

Underlying factors promoting nestedness of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba

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Abstract

Underlying factors promoting nestedness of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba.— Assessing the factors associated with nestedness patterns is a crucial aspect in studies of community structure. Bird assemblages in the Jardines de la Reina archipelago have a stable nested structure but the underlying influences have not been evaluated. We constructed a presence–absence data matrix based on a bird inventory obtained from 43 cays of this archipelago. We calculated nestedness using the NODF metric based on the overlap and decreasing fill and evaluated its significance by running 1,000 iterations of four null models. The matrix columns were rearranged to evaluate seven factors possibly related to the nestedness of bird communities. Bird assemblages exhibited a significant nested pattern (67.93) and all factors contributed ($p < 0.01$) to the nestedness patterns of bird communities. Habitat diversity and cay area and perimeter were the factors that contributed most to the nested structure. The nestedness pattern in the bird assemblages of the Jardines de la Reina archipelago was potentially caused by the interaction of selective extinction and differential colonization of species, with the former having a more remarkable effect.

Key words: Nested structure, Fragmented biota, Selective extinction, Differential colonization

Resumen

Factores subyacentes que promueven el anidamiento de ensamblajes de aves en cayos del archipiélago de los Jardines de la Reina, Cuba.— La evaluación de los factores asociados a los modelos de anidamiento se ha convertido en un aspecto esencial de los estudios sobre estructuración de comunidades. Los ensamblajes de aves del archipiélago de los Jardines de la Reina presentan una estructura anidada estable, aunque sus causas permanecen sin evaluar. Se elaboró una matriz de datos de presencia y ausencia a partir de un inventario de aves obtenido en 43 cayos de este archipiélago. Se calculó el anidamiento mediante el índice NODF basado en el relleno superpuesto y decreciente. La significación del anidamiento se evaluó mediante 1.000 iteraciones de cuatro modelos nulos. Las columnas de la matriz se reordenaron para evaluar siete factores que podrían estar relacionados con el anidamiento en las comunidades de aves. Los ensamblajes de aves presentaron un modelo de anidamiento significativo (67,93) y todos los factores contribuyeron ($p < 0,01$) a los modelos de anidamiento de las comunidades de aves. La diversidad de hábitats y el área y el perímetro de los cayos fueron los factores que más contribuyeron a la estructura anidada. El modelo de anidamiento de los ensamblajes de aves en los Jardines de la Reina podría estar causado por la interacción de la extinción selectiva y, en menor medida, por la colonización diferencial de especies.

Palabras clave: Estructura anidada, Biota fragmentada, Extinción selectiva, Colonización diferencial

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Introduction

Nestedness is a characteristic pattern in insular biotas (Rodríguez–Gironés & Santamaría, 2006; Moore & Swihart, 2007) although it may be uncommon in some oceanic islands (e.g., Florencio et al., 2015; Matthews et al., 2015). This model structure can be observed in fragmented scenarios, where the species of depauperated fragments constitute 'proper' subsets of those in richer fragments (Patterson & Atmar, 1986; Patterson, 1987). Nestedness could be generated by one or many factors, depending on the taxonomic entity and the biogeographical features of the study site in question. Wright et al. (1998) noted that any factor that favors or affects the assembly of species communities from a common pool, in a consistent order, may produce nested patterns. Elucidating the factor(s) promoting nested distributions can be a complicated process due to the confluence of many environmental variables, such as 'nuisance factors' (Méndez, 2004; González–Oreja et al., 2012).

Two mechanisms that play an essential role in the unfolding of nested structures in natural assemblages of species are selective extinction (species loss within fragments in a predictable sequence based on their adaptability) and species' differential colonization (occupancy of the fragments by species based on their dispersal capabilities) (Patterson & Atmar, 1986; González–Oreja et al., 2012). Selective extinction generates non–random losses because species requiring large minimum areas or forming small populations tend to be more prone to extinction events. In the differential colonization approach, stronger dispersers will take up more fragments than the rest, and this produces ordered differences of species between fragments.

Other factors promoting nestedness are the area and isolation among the fragments (Feeley, 2003), disturbances (Bloch et al., 2007), interspecific competition, habitat fragmentation and quality, behavioral responses and species' environmental tolerance, and landscape continuity (Méndez, 2004; González–Oreja et al., 2012). The effect of area upon nestedness rests on the fact that species requiring large home ranges/territories will occupy only large fragments, while species with more phenotypic flexibility regarding habitat exploitation strategies will occur in every fragment (Wright et al., 1998; Feeley, 2003). Isolation is related to the distance effect, in which species with greater dispersal capabilities can be found in all fragments (including the most isolated ones), while more sedentary species could occupy the fragments closest to the dispersion source (Wright et al., 1998; Longo–Sánchez & Blanco, 2009). The shape of fragments is another potential factor contributing to nestedness because islands with more complex shapes may exhibit greater topographic complexity and habitat heterogeneity, enabling the coexistence of a higher number of species (Hu et al., 2011).

Bloch et al. (2007) stated that intense disturbances would alter nestedness patterns at small spatial scales because these phenomena can lead to local extinction. Conversely, periodic disturbance can facilitate the coexistence of species that, in absence of disturbance,

might be mutually exclusive. In general, a disturbance can destroy nested structure if rare species are eliminated or if local extinctions are density–independent (Bloch et al., 2007). Nevertheless, González–Oreja et al. (2012) based their assertion on the differences of species' tolerance to consider disturbance as a promoter of nestedness.

