Effects of migrations on the nestedness structure of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba

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Abstract

Effects of migrations on the nestedness structure of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba.— The nested subset hypothesis states that species in fragmented, less species–rich biotas are non–random subsets of those inhabiting richer sites. The effect of migration on these models has not been yet fully addressed. We compared the phenological stages of the community during the spring and fall migrations. Presence–absence data of bird species occurring at 43 cays of the Jardines de la Reina archipelago was compiled and two incidence matrices were built for fall and spring periods. The degree of nestedness was estimated based on the overlap and decreasing fill, and its significance was assessed by means of 1,000 replicates of four null models. Bird assemblages showed a higher number of species during fall (67) than they did in spring (51). They also showed a significant and stable pattern of nestedness, although this was slightly higher in spring. Seasonal fluctuations caused by migratory movements thus barely affected the nested structure of bird assemblages.

Key words: Community organization, Nested subset, Fragmented biota, Selective extinction, Differential colonization, Null model

Resumen

Efecto de las migraciones sobre la estructura de anidamiento de los ensamblajes de aves en los cayos del archipiélago de los Jardines de la Reina, Cuba.— La hipótesis del subgrupo anidado plantea que, en biotas fragmentadas, las especies de los sitios empobrecidos constituyen subconjuntos no aleatorios de las especies de los sitios con mayor riqueza. El efecto de las migraciones sobre estos modelos aún no ha sido abordado plenamente. Se compararon los estados fenológicos de la comunidad durante las migraciones primaveral y otoñal. Se recogieron datos sobre las presencias y ausencias de las especies de aves en 43 cayos del archipiélago de los Jardines de la Reina. Luego se construyeron dos matrices de incidencia para los periodos otoñal y primaveral. El grado de anidamiento de las matrices se calculó mediante el índice de anidamiento basado en el relleno superpuesto y decreciente, y se evaluó su significación mediante 1.000 réplicas de cuatro modelos nulos. Los ensamblajes de aves presentaron un mayor número de especies en el periodo otoñal (67) que en el primaveral (51). También manifestaron un modelo de anidamiento significativo y estable, que fue ligeramente mayor durante el periodo primaveral. Así, las fluctuaciones estacionales debidas a los movimientos migratorios prácticamente no alteraron la estructura anidada de los ensamblajes de aves.

Palabras claves: Organización comunitaria, Subgrupo anidado, Biota fragmentada, Extinción selectiva, Colonización diferencial, Modelo nulo

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Introduction

One of the best studied and most controversial subjects within the ecological context is how communities are assembled (Patterson, 1990; Gotelli & McCabe, 2002; Bloch et al., 2007) because the fundamental disjunctive question regarding this topic is based on whether such structuring is deterministically or stochastically originated. Diamond's assembly rules, published in 1975, were supported by the idea that interspecific competition was the basic causative factor shaping community structure. These rules are still considered to be among the most remarkable assumptions explaining the natural organization of communities but their validity has been subjected to much discussion during the past quarter of the last century (Gotelli & McCabe, 2002). The hypothesis of the nested subgroup (Patterson & Atmar, 1986) stands out among the most widely known rules (Rohde et al., 1998; Bloch et al., 2007) as no causal factors are assumed *a priori*. The remaining assembly rules, despite being based on varying criteria, assume that interspecific competition is the crucial factor for the structuring of natural communities. In this regard, analysis of the nested subgroup provides methodological advantages for studies on community organization over many other approaches.

The core of the nested subgroup hypothesis rests on the fact that communities exhibit a nested structure if poor species assemblages are non–random subgroups of those with greater species richness (Rohde et al., 1998; Fernández–Juricic, 2000; Bloch et al., 2007). This issue is closely related to studies on fragmented or isolated biotas such as islands, mountaintops, parasite hosts, isolated forests, and caves. In all cases, if structure of communities or assemblages is described by a nested model, this differs significantly from any randomly generated organization.

The nestedness of species assemblage could be generated by one or many factors depending on the taxonomic group and main features of the study area. Basic factors promoting nested structures are selective extinction and differential colonizationof species (*i.e.* Patterson & Atmar, 1986; Patterson, 1990). Selective extinction induces species loss within ecosystems, forming a predictable sequence without replacements by nearby colonizers (species relaxation). This may provoke non–random losses because species requiring large minimum areas or those forming small populations face high risks of extinction. The origin of nestedness caused by differential colonization was based on the idea that the dispersal capability of differential species leads to the occupation of a larger number of sites by stronger dispersers. Further research has since revealed that other factors may influence nestedness patterns (*e.g.* Calmé & Desrochers, 1999; Ulrich et al., 2009), such as passive sampling, habitat nestedness, disturbances, fragmentation, and age and superficial extension of fragments.

Differential colonization of species shows great potential to promote such structural patterns among the causative factors of nestedness. However, its influence has only been studied taking into account the consequences of the species permanently oc-

cupying the sites (immigration) (*e.g.* Cook & Quinn, 1995; Rohde et al., 1998). For instance, birds' annual migrations —which may be described as temporal selective colonizations since each species follows its own migratory pathway and determines its wintering ground— await further scientific scrutiny. Such phenological events are known to bring about remarkable annual compositional changes in tropical bird communities within the Caribbean, depending on the migratory movements in question.

