamingoes and global warming is how it affects their mating season. Flamingoes depend on the rainfall to help them mate, so

prolonged periods of drought can adversely affect their survival rates (Johnson and Cézilly 2007). Global warming can also dry out the lagoons and swampy areas where flamingos live, also affecting water alkalinity (del Hoyo 1992). When the water becomes too acid, survival is affected and then birds need to relocate. They also rely upon the shallow lagoons to provide them with sources of food (del Hoyo 1992). The spatio-temporal distribution of non-breeding and breeding flamingos seems to be dependent on food density and climatic variation (Arengo and Baldassarre 1995; Baldassarre and Arengo 2000; Tuite 2000).

Another important aspect on habitat protection for American Flamingo are their breeding sites. As the models for future scenarios show, specifically in the most important sites for American Flamingo breeding in Cuba, the Delta del Cauto Faunal Refuge expects to have a considerable reduction of the suitable area until 2070. Delta del Cauto supports the second largest breeding site of the Cuban Archipelago with 20,000-30,000 reported nests (Denis et al. 2005). Therefore, it is extremely important for the conservation of the species to take our predictions into account. Instead, in Río Máximo Faunal Refuge, the reduction prediction of suitable area for this species was not drastic until 2070. However, the influence of sea level rise by the end of this century could be fatal for this important nesting site. About 100,000-120,000 individuals gather to nest each year in Río Máximo (Denis et al. 2002), being the largest nesting site in Cuba and the Caribbean. The American Flamingo Cuban population is one of the most important in the region (Ottenwalder 1991), producing at least 50% of annual recruitment (Morales 1996).

There are several evidences that breeding of flamingoes is affected by climate variations (Bechet and Johnson 2008; Bargas and Balow 2008; Bucher and Curto 2012). Flamingoes breeding habitat requires three essential conditions: i) precipitations to ensure its permanence, as they need fresh water, ii) maintenance of a water belt around the nests, as a

defense against terrestrial predators and iii) supply of sufficient food for adults and juveniles (Johnson 1983). Breeding colonies are dependent also of undisturbed places to protect eggs and chicks from terrestrial predators (Simmons 1996; Johnson and Cézilly 2007). Flamingoes nesting habitats can be considered unstable, since the lagoons are subject to drying out or pronounced retractions according to environmental conditions (Mascitti and Nicolossi 1992).

4.2 Reddish Egret

Our results showed that the current suitable habitat for Reddish Egret in Cuba would increase under the projected climate scenarios for 2050 and 2070. It seems that under a changing climate, some species will benefit by extending ranges into currently unsuitable areas (Jetz et al. 2007; Hu et al. 2010; Lu et al. 2012). This means that there is not a conservation concern for this species under climate change scenarios for the period of time evaluated in relation to the variables analyzed in our predictive model.

The fact that the suitable habitat increases for Reddish Egret in future climatic scenarios could be due to some factors. First, this species has a wider distribution range, with a greater latitude and longitude amplitude if we compare with the American Flamingo, which would allow a wider range of climate amplitude for this species. Also, even though this species is a coastal habitat specialist (Lowther and Paul 2002; Bates et al. 2016), its foraging and breeding sites are less specialized than for American Flamingo (del Hoyo 1992). On the other hand, there are no previous reports of breeding sites losses for Reddish Egret due to climatic variations or extreme droughts. The main factors documented for nesting sites losses in this species are human disturbance, coastal development and sea level rise (Hodgson and Paul 2011), as well as the presence of predators (Cox et al. 2019).

Nevertheless, this species can be affected indirectly by other variables associated to climate change that were not included in our models. Among these variables, alterations due to sea level rise, subsidence, and increased frequency and intensity of storms and flooding (Wilson et al. 2014) may lead to serious habitat losses. The Reddish Egret is completely dependent on coastal marine habitats for breeding and foraging, habitats which are vulnerable to sea level rise. Most of the current breeding sites used by the species could be permanently inundated and these changes may be irreversible (Wilson et al. 2014).