The influence of interspecific competition on nested structures may be ambiguous due to the existence of divergent criteria about this factor (Méndez, 2004). Bloch et al. (2007) consider that competitive exclusion reduces nestedness by preventing the co–occurrence of species that could otherwise share the same ecological niches. However, competition also affects nestedness by shifting the species composition or the checkerboard structure of the assemblages (Feeley, 2003; Almeida–Neto et al., 2007). Nevertheless, McLain & Pratt (1999) considered that competition along with habitat heterogeneity can reinforce nestedness because competitive exclusion becomes stronger as the fragments' habitat complexity decreases.

Hierarchical habitat distributions (habitat nestedness) also play an important role in species nestedness (Higgins et al., 2006; Ulrich et al., 2009; Watson et al., 2009). According to this factor, species nestedness is a direct outcome of non–random distribution of habitats. Despite the different ways that nestedness models can be generated, Ulrich et al. (2009) state that all underlying factors are usually defined by environmental or biological gradients leading to orderly changes of colonization and extinction events in fragmented areas.

Nestedness is a typical feature of a wide variety of insular biotas that include plants, arthropods, reptiles, birds and mammals (Calmé & Desrochers, 1999; Almeida–Neto et al., 2007). It characterizes the structure of meta–communities and describes species' spatial distributions in less discrete habitats (Bloch et al., 2007; Moore & Swihart, 2007). Nestedness has been used to estimate minimum viable population sizes, to evaluate fragment connectivity, to characterize the resilience of disturbed communities (Bloch et al., 2007), and to predict species' extinction rates (Azeria & Kolasa, 2008). It has also been widely used in decision–making in conflicting conservation scenarios to help determine whether the protection of small fragments should be prioritized over larger areas (Bloch et al., 2007).

In the Jardines de la Reina archipelago (JRA), south of Cuba, bird assemblages exhibit a stable nestedness pattern which becomes more remarkable during the spring season (García–Quintas & Parada, 2014). Owing to the relatively little geographic isolation (for birds) and the poor landscape complexity (with low habitat diversity) of the JRA, we proposed that factors related to physical characteristics of cays (e.g., area, shape) may play a crucial role in bird nestedness unfolding and its stability over time. We would thus expect that the effect of these factors on nestedness would be greater than any other factor studied herein. The objective of this work was to assess the effects of possible driving factors on the nested structures of avian assemblages in the JRA. Such data may be relevant to detect the ecological components that stabilize the nested pattern of birds in this insular region.

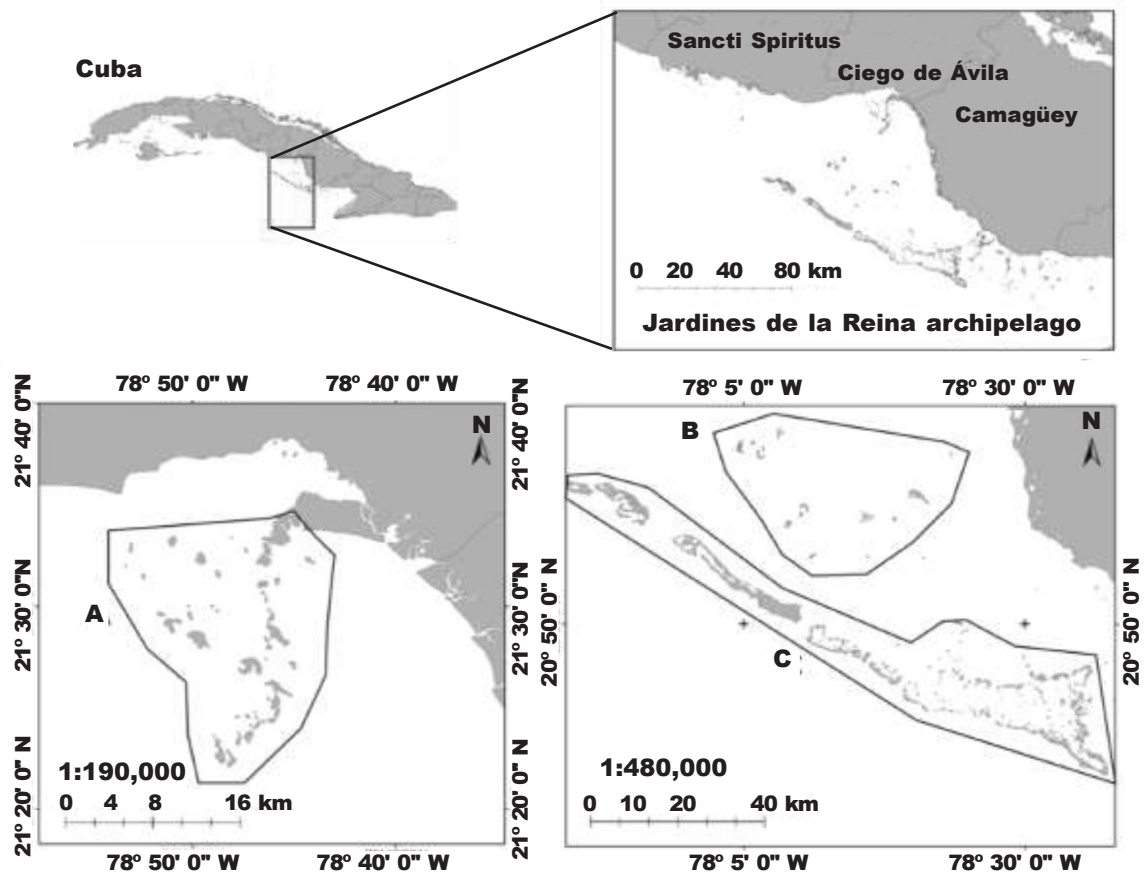


Fig. 1. Geographic location of the three main insular sub-groups of the Jardines de la Reina archipelago, Cuba: A. Cays of Ana María; B. Central cays of the gulf of Ana María; and C. Cays of Doce Leguas.

