

# Spatial distribution patterns of terrestrial bird assemblages on islands of the Sabana–Camagüey Archipelago, Cuba: evaluating nestedness and co-occurrence patterns

C. A. Mancina, D. Rodríguez Batista & E. Ruiz Rojas

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## Abstract

*Spatial distribution patterns of terrestrial bird assemblages on islands of the Sabana–Camagüey Archipelago, Cuba: evaluating nestedness and co-occurrence patterns.*— Using distribution data of 131 terrestrial bird species on 17 islands of the Archipelago Sabana–Camagüey, Cuba, we tested for non-randomness in presence–absence matrices with respect to co-occurrence and nestedness. We conducted separate analyses for the whole assemblage and sub-matrices according to trophic levels and residence status (breeding and migratory). We also explored the influence of weighting factors such as island area and isolation. The C-occurrence analyses were susceptible to the species subsets and the weighting factors. Unweighted analyses revealed a significant negative co-occurrence pattern for the entire assemblage and for most sub-matrices. The area weighted analyses always indicated strong non-random structure. However, an analysis with intra-guild species pairs showed that most pairs were randomly assembled; very few pairs had a significant segregated pattern. Bird assemblages followed a nested subset structure across islands. Nestedness was strongly correlated with area and unrelated with island isolation. Overall, this study suggests that terrestrial bird assemblages were shaped by extinction processes mediated through area effects rather than interspecific trophic guild competition. Data suggest that conservation of largest islands will guarantee high terrestrial bird richness on the archipelago.

Key words: Archipelago, Birds, Community ecology, Cuba, Macroecology, Null models.

## Resumen

*Patrones de distribución espacial de las agrupaciones de aves terrestres en las islas del archipiélago Sabana–Camagüey, Cuba: evaluación de los patrones de anidamiento y de coexistencia.*— Se emplearon datos de distribución de 131 especies de aves terrestres en 17 islas del archipiélago Sabana–Camagüey para analizar la no aleatoriedad en las matrices de presencia y ausencia con respecto a la coexistencia y el anidamiento. Los análisis se realizaron para todo el conjunto y para submatrices por grupos tróficos y estados de residencia (especies migratorias y reproductivas). Además, se analizó la influencia de factores de ponderación, como el área y el aislamiento de las islas. El patrón de coexistencia fue sensible a los grupos de especies y los factores de ponderación. Los análisis no ponderados revelaron un patrón de coexistencia significativamente negativo para todo el conjunto y la mayoría de los grupos. Cuando se usó el área de las islas como factor siempre se observó una estructura no aleatoria de las agrupaciones. Sin embargo, dentro de los gremios tróficos la mayoría de los pares de especies mostraron un patrón aleatorio y muy pocos pares tuvieron un patrón significativamente segregado. La distribución de las aves terrestres sigue una estructura anidada. El anidamiento estuvo fuertemente correlacionado con el área y no presentó relación con el aislamiento de las islas. De manera general este estudio sugiere que las agrupaciones de aves terrestres en este archipiélago están más estructuradas por procesos de extinción selectiva relacionados con el área de las islas, que por la competición interespecífica dentro de gremios tróficos. Los datos sugieren que la conservación de las islas de mayor área podría garantizar una elevada riqueza de especies en el archipiélago.

Palabras claves: Archipiélago, Aves, Ecología de comunidades, Macroecología, Modelos nulos.

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*Carlos A. Mancina & Daysi Rodríguez Batista, Inst. de Ecología y Sistemática, carretera de Varona km 3 ½ Capdevila, Boyeros, A. P. 8029, C. P. 10800, La Habana, Cuba; Edwin Ruiz Rojas, Centro de Estudios y Servicios Ambientales, Villa Clara (Cuba).*

Corresponding author: Carlos A. Mancina. E-mail: [mancina@ecologia.cu](mailto:mancina@ecologia.cu)

## Introduction

Recognition of patterns in ecological communities and understanding the mechanisms that produce these patterns are fundamental goals of ecology and conservation biology. An essential question is whether communities are composed of random species assemblages or whether deterministic processes such as competition influence the composition of species within communities. Diamond (1975) expanded this approach with his analyses of the distribution of terrestrial bird species on islands of the Bismarck Archipelago. He found that interspecific interactions determine non-random co-occurrence patterns and proposed rules known as assembly rules, including the checkerboard distribution, forbidden species combinations, and so on. Diamond's rules and other more recent community assembly rules (such as favored states, food-web structure, guild proportionality, and nested subset) are frequently examined in studies of metacommunities and community ecology (Fortuna et al., 2010; Beaudrot et al., 2013; Henriques-Silva et al., 2013).