Although the suitable habitat may increase in future scenarios for the Reddish Egret, and could meet the climatic conditions for its survival, these extensions of increased habitat may not include other specific conditions for this species, such as shallow coastal waters and salt-pans (González et al. 2016). There is some belief that foraging habitat might be limiting due to the relatively specific physical and hydrologic conditions required by the Reddish Egret to forage (Wilson et al. 2014) and this species is rarely record far from the coast. The Reddish Egret is the only Ardeid species to be restricted to coastal saline habitats. The critical need for this species appears to be proximity to shallow open waters suitable for its unique foraging technique (Wilson et al. 2014). Even if this species would increase its range in Cuba in the future, we believe it would not have a strong pressure for resource competition due to its current small population size. The number of Reddish Egrets using Cuban coastal ecosystems is about 500 birds and there are at least 155 breeding pairs, estimated at 13 breeding sites (Gonzales et al. 2016). Also, the number of nests at breeding sites of Reddish Egret in Cuba is small (ranged from two to 27; Gonzales et al. 2016), compared with others egret species in the country.

Few works have been carried out in species of Ardeidae family evaluating the potential impacts of climate change and using SDMs. One of them studied the White-eared Night

Heron *Gorsachius magnificus*, an endangered species of Asia (Hu and Liu 2014). The results showed that the extent of suitable habitat range may shrink by more than 35% under a predicted changing climate when assuming the most pessimistic condition, contrary to our results with Reddish Egret. In the same way, Steen and Powell (2012) projected range loss for American Bittern *Botaurus lentiginosus* close to 29% of their current range. However other research on waterbirds has shown also an increase under a changing climate, as is the case for Black-faced Spoonbill *Platalea minor*, endemic to Asia (Hu et al. 2010), so this is not an isolated result.

4.4 Modeling approach

There is skepticism about the reliability of predictive models and their application in conservation (Wiens et al. 2009; Dawson et al. 2011) because, in general, they do not consider all the complexity inherent in nature. For example, evolutionary processes and species ability to adapt (Skelly et al. 2007) or biotic relationships (e.g. competition and predation) (Anderson et al. 2002; Peterson et al. 2002; Hebblewhite et al. 2005; Gutiérrez et al. 2005), which could limit the permanence of the species despite suitable climatic environments (Kissling et al. 2012). Other factors impact species and their habitats (e.g., sociopolitical factors, invasive species and diseases), but these were not included in our models. Even though the complexity of the natural system constrains predictive power of models, the bioclimate envelope approach can provide a useful first approximation to the potentially dramatic impact of climate change on biodiversity (Pearson and Dawson 2003). They provide an effective way of looking into the future for the sake of conservation and

resource management (Wiens et al. 2009). Our study outlines an approach to assess vulnerability of two waterbird species under climate change scenarios.

Species detectability can also influence model results (Steen and Powell 2012). American Flamingo detectability is much easier than Reddish Egret's, which can be confused with other egret species, especially the white morph. Two types of errors, omission (exclusion of areas inhabited) and commission (inclusion of areas not actually inhabited), often exist in species distribution models (Fielding and Bell 1997). Commission error seems to be more frequent than omission error in many circumstances (Thuiller et al. 2006; Elith et al. 2006). This error could have influenced the results of Reddish Egret models, whereby it should be interpreted with more caution. Climate models are currently the strongest tools for simulating future climate scenarios, however, all climate models are not equally useful and contain a variety of uncertainties at all spatial and temporal scales (Beaumont et al. 2008).

4.5 Conservation implications

Results in the present study highlight the importance of incorporating climate change into habitat conservation planning of species. Our results show that American Flamingo is a highly sensitive species to climate change providing several important implications for conservation. First, new protected areas should be established in Cuban coast, specifically those including large mud flats and hyper-saline estuaries. Second, management actions should be focused on protecting known habitats and nesting sites, as well as raising awareness to reduce habitat degradation and human disturbance. Also for the successful breeding of American Flamingo in adverse climatic conditions, it is important the management of duration and magnitude of flooding flows of fresh and salty waters (Arthur et al. 2012),

regulating rivers and wetlands. Successful breeding of waterbirds is one of the most common objectives for the management of environmental flows (MDBA 2014). To prepare for these contingencies, we suggest that the conservation agencies and local Cuban governments place a priority on the establishment and maintenance of targeted wetlands.