Fig. 1. Ubicación geográfica de los tres subgrupos insulares principales del archipiélago de los Jardines de la Reina, Cuba: A. Cayos de Ana María; B. Cayos del centro del golfo de Ana María; C. Cayos de las Doce Leguas.

Material and methods

Study area

The JRA stretches along the southern coast of the Isle of Cuba and is made up of numerous cays, flats, sandbanks and coral reefs. The present study encompasses 43 cays from the three main sub-groups: cays of Ana María, cays of the central part of the Gulf of Ana María, and cays of Doce Leguas (fig. 1). In general, the study site is characterized by fragile ecosystems with low species richness, and the most representative vegetation type is mangrove forests. Xeromorphic scrub and complexes of sandy and rocky shoreline vegetation can also be found.

Zúñiga (2000) noted that the origin of the cays of Doce Leguas experienced a gradual growth along the E–W axis during the Holocene through various geological and climatic processes. This is evident

in the different geological development of the cays (more complex cays eastward), and the diversity and structural complexity of its vegetation. The emergence of these cays acted as a barrier, restricting water exchange between the Gulf of Ana María and the Caribbean Sea. This favored the accumulation of muddy sediments in the gulf, which in turn led to the origin of many other cays (e.g., cays of Ana María and the central keys of the Gulf of Ana María) (Zúñiga, 2000). Those cays and islets are characterized by an oceanic origin with a recent geological history.

Sampling effort

Current knowledge of species occurrence in the study site is spatially biased towards the larger cays with higher vegetation diversity. Most surveys to date have been conducted in such cays and more comprehensive sets of census techniques have been applied to

describe their avifauna. Differences in the inventories between cays have thus been minimized because the sampling effort was in accordance with the cays' characteristics. To test the effects of the sampling effort, we developed an indicator of sampling effort resulting from multiplying the number of surveys by the number of census techniques used in each cay, divided by the cay's area. High values of this indicator correspond to the best sampling efforts conducted. Nevertheless, due to the standardization of the sampling intensity with respect to the cays' area, we did not consider large differences in sampling efforts in our study (table 1s in supplementary material).

Nestedness analysis

We obtained the presence–absence data of bird species occurring at each surveyed cay from a recent work by García–Quintas & Parada (2014). This study comprised an up–to–date list of the published papers on species inventories carried out in the study area until 2012. We excluded species relying strongly on marine–oceanic habitats, as well as those with no explicit reference to their locality name when first reported. These steps aimed to increase the reliability of checklists and to avoid biases during the nestedness analysis. García–Quintas & Parada (2014) classified the migratory status of bird species at the JRA according to Garrido & Kirkconnell's (2011) criteria and based on their own knowledge on the local avifauna as follows: permanent resident, winter resident, summer resident or transient. Transients were excluded from the analyses because they usually occur in low numbers and exploit resources during limited timeframes while migrating through the area. We thus expected that these species could exert only a negligible influence on the communities' structure and functions.

We created a presence–absence (1–0) matrix whose rows and columns represented species and cays, respectively. Entries were arranged in the matrix in increasing order, starting from the number of cays occupied per species and the number of species per cay in the rows and columns, respectively. We calculated the degree of matrix nestedness using the nestedness metric based on the overlap and decreasing fill (NODF) (Almeida–Neto et al., 2008) by running the software ANINHADO 3.0.3 (Guimarães & Guimarães, 2006). NODF values ranged from 0 (no nestedness) to 100 (perfect nestedness) and this score was compared with those obtained from the simulations (1,000) of four null models (Er, Ce, Co and Li, Bascompte et al., 2003; Almeida–Neto et al., 2007) in order to estimate the significance level of the degree of overall nestedness. The null models followed these rules: Er. Presences are randomly assigned to any cell within the matrix (equal probability of presence of each species in each cay); Ce. The probability of a cell a_{ij} showing a presence is the average of the probabilities of occupancy of its row and column (probability of presence/occupancy is proportional to the degree of generalization in the ecological characteristics of the species and cays); Co. Presences are randomly assigned within the columns (species frequencies fixed with equiprobable site fre-

quencies); Li. Presences are randomly assigned within the rows (site frequencies fixed with equiprobable frequencies of species).

Underlying factors

Seven factors were used to assess their potential effects on the avian nested structures in the JRA. These factors included cay area, perimeter and shape, minimum distance between cays and from the Isle of Cuba (isolation measures), avian habitat diversity in the cays, and habitat nestedness.

We measured the perimeter and area of each island using an unsupervised classification (k –means method, change threshold set at 5%, and three iterations) of a mosaic made up by two *Landsat 5 TM* satellite images, sceneries 13–45 and 13–46, from 11 July and 22 April 2001, respectively. We used ENVI 4.7 software to perform the classification, which yielded seven classes. These were then grouped to help delimit deep waters from the remaining cover types (land, terrestrial vegetation and shallow waters). Thus, a mask file was created to discard information on deep waters, by assigning it a zero value, and to delineate the emerged land of cays and other critical habitats for waterbirds, such as shallow waters. The resulting image (once classified and filtered through the mask) was converted from raster to vector format to calculate the area and perimeter of the 43 cays. For the cays formed by many smaller fragments, the values of area and perimeter of each fragment were added up to obtain the total score of these two variables.