Many studies have relied on null models to test the community structure. Null models are randomization methods that exclude a target mechanism to determine whether a specific non-random pattern can be generated (Connor & Simberloff, 1979; Gotelli & Graves, 1996). Two of the most widely applied models are species co-occurrence (Gotelli, 2000) and nestedness (Patterson & Atmar, 1986). The co-occurrence patterns are attributed to competitive inter-specific interactions or environmental factors. Several co-occurrence indices are used to quantify patterns in presence-absence matrices, in many instances relating the observed patterns to Diamond's assembly rules (Gotelli & McCabe, 2002; Collins et al., 2011; Wang et al., 2011). Nested species subsets are a common pattern of community assembly characteristic of many types of fragmented landscapes and insular systems. Nestedness is a condition in which species distributions occur hierarchically so that the fauna of species-poor islands comprise a perfect subset of the fauna on increasingly species-rich islands (Ulrich et al., 2009). In contrast with co-occurrence models, nestedness is not directly related to competition events such as the structuring mechanism of communities. Rather, nested patterns could be related with differential colonization or extinction of species, passive sampling, and carrying capacities, distance or area effects (Patterson & Atmar, 1986; Wright et al., 1998; Ulrich et al., 2009).

Many studies of avian communities on archipelagos or isolated habitats have shown more segregated patterns of co-occurrence than expected by chance, suggesting that interspecific interactions are an underlying mechanism in structuring of bird communities (Stone & Roberts, 1992; Gotelli & McCabe, 2002; Feeley, 2003). Besides, nested patterns of insular bird assemblages are common and have been related to extinction and colonization processes (Lomolino, 1996), habitat nestedness (Calmé & Desrochers, 1999; Wang et al., 2011) and passive sampling (Wright et al., 1998).

The Sabana-Camagüey Archipelago (hereafter SCA) constitutes the largest system of islands or cays

in the Caribbean region (Alcolado et al., 2007). Several studies have contributed to the knowledge of avian richness of some islands (e.g. Garrido, 1973; Sánchez et al., 1994; Wallace et al., 1996, 1999; Rodríguez, 2000; Sánchez & Rodríguez, 2001; González et al., 2008), and 241 bird species have been reported from this archipelago, representing 65% of the whole Cuban ornithofauna (Rodríguez et al., 2007). However, the distribution patterns and factors that determine the species richness on these islands remain unexplored. The high species richness of birds, their geographic position, and the high number of islands that differ in area and landscape characteristics make this archipelago an appropriate scenario to test hypotheses on assembly and structure of bird communities. In this study, we used null model analysis to test for patterns of species co-occurrence and nestedness with data on presence-absence of terrestrial birds from a set of 17 islands from SCA. We explored the potential role of extinction and colonization events as underlying mechanism in the structure of bird assemblages by analyzing correlations of nestedness and island traits, such as area and isolation.

## Material and methods

### Study area and avifauna data

The Sabana-Camagüey Archipelago (SCA) is a chain of 2,515 islands or cays along 465 km of the north coast of Cuba; total area of the SCA is c. 3,414 km<sup>2</sup>. The islands range in area from < 0.1 km<sup>2</sup> to 680 km<sup>2</sup> Cayo Romano, the largest island of the SCA. The landscape heterogeneity and flora diversity tend to be higher on larger islands such as Sabinal, Coco, Romano and Guajaba (Priego-Santander et al., 2004). The vegetation is diverse and several plant communities have been described for the SCA. The mangrove forest is widespread along coasts and constitutes the main coverage on the smallest islands. The most extensive plant formations are the semi-deciduous and dry evergreen forests, xerophytic scrubs, and sandy coastal vegetation (Alcolado et al., 2007).

Data of bird communities across SCA were gathered from an extensive review of literature and our field data. Although information is available about the bird fauna of 86 islands, we selected only 17 islands because these have more complete information about their avian communities (largest number of surveys across several years and seasons). The selected islands range in area from 0.27 to 680 km<sup>2</sup> and are separated between 0.5 and 33 km from the main island of Cuba (table 1, fig. 1). These variables were obtained from digital maps using the software DIVA-GIS v 7.5 (Hijman et al., 2005).

We selected only terrestrial species because their assemblages should depend on the islands as breeding or feeding sites. The data were organized as a presence-absence matrix in which each row represents a species and each column an island. To ensure that the results were not biased by the inclusion of species with very different strategies in the habitat use, we

Table 1. Characteristics of the study islands in the Sabana–Camagüey Archipelago and number of terrestrial birds on each island: A. Area (in km<sup>2</sup>); I. Isolation (in km); N. Number of species. (Isolation is given as the nearest distance to the main island of Cuba.)