Long-term monitoring of waterbird populations (Kingsford et al. 2013; Hansen et al. 2015) provides a basis for the identification of trends, patterns of variation, and potential change drivers for particular species at specific wetlands (Colloff et al. 2015). Distribution modeling contribute to management decisions by determining how habitat availability varies between species with different habitat requirements, by highlighting changes in use of wetlands that have been historically breeding sites of waterbirds. Such monitoring will give a comprehensive assessment of wetland habitat availability, and provide basis for waterbird conservation and management in the future. In accordance with the results of the American Flamingo about climate change, it is urgent to update the status of this species in Cuba, population sizes, current nesting sites and to monitor these variables periodically.

According to the previous forecasts, it is necessary to develop stronger climate change adaptation and conservation strategies, coupled with designing and planning the National System of Protected Areas in Cuba. Also, we recommend a management plan aimed at wetlands conservation, in order to improve and increase the quality and extent of suitable protected habitats. These zones represent critical climatic shelters for the conservation and survival of the studied species and an important part of Cuba's and the regional biota. It is important to highlight that this work could be a reference and an inspiration to predict the climate change effect on other waterbirds species distribution for their future conservation in Cuba and the Caribbean.

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7. Supplementary materials

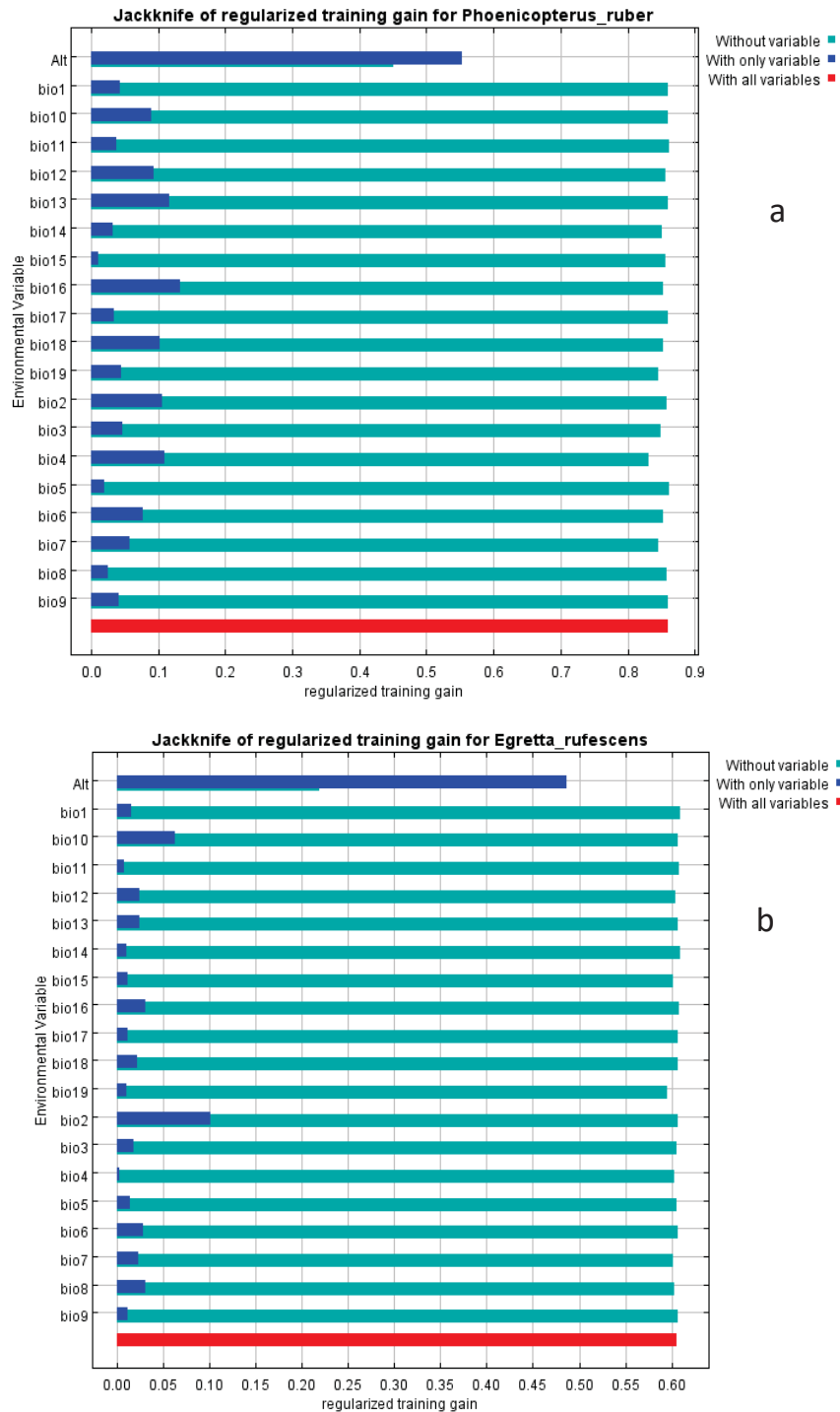
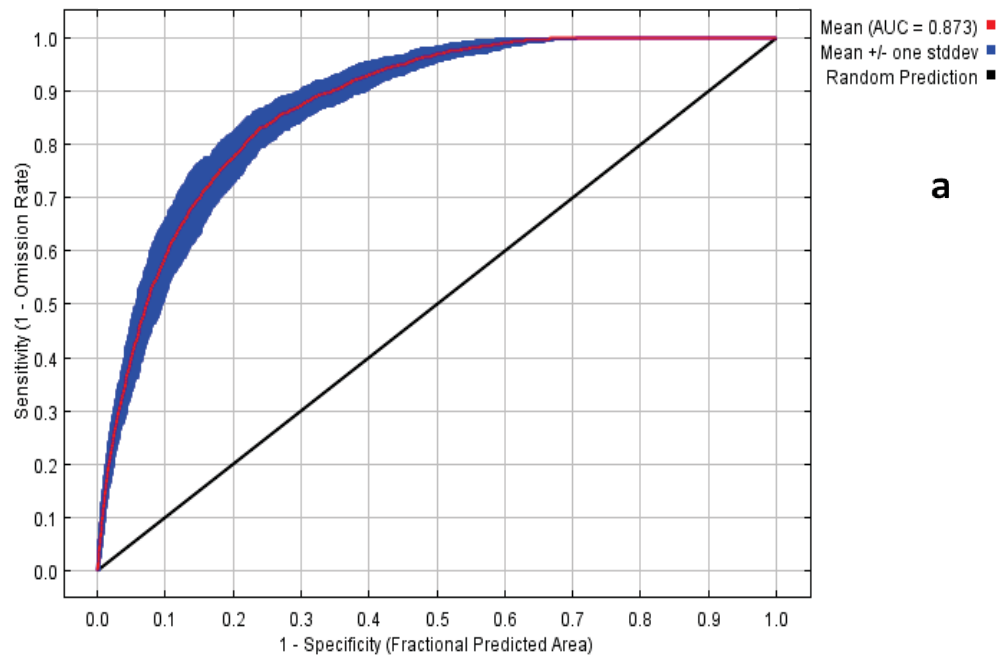
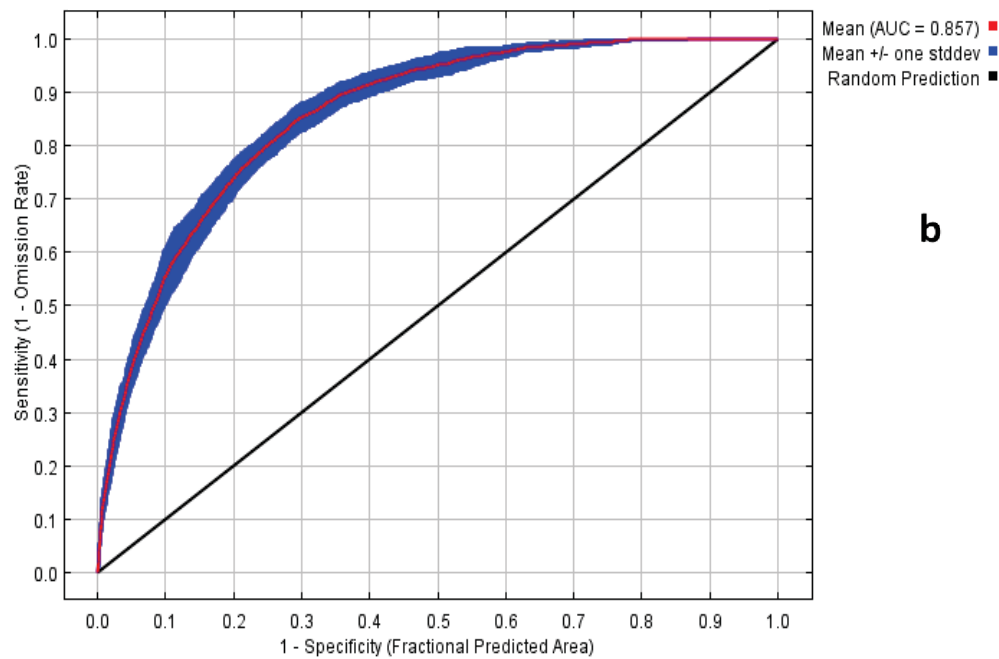