We used the shape index for islands (Hu et al., 2011) to characterize the shape complexity of the chosen cays. In this index, value one means circle–shaped fragment, and the score increases as shape tends to differ from the perfect circular symmetry. The isolation degree was calculated by measuring the minimum distance between each cay and the isle of Cuba (potential source–sink system) and the distance between each cay and its nearest neighbor (potential species flux). Distances were measured from the classified image by using ENVI 4.7 software. Seven habitat classes of critical importance to the avifauna were identified: sandy and rocky coasts, close inland lagoons, open inland lagoons, mangroves, sandy vegetation, rocky vegetation and secondary vegetation. The number of habitats per cay (habitat diversity) was recorded from field observations, information provided by specialists and available cartographic materials. Furthermore, these bird habitat classes were used to evaluate the existence of habitat nestedness through a nested analysis in a new matrix where the rows represented habitat classes instead of species (Wang et al., 2013). The last analysis was performed by using the NODF index and the same null models (Er, Ce, Co and Li).

We followed Lomolino's (1996) method to assess the influence of each factor on nestedness, although we used the NODF index to quantify the degree of nestedness. This method is regarded as one of the most suitable and broadly applied to infer the related factors of nestedness (Fernández–Juricic, 2000; Ulrich et al., 2009; Valencia–Pacheco et al., 2011).

Essentially, it is a way to evaluate the possible drivers of nestedness where it is assumed that immigration probability decreases whereas isolation increases, and the extinction probability decreases insofar as the area increases. The main advantage of this method lies in its flexibility to assess the effect of each factor from the principle of fragment rearrangement within the data matrix (Fernández–Juricic, 2000; Méndez, 2004). It also allows, though indirectly, the linking of the nestedness patterns with the processes of selective extinction (e.g., matrix with fragments ordered by area) and differential colonization (e.g., matrix with fragments ordered by isolation).

Thus, seven presence–absence matrices (one per factor) were assembled in the same way that the matrix was built for the general analysis of the nestedness, but columns (cays) within the matrices were rearranged according to the factor to be evaluated. Ordination criteria of the matrices' columns were arranged in a decreasing order from left to right for area, perimeter, shape and habitat diversity. Cay–to–cay and cay–isle of Cuba distances were arranged in descending order. If analysis of habitat nestedness was positive, then ordination of the columns to evaluate this factor would be equal to the matrix of habitat nestedness.

We evaluated the underlying factors of nestedness in the seven matrices through the NODF index and their level of significance was estimated by running 1,000 simulations of the null model Li per matrix. The selection of this null model is based on its unique capability to randomize presence within the matrices, but to keep the initial order of the columns unaltered, according to the Lomolino (1996) approach. The remainder of the null models (Er, Co and Ce) can not be used for this test because their randomization algorithms provoke changes in the order of the columns, limiting the evaluation of the nestedness factors. Factors whose matrices yielded significant scores on the NODF index were considered as factors related to the nestedness of the bird assemblages, and the index value also indicated how important the influence of each factor was on this pattern. Factors assessed were related, although indirectly, to selective extinction (area, perimeter, shape, bird habitat diversity and habitat nestedness) and species differential colonization (isolation). To calculate the descriptive statistics of the scores from null models, we used the software Statistica 8.0 (StatSoft, 2007) and evaluated statistical significance at three p values: < 0.1 , < 0.05 and < 0.01 .

Results

Main physical characteristics of the cays

Cays such as Cinco Balas and Grande were among the three localities with the highest scores of area and perimeter. Cayuelo, Obisipito and Quitasol showed the lowest values and have an almost circular shape (table 1). Highest isolation levels with respect to the nearest cays were reported in 75% of the cays

in the central part of the Gulf of Ana María; Palomo and Santa María cays showed distances over 10 km. The westernmost cays of the Doce Leguas group (Bretón, Alcatracito, Alcatraz and Cinco Balas) were the farthest from Cuba's southern coast (over 80 km offshore). Algodón Grande, Cachiboca, Caguama and Anclitas were the richest cays in terms of bird habitat diversity (table 1); with the exception of Anclitas, all these cays presented secondary vegetation, a fairly uncommon feature in the landscape of the JRA.

Nestedness of the avifauna of the JRA

A total of 77 bird species were found in the sampled cays (transients excluded), but *Fregata magnificens* (Magnificent Frigatebird) was discarded prior to the nestedness analyses due to its strong dependence on marine resources rather than on terrestrial ecosystems (table 2s in supplementary material). Bird assemblages in the JRA showed a significantly nested structure (NODF = 67.93; $p < 0.01$) with respect to those randomly generated by the four null models. The NODF simulated scores were 39.19 ± 1.25 [35.14–43.48], 43.41 ± 0.86 [40.57–46.04], 29.87 ± 0.96 [26.94–32.68] and 40.79 ± 0.53 [39.18–42.60] for Ce, Co, Er and Li, respectively.

Underlying nestedness factors

Overall distribution of bird habitats among cays was significantly nested (NODF_{obs} = 69.67; $p < 0.01$) according to the scores (mean \pm SD [min–max]) of three null models (NODF_{Ce} = 60.71 ± 3.46 [50.10–70.12], NODF_{Co} = 53.60 ± 1.32 [50.48–60.36], NODF_{Er} = 54.59 ± 3.34 [44.79–65.86]). Only Li showed low probabilities (for the three levels of p significance) of occurrence of this pattern (NODF_{Li} = 65.54 ± 3.77 [49.26–75.63]; $p = 0.13$).

We found that all factors contributed to the nestedness of bird assemblages in the JRA (table 2). Hierarchically, bird habitat diversity reached the highest value of the NODF index, which means that it was the main driving factor of nested structures and the existence of strong habitat–bird associations in the study site. The latter statement was further supported by the habitat nestedness' contribution. The area, perimeter and shape of the cays were also important factors related with the observed nestedness degree of bird assemblages (table 2). However, the isolation of the cays (minimum distances) also contributed, although to a lesser extent than other factors.