*Tabla 1. Características de las islas estudiadas del archipiélago Sabana–Camagüey y número de especies de aves por islas: A. Área (en km<sup>2</sup>); I. Aislamiento (en km); N. Número de especies. (El valor de aislamiento es la distancia más cercana a la isla de Cuba.)*

Island	A (km <sup>2</sup> )	I (km)	N
Aguada	2.29	5.47	36
Coco	334.52	21.43	117
Cruz	26.14	29.95	49
Ensenachos	1.45	27.75	39
Fábrica	0.79	4.07	40
Francés	6.22	26.66	40
Guajaba	105.2	10.47	89
Guillermo	15.65	24.42	63
Las Brujas	7.23	24.79	61
Lucas	3.16	5.74	45
Mégano Grande	7.55	31.8	24
Palma	0.27	0.49	46
Paredón Grande	10.71	32.99	84
Romano	680	14.16	88
Sabinal	338.3	2.16	90
Salinas	1.08	4.72	41
Santa María	21.9	28.69	85

generated presence–absence submatrices for two species subsets: 1) breeding vs. migratory species (including winter residents), and 2) four trophic guilds of breeding birds (omnivores, predators, insectivores and phytophagous) based on our field observations and published data (e.g. Kirkconnell et al., 1992). Vagrants, transients or very rare migrants in the Cuban archipelago were excluded from data analyses (Llanes et al., 2002; Garrido & Kirkconnell, 2010).

#### Co-occurrence and nestedness analysis

To estimate whether bird species co-occurred more or less than expected by chance, we used the checkerboard score (C–score) index (Stone & Roberts, 1990). C–score measures the average number of 'checkerboard units' among all possible pairs of species. This index measures the extent to which species

are segregated across islands but does not require perfect checkerboard distributions; the C–score should be significantly larger than expected by chance in communities structured by interspecific interactions (Gotelli, 2000).

The C–score index was compared to those of 5,000 randomly assembled communities using the software EcoSim 7.0 (Gotelli & Entsminger, 2001). We used the sequential–swap algorithm to generate random null matrices (Manly, 1995). Simulated matrices were generated under two null models that differ in the way row and column totals are treated: 1) a fixed–fixed (FF) algorithm, where both the row and the column totals of the original matrix are fixed (the biological justification for this model is that it preserves in the null matrices the observed differences between sites in species richness—column totals—and observed differences among species in their frequency of occurrence or row totals, Gotelli, 2000); and 2) a fixed–weighted (FW) algorithm (Gotelli & Entsminger, 2001; Jenkins, 2006), where columns are weighted by factors that during randomization contribute to inter–island differences in community composition. We separately used two weighting factors: the island area (FW<sub>area</sub>) and the distance (FW<sub>isolation</sub>) from the main island of Cuba (used as an isolation criterion).

We calculated a standardized effect size (SES) as [(observed score–mean simulated score)/standard deviation of simulated score]; SES indicates the number of standard deviations that the observed index is above or below the mean index of simulated matrices. Non–random matrices generally have SES for the C–score > |2| (Gotelli & McCabe, 2002). In addition, we used Bayes methods implemented by Gotelli & Ulrich (2010) to identify particular species pairs for each trophic guild that contributes to observed patterns, and to determine those random, segregated or aggregated species pairs. We used the criteria mean–based (Bayes M criterion) and confidence interval (Bayes CL criterion) (Gotelli & Ulrich, 2010) calculated with the software 'Pairs' (Ulrich, 2008).

For nestedness analysis, we used a metric–based on overlap and decreasing fill, NODF (Almeida–Neto et al., 2008). NODF calculates nestedness independently among rows and columns, evaluating nestedness only among islands (i.e. species richness) or only among species (i.e. species occupancy). NODF varies from 0 to 100 and higher values indicate more nested assemblage. The nestedness significance was estimated on 1,000 random matrices. We used a null model with a fixed–equiprobable algorithm, where the number species in an island is allowed to vary during randomization; this random model represents a scenario where the probability of colonization of all species is equal for all islands (Gotelli, 2000; Ulrich et al., 2009). Nestedness analyses and randomizations were conducted using the software 'NODF' (Almeida–Neto & Ulrich, 2011).

To explore the role of extinction and colonization events upon nestedness we used Spearman rank correlations between island rank order in the maximally packed matrix, and island area and isolation, respectively (Patterson & Atmar, 2000). This method has