Many authors (*e.g.* Cook & Quinn, 1995; Rohde et al., 1998; Calmé & Desroches, 1999; Fernández–Juricic, 2000; Bloch et al., 2007) have referred to the differential or selective colonization as one of the main forces generating nestedness patterns within the species' natural assemblages. This may imply that the differential occupancy experienced by many migratory bird species in several archipelagos during each season should increase the degree of nestedness on the assemblages of which they temporarily form part. On the contrary, Patterson & Atmar (1986), Patterson (1990), and Calmé & Desrochers (1999) disregard the role of colonization as a critical process to unfolding nested structures in species' assemblages.

This scientific paradox can be assessed in the bird communities of the Jardines de la Reina archipelago, off the southern coast of Cuba because the area is a critical site for residence and transit of migrant bird species (Parada & García–Quintas, 2012). One tentative hypothesis to the aforementioned contradiction is that bird assemblages inhabiting the Jardines de la Reina archipelago have a stable nested pattern under the influence of the many migratory species. If such an assertion is true, then annual fluctuations in the composition of bird species in the Jardines de la Reina archipelago do not affect the nestedness degree of assemblages. To test this hypothesis, the bird assemblages of the Jardines de la Reina archipelago should be assessed and compared in different phenological stages, that is to say, during the periods of highest turnover rates when the influx of neotropical migrants from northern latitudes in September–October and of migrants from southern latitudes in March–April take place on an annual basis.

Material and methods

Study area

The present study was conducted in 43 cays of the Jardines de la Reina archipelago which stretches along the southern coast of Cuba from the Ancon peninsula (Sancti Spíritus province) to Cabo Cruz (Granma province) and comprises numerous islets, shoals and reefs. Three main insular groups can be distinguished: the Ana María cays, the central cays of the gulf of Ana María, and the Doce Leguas cays (fig. 1).

Terrestrial landscapes tend to have a relatively small area (table 1), early geological evolution, and high ecological fragility due to exposure to extreme physical–geographic conditions (*i.e.* strong winds and tidal waves, high salinization and evaporation rates,
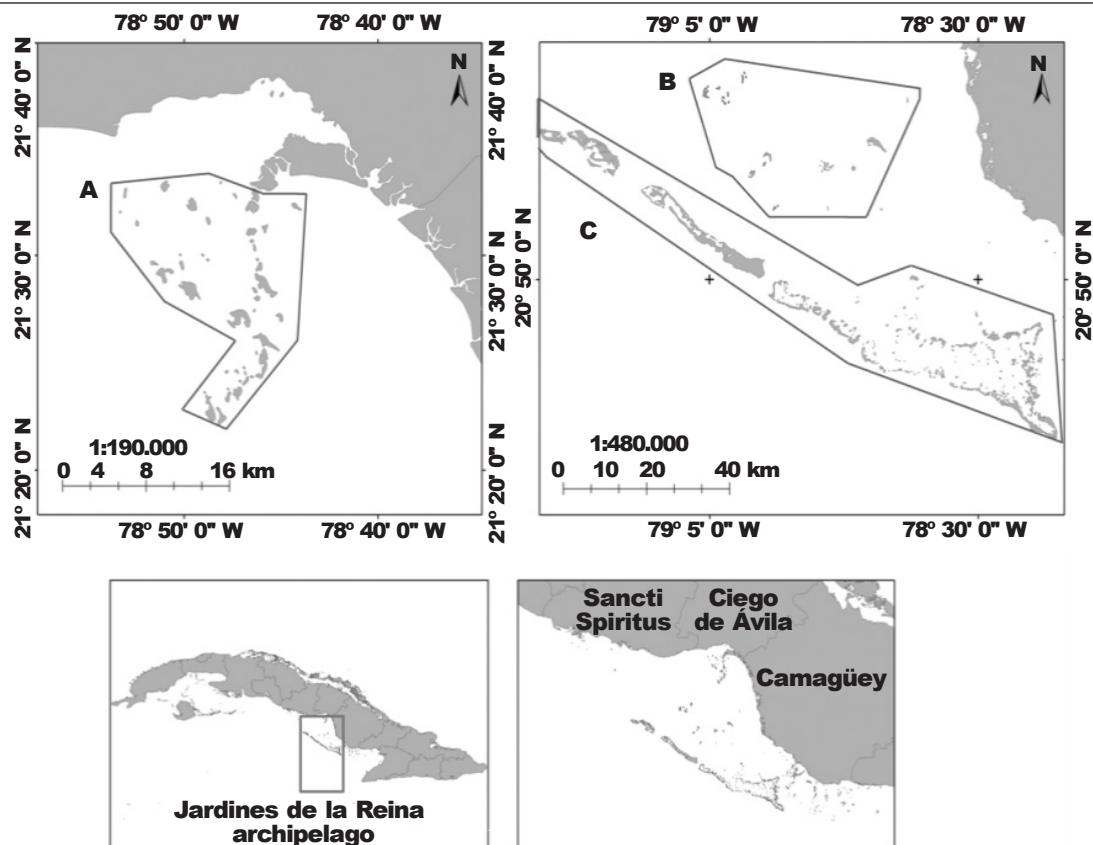
Fig. 1. Study area where the seasonality effect of the avian composition on the structure of bird assemblages in 43 cays of the Jardines de la Reina archipelago, Cuba, was evaluated. A. Ana María cays, B. Central cays of the gulf of Ana María; C. Doce Leguas cays.