Fig. S1 Jackknife results plot for initial MaxEnt model, provided by MaxEnt output for American Flamingo *Phoenicopterus ruber* (a) and Reddish Egret *Egretta rufescens* (b)



a



b

Fig. S2 Accuracy assessment of the Maxent models (30 runs) through the receiver operating characteristic curve (ROC) and area under curve (AUC) value for American Flamingo (a) and Reddish Egret (b)

Table S1. Bioclimatic variables extracted from WorldClim (<http://www.worldclim.org/>) and used to test the effects of climate change on the distribution of American Flamingo and Reddish Egret

bio1 = Annual mean temperature
bio2 = Mean diurnal temperature range (mean of monthly (max temp - min temp))
bio 3 = Isothermality (BIO2/BIO7) (* 100)
bio 4 = Temperature seasonality (standard deviation *100)
bio5 = Max temperature of warmest month
bio6 = Min temperature of coldest month
bio7 = Temperature annual range (BIO5-BIO6)
bio8 = Mean temperature of wettest quarter
bio9 = Mean temperature of driest quarter
bio10 = Mean temperature of warmest quarter
bio11 = Mean temperature of coldest quarter
bio12 = Annual precipitation
bio13 = Precipitation of wettest month
bio14 = Precipitation of driest month
bio15 = Precipitation seasonality (coefficient of variation)
bio16 = Precipitation of wettest quarter
bio17 = Precipitation of driest quarter
bio18 = Precipitation of warmest quarter
bio19 = Precipitation of coldest quarter

Table S2 Pairwise Pearson correlation coefficients among 19 bioclimatic variables for species distribution modeling of American Flamingo *Phoenicopterus ruber*. In bold are predictors and values with correlation > 0.8 . Abbreviation of bioclimatic variables used as columns and rows are defined in Table S1

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18
bio1	1																	
bio2	-0.72	1																
bio3	0.61	-0.59	1															
bio4	-0.73	0.76	-0.92	1														
bio5	0.30	0.25	-0.37	0.36	1													
bio6	0.93	-0.85	0.80	-0.91	-0.03	1												
bio7	-0.77	0.88	-0.87	0.98	0.35	-0.95	1.00											
bio8	0.72	-0.36	0.30	-0.40	0.44	0.59	-0.41	1.00										
bio9	0.85	-0.65	0.64	-0.72	0.18	0.86	-0.75	0.44	1.00									
bio10	0.67	-0.24	-0.08	0.00	0.86	0.39	-0.09	0.64	0.49	1								
bio11	0.95	-0.79	0.81	-0.91	0.02	0.99	-0.92	0.62	0.86	0.41	1.00							
bio12	0.40	-0.47	0.66	-0.57	-0.23	0.53	-0.57	0.07	0.46	-0.02	0.51	1.00						
bio13	0.47	-0.46	0.68	-0.64	-0.19	0.58	-0.61	0.16	0.50	0.00	0.58	0.92	1.00					
bio14	0.17	-0.30	0.43	-0.28	-0.22	0.26	-0.31	-0.06	0.23	-0.05	0.23	0.77	0.50	1.00				
bio15	-0.01	0.29	-0.09	0.00	0.13	-0.06	0.10	0.23	-0.08	-0.02	0.00	-0.48	-0.17	0.00				
bio16	0.46	-0.46	0.69	-0.64	-0.19	0.58	-0.60	0.15	0.51	0.00	0.58	0.93	0.99	0.53	-0.20	1.00		
bio17	0.19	-0.32	0.45	-0.30	-0.23	0.28	-0.34	-0.06	0.26	-0.05	0.25	0.81	0.55	0.99	-0.73	0.58	1.00	

bio18	0.15	-0.25	0.38	-0.33	-0.33	0.24	-0.33	0.03	0.14	-0.15	0.24	0.66	0.52	0.70	-0.37	0.53	0.71	1.00
bio19	0.38	-0.38	0.60	-0.48	-0.09	0.48	-0.47	0.06	0.48	0.06	0.46	0.86	0.83	0.57	-0.37	0.85	0.62	0.29

