

Taxonomic nestedness based on guilds? Bird assemblages of the Jardines de la Reina National Park, Cuba, as study case

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Abstract

Taxonomic nestedness based on guilds? Bird assemblages of the Jardines de la Reina National Park, Cuba, as study case. Nestedness is a widely known structuring model in insular and fragmented biotas that has often been assessed, but most studies to date have used a taxonomic approach. However, the relevance of an approach using functional groups has become increasingly highlighted in community ecology research. In this study, we evaluated the occurrence of nested structure in the Jardines de la Reina National Park bird assemblages as a whole, and its trophic guilds by following three different grouping criteria. We constructed species presence–absence matrices for each guild and estimated the degree of nestedness with the metric based on the overlap and decreasing fill, assessing its significance by means of two null models. Overall bird assemblage was significantly nested (NODF = 76.99; $p = 0.01$) whereas terrestrial insectivores (NODF = 81.32) and insectivores (NODF = 80.04) were the only trophic guilds (out of 19) that showed significant nestedness ($p \leq 0.01$). These results could provide evidence of the structural and functional cohesion of avifauna at the study site, especially among its insect–eating taxa. Taxonomic nestedness based on a guilds approach may help identify suitable conservation strategies for avian communities inhabiting naturally fragmented areas such as the Jardines de la Reina National Park.

Key words: Functional grouping, Low–lying islands, Nested community, Null model, Protected area, Trophic guild

Resumen

¿Anidamiento taxonómico basado en gremios? Los ensamblajes de aves del Parque Nacional Jardines de la Reina, en Cuba, como caso de estudio. El anidamiento es un modelo de estructuración bien conocido en biotas insulares y fragmentadas que se ha estudiado a menudo, aunque en la mayoría de los estudios realizados hasta la fecha se ha hecho desde un enfoque taxonómico. No obstante, en los estudios sobre ecología de comunidades se resalta cada vez más la importancia de adoptar un enfoque que utilice grupos funcionales. En este estudio se evaluó el grado de estructura de anidamiento en los ensamblajes de aves del Parque Nacional Jardines de la Reina en general y en sus gremios tróficos, siguiendo tres criterios de clasificación. Se confeccionaron matrices de presencia–ausencia de especies para cada gremio, se calculó el grado de anidamiento a partir del relleno superpuesto y decreciente y se analizó su significación mediante dos modelos nulos. La comunidad general de aves estuvo significativamente anidada (NODF = 76,99; $p = 0,01$) mientras que los insectívoros terrestres (NODF = 81,32) y los insectívoros (NODF = 80,04) fueron los únicos gremios tróficos que presentaron anidamiento significativo ($p \leq 0,01$). Estos resultados podrían poner de manifiesto la cohesión estructural y funcional de la avifauna en la zona del estudio, especialmente en los taxones insectívoros. Así, el enfoque del anidamiento taxonómico basado en gremios puede ayudar a determinar las estrategias de conservación adecuadas para las comunidades de avifauna que habitan en zonas naturalmente fragmentadas, como el Parque Nacional Jardines de la Reina.

Palabras clave: Agrupamiento funcional, Islas bajas, Comunidad anidada, Modelo nulo, Zona protegida, Gremio trófico

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Introduction

The complexity of natural communities has long proved a fruitful theoretical framework for the inception of numerous hypotheses related to and assembly rules at explaining species coexistence patterns. The most prevalent of these patterns are aggregation, segregation, turnover, and nestedness (Ulrich and Gotelli, 2013). Although these patterns and their underlying mechanisms have been the subject of considerable research efforts, tackling these theoretical principles separately is still a pervasive approach across many such studies. However, different structural patterns of species assemblages may well coexist in any given matrix (Ulrich and Gotelli, 2012). Ulrich et al. (2017) stated that species interactions, distribution of functional traits and stochastic events of colonization and extinction can be readily inferred from the analysis of presence-absence.

Among these patterns, biotic nestedness has become a recurring topic of ecological research in the past few decades (e.g., Patterson and Atmar, 1986; Patterson, 1987; Wright et al., 1998; Almeida-Neto et al., 2008; Ulrich et al., 2009). Interestingly, prevalence of this particular phenomenon across natural communities has shifted from commonplace to scarce through continued improvements of statistical toolkits (Matthews et al., 2015). While the definition of nestedness itself has been targeted for extensive criticism and revision (Dormann et al., 2009), its essence has remained nearly unchanged in that 'communities exhibit nested structures if poor species assemblages are non-random subgroups of those with greater species richness' (Patterson, 1987). More recently, Matthews et al. (2015) noted that ecological similarities among species may be overlooked by the traditional taxonomic approach (species composition), which could result in functional redundancy of the ecosystems. This latter subject stresses the need to include functional criteria in nestedness studies by providing a more accurate ecological context.

The concept of functional diversity, i.e. the breadth of ecological functions within any species assemblage (Petchey and Gaston, 2006; Bender et al., 2017), has been applied to the nestedness approach (e.g. Matthews et al., 2015; Bender et al., 2017; Aspin et al., 2018; Peláez and Pavanelli, 2018). Thus, functional nestedness was defined as the degree to which the set of functions present in a species-poor site are also present in richer sites, with a greater number of species, revealing a gradient in functional redundancy (Matthews et al., 2015; Bender et al., 2017). The core of this nestedness type is the 'species eco-functional traits' such as physiological, morphological, biochemical and behavioral characteristics of the individuals, related to the functions of the ecosystems (Gómez-Ortiz and Moreno, 2017). Similar to its taxonomic homologous, functional nestedness can be represented in a presence-absence matrix with the difference that the eco-functional traits substitute the species' names (see Bender et al., 2017). To date, this is the most widely accepted approach to assess the functional nestedness within the natural species assemblages.

Nevertheless, since Bender et al. (2017) and Gómez-Ortiz and Moreno (2017) state that functional diversity may be too quantified through functional groups or guilds, we suggest that another new approach can be used to assess the species functional roles in the nestedness context. Guilds constitute 'groups of species that exploit the same kind of environmental resources in a similar manner' (Simberloff and Dayan, 1991; Heino, 2009), and are defined based on a set of eco-functional traits shared among the species within the guild in question. Therefore, nestedness can be potentially assessed for any given species assemblages by using the concept of guilds/functional groups. A hypothetical presence-absence matrix (species vs. sites) may or may not be taxonomically nested, but different degrees of nestedness between some of its underlying submatrices can still occur. If such submatrices are built based on a given guild classification system, we would be using a similar procedure to that of the functional nestedness within the overall species assemblage (fig. 1).