Fig. 1. Área de estudio donde se evaluó la influencia de la estacionalidad de la composición de especies sobre la estructura de anidamiento de los ensamblajes de aves en 43 cayos 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.

seasonal droughts, and intense hydromorphism). The main vegetation forms are mangrove forests, xeromorphic scrub, and sandy and rocky shoreline vegetation, which are best represented in the cays of Doce Leguas (larger and older cays). Lower levels of floral diversity can be found in the cays along the Ana María gulf, where mangrove forests are the prevailing vegetation and may even cover all the emerged land in the Bergantines, Cuervo, Cayuelo and Balandras cays. Some shallow lagoons are also a notable feature in the terrestrial landscapes of many of these cays.

Data source and filtering on the species presence–absence

Presence–absence data was obtained from two different sources. First, we carried out a thorough search encompassing most of the available researches on the study site and extracted many inventory lists. This insular region has been little surveyed and its avifauna is broadly considered among the least studied within the Cuban archipelago. Therefore, most information on the species occurrence was restricted to a few compilation works such as Garrido & García (1975), Buden & Olson (1989), Parada et al. (2012), and Parada & García–Quintas (2012). Second, three surveys conducted in the Caguama (March, July, 2012), and Grande and Caguama (October, 2012) cays were also included to enlarge the final dataset for further analyses. On the March and July field expeditions, visual counts were used to detect bird species inhabiting main vegetation types in Caguama cay. In October, data from visual counts conducted along the south coastline of Grande and Caguama cays during early mornings along with a mist–netting protocol described by Parada et al. (2012) were also used.

Inventory lists per cay were then put together and species exclusively exploiting the ecological resources

Table 1. Main features of the 43 sampled cays of Jardines de la Reina archipelago, Cuba: AMC. Ana María cays; CCG. Central cays of the gulf of Ana María; DLC. Doce Leguas cays; * Information obtained through a classified Landsat image; ** Information gathered from field censuses and specialists´ personal communications.

*Tabla 1. Características principales de los 43 cayos muestreados del archipiélago de los Jardines de la Reina, Cuba: AMC. Cayos de Ana María; CCG. Cayos del centro del golfo de Ana María; DLC. Cayos de las Doce Leguas; * Información obtenida mediante una imagen Landsat clasificada; ** Información obtenida a través de los censos de aves y por comunicaciones personales de especialistas.*

Cays	Insular subgroup	Area* (km^2)	Perimeter* (km^2)	Number of birds per habitat**
Cayuelo	AMC	0.02	0.72	1
Obispito	AMC	0.03	0.84	4
Quitasol	AMC	0.05	1.02	2
La Loma	AMC	0.06	1.50	2
Obispo	AMC	0.09	2.76	4
Guinea	AMC	0.13	1.92	4
La Tea	AMC	0.17	2.46	2
Caoba	AMC	0.26	3.84	3
Flamenco	AMC	0.84	7.50	4
Cana	AMC	0.91	11.34	5
Arenas	AMC	0.97	9.84	4
Tío Joaquín	AMC	1.21	11.07	5
Providencia	AMC	1.29	13.38	5
Guásimas	AMC	1.59	8.70	4
Balandras	AMC	1.62	15.36	2
Punta de Los Machos	AMC	2.14	26.61	3
Cargado	CCG	0.15	3.48	4
Bergantines	CCG	0.22	4.20	4
Palomo	CCG	0.28	6.84	4
Santa María	CCG	0.29	3.12	4
Algodoncito	CCG	0.77	5.82	4
Manuel Gómez	CCG	2.11	34.80	4
Cuervo	CCG	2.16	35.28	5
Algodón Grande	CCG	3.64	32.70	6
Boca Rica	DLC	0.36	6.96	2
Largo	DLC	0.48	7.32	3
Juan Grin	DLC	0.63	16.74	3
Camposanto	DLC	0.82	6.42	4
Alcatracito	DLC	1.34	11.04	4
Boca de la Piedra de Piloto	DLC	1.52	19.14	4
Piedra Grande	DLC	1.53	16.51	5
Boca Seca	DLC	1.76	30.24	2
Alcatraz	DLC	1.84	16.38	4
Cachiboca	DLC	2.44	57.00	6
Boca Piedra Chiquita	DLC	2.88	11.28	5
Las Cruces	DLC	3.64	55.37	4

Table 1. (Cont.)

Cays	Insular subgroup	Area* (km²)	Perimeter* (km²)	Number of birds per habitat**
Cabeza del Este	DLC	6.82	94.44	5
Bretón	DLC	7.51	71.46	4
Caguama	DLC	7.66	87.42	6
Anclitas	DLC	9.06	158.64	6
Grande	DLC	24.29	193.17	5
Caballones	DLC	33.52	73.68	5
Cinco Balas	DLC	43.56	151.20	3

from coastal waters were removed as were all those without any explicit reference of their locality name when first reported. These two simple steps increased the reliability of checklists reliability and avoided associated biases when the numerical analyses were run. The migratory status of bird species occurring in the Jardines de la Reina archipelago was categorized into four main groups: permanent resident (PR), winter resident (WR), summer resident (SR) or transient (Tr), following the criteria of Garrido & Kirkconnell (2011) and those of knowledgeable researchers on the study area avifauna.