Table S3 Pairwise Pearson correlation coefficient among 19 bioclimatic variables for species distribution modeling of Reddish Egret *Egretta rufescens*. In bold are predictors and values with correlation > 0.8 . Abbreviation of bioclimatic variables used as column and row are defined in a Table S1

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18
bio1	1																	
bio2	-0.64	1																
bio3	0.68	-0.35	1.00															
bio4	-0.81	0.57	-0.93	1.00														
bio5	0.46	0.09	-0.04	0.05	1.00													
bio6	0.96	-0.71	0.81	-0.93	0.22	1.00												
bio7	-0.85	0.75	-0.84	0.97	0.06	-0.96	1.00											
bio8	0.73	-0.44	0.35	-0.45	0.44	0.62	-0.51	1.00										
bio9	0.79	-0.46	0.67	-0.75	0.29	0.82	-0.75	0.32	1.00									
bio10	0.78	-0.44	0.15	-0.27	0.83	0.59	-0.37	0.70	0.51	1.00								
bio11	0.97	-0.63	0.83	-0.93	0.27	0.99	-0.94	0.64	0.82	0.60	1.00							
bio12	0.40	-0.53	0.44	-0.46	-0.12	0.48	-0.52	0.20	0.36	0.16	0.44	1.00						
bio13	0.53	-0.52	0.59	-0.63	-0.06	0.61	-0.64	0.31	0.47	0.20	0.59	0.91	1.00					
bio14	-0.03	-0.31	-0.13	0.09	-0.17	-0.02	-0.03	-0.05	-0.01	0.03	-0.07	0.66	0.36	1.00				
bio15	0.39	0.11	0.51	-0.50	0.15	0.40	-0.36	0.30	0.33	0.12	0.46	-0.16	0.18	-0.64	1.00			
bio16	0.50	-0.50	0.59	-0.61	-0.08	0.59	-0.63	0.28	0.45	0.17	0.57	0.93	0.99	0.39	0.16	1.00		
bio17	0.00	-0.35	-0.11	0.07	-0.17	0.01	-0.06	-0.03	0.02	0.05	-0.04	0.70	0.40	0.99			1.00	
bio18	0.33	-0.42	0.25	-0.33	-0.14	0.35	-0.40	0.33	0.19	0.16	0.34	0.72	0.69	0.57	-0.04	0.70	0.58	1.00
bio19	0.21	-0.33	0.31	-0.28	-0.06	0.29	-0.32	-0.01	0.30	0.07	0.25	0.80	0.69	0.50	-0.21	0.71	0.54	0.3

Table S4 Extent of suitable area (km²), based on binary maps, in current (2000) and future climate scenarios (RCP 2.6 W/m² and RPC 8.6 W/m²) for 2050 and 2070 for American Flamingo and Reddish Egret in Cuba

Specie	Year (Scenario)	Suitable areas	Stability	Contraction	Expansion
	RCP W/m ²	km ²	% (km ²)	% (km ²)	% (km ²)
American					
Flamingo	2000	11,231.2			
	2050 (2.6)	10,008.8	90 (10,008.8)	10 (1,123)	0
	2050 (8.5)	8,108.8	72.2 (8,108.8)	27.8 (3,123)	0
	2070 (2.6)	8,018.4	71.4 (8,018.4)	28.6 (3,213)	0
	2070 (8.5)	6,934.4	61.7 (6,934)	38.3 (4,297)	0
Reddish Egret					
Reddish Egret	2000	15,331.2			
	2050 (2.6)	19,489.6	100	0	27.1 (4,158)
	2050 (8.5)	19,412.8	100	0	26.6 (4,081)
	2070 (2.6)	2,0776	100	0	35.5 (5,445)
	2070 (8.5)	22,124	100	0	44.3 (6,793)