Taxonomic nestedness based on guilds could be an ecologically meaningful approach since it enables researches for several reasons: first, to detect the true nested species subgroups according to its functional role within entire species assemblage; second, to identify important ecological functions (determined by the nested guilds) that contribute to the communities' stability and structural cohesion in fragmented landscapes; and third, to prioritize conservation efforts towards species subgroups relevant in maintaining the assemblages' natural cohesion/organization over individual species. Further studies focused on the underpinnings of functional nestedness could shed light on how to assess the effects of biological conservation threads at varying spatio-temporal scales from long-term population datasets. Trophic guilds are particularly useful as they inform us about trophic web structures and the ecosystems' energy flow.

In Cuba, bird assemblages of the Jardines de la Reina archipelago (JRA) show a consistent year-round nested structure throughout the annual cycle, unaltered by migration-driven species turnovers (García-Quintas and Parada, 2014). The Jardines de la Reina National Park (JRNP), the largest marine protected area with the highest number of cays in the Caribbean, is located within this insular region. Species relationships with its habitats and critical food resources are well known to shape birds' distribution patterns at varying spatial scales. Thereby, marine bird assemblages tend to display extensive and homogeneous distributional areas due to the spatial representativeness and interconnectivity of foraging sites across insular regions. On the contrary, trophic guilds whose species rely heavily on terrestrial food resources would naturally show comparatively more patchy and reduced distribution ranges due to differences on food items (availability and quality) among habitats and locations.

Therefore, we would expect that the nestedness degree of bird assemblages in the JRNP increases from the trophic guilds that include species dependent on the marine resources to the guilds composed by species consuming exclusively terrestrial items. Thus,

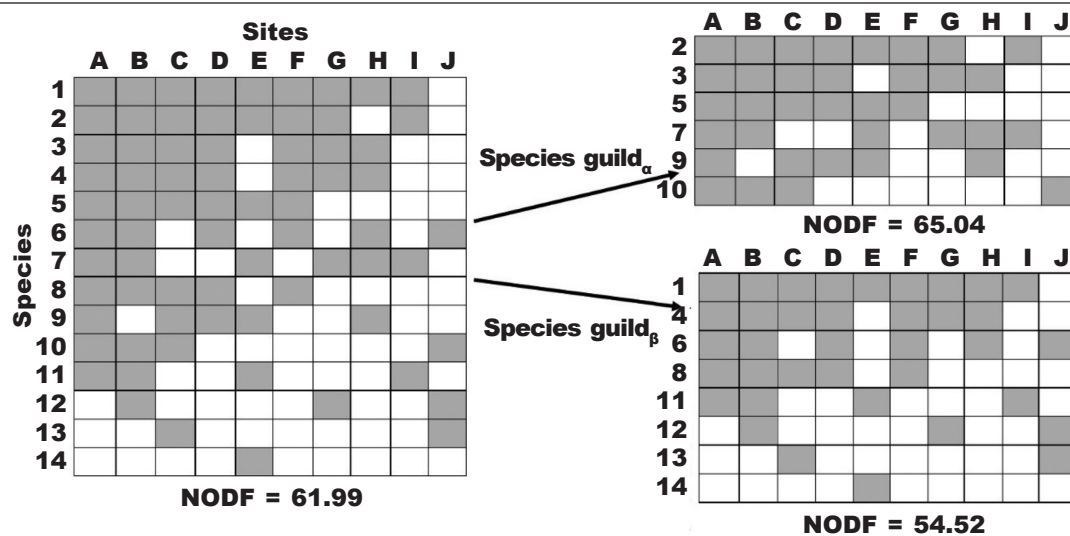


Fig. 1. A theoretical example of the taxonomic nestedness based on guilds. The example on the left represents a general matrix (species vs. sites) sorted according to the classical taxonomic nestedness approach. On the right we showed two submatrices of the general matrix where its species compositions constitute distinct functional groups (α and β guilds): gray squares, presences; white squares, absences. Differences between NODF (nestedness metric based on the overlap and decreasing fill) values show that several nested statuses, corresponding to distinct guilds, can coexist into either matrix.

Fig. 1. Ejemplo teórico del anidamiento taxonómico basado en gremios. A la izquierda está representada una matriz general (especies frente a sitios) ordenada según el enfoque del anidamiento taxonómico clásico. A la derecha se presentan dos submatrices de la matriz general cuyas composiciones de especies constituyen grupos funcionales distintos (gremios α y β): cuadros grises, presencias; cuadros blancos, ausencias. Las diferencias entre los valores de NODF (índice de anidamiento basado en el relleno superpuesto y decreciente) muestran que en cualquier matriz pueden coexistir varios estados anidados correspondientes a gremios distintos.

the aims of this study are: 1) to test out the occurrence of varying degrees of nestedness between different trophic guilds underlying the overall taxonomic nestedness in the JRNP; 2) to evaluate and compare the nested pattern between trophic guilds based on distinct grouping schemes; and 3) to identify functional groups of birds which significantly contribute to the overall nested structure in the archipelago as priority conservation targets.

Material and methods

Study area

The JRA stretches along Cuba's south-eastern coast from the Ancón Peninsula (Sancti Spíritus province) to Cabo Cruz (Granma province) and it comprises about 661 cays and islets. Among the three main insular sub-regions in this archipelago, the Doce Leguas cays, which encompass the JRNP, are the most extensive. This protected area extends across 87 km south of Ciego de Ávila and Camagüey provinces and includes relatively large cays such as Caguama (7.7 km²), Grande (24.3 km²) and Caballones (33.5 km²) (fig. 2).

This insular region encompasses relatively small and low-lying islands of recent geological history and oceanic origin that have arisen from storm movement of offshore sediments (García-Quintas and Parada, 2017). Sandy shores, dunes and shallow coastal lagoons constitute the most remarkable landscape features in these cays. In the JRNP, there are three main vegetation types, namely, mangrove forests (mostly dominated by *Rhizophora mangle*), sandy coastal scrubs (typical plant species are *Metopium toxiferum*, *Coccothrinax littoralis*, *Erithalis fruticosa*, *Chamaecrista lineata*, *Salvia bahamensis* and *Crossopetalum rhacoma*), and sandy and rocky vegetation complexes. Mangrove forests are the most widely distributed vegetation type, featuring floristic and physiognomic variants throughout the archipelago (Parada and García-Quintas, 2012). In general, these coastal vegetation complexes harbor low plant species richness and some of their floristic features can be found intermixed with those of adjacent coastal scrubs. Vascular flora of the JRA is represented by 40 families, 97 genera and 113 infra-generic taxa with 4.5% taxa being endemic to Cuba (Acevedo, 2013).