Analysis

Transients were excluded from further analyses as they occur at low numbers and exploit ecological niches over only a few days while migrating; the structuring of communities is therefore unlikely to be significantly affected by them. Two matrices containing the remainder of the bird species were then built in order to represent each phenological phase: fall (PR + WR) and spring (PR + SR) migrations. Within each matrix, entries indicated the presence (1) or absence (0) of a species at a site. Typically, matrices were ordered according to the marginal row and column sums. Common species were placed in the upper rows, and species–rich sites placed in the left–hand columns.

Nestedness was calculated by means of two indexes: matrix temperature (T) (Atmar & Patterson, 1993) and a nestedness metric based on overlap and decreasing fill (NODF) (Almeida–Neto et al., 2008) by running the software ANINHADO 3.0.3 (Guimarães & Guimarães, 2006). The former index was solely calculated to allow comparisons with many earlier works on communities' nestedness owing to its vast usage in the specialized literature. The T index values were relativized using the Lomolino (1996) formula to calculate the percentage of perfect nestedness (PN). Nested presence–absence matrices were visualized using the nestedness temperature calculator (Atmar & Patterson, 1995).

Four null models (Er, Ce, Co and Li) provided by the software ANINHADO 3.0.3 were used to assess whether the bird assemblages were nested or randomly structured by generating 1,000 iterations for each one. The calculation of PN was only evaluated using the Er null model. All the randomization algorithms of the null models followed the following rules: (1) Er, presences are randomly assigned to any cell within the matrix; (2) Ce, probability of a cell a_{ij} show the average of the probabilities of occupancy of its row and column (equation 1); (3) Co, presences are randomly assigned within the columns; and (4) Li, presences are randomly assigned within the rows:

$$[(P_i / C) + (P_j / R)] / 2 \qquad \text{(equation 1)}$$

where P_i is the number of presences in the i row, P_j is the number of presences in the j column, and C and R are the number of columns and rows, respectively.

Statistical tools were used as null models to compare the degree of nestedness between the spring and fall migrations. To do this, the difference between the values of NODF in the two seasonal stages was calculated (size effect). Afterwards, an overall presence–absence matrix which comprised all the species contained in the two former matrices and all the sampled cays was built up. This matrix was then organized following the general requirements to unfold the nestedness analysis, and randomized twice using the four null models provided by the software ANINHADO 3.0.3. The difference between the simulated values of the NODF generated by each null model was calculated per pairs of iterations/replicates. The statistical significance of the observed difference (size effect) was calculated in terms of its associated probability from the differences simulated by the four null models. To calculate the descriptive statistics of the values generated by the null models, the software *Statistica* 8.0 (StatSoft, 2007) was used and significance level was set at $p < 0.1$.

Results

Avifauna in the study area

The regional avifauna was made up of 120 species, although *Phoenicopterus ruber* (Greater Flamingo), *Anas acuta* (Northern Pintail), *Tringa solitaria* (Solitary Sandpiper), *Antrostomus carolinensis* (Chuck–will's–widow) and *Vermivora chrysoptera* (Golden–winged Warbler) were excluded as their locality names where they were first recorded are unknown (table 2). We also excluded *Fregata magnificens* (Magnificent Frigatebird) as reports of this species were mostly based on individuals in flight exploiting several aerial strata along vast areas, including the surrounding waters. Permanent residents accounted for 37.4% of the species whereas transients were represented by 38 species for the archipelago as a whole. Summer and winter residents were represented by nine and 25 species, respectively (table 2).

Patterns of nestedness

Assemblages were made up by 67 and 51 species during the fall and spring migrations, respectively, and matrices of organized data showed filling values of 28.36% (fall) and 33.01% (spring). The degree of nestedness in spring was greater than in fall (fig. 2), though bird assemblages exhibited patterns of nested structures in both seasons since their NODF values showed significant differences with regard to the simulated values generated by the four null models (table 3).

Comparison between the degrees of nestedness during the two seasonal periods yielded a difference of 1.95. This was not significant if compared to the simulated differences generated by most null models (table 4). The seasonal migrations did not therefore promote any major changes in the degree of nestedness of bird assemblages.

Discussion

Research analyzing the compliance of species´ assembly rules can enrich our knowledge of community ecology and help in the planning and implementation of management and conservation efforts. Pianka (1999) and Bloch et al. (2007) stated that nestedness patterns on the community structure provide useful solid grounds for the designing and planning of fragmented protected areas, ecosystem management and meta–communities studies.

Our findings provide additional clues to the growing body of evidence pointing to nestedness as a ubiquitous phenomenon underlying community structure in fragmented biotas. Many authors (*e.g.* Patterson, 1990; Calmé & Desrochers, 1999; Fernández–Juricic, 2000) have found nested structures in numerous bird assemblages, and Méndez (2004) has referred to birds as one of most widely used taxonomic entities in studies focused on community structure. In the study site, a higher degree of in spring could be explained by the lower number of coexisting species and the

ecological relationships among them. Accordingly, nestedness could be produced by the ecological differences among species (Azeria & Kolasa, 2008).