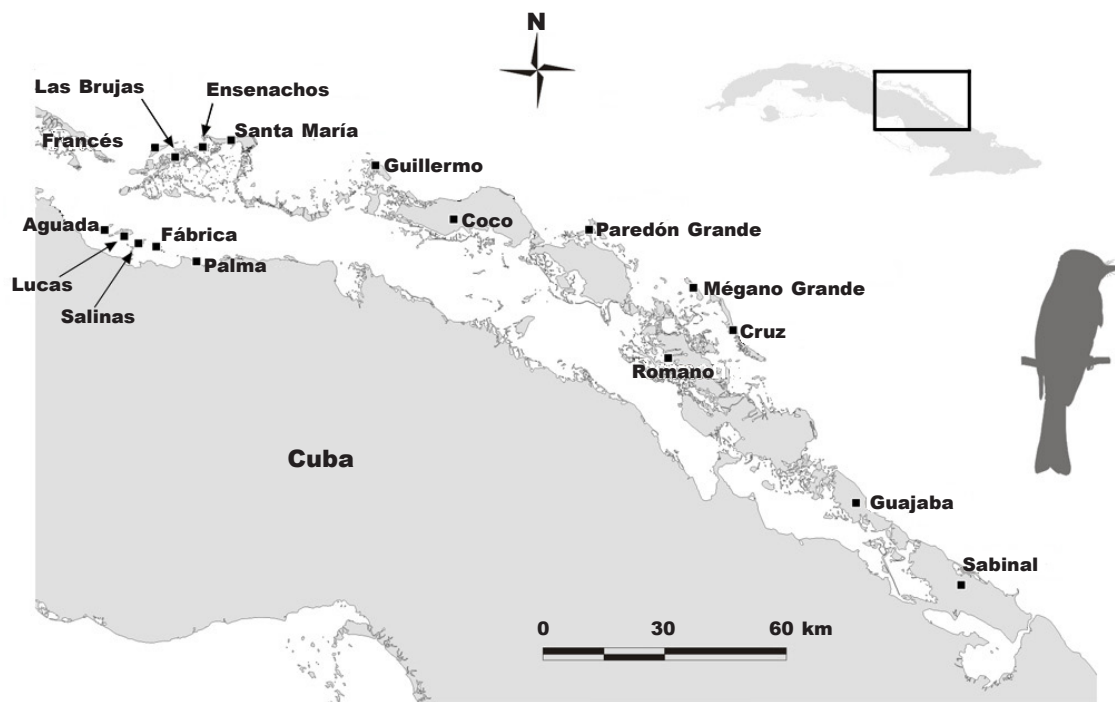


Fig. 1. Map of the Sabana–Camagüey Archipelago, Cuba; islands included in the study are named.

Fig. 1. Mapa del archipiélago Sabana–Camagüey, Cuba; se indican las islas incluidas en el estudio.

proven useful for indicating the possible mechanisms involved in a nested pattern; for example, a significant correlation between isolation and maximal nestedness will be related with immigration or colonization events. However, correlation with the island area suggests that extinction processes should determine the nested pattern (Lomolino, 1996; Patterson & Atmar, 2000; Fernández–Juricic, 2002).

## Results

A total of 131 terrestrial bird species were found to inhabit the islands considered in this study (appendix 1). There are similar numbers of breeding (67 species, 51.2%) and migrant (64 species, 48.8%) species; the species number ranges from 24 to 117 species across islands (table 1). Species richness on the islands is significantly correlated with island area ( $p < 0.001$ ; both variables in logarithm) which explained 56% of the variance. Species richness is not correlated with the island isolation ( $p = 0.7$ ).

### Co-occurrence patterns

Our results were influenced by the type of null model algorithm used (table 2). The observed C-scores for most subsets, under the F–F model, were significantly higher than expected by chance, suggesting segrega-

ted patterns of species co-occurrence. The C-score did not differ from null model figures only for phytophagous and predators, indicating random species co-occurrence. When the island area was used as a weighting factor ( $FW_{area}$ ), all subsets were significant (segregated patterns), being stronger ( $Z$  value  $> 10$ ) for the whole assemblage, and for breeding and omnivorous species. On the other hand, when using isolation as the weighting factor ( $FW_{isolation}$ ) the null hypothesis was not rejected, suggesting random co-occurrence patterns. The C-score was found to be marginally significant only for the omnivorous species (observed score = 5.27, expected score = 3.92,  $p = 0.04$ ), suggesting a weak pattern of interspecific segregation.

Analysis of species pairs showed that most of them were randomly assembled. For each trophic guild, very few pairs had a significant segregated pattern. Neither species pairs showed an aggregated pattern. The highest percentage of species pairs occurred for omnivorous and insectivorous species; the Bayes confidence interval criterion identified only 4.5% and 2.2% of segregated pairs, respectively. Table 3 shows the significantly segregated species pairs with highest values of C-Score; other species-pairs such as Gray Kingbird (*Tyrannus dominicensis*) – Oriente Warbler (*Teretistris fornsi*), Mangrove Cuckoo (*Coccyzus minor*) – Cuban Tody (*Todus multicolor*), and Smooth Billed Ani (*Crotophaga ani*) – Bahama Mockingbird (*Mimus gundlachi*), had values significantly

Table 2. Results from the analysis of species co-occurrence of terrestrial bird assemblages inhabiting 17 islands of the Sabana-Camagüey Archipelago. The observed C-Score, the values expected by chance, and standardized effect size (in parentheses) are shown for each species subset. (Significant results in bold.)

Tabla 2. Resultados de los análisis de coexistencia de las especies en las agrupaciones de aves terrestres que habitan en las islas del archipiélago Sabana-Camagüey. Para cada subgrupo de especies se muestran el valor del conteo C observado, los valores esperados por efecto del azar y el valor del tamaño del efecto estandarizado (entre paréntesis). (Los resultados significativos se indican con negritas.)