Discussion

Bird assemblages of JRA were nested, showing a cohesive and non–random structure at the level of the regional meta–community. Formally, the implications of the nestedness patterns for biological studies focus on the associated factor(s) leading to such structuring (Cutler, 1994). Nestedness of bird assemblages in this archipelago was influenced by several factors, but bird habitat diversity played a fundamental role. Factors

Table 1. General features of 43 cays of the Jardines de la Reina archipelago, Cuba. The shape index (SI) describes the contour of the cays based on a perfect circular shape (SI = 1): C-C. Cay-to-cay; C-I. Cay-to-isle of Cuba; NBh. Number of bird habitats; NBsp. Number of bird species.

Tabla 1. Características generales de 43 cayos del archipiélago de los Jardines de la Reina, Cuba. El índice de forma (SI) describe el contorno de los cayos a partir de la forma de un círculo perfecto (SI = 1). (Para consultar las abreviaturas, véase arriba.)

Cay	Area (km ²)	Perimeter (km)	SI	Minimum distance (km)		NBh	NBsp
				C-C	C-I		
Cayuelo	0.02	0.72	1.44	0.52	11.50	1	3
Obispito	0.03	0.84	1.38	1.08	6.21	4	8
Quitasp	0.05	1.02	1.34	0.48	11.95	2	5
La Loma	0.06	1.50	1.72	0.55	17.64	2	6
Obispo	0.09	2.76	2.66	1.08	4.32	4	14
Guinea	0.13	1.92	1.50	1.55	7.30	4	11
Cargado	0.15	3.48	2.50	8.21	46.16	4	20
La Tea	0.17	2.46	1.71	1.06	8.00	2	8
Bergantines	0.22	4.20	2.54	7.14	35.66	4	18
Caoba	0.26	3.84	2.14	1.52	11.85	3	17
Palomo	0.28	6.84	3.63	14.72	40.20	4	23
Santa María	0.29	3.12	1.63	10.85	13.17	4	22
Boca Rica	0.36	6.96	3.27	0.71	37.75	2	12
Largo	0.48	7.32	2.98	5.20	37.88	3	5
Juan Grin	0.63	16.74	5.93	0.05	39.25	3	16
Algodoncito	0.77	5.82	1.88	3.66	28.07	4	29
Camposanto	0.82	6.42	2.00	0.12	38.50	4	11
Flamenco	0.84	7.50	2.31	0.29	11.86	4	35
Cana	0.91	11.34	3.35	0.20	18.69	5	16
Arenas	0.97	9.84	2.81	1.18	20.05	4	18
Tío Joaquín	1.21	11.07	2.84	0.00	13.64	5	18
Providencia	1.29	13.38	3.32	1.52	8.86	5	5
Alcatracito	1.34	11.04	2.69	0.48	85.64	4	19
Boca de la Piedra de Piloto	1.52	19.14	8.38	0.64	45.05	4	25
Piedra Grande	1.53	16.51	3.76	0.09	46.28	5	20
Guásimas	1.59	8.70	1.95	1.00	12.63	4	6
Balandras	1.62	15.36	3.41	0.54	12.36	2	3
Boca Seca	1.76	30.24	6.44	0.05	37.49	2	25
Alcatraz	1.84	16.38	3.40	0.08	81.93	4	14
Manuel Gómez	2.11	34.80	6.76	3.66	33.03	4	11
Punta de Los Machos	2.14	26.61	5.13	0.00	14.88	3	9
Cuervo	2.16	35.28	6.78	8.21	46.85	5	27
Cachiboca	2.44	57.00	10.30	1.83	42.37	6	26
Boca Piedra Chiquita	2.88	11.28	1.88	0.42	46.47	5	24
Algodón Grande	3.64	32.70	4.84	5.42	21.10	6	50
Las Cruces	3.64	55.37	8.19	0.09	43.42	4	29
Cabeza del Este	6.82	94.44	10.20	0.07	31.44	5	34
Bretón	7.51	71.46	7.36	0.77	91.00	4	37
Caguama	7.66	87.42	8.92	0.68	34.38	6	60
Anclitas	9.06	158.64	14.87	0.42	46.65	6	68
Grande	24.29	193.17	11.06	0.00	58.23	5	61
Caballones	33.52	73.68	3.59	0.00	52.65	5	47
Cinco Balas	43.56	151.20	6.46	0.08	81.43	3	27

Table 2. Evaluation of the effects of seven factors potentially related to the nestedness of bird assemblages in 43 cays of the Jardines de la Reina archipelago, Cuba. The simulated scores ($N = 1,000$) of the null model L_i are shown as mean \pm SD (min–max); NODF. Nestedness metric based on overlap and decreasing fill; P . Probability.

Tabla 2. Evaluación del efecto de siete factores que podrían estar relacionados con el anidamiento de los ensamblajes de aves en 43 cayos del archipiélago de los Jardines de la Reina, Cuba. Los valores simulados ($N = 1.000$) del modelo nulo L_i se muestran como media \pm DE (mín–máx): NODF. Índice de anidamiento basado en el relleno superpuesto y decreciente; P . Probabilidad.

Factor	NODF _{obs}	NODF _{L_i}	P
Area	64.90	35.52 \pm 0.73 (33.51 - 37.88)	< 0.01
Perimeter	64.82	35.53 \pm 0.73 (33.57 - 38.21)	< 0.01
Shape	64.26	35.58 \pm 0.76 (32.94 - 38.39)	< 0.01
Minimum distance (cay–to–cay)	61.42	35.51 \pm 0.73 (33.34 - 38.05)	< 0.01
Minimum distance (cay–isle of Cuba)	57.16	35.56 \pm 0.72 (33.41 - 37.93)	< 0.01
Bird habitat diversity	65.85	35.52 \pm 0.70 (33.09 - 37.91)	< 0.01
Bird habitat nestedness	64.11	35.52 \pm 0.74 (33.27 - 38.34)	< 0.01

associated with the physical characteristics of the cays (area, perimeter and shape) also contributed to the nested structure in a significant way. We indirectly inferred that selective extinction could be the principal historical mechanism that triggers and stabilizes the observed nested patterns, without excluding the contribution of differential colonization events.