A smaller number of species occurring during spring may have favored many processes, such as spatial segregation, habitat selection and territoriality which are especially remarkable during the breeding season, as in the case of most permanent and summer resident landbirds. These behavioral patterns may promote the species segregation between cays. Thus, the habitat quality, resources availability and intra– and inter–specific hierarchical organizations may have played crucial roles in the differential occupation of species in the cays. For instance, small fragments usually lack sufficient resources to permanently support populations of fruit–eating species (Feeley et al., 2007), causing these birds to move towards larger cays with higher food availability. The numbers of nectarivore (*Chlorostilbon ricordii* only) and frugivore (*Spindalis zena* not currently reported) species in the Jardines de la Reina, for example, is extremely low as they rely on food items that have marked spatial and temporal availability. These species tend to be patchily distributed and may face higher risks of extinction.

Lastly, the increase in nestedness of bird assemblages during spring may be due to the fact that the study site is inhabited by a lower overall number of species, made up only of the breeding populations of summer and permanent residents. In turn, these populations tend to be relatively large and widely distributed across the archipelago´s mangroves and coastal ponds. Aggressive displays by large breeding colonies of cormorants, egrets, pelicans, terns and gulls, and also the presence of *Buteogallus gundlachii* (Cuban Black Hawk) and *Tyrannus caudifasciatus* (Loggerhead Kingbird), which do not breed colonially, may force other birds to shift to cays capable of supporting higher numbers, possibly increasing the degree of nestedness during this period. Likewise, when a larger set of species coexist during fall, the degree of nestedness could decrease given the possible increase in competitive interactions among species, as suggested by Albrecht & Gotelli (2001). Nonetheless, Bloch et al. (2007) pointed out that competitive exclusion reduces the nestedness by preventing the coexistence of species that could otherwise could share the same habitats and resources. On this point, Méndez (2004) believes that nested structures may be ambiguously influenced by the interspecific competition.

In addition, species segregation caused by the ecological dominance among species may lead to weak species being displaced towards resource–poorer habitats (Mac Nally & Timewell, 2005). The density of generalist species may have strong effects on the dynamics of local communities, and therefore the suitability of species assemblages is differentially modulated (Azeria & Kolasa, 2008). Extreme environmental conditions, or the introduction of exotic or invasive species (strong competitors), for example, may have more profound effects on specialist species than those exploiting a much broader range

Table 2. Bird species reported in 43 cays of the Jardines de la Reina archipelago, Cuba: Tr. Transient; PR. Permanent resident; WR. Winter resident; SR. Summer resident; * Number of cays where each species was reported.

*Tabla 2. Especies de aves registradas en 43 cayos del archipiélago de los Jardines de la Reina, Cuba: Tr. Transeúnte; PR. Residente permanente; WR. Residente invernal; SR. Residente veraniego; * Número de cayos en los que fue registrada cada especie.*

Species	Common name	Permanence status	Cays*
Anas discors	Blue–winged Teal	Tr	2
Mergus serrator	Red–breasted Merganser	Tr	1
Fregata magnificens	Magnificent Frigatebird	PR	32
Sula leucogaster	Brown Booby	PR	1
Phalacrocorax auritus	Double–crested Cormorant	PR	30
Anhinga anhinga	Anhinga	PR	12
Pelecanus occidentalis	Brown Pelican	PR	22
Ardea herodias	Great Blue Heron	PR	32
Ardea alba	Great Egret	PR	19
Egretta thula	Snowy Egret	PR	7
Egretta caerulea	Little Blue Heron	PR	13
Egretta rufescens	Reddish Egret	PR	19
Egretta tricolor	Tricoloured Heron	PR	17
Bubulcus ibis	Cattle Egret	Tr	6
Butorides virescens	Green Heron	PR	20
Nyctanassa violacea	Yellow–crowned Night–heron	PR	5
Eudocimus albus	White Ibis	PR	14
Platalea ajaja	Roseate Spoonbill	PR	10
Cathartes aura	Turkey Vulture	PR	18
Pandion haliaetus	Osprey	PR	23
Buteogallus gundlachii	Cuban Black Hawk	PR	14
Buteo jamaicensis	Red–tailed Hawk	Tr	2
Falco peregrinus	Peregrine Falcon	Tr	4
Falco columbarius	Merlin	Tr	6
Rallus longirostris	Clapper Rail	PR	13
Pluvialis squatarola	Grey Plover	WR	10
Charadrius wilsonia	Wilson's Plover	SR	27
Charadrius semipalmatus	Semipalmated Plover	WR	3
Charadrius vociferus	Killdeer	PR	5
Himantopus mexicanus	Black–necked Stilt	PR	5
Actitis macularius	Spotted Sandpiper	WR	11
Tringa melanoleuca	Greater Yellowlegs	WR	3
Tringa semipalmata	Willet	PR	5
Numenius phaeopus	Whimbrel	Tr	1
Arenaria interpres	Ruddy Turnstone	WR	19
Calidris minutilla	Least Sandpiper	WR	10

Table 2. (Cont.)