Subset (# species)	Observed C-score	Simulated C-scores		
		F-F	FW <sub>area</sub>	FW <sub>isolation</sub>
All species (131)	3.41	3.18 ( <b>6.61</b> )	1.02 ( <b>19.98</b> )	3.98 (-2.65)
Migratory (64)	2.71	2.55 ( <b>2.65</b> )	1.19 ( <b>7.62</b> )	5.11 (-6.73)
Breeding (67)	2.83	2.61 ( <b>5.17</b> )	0.85 ( <b>13.21</b> )	3.04 (-0.74)
Phytophagous (16)	0.82	0.71 (1.27)	0.37 ( <b>2.36</b> )	1.43 (-1.68)
Omnivorous (15)	5.27	4.86 ( <b>2.54</b> )	1.02 ( <b>11.22</b> )	3.92 ( <b>1.76</b> )
Predators (10)	2.22	2.08 (0.72)	0.92 ( <b>2.63</b> )	3.82 (-1.61)
Insectivorous (14)	2.84	2.60 (2.13)	0.93 ( <b>5.22</b> )	2.33 (0.81)

segregated but with low C-scores, suggesting weakly segregated patterns between these species pairs.

#### Nestedness

The entire community of terrestrial birds showed a significantly nested pattern (NODF = 78.41,  $p < 0.0001$ ). The breeding subset of bird species showed higher degrees of nestedness than the migratory assemblage. The degree of nestedness of species richness among islands

(columns) was higher than the degree of nestedness in species occupancy (rows) for whole assemblage and for migratory and breeding subset separately (table 4). Spearman rank correlations between species order in the maximally nested matrix with island area and isolation indicate that area is the most important factor in nestedness (table 5). The analysis suggests that the distance to main island of Cuba has no influence on the degree of nestedness of avian assemblages from the Sabana-Camagüey Archipelago.

Table 3. Species pairs with the highest and most significant figures of C-Score (Obs.) denoting segregated distribution patterns. The number of occurrences and the number of islands with joint occurrences (U) are shown in brackets. For each species pairs, the values expected by chance (Sim.) and standardized effect size (SES) are shown.

Tabla 3. Parejas de especies con los índices de conteo C (Obs.) más elevados y significativos, indicando patrones significativamente segregados. Se muestran entre paréntesis el número de observaciones y la cantidad de islas donde coexisten (U). Para cada pareja de especies se muestra los valores esperados por efecto del azar (Sim.) y el valor del tamaño del efecto estandarizado (SES).

Species 1	Species 2	U	Obs.	Sim. (SES)
<i>Mimus gundlachii</i> (8)	<i>Dives atrovioleaceus</i> (5)	0	1.0	0.212 ( <b>5.42</b> )
<i>Mimus gundlachii</i> (8)	<i>Priotelus temnurus</i> (4)	0	1.0	0.215 ( <b>4.88</b> )
<i>Icterus melanopsis</i> (7)	<i>Dives atrovioleaceus</i> (5)	1	0.68	0.227 ( <b>3.07</b> )
<i>Glaucidium siju</i> (9)	<i>Accipiter striatus</i> (3)	1	0.59	0.082 ( <b>3.79</b> )
<i>Geotrygon chrysis</i> (7)	<i>Tiaris bicolor</i> (3)	1	0.57	0.072 ( <b>4.31</b> )

Table 4. Results of nestedness analyses for the terrestrial bird assemblages on islands of the Sabana–Camagüey Archipelago. The table shows observed ( $NODF_{obs}$ ) and expected by chance ( $NODF_{sim}$ ) values, and also the degree of nestedness independently for columns and rows. (The standardized effect size is shown in brackets; all combinations were significantly nested, in bold.)

*Tabla 4. Resultados de los análisis de anidamiento de las agrupaciones de aves terrestres en las islas del archipiélago Sabana–Camagüey. Se muestran los valores del índice observado ( $NODF_{obs}$ ) y los valores esperados por efecto del azar ( $NODF_{sim}$ ), así como el grado de anidamiento para filas y columnas de forma independiente. (Entre paréntesis se muestra el valor del tamaño del efecto estandarizado; todas las combinaciones fueron significativamente anidadas, en negrita.)*

	Total		Columns		Rows	
	$NODF_{obs}$	$NODF_{sim}$	$NODF_{obs}$	$NODF_{sim}$	$NODF_{obs}$	$NODF_{sim}$
All species	78.41	61.26 ( <b>72.75</b> )	83.58	62.79 ( <b>11.62</b> )	78.32	61.23 ( <b>73.2</b> )
Migratory	78.15	51.36 ( <b>49.43</b> )	80.47	53.12 ( <b>13.29</b> )	78.00	51.24 ( <b>55.17</b> )
Breeding	84.46	69.13 ( <b>31.37</b> )	86.15	68.75 ( <b>6.88</b> )	84.36	69.15 ( <b>37.64</b> )

## Discussion

Our analyses show that terrestrial bird species co-occurred less frequently than expected by chance on islands from the Sabana–Camagüey Archipelago, suggesting that these avian communities are probably structured by negative interspecific interactions. However, similar to other studies (e.g. Meyer & Kalko, 2008), the results were susceptible to the species subsets and the weighting factors. When the fixed–fixed model was used we found random co-occurrence patterns for predators and phytophagous species. However, using area as weighting, all subsets showed significant segregated co-occurrence patterns. Contrarily, weighting analyses by island isolation showed random patterns for most species subsets. This result suggests that because of the short distance between the archipelago and the main island of Cuba, the differential dispersal abilities of the bird species would not be an important factor in the structure of the avian assemblages. On the other hand, island area and other attributes associated with of area, such as landscape diversity or the number of plant formations (see Priego–Santander et al., 2004), have a more important role structuring the bird communities of the Sabana–Camagüey Archipelago.