Diversity of avian habitats was the most influential ecological factor regarding nestedness in the JRA. Although this factor may not overshadow the effects of other factors, it could diminish their effects. In this regard, Calmé & Desrochers (2000) consider that if species richness is correlated with habitat diversity, the area per se constitutes a secondary factor. The latter could be related to marked preferences of certain groups of species over some specific habitats (Calmé & Desrochers, 1999). While shorebirds, gulls, herons and other waterbirds exploited common habitats (e.g., mangroves, coasts, lagoons) in most cays, several species of warblers, cuckoos and thrushes were restricted to sandy vegetation, a bird habitat present in fewer cays. Seemingly, the habitat factor plays a key role in the nestedness patterns of the avian communities inhabiting the JRA. This may well reinforce the intricate species–habitat relationships even further as a pivotal ecological factor determining species distribution patterns, mainly because birds are a highly–mobile group with great dispersal capability.

The contributions of habitat nestedness reinforce the effect of habitat diversity, but represent a superior level of organization. The relationship between this pattern and the birds' nested structures reflects the strong dependence of bird species upon their habitats, since such habitats constitute their sources of foraging, reproduction and refuge. Habitat nestedness is

thought to be among those processes that explain the nested structures found in bird communities that have eluded much criticism since it rests mostly on the links between birds and their habitats, and disregards species' population dynamics and natural history (Calmé & Desrochers, 1999; Wang et al., 2013). Thereby, species exploiting common habitats should be widespread whereas species depending on uncommon habitats should be confined to a few sites (Wright et al., 1998).

Hu et al. (2011) summarize that area, isolation and shape of the fragments are among the main factors shaping species richness patterns and meta-community assemblages. Shape may be related to the physical complexity of fragments, and thus to their potential capacity for supporting more or fewer numbers of species. Perimeter might also influence the degree of nestedness of the fragments (e.g., cays made up by several fragments) or the habitat availability in transition zones. For instance, the water/land interface offers habitats and food webs exploited by terrestrial, marine and those organisms confined to this ecotone (Pizarro et al., 2012), which in turn might generate nested patterns.

The strong species–area relationships, long considered a cornerstone of the MacArthur & Wilson (1967) Theory of Biogeography of Isles, can reflect features of habitat spatial distribution, growth dynamics and population extinction as well as the dispersion and habitat selection statistics (Coleman et al., 1982). In the JRA, the area of the cays was one of the factors generating nestedness of bird communities, as illustrated by the finding that larger cays (e.g., Grande, Caguama) supported higher species richness than smaller ones, and bird richness in small cays is a subset of the big cays.

This coincided with the results of Ambuel & Temple (1983) and Fernández-Juricic (2000), who focused on the avian assemblages associated with the fragmented deciduous forests of eastern North America and the urban parks of Madrid, respectively.

Isolation metrics (cay-to-cay and cay-isle of Cuba) contributed less than other factors to the avian communities' nestedness detected in the JRA. Of these metrics, minimum distance between cays was the most important factor, probably due to the different degrees of isolation between the three insular subgroups. In this regard, the central cays of the gulf of Ana María were the most isolated ones in the study site, whereas many cays of Doce Leguas are closer to one another. These isolation differences along with the varying dispersal capability shown by bird species may favor the development of the nestedness structures in the JRA's avian assemblages. Longo-Sánchez & Blanco (2009) mentioned that the effect of distance or isolation could be accounted for by the geographical isolation and the species dispersal skills.

The curved shape of the southern coast of central Cuba, along with the relative position of the cays in the study site (fig. 1), clearly illustrates their proximity to the mainland. This condition may favor the flux of species between these two areas, especially for birds, which in turn, would account for the minor contribution (among the factors evaluated) of the distance among cays and between the cays and the Isle of Cuba to the development of nested structures. The species dispersal movements may also be favored by the low isolation of the cays of each insular subgroup and because birds are among the vertebrates with the greatest dispersal skills over the water (Cook & Quinn, 1995). Lees & Peres (2006) assert that the distance and isolation metrics become relevant at predicting species richness when habitat fragments are scattered in ranges from 100 to 10,000 m. Most of the minimum distances reported in the JRA fall within this range. Moreover, Higgins et al. (2006) considered that population dynamics of the birds inhabiting the Greater Antilles are largely determined by natality and mortality processes rather than by the species migratory behavior, given the long distances separating the islands. This view should not be generalized, however, because an important assortment of the Cuban avifauna is made up of migratory species coming from various regions of the American continent.

Area, perimeter and shape of the cays in the JRA were the factors related to the selective extinction of species. This finding relies on the potential effects of these mechanisms regarding the capability of the cays for harboring bird species as well as on the species' adaptability. The isolation metrics were indirectly correlated with the species' dispersal capacity, a key element for analyzing the differential colonization process. Differences in the diversity of bird habitat among the sampled cays favored extinction over the colonization process, as the degree of isolation does not appear to pose an effective barrier for preventing most of the species from wandering across this insular region.