Species	Common name	Permanence status	Cays*
Calidris mauri	Western Sandpiper	Tr	3
Limnodromus griseus	Short–billed Dowitcher	Tr	1
Leucophaeus atricilla	Laughing Gull	PR	13
Sternula antillarum	Least Tern	SR	7
Thalasseus maximus	Royal Tern	PR	27
Hydroprogne caspia	Caspian Tern	WR	4
Thalasseus sandvicensis	Sandwich Tern	SR	15
Geotrygon montana	Ruddy Quail–dove	Tr	1
Patagioenas squamosa	Scaly–naped Pigeon	PR	3
Patagioenas leucocephala	White–crowned Pigeon	PR	27
Zenaida asiatica	White–winged Dove	PR	23
Zenaida aurita	Zenaida Dove	PR	2
Zenaida macroura	Mourning Dove	PR	19
Columbina passerina	Common Ground–dove	PR	4
Coccyzus americanus	Yellow–billed Cuckoo	SR	5
Coccyzus minor	Mangrove Cuckoo	PR	1
Crotophaga ani	Smooth–billed Ani	PR	4
Tyto alba	Barn Owl	Tr	1
Chordeiles minor	Common Nighthawk	Tr	1
Chordeiles gundlachii	Antillean Nighthawk	SR	18
Chlorostilbon ricordii	Cuban Emerald	PR	18
Megaceryle alcyon	Belted Kingfisher	WR	12
Sphyrapicus varius	Yellow–bellied Sapsucker	Tr	4
Xiphidiopicus percussus	Cuban Green Woodpecker	PR	8
Contopus caribaeus	Greater Antillean Pewee	PR	19
Contopus virens	Eastern Wood–pewee	Tr	1
Myiarchus sagrae	La Sagra's Flycatcher	PR	14
Tyrannus dominicensis	Grey Kingbird	SR	22
Tyrannus caudifasciatus	Loggerhead Kingbird	PR	21
Vireo griseus	White–eyed Vireo	WR	2
Vireo olivaceus	Red–eyed Vireo	Tr	3
Vireo altiloquus	Black–whiskered Vireo	SR	20
Progne cryptoleuca	Cuban Martin	SR	6
Petrochelidon fulva	Cave Swallow	SR	5
Hirundo rustica	*Barn Swallow*	*Tr*	*12*
Catharus minimus	Grey–cheeked Thrush	Tr	1
Catharus fuscescens	Veery	Tr	1
Turdus plumbeus	Red–legged Thrush	PR	3
Dumetella carolinensis	Grey Catbird	WR	5
Mimus polyglottos	Northern Mockingbird	PR	3

Table 2. (Cont.)