Although the avifauna assemblages showed a wide segregated pattern, we found that species pairs, within each trophic guild, showed random patterns. This result suggests competitive exclusion could be rare in these bird assemblages. A similar result was obtained for other avifauna on archipelagos (Gotelli & Ulrich, 2010; Collins et al., 2011), and might reflect widespread, but weak species interactions or mechanisms of species segregation that are not related to direct species interactions but to historical events or resource abundance (Gotelli & McCabe, 2002; Gotelli & Ulrich, 2010).

The analyses indicate a strong nested structure in the entire assemblage and for breeding and migratory birds. Common and widespread species (e.g. Greater Antillean Grackle, Cuban Emerald, Yellow Warbler, etc.) tended to comprise the avifauna of islands with lesser species richness, while richer islands included these species in addition to other rare species or with restricted ranges. We found that island nested rank order was significantly correlated with the rank order of island area but not with island isolation. This result, together with the significant species–area relationship, suggests that the terrestrial bird assemblages at SCA are structured through

Table 5. Results of Spearman Rank correlations of island order in the maximally nested matrix with the values of area and isolation;  $p$  values were generated by 1,000 Monte Carlo simulations: A. Area; I. Isolation.

*Tabla 5. Resultados de la correlación por rangos de Spearman entre los valores ordinales que le corresponde a cada isla en la matriz de máximo anidamiento y sus valores de área y aislamiento; los valores  $p$  fueron generados por 1.000 simulaciones de Monte Carlo: A. Área; I. Aislamiento.*

Subset	$A r_s$	$p$	$I r_s$	$p$
All species	−0.76	0.0003	0.078	0.76
Migratory	−0.74	0.0005	−0.24	0.34
Breeding	−0.73	0.00004	0.16	0.53

local extinction rather than through colonization or immigration processes from the main island of Cuba (Lomolino, 1996; Wright et al., 1998).

The lower nested pattern observed in the migratory assemblages would be related to habitat generalists with high dispersal abilities (e.g. some wintering migrant passerines such as Black and White Warbler, Palm Warbler, American Redstart; Rappole, 1995; Wallace et al., 1996; Latta et al., 2003). The highest nested patterns of breeding birds would be related to the low habitat diversity or limited resource abundance on the small islands, although these would be limiting factors mainly for those breeding species with large area requirements or habitat specialists (e.g. Gundlach's Hawk, Zapata Sparrow, Fernandina's Flicker, Cuban Grassquit, etc.). Among the islands smaller than 15 km<sup>2</sup>, Cayo Paredón Grande had the highest species richness, with 84 bird species. This island has unusually high landscape heterogeneity and floristic diversity (Priego-Santander et al., 2004), supporting the idea that habitat diversity is an important factor in explaining the distribution and species richness on the archipelago.

Ours results are consistent with several studies that show that nested avian assemblages on islands or fragmented habitat are apparently shaped by selective extinction processes through island or patch area and the habitat diversity effects rather than interspecific guild competition. (Fernández-Juricic, 2000; Feeley, 2003; Wang et al., 2011). The strong nested patterns and significant species-area relationships of the avian assemblages suggest, from a conservation perspective, that the protection of the largest islands with the most species rich assemblages (e.g. Romano, Sabinal, Coco, Guajaba and Santa María) will warrant high terrestrial bird richness. However, an adequate conservation strategy will be to conserve small and large islands with the purpose of maintaining a high heterogeneity in the environmental conditions on the Sabana-Camagüey Archipelago (Fischer & Lindenmayer, 2005).

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Appendix 1. List of terrestrial bird species included in this study, ordering species according to the maximally nested matrix. Status (B. Breeding, M. Migratory). Trophic group (TG: O. Omnivores, P. Predators, I. Insectivores, Ph. Phytophagous). The last column shows the number of islands where each species was recorded. Nomenclature follows A.O.U. (2011).

Apéndice 1. Listado de las especies de aves terrestres incluidas en este estudio, ordenadas acorde a su posición en la matriz de máximo anidamiento. Status (B. Reproductora, M. Migratoria). Grupo trófico (TG: O. Omnívora, P. Depredadora, I. Insectívora; Ph. Fitófaga). En la última columna se indica el número de islas donde la especie han sido registrada. Taxonomía según la A.O.U. (2011).