Nevertheless, the isolation of the cays could limit the distribution of some species of birds with rather

low dispersion in the JRA. It is of interest that endemic taxa such as *Xiphidiopicus percussus*, with common and broadly distributed year-round populations in many cays of Doce Leguas, are not known to occur in the central and northern cays of the Gulf of Ana María, although they are closer to the southern coast of central Cuba, where the species' preferred habitats are highly represented (mangrove forests) (Parada & García-Quintas, 2012). Further evidence regarding the limited connectivity between the JRA and the mainland bird populations comes from the possible relictual populations of *Quiscalus niger*, with the subspecies *Q. n. caribaeus* persisting in the northern and southern archipelagos, including the Isle of Pines and the westernmost region of the mainland, having apparently been replaced elsewhere on the mainland by *Q. n. gundlachi* (Buden & Olson, 1989).

Patterson & Atmar (1986), Wright et al. (1998) and Feeley (2003) state that selective extinction is, in natural archipelagos, a more frequent phenomenon rendering higher nestedness scores over the species' differential colonization. However, the presumed prevalence of extinction over colonization as a mechanism that promotes nested structures is not generalized. In the JRA, as in the study of Valencia-Pacheco et al. (2011), both colonization and extinction played essential roles in the development of nestedness patterns, coinciding with Murgui (2010), who considers these two processes as not mutually exclusive. Nonetheless, the effects of the other factors suggest that species' selective extinction could contribute to the avian assemblages' nestedness in the JRA. This insular region possesses peculiar features such as an oceanic origin and location not far from larger landmasses (e.g., the Isle of Cuba, the North American continent). Such location may have facilitated connectivity between the avifauna of the JRA and the neighboring emerged lands as the flux of species should have not been highly restricted.

Despite the differences in the sampling effort across the study site, the probable absence of true nestedness patterns was ruled out. As shown by the sampling effort indicator, survey intensity corresponded to the cays' area. Furthermore, cays such as Caguama, Anclitas, Grande and Algodon Grande have been surveyed more frequently with the aid of several census techniques, as it was long assumed that they may harbour higher levels of avian biodiversity. The least surveyed cays are generally characterized by more homogeneous vegetation and fewer habitat types. For example, Cayuelo, Quitasol and La Tea are small cays that have a low diversity of bird habitat and predominance of mangrove forests. In these cays, bird species can be detected in few sampling sections. However, it will be important to improve the sampling design to reduce or eliminate the associated biases and use other metrics to quantify the sampling intensity.

We believe that the nested structures detected in the JRA avifauna may have initially been generated by differential colonization (due to the oceanic origin of the JRA), and later reinforced by the selective extinction of species. Such extinction events could have taken place through demographic processes such as

mortality and emigration, as well as by displacement of certain species via competitive exclusion. Differential colonization may contribute to nestedness stability but does not seem determinant in this insular region, as reflected by the lack of influence of the annual migrations on the degree of assemblages' nestedness, as shown by García-Quintas & Parada Isada (2014). Therefore, cays with greater habitat diversity, larger area and higher bird species richness will act as source patches within the JRA and thus preserve the nestedness of avian assemblages. In this case, Ancítas, Grande, Caguama, Caballones and Algodón Grande cays are the most important sites for avian conservation. The latter is not currently included within the Cuban system of protected areas and its future inclusion might well be the next step towards the efficient design of regional reserve networks in which the avifauna's functional connectivity and nestedness are pivotal theoretical frameworks.

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Supplementary material

Table 1s. Evaluation of the sampling effort in 43 cays of the Jardines de la Reina archipelago, Cuba, for a study about the nested structure of the bird assemblages in these cays: Ns. Number of surveys; Nct. Number of census techniques; Ise. Indicator of sampling effort. (Values of areas are given in table 1.)

Tabla 1s. Evaluación del esfuerzo de muestreo en 43 cayos del archipiélago de los Jardines de la Reina, Cuba, para un estudio sobre la estructura anidada de los ensamblajes de aves de estos cayos: Ns. Número de muestreos; Nct. Número de técnicas de censo; Ise. Indicador del esfuerzo de muestreo. (Los valores de las áreas se presentan en la tabla 1.)

Cays	Ns	Nct	Ise	Cays	Ns	Nct	Ise
Cinco Balas	2	1	0.05	Algodoncito	1	1	1.30
Caballones	2	1	0.06	Piedra Grande	2	1	1.31
Cabeza del Este	1	1	0.15	Boca de la Piedra de Piloto	2	1	1.32
Bretón	2	1	0.27	Juan Grin	1	1	1.59
Punta de Los Machos	1	1	0.47	Largo	1	1	2.08
Manuel Gómez	1	1	0.47	Anclitas	7	3	2.32
Alcatraz	1	1	0.54	Caguama	6	3	2.35
Las Cruces	2	1	0.55	Camposanto	2	1	2.44
Balandras	1	1	0.62	Caoba	1	1	3.85
Guásimas	1	1	0.63	Boca Rica	2	1	5.56
Boca Piedra Chiquita	2	1	0.69	La Tea	1	1	5.88
Alcatracito	1	1	0.75	Santa María	2	1	6.90
Providencia	1	1	0.78	Palomo	2	1	7.14
Cachiboca	2	1	0.82	Guinea	1	1	7.69
Algodón Grande	3	1	0.82	Bergantines	2	1	9.09
Tío Joaquín	1	1	0.83	Obispo	1	1	11.11
Cuervo	2	1	0.93	Cargado	2	1	13.33
Grande	8	3	0.99	La Loma	1	1	16.67
Arenas	1	1	1.03	Quitasol	1	1	20.00
Cana	1	1	1.10	Obispito	1	1	33.33
Boca Seca	2	1	1.14	Cayuelo	1	1	50.00
Flamenco	1	1	1.19				