| Species	Common name	Permanence status	Cays*
Seiurus aurocapilla	Ovenbird	WR	7
Helmitheros vermivorum	Worm–eating Warbler	WR	2
Parkesia noveboracensis	Northern Waterthrush	WR	19
Mniotilta varia	Black–and–white Warbler	WR	9
Protonotaria citrea	Prothonotary Warbler	Tr	1
Oreothlypis peregrina	Tennessee Warbler	Tr	1
Geothlypis trichas	Common Yellowthroat	WR	11
Setophaga citrina	Hooded Warbler	Tr	2
Setophaga ruticilla	American Redstart	WR	16
Setophaga tigrina	Cape May Warbler	WR	4
Setophaga americana	Northern Parula	WR	10
Setophaga castanea	Bay–breasted Warbler	Tr	1
Setophaga fusca	Blackburnian Warbler	Tr	1
Setophaga petechia	Yellow Warbler	PR	40
Setophaga caerulescens	Black–throated Blue Warbler	WR	10
Setophaga palmarum	Palm Warbler	WR	15
Setophaga dominica	Yellow–throated Warbler	WR	8
Setophaga discolor	Prairie Warbler	WR	21
Icteria virens	Yellow–breasted Chat	Tr	1
Tiaris olivaceus	Yellow–faced Grassquit	PR	1
Piranga rubra	Summer Tanager	Tr	1
Piranga olivacea	Scarlet Tanager	Tr	2
Pheucticus ludovicianus	Rose–breasted Grosbeak	Tr	2
Passerina caerulea	Blue Grosbeak	Tr	1
Passerina cyanea	Indigo Bunting	Tr	5
Dolichonyx oryzivorus	Bobolink	Tr	1
Agelaius humeralis	Tawny–shouldered Blackbird	PR	14
Quiscalus niger	Greater Antillean Grackle	PR	31
Icterus galbula	Baltimore Oriole	Tr	1
Asio dominguensis	Short–eared Owl	Tr	1
Sula dactylatra	Masked Booby	Tr	1
Icterus melanopsis	Cuban Oriole	Tr	1
Catharus ustulatus	Swainson's Thrush	Tr	1
Mycteria americana	Wood Stork	Tr	1
Haematopus palliatus	American Oystercatcher	WR	1
Tringa flavipes	Lesser Yellowlegs	WR	1
Calidris alba	Sanderling	WR	5
Polioptila caerulea	Blue–grey Gnatcatcher	Tr	1
Oreothlypis ruficapilla	Nashville Warbler	Tr	1
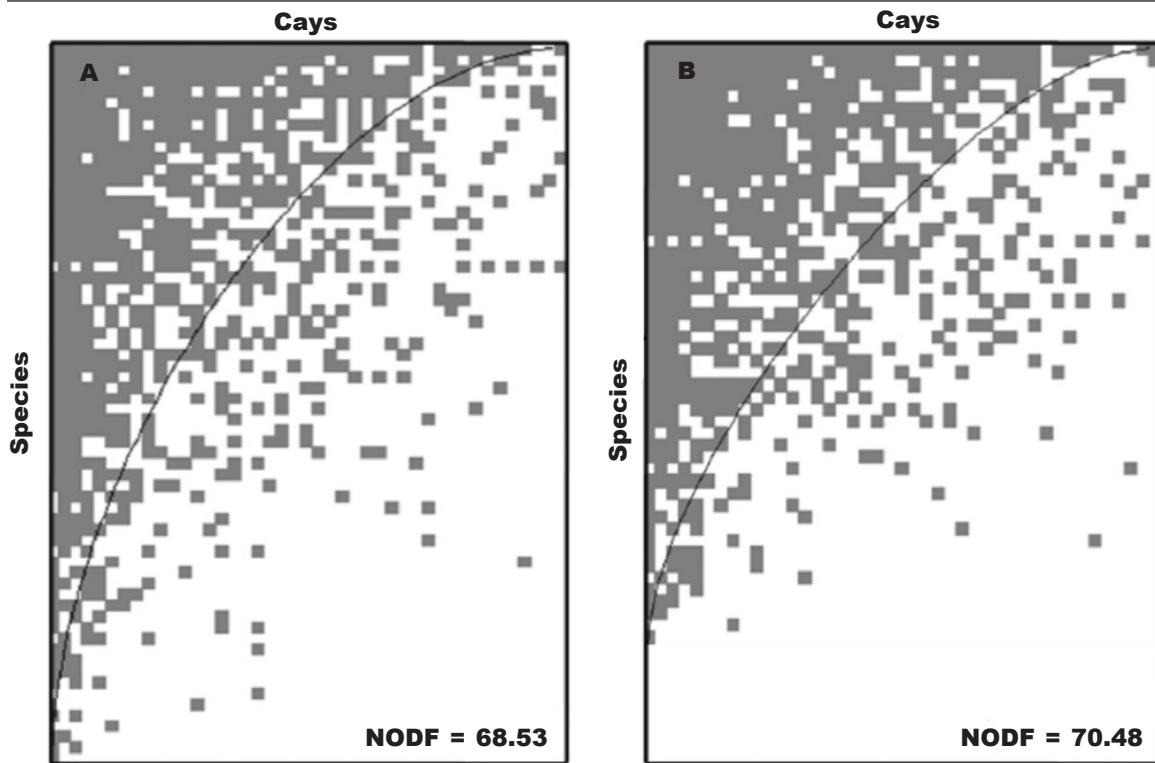
Fig. 2. Nestedness degree of the bird assemblages inhabiting 43 cays of the Jardines de la Reina archipelago, Cuba, during fall (A) and spring (B) migrations. Assemblages made up by 67 and 51 species in A and B, respectively: grey squares, presence; white squares, absence; central line, isocline of perfect nestedness; NODF. Nestedness metric based on overlap and decreasing fill.

Fig. 2. Grado de anidamiento de los ensamblajes de aves presentes en 43 cayos del archipiélago de los Jardines de la Reina, Cuba, durante las migraciones otoñal (A) y primaveral (B). Ensamblajes compuestos por 67 y 51 especies en A y B, respectivamente: cuadros grises, presencias; cuadros blancos, ausencias; línea central, isoclina de anidamiento perfecto; NODF. Índice de anidamiento basado en el relleno superpuesto y decreciente.

of ecological niches. These effects could change species composition, and therefore nested patterns. Generalist species such as herons and doves, both widely distributed populations across the Jardines de la Reina archipelago, could favor the generation of nested structures. Azeria & Kolasa (2008) highlight the importance of thoroughly assessing the relative role of the ecological differences among species (*e.g.* niche breadth) as a cause of nestedness and its temporal stability.

It is plausible to consider that many species may have developed behavioral and morphological adaptations to tolerate higher levels of niche overlapping from other species during fall migrations. Morphological differences (*i.e.* bill size and structure) in similar–sized bird species occupying the same habitat might promote coexistence through feeding niche differentiation as referred in many earlier works (Conant, 1988; Grant, 1999). Such adaptive strategies aiming to minimize the effects of ecological competition upon the arrival of

numerous neartic–neotropical migrants to the Jardines de la Reina archipelago may, to some extent, facilitate species coexistence across this insular region. This would in turn lead to homogenization of the compositional features of bird communities and thus decrease the degree of nestedness on the assemblages.

We agree with Almeida–Neto et al. (2008) and Ulrich et al. (2009) on considering the NODF metric as the most sensible index to evaluate the degree of nestedness given by its properties, which are deemed to be more statistically suitable than the T and D (nestedness discrepancy) indexes (Hu et al., 2011). In fact, this index not only far exceeds the remainder of conventional metrics, but also functions adequately within the null models framework (Almeida–Neto et al., 2008). On the other hand, the use of the T index may yield not only overestimated degrees of nestedness but also contrasting results compared to those obtained by the NODF metric. Such discrepancy was also verified in the present study since bird assemblages exhibited a

Table 3. Assessment of the nestedness degree (NODF index) in the bird assemblages of 43 cays of the Jardines de la Reina archipelago, Cuba, during fall and spring migrations, by comparing the observed (obs.) and the four null models (Er, Ce, Co and Li) simulated values (N = 1,000) of NODF (nestedness metric based on the overlap and decreasing fill): T. Matrix temperature; PNEr. % of perfect nestedness with respect to Er model. All values are expressed as mean ± SD (min–max). There was a significant nestedness (< 0.01) for all the cases.