Common name	Scientific name	Status	TG	Islands
Greater Antillean Grackle	<i>Quiscalus niger</i>	B	O	17
Turkey Vulture	<i>Cathartes aura</i>	B	P	17
White Crowned Pigeon	<i>Patagioenas leucocephala</i>	B	Ph	17
Cuban Pewee	<i>Contopus caribaeus</i>	B	I	17
Cuban Emerald	<i>Chlorostilbon ricordii</i>	B	Ph	17
Common Ground Dove	<i>Columbina passerina</i>	B	Ph	17
Yellow Warbler	<i>Setophaga petechia</i>	B	I	17
Yellow-faced Grassquit	<i>Tiaris olivaceus</i>	B	Ph	16
American Kestrel	<i>Falco sparverius</i>	B	P	16
Black and White Warbler	<i>Mniotilta varia</i>	M	I	16
Northern Mockingbird	<i>Mimus polyglottos</i>	B	O	16
Palm Warbler	<i>Setophaga palmarum</i>	M	I	16
American Redstart	<i>Setophaga ruticilla</i>	M	I	16
Western Spindalis	<i>Spindalis zena</i>	B	Ph	16
La Sagra's Flycatcher	<i>Myiarchus sagrae</i>	B	I	16
Cuban Bullfinch	<i>Melopyrrha nigra</i>	B	Ph	16
Ovenbird	<i>Seiurus aurocapilla</i>	M	I	15
Cuban Green Woodpecker	<i>Xiphidiopicus percussus</i>	B	O	15
Gray Kingbird	<i>Tyrannus dominicensis</i>	B	I	15
White-winged Pigeon	<i>Zenaida asiatica</i>	B	Ph	15
Loggerhead Kingbird	<i>Tyrannus caudifasciatus</i>	B	I	15
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	M	I	15
Common Yellowthroat	<i>Geothlypis trichas</i>	M	I	15
Mourning Dove	<i>Zenaida macroura</i>	B	Ph	15
Killdeer	<i>Charadrius vociferus</i>	B	O	14
Great Lizard-Cuckoo	<i>Coccyzus merlini</i>	B	P	14
Gray Catbird	<i>Dumetella carolinensis</i>	M	O	14
Black-whiskered Vireo	<i>Vireo altiloquus</i>	B	I	14
Red-legge Thrush	<i>Turdus plumbeus</i>	B	O	14
Smooth Billed Ani	<i>Crotophaga ani</i>	B	O	13
Cuban Vireo	<i>Vireo gundlachii</i>	B	I	13
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	M	I	13
Zenaida Dove	<i>Zenaida aurita</i>	B	Ph	12
Northern Parula	<i>Setophaga americana</i>	M	I	12
Praire Warbler	<i>Setophaga discolor</i>	M	I	12

## Appendix 1. (Cont.)

Common name	Scientific name	Status	TG	Islands
Northern Waterthrush	<i>Parkesia noveboracensis</i>	M	I	12
Barn Owl	<i>Tyto alba</i>	B	P	12
Indigo Bunting	<i>Passerina cyanea</i>	M	Ph	11
West Indian Woodpecker	<i>Melanerpes superciliaris</i>	B	O	11
Yellow-throated Vireo	<i>Vireo flavifrons</i>	M	I	11
Yellow-throated Warbler	<i>Setophaga dominica</i>	M	I	11
Crested Caracara	<i>Caracara cheriway</i>	B	P	10
Merlin	<i>Falco columbarius</i>	M	P	10
Magnolia Warbler	<i>Setophaga magnolia</i>	M	I	10
Cape May Warbler	<i>Setophaga tigrina</i>	M	I	10
Red-tailed Hawk	<i>Buteo jamaicensis</i>	B	P	10
Mangrove Cuckoo	<i>Coccyzus minor</i>	B	I	10
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	M	I	10
Peregrine Falcon	<i>Falco peregrinus</i>	M	P	9
Cuban Pygmy-Owl	<i>Glaucidium siju</i>	B	P	9
Cuban Tody	<i>Todus multicolor</i>	B	I	9
Blue Grosbeak	<i>Passerina caerulea</i>	M	Ph	9
Cave Swallow	<i>Petrochelidon fulva</i>	B	I	9
Painted Bunting	<i>Passerina ciris</i>	M	Ph	9
Antillean Nighthawk	<i>Chordeiles gundlachii</i>	B	I	8
Greater Antillean Nighthawk	<i>Caprimulgus cubanensis</i>	B	I	8
Bahama Mockingbird	<i>Mimus gundlachii</i>	B	O	8
Cuban Gnatcatcher	<i>Polioptila lembeyei</i>	B	I	8
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	M	I	7
Northern Flicker	<i>Colaptes auratus</i>	B	O	7
White-eyed Vireo	<i>Vireo griseus</i>	M	I	7
Key West Quail-Dove	<i>Geotrygon chrysis</i>	B	Ph	7
Bobolink	<i>Dolichonyx oryzivorus</i>	M	O	7
Blackpoll Warbler	<i>Setophaga striata</i>	M	I	7
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	B	I	7
Cuban Oriole	<i>Icterus melanopsis</i>	B	O	7
Oriente Warbler	<i>Teretistris fornsi</i>	B	I	7
Baltimore Oriole	<i>Icterus galbula</i>	M	O	6
Yellow-rumped Warbler	<i>Setophaga coronata</i>	M	I	6
Scarlet Tanager	<i>Piranga olivacea</i>	M	Ph	6
Chuck-will'swidow	<i>Caprimulgus carolinensis</i>	M	I	6
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	M	Ph	6
Ruddy Quail-Dove	<i>Geotrygon montana</i>	B	Ph	6
Tawny-shouldered Blackbird	<i>Agelaius humeralis</i>	B	O	6
Cuban Blackbird	<i>Dives atrovioleaceus</i>	B	O	5
Cuban Martin	<i>Progne cryptoleuca</i>	B	I	5