Recent contributions to the study of the avifaunal distribution within the JRA have improved knowledge

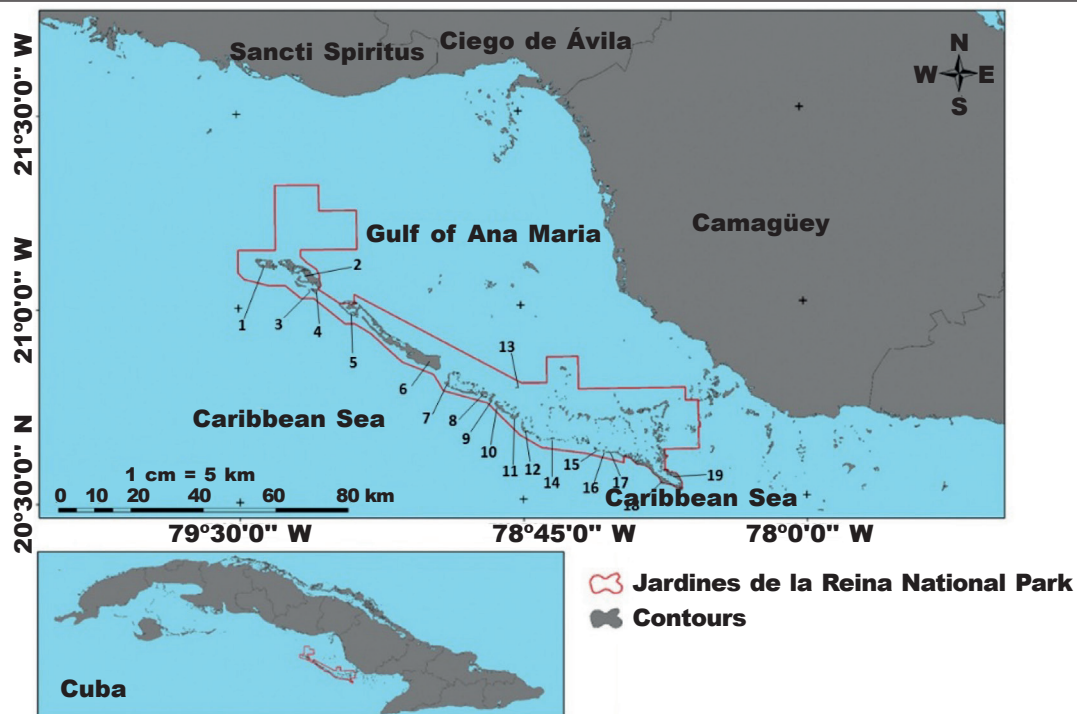


Fig. 2. Geographical location of the Jardines de la Reina National Park south of Ciego de Ávila and Camagüey provinces, southern Cuba. Studied cays: 1, Bretón; 2, Cinco Balas; 3, Alcatracito; 4, Alcatraz; 5, Grande; 6, Caballones; 7, Anclitas; 8, Boca Piedra Chiquita; 9, Boca de la Piedra de Piloto; 10, Piedra Grande; 11, Las Cruces; 12, Cachiboca; 13, Largo; 14, Boca Rica; 15, Juan Grin; 16, Boca Seca; 17, Camposanto; 18, Caguama; 19, Cabeza del Este.

Fig. 2. Ubicación geográfica del Parque Nacional Jardines de la Reina, al sur de las provincias Ciego de Ávila y Camagüey, en el sur de Cuba. (Para las abreviaturas de los cayos estudiados, véase arriba).

of the JRA biodiversity, a previously relatively poorly studied area compared to other Cuban insular and coastal regions (Parada and García–Quintas, 2012). At present, 92.6% of the avifauna documented in JRA (121 species, Parada et al., 2015) is represented in JRNP. Three taxa are regarded as Near Threatened: reddish egret (*Egretta rufescens*), Cuban black hawk (*Buteogallus gundlachii*) and white crowned pigeon (*Patagioenas leucocephala*) (Birdlife International, 2018).

Data source and processing

We obtained the presence–absence data of bird species occurring in 19 of the Doce Leguas cays from earlier works (Parada and García–Quintas, 2012; García–Quintas and Parada, 2017), along with our latest documented occurrences in the study site. General physical attributes of these cays and the sampling effort employed by each one are in García–Quintas and Parada (2017). We created a presence–absence (1–0) matrix whose rows and columns represented species and cays (taxonomic approach), respectively. Data were entered in the matrix in increasing order; starting with most widely distributed species on the top row and the cay with the highest species richness on the left column.

We excluded species with no explicit reference to their locality name when first reported in the study area (e.g., solitary sandpiper *Tringa solitaria*, chuck–will’s–widow *Antrostomus carolinensis*).

Species were grouped into trophic guilds according to three distinct classification schemes: most detailed and comprehensive criteria used for the Cuban avifauna (Kirkconnell et al., 1992), a parsimonious simplification of previous criteria (Andraca, 2010: Variant III) and the simplest and most inclusive criteria (Pizarro et al., 2012) (table 1s in supplementary material). Presence–absence matrices were created limited to the species in a trophic guild, for each guild of each of the three grouping schemes (based on guilds approach), separately, and arranged the same way as the combined matrix. Trophic guilds made up by fewer than five species were excluded from analyses to avoid small matrices.

To estimate nestedness, we used the nestedness metric based on the overlap and decreasing fill NODF (Almeida–Neto et al., 2008) featured in NODF 2.0 (Almeida–Neto and Ulrich, 2010). NODF values ranged from 0 (no nestedness) to 100 (perfect nestedness), and were compared with those obtained from 1,000 simulations of two null models. We used null models

Table 1. Trophic guilds structure (guilds ≥ 5 species) of bird assemblages in 19 cays of the Jardines de la Reina National Park, southern Cuba: FGI, foliage-gleaner insectivore; ASI, air-sallier insectivore; PGIF, pecker-gleaner insectivore-frugivore; FGIF, foliage-gleaner insectivore-frugivore; GGG, ground-gleaner granivore; WAC, water-ambusher carnivore; WPP, water-plunger piscivore; SGC, shoreline-gleaner carnivore; SPC, shoreline-prober carnivore; TI, terrestrial insectivore; AI, aerial insectivore; G_A , granivore (Andraca, 2010); GCIF, ground-dwelling insectivore-frugivore; FIF, foliage insectivore-frugivore; P, predator; CAR_A , carnivore (Andraca, 2010); I, insectivore; G_P , granivore (Pizarro et al., 2012); CAR_P , carnivore (Pizarro et al., 2012).

Tabla 1. Estructura en gremios tróficos (gremios ≥ 5 especies) de los ensamblajes de aves en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba: FGI, insectívoro de follaje con espiguelo; ASI, insectívoro aéreo; PGIF, insectívoro-frugívoro con picoteo y espiguelo; FGIF, insectívoro-frugívoro de follaje con espiguelo; GGG, granívoro de suelo con espiguelo; WAC, carnívoro acuático con vuelo en picada; WPP, piscívoro buceador; SGC, carnívoro de orilla con espiguelo; SPC, carnívoro de orilla-prober; TI, insectívoro terrestre; AI, insectívoro aéreo; G_A , granívoro (Andraca, 2010); GCIF, insectívoro-frugívoro de suelo; FIF, insectívoro-frugívoro de follaje; P, depredador; CAR_A , carnívoro (Andraca, 2010); I, insectívoro; G_P , granívoro (Pizarro et al., 2012); CAR_P , carnívoro (Pizarro et al., 2012).