Table 2s. Incidence matrix of non-transient bird species occurring in 43 cays in the Jardines de la Reina archipelago, Cuba: A. Anclitas; B. Grande; C. Caguama; D. Algodón Grande; E. Caballones; F. Bretón; G. Flamenco; H. Cabeza del Este; I. Las Cruces; J. Algodoncito; K. Cinco Balas; L. Cuervo; M. Cachiboca; N. Boca de la Piedra de Piloto; O. Boca Seca; P. Boca Piedra Chiquita; Q. Palomo; R. Santa María; S. Piedra Grande; T. Cargado; U. Alcatracito; V. Arenas; W. Tío Joaquín; X. Bergantines; Y. Caoba; Z. Juan Grin; a. Cana; b. Alcatraz; c. Obispo; d. Boca Rica; e. Camposanto; f. Guinea; g. Manuel Gómez; h. Punta de Los Machos; i. La Tea; j. Obispito; k. La Loma; l. Guásimas; m. Providencia; n. Quitasol; o. Largo; p. Cayuelo; q. Balandras; * Presence; – Absence.

Species	Cay																			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	
<i>Setophaga petechia</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Ardea herodias</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Quiscalus niger</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	–	*	*	*
<i>Phalacrocorax auritus</i>	*	*	*	*	*	*	–	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Charadrius wilsonia</i>	*	*	*	*	*	–	*	*	*	*	*	*	–	*	–	*	*	*	*	
<i>Thalasseus maximus</i>	*	*	*	*	*	–	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Patagioenas leucocephala</i>	*	*	*	*	*	*	*	*	*	–	*	–	*	*	*	*	*	–	–	*
<i>Pandion haliaetus</i>	*	*	*	*	*	*	–	*	*	*	*	*	*	*	*	*	*	*	–	–
<i>Zenaida asiatica</i>	*	*	*	*	*	*	–	*	*	–	*	–	*	*	*	*	*	*	–	*
<i>Pelecanus occidentalis</i>	*	*	*	*	*	*	–	*	*	*	*	*	*	*	*	*	*	*	–	–
<i>Tyrannus dominicensis</i>	*	*	*	*	*	*	*	*	*	–	*	–	*	*	*	*	*	–	–	–
<i>Tyrannus caudifasciatus</i>	*	*	*	–	*	*	*	*	*	*	–	–	*	*	–	–	–	–	–	–
<i>Setophaga discolor</i>	*	*	*	*	*	*	*	*	–	*	–	*	*	–	*	*	*	*	*	–
<i>Butorides virescens</i>	*	*	*	*	*	*	*	*	–	*	*	*	–	*	*	–	*	–	*	*
<i>Vireo altiloquus</i>	*	*	*	*	*	*	*	–	*	–	*	*	*	–	*	–	–	–	*	*
<i>Ardea alba</i>	*	*	*	*	*	*	*	*	*	–	*	–	*	*	*	*	*	–	–	*
<i>Egretta rufescens</i>	*	*	*	*	*	*	–	–	*	*	*	*	*	*	*	*	*	*	–	–
<i>Arenaria interpres</i>	*	*	*	*	*	–	–	–	–	–	*	*	–	*	*	*	*	*	*	*
<i>Contopus caribaeus</i>	*	*	*	*	*	*	*	*	*	*	–	–	–	*	–	–	–	–	–	–
<i>Parkesia noveboracensis</i>	*	*	*	*	*	*	*	*	–	*	–	*	–	–	–	*	*	*	*	–
<i>Zenaida macroura</i>	–	–	*	*	–	–	*	*	*	–	*	–	–	*	*	–	–	*	–	–
<i>Cathartes aura</i>	*	*	*	*	*	*	*	*	*	–	*	–	*	–	*	–	–	*	*	*
<i>Chordeiles gundlachii</i>	*	*	*	*	–	–	*	–	*	–	–	–	*	*	–	*	–	–	*	*
<i>Chlorostilbon ricordii</i>	*	*	*	*	*	*	*	–	*	*	*	–	–	*	*	*	–	–	*	*
<i>Egretta tricolor</i>	*	*	*	*	*	*	*	*	*	–	*	*	*	–	*	–	–	–	–	*
<i>Setophaga ruticilla</i>	*	*	*	*	*	*	*	*	–	*	–	*	–	*	–	*	*	*	*	–
<i>Thalasseus sandvicensis</i>	*	*	*	*	–	–	–	*	–	*	–	*	–	–	–	*	–	–	–	–
<i>Setophaga palmarum</i>	*	*	*	*	*	–	*	–	–	*	*	*	–	–	–	–	*	*	*	–
<i>Eudocimus albus</i>	*	*	*	–	*	–	*	–	*	–	–	–	*	*	*	–	–	–	–	*
<i>Buteogallus gundlachii</i>	*	*	*	*	*	*	–	*	*	–	*	*	*	–	*	–	–	–	–	–
<i>Myiarchus sagrae</i>	*	*	*	*	*	*	*	*	*	–	–	–	*	*	–	–	–	–	–	*
<i>Agelaius humeralis</i>	*	*	*	–	*	–	–	*	*	–	–	–	*	*	*	*	–	–	*	*
<i>Egretta caerulea</i>	*	*	*	*	–	*	–	*	–	*	*	*	–	–	–	–	–	–	–	*
<i>Rallus longirostris</i>	*	*	*	*	–	*	–	*	–	*	–	*	–	–	–	–	*	–	–	–
<i>Leucophaeus atricilla</i>	*	*	*	*	–	–	*	–	–	*	–	*	–	*	–	*	–	*	–	–
<i>Anhinga anhinga</i>	*	*	*	–	*	*	–	*	*	–	*	–	–	–	–	*	–	–	–	–
<i>Megaceryle alcyon</i>	*	*	*	*	*	*	*	–	–	*	–	*	–	–	–	–	*	*	–	–