FINAL CONSIDERATIONS

The results of this thesis provide key information for future management and conservation of waterbirds in Cuba and North America, as most species are winter migrants. Chapter one contains the most comprehensive study on waterbird assemblages in Cuban natural wetlands, consisting of a long-term assessment of an extensive area of wetlands using standardized methods, in which we registered 110 bird species. The study area covers a fourth of Cuban coastal area, representing 40 % of the wetlands in the island. Cuba is the largest of the Caribbean islands, encompassing most of the wetlands and receiving, each year, a significant flow of migratory waterbirds from North America. Based on our results, we developed suggestions for wetlands management in order to enhance waterbirds conservation. Our results show the seasonal and interannual stability of waterbirds assemblage, the good level of protection of Cuban southern coast, and also highlight the global importance of waterbird conservation in this area and its wetlands, mainly in fall migration. We found that 12 species exceeded 1 % criterion of world population and we encouraged the creation of two new Ramsar sites, a new protected area, and one Important Bird Areas (IBAs), in addition to the reaffirmation of the status of several sites within these categories. This work could be also relevant because it gives a good information about coastal wetlands of international importance in the Caribbean, still unexplored.

In the second chapter, we present another relevant result relative to the effect of landscape configuration at different spatial scales on the structure of waterbird communities in coastal wetlands in a conservation gradient in Cuban southwest. This study shows that landscape context of coastal wetlands influences waterbird abundance, species composition and waterbird diversity. The effects of landscape variables varied according to the scale and

the sensitivity of the waterbird community descriptor. Our results show that the scale at which the landscape structure of coastal wetland is measured predicts abundance, waterbird composition and diversity. In our wider scale of measurement (6 km), the mean patch area of mangrove had a negative influence on waterbird abundance, while at the narrower spatial scale (2 km) the percentage of landscape covered by lagoons, salt marshes and rivers had a positive effect. Instead, a higher percentage of landscape covered by mangroves and a percentage of landscape covered by lagoons, salt marshes and rivers had a positive effect in waterbird composition at 2 km. The percentage of landscape covered by mangroves had a negative effect in waterbird diversity at the 4 km spatial scale. The percentage of anthropogenic land use has not influenced in any response variable at the evaluated scales.

Several recommendations regarding the effective management of waterbirds to contribute to adequate protected area planning on Cuban south coast are given, based on these results. First, management plans need to be implemented at the regional level addressing conservation and restoration of heterogeneous landscapes at different spatial scales. The maintenance of larger open water lagoons combined with small mangrove patches would favor increasing waterbird abundance during migration congregation. Also, the definition of boundaries of protected wetlands should take into account the results of scale of effect, in both new and existing reserves. Even non-protected areas should be protected by biodiversity protection laws, such as the Cuban coastal law, which must be adequately implemented in order to protect lagoons, salt marshes and mangroves. The protected areas of this region should follow similar management protocols for all suitable waterbird habitats, respecting the suggested scales.

In chapter 3, current and future distributions of American Flamingo *Phoenicopterus ruber* and Reddish Egret *Egretta rufescens* were predicted using species distribution models.

Our results show that the current distribution of American Flamingo is predicted to reduce 38 % under a changing future climate, in the most pessimistic scenario of 2070, while the current distribution size of Reddish Egret is predicted to increase in 44 %. The suitable potential habitat of American Flamingo in the most pessimistic scenario of 2070 would distribute 51 % outside the National System of Protected Areas of Cuba. From this study we can conclude that American Flamingo is a highly-sensitive species to climate change and we discuss several implications for this species conservation. New protected areas should be established in Cuban coast and management actions should be focused on protecting known habitats and nesting sites, as well as raising awareness to reduce habitat degradation and human disturbance. Also, for the successful breeding of American Flamingo in adverse climatic conditions, it is important to manage the duration and magnitude of flooding flows of fresh and salty waters, coming from nearby rivers and wetlands. We suggest that the conservation agencies and local Cuban governments prioritize the establishment and maintenance of targeted wetlands. It is necessary to implement a long-term monitoring plan to urgently update the status of American Flamingo in Cuba, assess population sizes and current nesting sites. Also, it is necessary to design and plan the National System of Protected Areas of Cuba in a short term, taking into account conservation strategies adapted to climate change., as well as to guide management measures aimed at wetlands conservation and fragmentation reduction.

Birds are very sensitive to threats like habitat loss, habitat fragmentation and degradation, pollution, climate change and unregulated harvest. The results of this thesis not only highlights the good health of several Cuban wetlands through high quality waterbirds data, but encourage their management at the landscape level to prevent their habitat loss, and the prediction of the possible effects of future climate changes upon charismatic species.

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