Species	Kirkconnell et al. (1992)	Andraca (2010) Variant III	Pizarro et al. (2012)
<i>Setophaga petechia</i>	FGI	TI	I
<i>Setophaga tigrina</i>	FGI	TI	I
<i>Setophaga americana</i>	FGI	TI	I
<i>Setophaga palmarum</i>		TI	I
<i>Setophaga ruticilla</i>		AI	I
<i>Seiurus aurocapilla</i>		TI	I
<i>Parkesia noveboracensis</i>		TI	I
<i>Bubulcus ibis</i>		TI	I
<i>Charadrius vociferus</i>		TI	I
<i>Oreothlypis peregrina</i>	FGI	TI	I
<i>Vireo olivaceus</i>	FGI	TI	I
<i>Vireo altiloquus</i>	FGI	TI	I
<i>Vireo griseus</i>	FGI	TI	I
<i>Sphyrapicus varius</i>		TI	I
<i>Xiphidiopicus percussus</i>		TI	I
<i>Mniotilta varia</i>		TI	I
<i>Geothlypis trichas</i>		TI	I
<i>Setophaga caerulescens</i>		TI	I
<i>Setophaga dominica</i>		TI	I
<i>Setophaga discolor</i>		TI	I
<i>Chlorostilbon ricordii</i>			I
<i>Contopus caribaeus</i>	ASI	AI	I
<i>Contopus virens</i>	ASI	AI	I
<i>Myiarchus sagrae</i>	ASI	AI	I
<i>Tyrannus dominicensis</i>	ASI	AI	I
<i>Tyrannus caudifasciatus</i>	ASI	AI	I
<i>Chordeiles gundlachi</i>		AI	I
<i>Hirundo rustica</i>		AI	I
<i>Progne cryptoleuca</i>		AI	I

Table 1. (Cont.)

Species	Kirkconnell et al. (1992)	Andraca (2010) Variant III	Pizarro et al. (2012)
<i>Petrochelidon fulva</i>		AI	I
<i>Chordeiles minor</i>		AI	I
<i>Zenaida asiatica</i>	GGG	G _A	G _P
<i>Zenaida macroura</i>	GGG	G _A	G _P
<i>Zenaida aurita</i>	GGG	G _A	G _P
<i>Columbina passerina</i>	GGG	G _A	G _P
<i>Geotrygon montana</i>	GGG	G _A	G _P
<i>Tiaris olivaceus</i>		G _A	G _P
<i>Passerina caerulea</i>		G _A	G _P
<i>Passerina cyanea</i>		G _A	G _P
<i>Agelaius humeralis</i>		G _A	G _P
<i>Coccyzus americanus</i>	PGIF	GCIF	I
<i>Coccyzus minor</i>	PGIF	GCIF	I
<i>Crotophaga ani</i>	PGIF	GCIF	I
<i>Dumetella carolinensis</i>	PGIF	GCIF	I
<i>Mimus polyglottos</i>	PGIF	GCIF	I
<i>Quiscalus niger</i>	PGIF	GCIF	I
<i>Turdus plumbeus</i>		GCIF	I
<i>Piranga rubra</i>	FGIF	FIF	I
<i>Piranga olivacea</i>	FGIF	FIF	I
<i>Pheucticus ludovicianus</i>	FGIF	FIF	I
<i>Icterus galbula</i>	FGIF	FIF	I
<i>Icterus melanopsis</i>	FGIF	FIF	I
<i>Falco columbarius</i>		D	CAR _P
<i>Falco peregrinus</i>		D	CAR _P
<i>Buteo jamaicensis</i>		D	CAR _P
<i>Tyto alba</i>		D	CAR _P
<i>Asio dominguensis</i>		D	CAR _P
<i>Spatula discors</i>			CAR _P
<i>Nyctanassa violacea</i>			CAR _P
<i>Buteogallus gundlachi</i>			CAR _P
<i>Ardea alba</i>	WAC	CAR _A	CAR _P
<i>Ardea herodias</i>	WAC	CAR _A	CAR _P
<i>Butorides virescens</i>	WAC	CAR _A	CAR _P
<i>Egretta tricolor</i>	WAC	CAR _A	CAR _P
<i>Egretta rufescens</i>	WAC	CAR _A	CAR _P
<i>Egretta caerulea</i>	WAC	CAR _A	CAR _P
<i>Egretta thula</i>	WAC	CAR _A	CAR _P
<i>Eudocimus albus</i>		CAR _A	CAR _P
<i>Platalea ajaja</i>			CAR _P

Table 1. (Cont.)

Species	Kirkconnell et al. (1992)	Andraca (2010) Variant III	Pizarro et al. (2012)
<i>Pelecanus occidentalis</i>	WPP	CAR _A	CAR _P
<i>Hydroprogne caspia</i>	WPP	CAR _A	CAR _P
<i>Thalasseus maximus</i>	WPP	CAR _A	CAR _P
<i>Sternula antillarum</i>	WPP	CAR _A	CAR _P
<i>Sula leucogaster</i>	WPP	CAR _A	CAR _P
<i>Sula dactylatra</i>	WPP	CAR _A	CAR _P
<i>Pandion haliaetus</i>	WPP	CAR _A	CAR _P
<i>Leucophaeus atricilla</i>		CAR _A	CAR _P
<i>Charadrius wilsonia</i>	SGC	CAR _A	CAR _P
<i>Charadrius semipalmatus</i>	SGC	CAR _A	CAR _P
<i>Actitis macularius</i>	SGC	CAR _A	CAR _P
<i>Pluvialis squatarola</i>	SGC	CAR _A	CAR _P
<i>Calidris minutilla</i>	SGC	CAR _A	CAR _P
<i>Calidris mauri</i>	SGC	CAR _A	CAR _P
<i>Calidris alba</i>	SGC	CAR _A	CAR _P
<i>Arenaria interpres</i>	SGC	CAR _A	CAR _P
<i>Tringa melanoleuca</i>	SPC	CAR _A	CAR _P
<i>Tringa semipalmata</i>	SPC	CAR _A	CAR _P
<i>Himantopus mexicanus</i>	SPC	CAR _A	CAR _P
<i>Limnodromus griseus</i>	SPC	CAR _A	CAR _P
<i>Rallus crepitans</i>	SPC	CAR _A	CAR _P
<i>Phalacrocorax auritus</i>		CAR _A	
<i>Megasceryle alcyon</i>		CAR _A	

Fixed–Fixed (FF) (Connor and Simberloff, 1979; Gotelli, 2000) and Proportional–Proportional (PP) (Ulrich and Gotelli, 2012) to estimate the significance level of the nestedness degree at $p \leq 0.01$. Results from FF null model were prioritized over those obtained from the PP null model when matrix filling ranged between 35 and 45% according to Ulrich and Gotelli's (2012, 2013) recommendations. The nestedness degree was compared between trophic guilds using the Z–transformed score ($\text{NODF}_{\text{obs}} - \text{NODF}_{\text{exp}} / \text{SD}_{\text{exp}}$).