Tabla 3. Evaluación del grado de anidamiento (índice NODF) en los ensamblajes de aves de 43 cayos del archipiélago de los Jardines de la Reina, Cuba, durante las migraciones otoñal y primaveral, mediante la comparación de los valores observados (obs.) y los simulados (N = 1.000) de los cuatro modelos nulos (Er, Ce, Co y Li) del NODF (Índice de anidamiento basado en el relleno superpuesto y decreciente): T. Temperatura de la matriz; PNEr. % de anidamiento perfecto respecto al modelo Er. Todos los valores se expresan como la [media ± DE (mín–máx)]. En todos los casos el anidamiento fue significativo (< 0,01).

| | Sampling periods | |
Index	Fall	Spring
T (PNEr)	12.68 (82.57)	13.06 (82.38)
NODFobs.	68.53	70.48
NODFEr	29.41 ± 1.04 (25.43–32.55)	34.00 ± 1.21 (30.27–37.50)
NODFCe	39.01 ± 1.38 (34.56–44.35)	43.55 ± 1.51 (38.67–48.23)
NODFCo	43.11 ± 0.90 (39.22–46.10)	46.37 ± 0.87 (43.30–49.56)
NODFLi	40.74 ± 0.62 (38.78–42.84)	46.18 ± 0.81 (43.40–48.56)

higher degree of nestedness in fall and spring according to the T and NODF indexes, respectively.

A limitation of the present study is that data on species' occurrence was not homogeneous across the study area due to the differences in the number of visits and census techniques used per cay. This may have underestimated the numbers of species along the sampled sites, and may therefore have generated false nested structures. For this reason published compilation works providing the most comprehensive and thorough species checklists were targeted as the ideal currently available information sources (*i.e.* Parada & García–Quintas, 2012; Parada et al., 2012). The inclusion of

Table 4. Comparisons of nestedness degree of the bird assemblages in 43 cays of the Jardines de la Reina archipelago, Cuba, between fall and spring migrations. Differences in the simulated values of NODF index (N = 1,000) are shown as mean ± SD (min–max): NODF. Nestedness metric based on the overlap and decreasing fill; [*] Statistical significance.

*Tabla 4. Comparación del grado de anidamiento de los ensamblajes de aves en 43 cayos del archipiélago de los Jardines de la Reina, Cuba, entre las migraciones otoñal y primaveral. Las diferencias de los valores simulados del NODF (N = 1.000) se muestran como media ± DE (mín–máx): NODF. Índice de anidamiento basado en el relleno superpuesto y decreciente; * Significación estadística.*

Null models	Differences between pairs of NODF values of replicates	Size effect	Probability
Er	1.11 ± 0.85 (0.00–5.46)	1.95	0.17
Ce	1.39 ± 1.06 (0.00–6.26)	1.95	0.25
Co	0.92 ± 0.71 (0.00–4.20)	1.95	0.10
Li	0.59 ± 0.46 (0.00–2.42)	1.95	0.01*

inventory datasets from over 50 years ago (*i.e.* data from September 1930 published in Buden & Olson, 1989) could influence the nested patterns, if we consider the colonization–extinction dynamics of natural communities. However, we believe that this did not pose a serious problem because most of the species reported by Buden & Olson (1989) and Garrido (1978) are still abundant and widely distributed throughout Jardines de la Reina archipelago. The exceptions are a few vagrant species (*Antrostomus carolinensis* and *Chordeiles minor*) reported on a single occasion some decades ago and *Turdus plumbeus* whose formerly scarce and locally distributed populations may have become extinct as far back as the late 1990s.

Furthermore, the significant differences expressed by the null model Li in the degree of nestedness between migratory seasons may reflect the drawbacks of the randomization algorithm in this model to generate many replicates. Indeed, it produced a narrower range of simulated values than the other models by randomizing the presence of the matrix with row totals kept constant. Thus, the variability of the simulated size effect may have been small enough to bias the detection probabilities of significant differences.

Overall, studies of the temporal changes on nested structures have been little studied to date (Bloch et al., 2007) even though temporal–spatial variations in distribution patterns of non–random species have long been a cornerstone in the ecology of community (Longo–Sánchez & Blanco, 2009). In this regard, no significant differences between the degree of nestedness of assemblages in the two distinct phenological stages (spring and fall seasons) was detected. This indicates that bird communities inhabiting the Jardines de la Reina archipelago showed a stable nested structure despite the influence of many migrants causing seasonal changes on species composition, with higher values of nestedness recorded in spring migrations.

We believe that causative factors such as the isolation of the cays and the habitat nestedness may have a significant role in the generation of nestedness patterns of bird communities in Jardines de la Reina. However, the effects of passive sampling should not be ruled out a priori taking into account the limitations and biases of the currently available datasets. Further identification and evaluation of the factors that promote nested structures among the avifauna in the study site may become relevant to establish conservation priorities and goals in the archipelago and thus maintain the stability of its bird assemblages.

Acknowledgments

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