## Appendix 1. (Cont.)

Common name	Scientific name	Status	TG	Islands
Barn Swallow	<i>Hirundo rustica</i>	M	I	5
Tree Swallow	<i>Tachycineta bicolor</i>	M	I	5
Bay-breasted Warbler	<i>Setophaga castanea</i>	M	I	5
Bananaquit	<i>Coereba flaveola</i>	M	I	5
Prothonotary Warbler	<i>Protonotaria citrea</i>	M	I	5
Black-throated Green Warbler	<i>Setophaga virens</i>	M	I	5
Hooded Warbler	<i>Setophaga citrina</i>	M	I	5
Burrowing Owl	<i>Athene cunicularia</i>	B	P	5
Northern Harrier	<i>Circus cyaneus</i>	M	P	5
Cuban Crow	<i>Corvus nasicus</i>	B	O	4
Grasshopper Sparrow	<i>Ammodramus savannarum</i>	M	Ph	4
Eastern Meadowlark	<i>Sturnella magna</i>	B	O	4
Orchard Oriole	<i>Icterus spurius</i>	M	O	4
Blackburnian Warbler	<i>Setophaga fusca</i>	M	I	4
Swainson's Warbler	<i>Limnithlypis swainsonii</i>	M	I	4
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	M	I	4
Bare-legged Owl	<i>Gymnoglaux lawrencii</i>	B	P	4
Summer Tanager	<i>Piranga rubra</i>	M	Ph	4
Cuban Trogon	<i>Priotelus temnurus</i>	B	O	4
Swainson's Thrush	<i>Catharus ustulatus</i>	M	O	4
Eastern Wood-Pewee	<i>Contopus virens</i>	M	I	4
Red-eyed Vireo	<i>Vireo olivaceus</i>	M	I	4
Scaly-naped Pigeon	<i>Patagioenas squamosa</i>	B	Ph	4
Gundlach's Hawk	<i>Accipiter gundlachi</i>	B	P	3
Broad-winged Hawk	<i>Buteo platypterus</i>	B	P	3
Black-faced Grassquit	<i>Tiaris bicolor</i>	B	Ph	3
Sharp-shinned Hawk	<i>Accipiter striatus</i>	B	P	3
Plain Pigeon	<i>Patagioenas inornata</i>	B	Ph	3
Savannah Sparrow	<i>Passerculus sandwichensis</i>	M	Ph	3
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	M	I	3
Louisiana Waterthrush	<i>Parkesia motacilla</i>	M	I	3
Short-eared Owl	<i>Asio flameus</i>	B	P	3
Gray-cheeked Thrush	<i>Catharus minimus</i>	M	O	3
Kentucky Warbler	<i>Geothlypis formosa</i>	M	I	2
Orange-crowned Warbler	<i>Oreothlypis celata</i>	M	I	2
Tennessee Warbler	<i>Oreothlypis peregrina</i>	M	I	2
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	M	I	2
Wilson's Warbler	<i>Cardenilla pusilla</i>	M	I	2
Stygian Owl	<i>Asio stygius</i>	B	P	2
Veery	<i>Catharus fuscescens</i>	M	O	2
Wood Thrush	<i>Hylocichla mustelina</i>	M	O	2

## Appendix 1. (Cont.)

Common name	Scientific name	Status	TG	Islands
Thick-billed Vireo	<i>Vireo crassirostris</i>	B	I	2
Philadelphia Vireo	<i>Vireo philadelphicus</i>	M	I	2
Cedar Waxwing	<i>Bombycilla cedrorum</i>	M	Ph	2
Cuban Grassquit	<i>Tiaris canorus</i>	B	Ph	2
Zapata Sparrow	<i>Torreornis inexpectata</i>	B	O	2
Clay-colored Sparrow	<i>Spizella pallida</i>	M	Ph	2
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	M	I	2
Shiny Cowbird	<i>Molothrus bonariensis</i>	B	O	2
Yellow-breasted Chat	<i>Icteria virens</i>	M	I	2
Northern Bobwhite	<i>Colinus virginianus</i>	B	Ph	1
Fernandina's Flicker	<i>Colaptes fernandinae</i>	B	I	1
Red-legged Honeycreeper	<i>Cyanerpes cyaneus</i>	B	Ph	1
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	M	Ph	1
Sandhill Crane	<i>Grus canadensis</i>	B	O	1