Results

We analysed a total of 115 bird species based on revised compilation works (table 2s in supplementary material). These included the latest additions to Caballones cay: semipalmated plover (*Charadrius semipalmatus*), zenaida dove (*Zenaida aurita*), gray catbird (*Dumetella carolinensis*), common yellowthroat

(*Geothlypis trichas*) and yellow–throated warbler (*Setophaga dominica*). Highest species numbers were documented in Anclitas (88), Caguama (76) and Grande (74). Species such as white–winged pigeon (*Zenaida asiatica*) and yellow warbler (*Setophaga petechia*) showed the widest distributional ranges across JRNP (18 cays). Avian guild structure yielded nine–, seven– and three– trophic groupings in accordance to classification criteria of Kirkconnell et al. (1992), Andraca (2010) (Variant III) and Pizarro et al. (2012), respectively (table 1). Guilds comprising the highest species numbers were Insectivore (43) and Carnivore (38) according to this latter classification scheme, whereas the best represented ones by the first two criteria (*i.e.*, Kirkconnell's and Andraca's) were shoreline pecker Carnivore (eight) and Carnivore (31), respectively.

Overall, avian assemblages in the JRNP showed a significant nested structure based on the difference between the observed (76.99) and simulated NOFD

Table 2. Mean \pm SD of nestedness degree ($CL_{lower} - CL_{upper}$ 95%) of avian trophic guilds (≥ 5 species) in 19 cays of the Jardines de la Reina National Park, southern Cuba. Grouping classifications were based on criteria of Kirkconnell et al. (1992), Andraca (2010) and Pizarro et al. (2012): NODF, nestedness metric based on overlap and decreasing fill; $NODF_{pp}$, null model 'proportional-proportional'; p , probability.

Tabla 2. Media \pm DE ($LC_{inferior} - LC_{superior}$ 95%) del grado de anidamiento de los gremios tróficos de aves (≥ 5 especies) en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba. Las clasificaciones en grupos se basaron en los criterios de Kirkconnell et al. (1992), Andraca (2010) y Pizarro et al. (2012): NODF, índice de anidamiento basado en el relleno superpuesto y decreciente; $NODF_{pp}$ modelo nulo "proporcional-proporcional"; p , probabilidad.

Trophic guilds	Matrix fill (%) / size (columns x rows)	$NODF_{obs}$	$NODF_{pp}$ N = 1000	p
Kirkconnell et al. (1992)				
Water-ambusher	58.6/19 x 7	78.79	77.10 \pm 3.40	0.34
Carnivore			(69.44–82.86)	
Water-plunger	41.4/19 x 7	69.18	67.61 \pm 5.78	0.44
Piscivore			(55.10–76.94)	
Shoreline-gleaner	28.3/19 x 8	42.12	40.00 \pm 3.12	0.24
Carnivore			(34.20–46.44)	
Shoreline-prober	16.8/19 x 5	13.44	12.96 \pm 1.66	0.40
Carnivore			(9.71–16.35)	
Ground-gleaner	31.6/19 x 5	54.42	54.28 \pm 2.60	0.43
Granivore			(48.62–58.29)	
Foliage-gleaner	33.8/19 x 7	69.79	64.43 \pm 4.43	0.09
Insectivore			(54.94–72.41)	
Air-sallier	52.6/19 x 5	49.62	49.05 \pm 5.50	0.48
Insectivore			(39.17–60.09)	
Pecker-gleaner	28.9 / 19 x 6	48.43	49.11 \pm 3.45	0.43
Insectivore-frugivore			(41.91–55.73)	
Foliage-gleaner	6.3/19 x 5	1.93	1.68 \pm 0.39	0.50
Insectivore-frugivore			(1.10–2.21)	
Andraca (2010) (Variant III)				
Carnivore	39.0/19 x 31	81.72	77.58 \pm 2.42	0.03
			(72.76–81.99)	
Predator	9.5/19 x 5	2.76	3.80 \pm 0.80	0.14
			(2.21–5.25)	
Granivore	28.7/19 x 9	61.07	59.19 \pm 4.51	0.33
			(49.66–67.98)	
Aerial Insectivore	40.2/19 x 11	61.06	61.46 \pm 3.87	0.48
			(54.54–69.37)	
Foliage	6.3/19 x 5	1.93	1.66 \pm 0.41	0.50
Insectivore-frugivore			(1.10–2.21)	
Ground-dwelling	27.1/19 x 7	49.52	50.18 \pm 3.68	0.44
Insectivore-frugivore			(43.39–57.36)	
Terrestrial Insectivore	29.1/19 x 19	81.32	70.50 \pm 3.43	0.00
			(63.56–76.93)	

Table 2. (Cont.)

Trophic guilds	Matrix fill (%) / size (columns x rows)	NOFD _{obs}	NOFD _{PP} N = 1000	<i>p</i>
Pizarro et al. (2012)				
Carnivore	33.2/19 x 38	77.08	74.17 ± 2.47 (69.18 – 78.72)	0.12
Granivore	28.7/19 x 9	61.07	59.39 ± 4.47 (50.55 – 68.21)	0.35
Insectivore	29.9/19 x 43	80.04	73.27 ± 2.40 (68.43 – 78.06)	0.00

values according to the PP null model (NOFD = 2.54; $p = 0.01$). Results from FF null model (NOFD = 76.68; $p = 0.28$) were not considered for analyses because its matrix filling just reached the 30.3%. In contrast, most of the trophic guilds that we assessed did not exhibit nested structure, except for Terrestrial Insectivore (TI) and Insectivore (I) by Andraca's (2010) and Pizarro et al. (2012) classifications, respectively (table 2), with the highest nestedness degree reported in TI (fig. 3). On these matrices, no FF null model results were considered for the same reason of the matrix fill (table 3s in supplementary material).

Discussion

Firstly, our results suggest that the overall avian assemblage in the JRNP is taxonomically nested. Such structuring corresponds to the interspecific differences of abundance and distribution patterns since the most abundant species at a local scale tend to influence neighbouring species assemblages to a greater extent than less common species (Patterson and Atmar, 1986). Thus, at our study site, avifauna inhabiting cays with relatively lower habitat diversity (reduced resources/niches) may become impoverished through extinction, colonization avoidance by dispersing birds that perceive no suitable habitat, and competitive exclusion, as opposed to avifauna in cays with higher landscape complexity or more resources for species to coexist.

Avian nestedness within the JRNP is consistent with findings from similar works focused at a broader spatial scale, namely, the Jardines de la Reina Archipelago as a whole (García-Quintas and Parada, 2014, 2017). This lends further support to the idea of nestedness persistence at varying spatial scales; an aspect which has remained poorly studied (Méndez, 2004). It is plausible to assert that nestedness within the cays of Laberinto de las Doce Leguas (where JRNP is located) accounts for much of the observed nested structures in the entire archipelago, because these cays exhibit the highest number of habitats for birds. Indeed, this factor is thought to be pivotal in the unfolding and persistence of nestedness in

avian metacommunities throughout the archipelago (García-Quintas and Parada, 2017).

Up to 42 species appear to be prone to local extirpation according to observed avian nestedness, owing to their spatially patchy occurrence (table 2s in supplementary material). The inclusion of these uncommon species among the main conservation targets of the protected area should not be entirely based on their scarcity in the JRNP. These species encompass waterfowl (e.g., blue-winged teal (*Spatula discors*), red-breasted merganser (*Mergus serrator*), greater

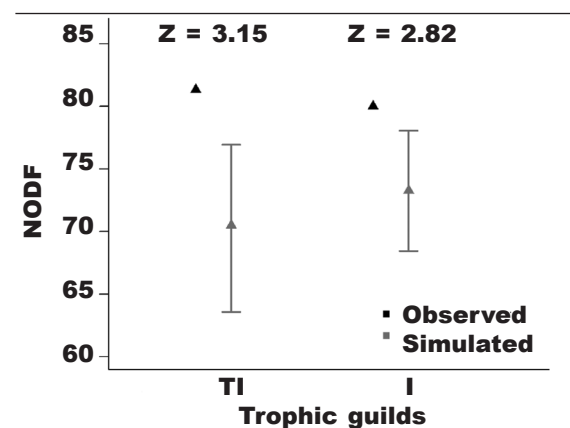


Fig. 3. Comparisons of nestedness degree between insectivore bird species groupings (Z-transformed score) in 19 cays of the Jardines de la Reina National Park, southern Cuba. Trophic guilds: TI, terrestrial insectivore (Andraca, 2010); I, insectivore (Pizarro et al., 2012).

Fig. 3. Comparación del grado de anidamiento entre grupos de especies de aves insectívoras (puntuación Z-transformada) en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba. Gremios tróficos: TI, insectívoro terrestre (Andraca, 2010); I, insectívoro (Pizarro et al., 2012).

yellowlegs (*Tringa melanoleuca*), sanderling (*Calidris alba*), short-billed dowitcher (*Limnodromus griseus*) and raptors (e.g., red-tailed hawk (*Buteo jamaicensis*), peregrine falcon (*Falco peregrinus*), barn owl (*Tyto alba*)), that are usually regarded as generalist species that exploit food resources across vast areas of broadly represented habitats. Rare occurrence of avian species in the study site is likely explained by the absence of critical habitats/ecological niches, which in turn, highlights the drawbacks of nestedness studies to facilitate fact-based decisions in prioritizing conservation goals when used as the sole set of criteria (Cutler, 1994).

However, the fact that significant nestedness was only reported in a small number of the trophic guilds in the JRNP avifauna may be an indication of a differential contribution of these functional groups to the overall nested structure. Thus, the occurrence of nestedness of functional groups of species brings to light ecological and biogeographical features frequently overlooked by studies focused on taxonomic nestedness only. For this reason Ulrich et al. (2017) proposed that robust identification of nested structures in natural communities demands the collection of environmental data and functional traits related to its component species.

In this study, nested trophic guilds grouped the insectivore species, more specifically, the TI guild which was exclusively made up of terrestrial species. Therefore, it appears that nestedness of terrestrial insect-eating bird species could be driven by differences in food availability (insects and spiders) throughout the JRNP which, in turn, may be linked to ecological and landscape features of these cays (vegetation types, substrates, seasonal bodies of water). Species clustered in the remaining trophic guilds either relied upon different food sources (e.g., seeds, fruits, larger living preys), or foraged mostly along coastal wetlands such as shorelines and shallow coastal waters (e.g., shorebirds, piscivores, wading birds), or exploited vast foraging areas (e.g., raptors). In general, weak reliance of these species on terrestrial habitats through frequent dispersal/foraging movements between fragments (cays) and the matrix (sea water) may have diluted the effects of nestedness-generating factors. Besides, the assumption of a total isolation between islands and the neighbouring sea biotas may not be very realistic (Herrera, 2011).

Although the overall species assemblage in the JRNP is organized in a nested structure, insectivore species were the only significantly nested trophic guild. This indicates that taxonomic nestedness based on guilds may shed light on finer-grain structuring patterns in metacommunities that are otherwise unnoticed if analyzed through the taxonomic approach alone. Additionally, this also highlights the importance of the insect-eating avifauna in shaping avian terrestrial communities in JRNP as a whole. As a result, our analyses provided a list of 13 locally extinction-prone species (those occurring in one or two cays in JRNP) when terrestrial insectivore (Andraca, 2010) and insectivore (Pizarro et al., 2012) guilds were combined (table 4s in supplementary material).

Pizarro et al.'s (2012) classification scheme was the broadest of all three and included few trophic guilds,

with the highest species number per grouping. On the contrary, numerous guilds made up of much fewer species were identified by the criteria of Kirkconnell et al. (1992), with a small portion of those included in the analyses (> 5 species). This is largely due to the high degree of specificity (type of food, foraging substrate and behavior) by which any given species is assigned to a trophic guild. The variant III from Andraca (2010) rendered a trade-off between classification specificity and the resulting number of groupings, and was thus being the most parsimonious approach we assessed. This classification scheme may be suitable to characterize avifaunas at both regional (e.g., nation-wide, large mountain ranges) and local scales (e.g., sub-archipelagos). Nonetheless, no classification system should be deemed more adequate *per se* over others unless the study spatial scale, research objectives and species assemblages' main features are taken into consideration. Our findings lend further support to the plausibility of using several guild classification criteria in the same hypothesis-testing framework as the recommended approach by Milesi et al. (2002), since detection of nested trophic guilds may be partly influenced by the chosen classification scheme. Therefore, we ratify the usage of various grouping criteria, or recommend using those classification systems that are neither too broad nor too detailed.

The conservation status of avian functional groups and the ecosystem implications of bird declines have been widely addressed (Sekercioglu et al., 2004), as has the importance of tropical insectivorous birds to various types of landscapes and habitats (Gradwohl and Greenberg, 1982; Greenberg et al., 2000; Van Bael et al., 2003; Perfecto et al., 2004). Accordingly, insectivore species may require the implementation of specific management and conservation strategies given their high sensitivity to orderly loss of nested guilds based on the fragments' surface area (Matthews et al., 2015). Moreover, its functional extinction/deficiency may likely cause trophic cascades (Sekercioglu et al., 2004), especially when in absence of other functionally equivalent taxa that can replace these birds' ecosystem services. While none of the insectivore species in JRNP is currently classified as endangered, their numerical importance has been highlighted by greater species number per family (e.g., Parulidae and Tyrannidae) and individual species abundance (e.g., yellow warbler, prairie warbler *Setophaga discolor*) (Parada et al., 2015). Therefore, we recommend the inclusion of the bird species of this trophic guild among the conservation goals of the next JRNP Management Plan since this will target its functional roles in the entire ecosystem for protection as opposed to the typical taxonomic-based conservation.

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References

- Acevedo, C. J., 2013. Lista florística del archipiélago de los Jardines de la Reina, Cuba. *Revista Cubana de Ciencias Biológicas*, 2(3): 62–72.
- Almeida-Neto, M., Guimarães, P., Guimarães, P. R. Jr., Loyola, R. D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117: 1227–1239.
- Almeida-Neto, M., Ulrich, W., 2010. A straightforward computational approach for quantifying nestedness using abundance data. *Environmental Modelling & Software*, 26: 173–178.
- Andraca, L., 2010. Reglas de ensamblaje y modelos de coexistencia de especies en las comunidades de aves cubanas. Tesis de licenciatura, Universidad de La Habana.
- Aspin, T. W. H., Matthews, T. J., Khamis, K., Milner, A. M., Wang, Z., O'callaghan, M. J., Ledger, M. E., 2018. Drought intensification drives turnover of structure and function in stream invertebrate communities. *Ecography*, 41(12): 1992–2004.
- Bender, M. G., Leprieux, F., Mouillot, D., Kulbicki, M., Parravicini, V., Pie, M. R., Barneche, D. R., Oliveira-Santos, L. G. R., Floeter, S. R., 2017. Isolation drives taxonomic and functional nestedness in tropical reef fish faunas. *Ecography*, 40(3): 425–435.
- Connor, E. F., Simberloff, D., 1979. The assembly of species communities: chance or competition? *Ecology*, 60(6): 1132–1140.
- Cutler, A. H., 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape and Urban Planning*, 28: 73–82.
- Dormann, C. F., Fründ, J., Blüthgen, N., Gruber, B., 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2: 7–24.
- García-Quintas, A., Parada, A., 2014. Effects of migrations on the nestedness structure of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba. *Animal Biodiversity and Conservation*, 37(2): 127–139.
- 2017. Underlying factors promoting nestedness of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba. *Animal Biodiversity and Conservation*, 40(1): 7–16, <https://doi.org/10.32800/abc.2017.40.0007>
- Gómez-Ortiz, Y., Moreno, C. E., 2017. La diversidad funcional en comunidades animales: una revisión que hace énfasis en los vertebrados. *Animal Biodiversity and Conservation*, 40(2): 165–174, <https://doi.org/10.32800/abc.2017.40.0165>
- Gotelli, N. J., 2000. Null model analysis of species co-occurrence patterns. *Ecology*, 81(9): 2606–2621.
- Gradwohl, J., Greenberg, R., 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. *Ecology*, 63: 581–583.
- Greenberg, R., Bichier, P., Cruz, A., MacVean, C., Perez, R., Cano, E., 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology*, 81(6): 1750–1755.
- Heino, J., 2009. Species co-occurrence, nestedness and guild-environment relationships in stream macroinvertebrates. *Freshwater Biology*, 54: 1947–1959.
- Herrera, J. M., 2011. El papel de la matriz en el mantenimiento de la biodiversidad en hábitats fragmentados. De la teoría ecológica al desarrollo de estrategias de conservación. *Ecosistemas*, 20(2): 21–34.
- Kirkconnell, A., Garrido, O. H., Posada, R. M., Cubillas, S. O., 1992. Los grupos tróficos en la avifauna cubana. *Poeyana*, 415: 1–21.
- Matthews, T. J., Sheard, C., Cottee-Jones, H. E. W., Bregman, T. P., Tobias, J. A., Whittaker, R. J., 2015. Ecological traits reveal functional nestedness of bird communities in habitat islands: a global survey. *Oikos*, 124: 817–826.
- Méndez, M., 2004. La composición de especies de aves en islas y paisajes fragmentados: un análogo ecológico de las muñecas rusas. *El Draque*, 5: 199–212.
- Milesi, F. A., Marone, L., Lopez de Casenave, J., Cueto, V. R., Mezquida, E. T., 2002. Gremios de manejo como indicadores de las condiciones del ambiente: un estudio de caso con aves y perturbaciones del hábitat en el Monte central, Argentina. *Ecología Austral*, 12: 149–161.
- Parada, A., García-Quintas, A., 2012. Avifauna de los archipiélagos del sur de Ciego de Ávila y Camagüey, Cuba: una revisión taxo-ecológica actualizada. *Mesoamericana*, 16(1): 35–55.
- Parada, A., García-Quintas, A., Hernández, D., 2015. The avifauna of sandy coastal vegetation during migration in the Laberinto de las Doce Leguas sub-archipelago, southern Cuba. *Cotinga*, 37: 48–58.
- Patterson, B. D., 1987. The principle of nested subsets and its implications for biological conservation. *Conservation Biology*, 1(4): 323–334.
- Patterson, B. D., Atmar, W., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28: 65–82.
- Peláez, O., Pavanelli, C. S., 2018. Environmental heterogeneity and dispersal limitation explain different aspects of β diversity in Neotropical fish assemblages. *Freshwater Biology*, 64(3): 497–505, <https://doi.org/10.1111/fwb.13237>
- Perfecto, I., Vandermeer, J. H., López, G., Ibarra, G., Greenberg, Bichier, P., Langridge, S., 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology*, 85(10): 2677–2681.
- Petchey, O. L., Gaston, K. J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters*, 9: 741–758.
- Pizarro, J. C., Anderson, C. B., Rozzi, R., 2012. Birds as marine-terrestrial linkages in sub-polar archipelagic systems: avian community composition, function and seasonal dynamics in the Cape Horn Biosphere Reserve (54–55°S), Chile. *Polar Biology*, 35: 39–51.
- Sekercioglu, C. H., Daily, G. C., Ehrlich, P. R., 2004.

- Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences, USA*, 101: 18042–18047.
- Simberloff, D., Dayan, T., 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*, 22: 115–143.
- Ulrich, W., Almeida-Neto, M., Gotelli, N. J., 2009. A consumer's guide to nestedness analysis. *Oikos*, 118: 3–17.
- Ulrich, W., Gotelli, N. J., 2012. A null model algorithm for presence–absence matrices based on proportional resampling. *Ecological Modelling*, 244: 20–27.
- 2013. Pattern detection in null model analysis. *Oikos*, 122: 2–18.
- Ulrich, W., Kryszewski, W., Sewerniak, P., Puchalka, R., Strona, G., Gotelli, N. J., 2017. A comprehensive framework for the study of species co-occurrences, nestedness and turnover. *Oikos*, doi: 10.1111/oik.04166.
- Van Bael, S. A., Brawn, J. D., Robinson, S. K., 2003. Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences, USA*, 100(14): 8304–8307.
- Wright, D. H., Patterson, B. D., Mikkelsen, G. M., Cutler, A., Atmar, W., 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia*, 113: 1–20.
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Supplementary material

Table 1s. Trophic guilds of the avian assemblages in the Jardines de la Reina National Park, Cuba, according to three classification systems.

Tabla 1s. Gremios tróficos de los ensamblajes de aves en el Parque Nacional Jardines de la Reina, en Cuba, según tres sistemas de clasificación.

Kirkconnell et al. (1992)			
Bark–gleaner insectivore	BGI	Frugivore	F
Bark–excavator insectivore	BEI	Frugivore–granivore	FG
Foliage–gleaner insectivore	FGI	Ground–and foliage pecker–and–gleaner	
Bark–and–foliage gleaner insectivore	BFGI	Granivore–insectivore	GFPGGI
Ground–ambusher insectivore	GAI	Aerial Predator	AP
Ground–pecker insectivore	GPI	Aerial nocturnal predator	ANP
Ground–and–water pecker insectivore	GWPI	Air–sallier nocturnal predator	ASNP
Ground–and–bark–excavator insectivore	GBEI	Insectivore and small–vertebrate predator	ISIP
Ground–and–foliage gleaner–pecker	GFGPI	Crustaceovore	C
Air–sallier lower–canopy–gleaner	ASLCGI	Molluscovore	M
Air–sallier insectivore	ASI	Omnivore	O
Aerial insectivore	AI	Scavenger	Scav
Aerial nocturnal insectivore	ANI	Water–ambusher carnivore	WAC
Air–sallier insectivore–frugivore	ASIF	Shoreline–prober carnivore	SPC
Air–sallier–and–forager insectivore–frugivore	ASFIF	Shoreline–gleaner carnivore	SGC
	ASFIF	Water–plunger piscivore	WPP
Foliage–gleaner insectivore–frugivore	FGIF	Water–prober carnivore–phytophage	WPCP
Pecker–gleaner insectivore–frugivore	PGIF	Pecker phytophage–carnivore	PPC
Ground–forager insectivore–frugivore	GFIF	Diver carnivore–phytophage	DCP
Floral–hover–gleaner nectarivore–insectivore	FHGNi	Mud strainer	MS
	FHGNi	Water–dabbler omnivore	WDO
Frugivore–nectarivore	FN	Water–dabbler–and–diver piscivore	WDDP
Ground–gleaner granivore	GGG	Air–sallier–and water–diver piscivore	ASWDP
Ground–and–foliage granivore	GFG	Water–diver piscivore	WDP
Andraca (2010) (Variant III)		Pizarro et al. (2012)	
Terrestrial Insectivore	IT	Insectivore	I
Aerial–insectivore	IAA	Frugivore	FP
Foliage insectivore–frugivore	FIF	Granivore	GP
Ground–dwelling insectivore–frugivore	GIF	Carnivore	CARP
Nectarivore–insectivore	NI	Carnivore–scavenger	CAR–S
Frugivore	FA	Scavenger	SCAV
Granivore	G	Omnivore	OP
Predator	D	Piscivore	PIS
Insectivore	GFGPI	Crustaceovore	CA
Insectivore	ASLCGI	Molluscovore	MA
Omnivore	OA		
Scavenger	SCAVA		
Carnivore–phytophage	C–P		
Water–dabbler	WDA		
Carnivore	CAR		

Table 2s. Incidence matrix of 115 bird species occurring in 19 cays of the Jardines de la Reina National Park, southern Cuba: * presence; blank, not recorded; Oo, overall occurrence.

Tabla 2s. Matriz de incidencia de 115 especies de aves presentes en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba: * presencia; vacío, no registrada; Oo, presencia generalizada.

Species/Cay		Anc	Cag	Gra	Cab	Bre
<i>Zenaida asiatica</i>	White-winged pigeon	*	*	*	*	*
<i>Setophaga petechia</i>	Yellow warbler	*	*	*	*	*
<i>Thalasseus maximus</i>	Royal tern	*	*	*	*	
<i>Patagioenas leucocephala</i>	White crowned pigeon	*	*	*	*	*
<i>Phalacrocorax auritus</i>	Double-crested cormorant	*	*	*	*	*
<i>Ardea alba</i>	Great egret	*	*	*	*	*
<i>Quiscalus niger</i>	Greater Antillean grackle	*	*	*	*	*
<i>Pelecanus occidentalis</i>	Brown pelican	*	*	*	*	*
<i>Pandion haliaetus</i>	Osprey	*	*	*	*	*
<i>Tyrannus dominicensis</i>	Gray kingbird	*	*	*	*	*
<i>Ardea herodias</i>	Great blue heron	*	*	*	*	*
<i>Fregata magnificens</i>	Magnificent frigatebird	*	*	*	*	*
<i>Agelaius humeralis</i>	Tawny-shouldered blackbird	*	*	*	*	
<i>Vireo altiloquus</i>	Black whiskered vireo	*	*	*	*	*
<i>Chlorostilbon ricordii</i>	Cuban emerald	*	*	*	*	*
<i>Charadrius wilsonia</i>	Wilson's plover	*	*	*	*	
<i>Tyrannus caudifasciatus</i>	Loggerhead kingbird	*	*	*	*	*
<i>Butorides virescens</i>	Green heron	*	*	*	*	*
<i>Cathartes aura</i>	Turkey vulture	*	*	*	*	*
<i>Anhinga anhinga</i>	Anhinga	*	*	*	*	*
<i>Buteogallus gundlachi</i>	Cuban black hawk	*	*	*	*	*
<i>Egretta tricolor</i>	Tricolored heron	*	*	*	*	*
<i>Egretta rufescens</i>	Reddish egret	*	*	*	*	*
<i>Contopus caribaeus</i>	Cuban pewee	*	*	*	*	*
<i>Myiarchus sagrae</i>	La Sagra's flycatcher	*	*	*	*	*
<i>Eudocimus albus</i>	White ibis	*	*	*	*	
<i>Setophaga discolor</i>	Prairie warbler	*	*	*	*	*
<i>Arenaria interpres</i>	Ruddy turnstone	*	*	*	*	
<i>Chordeiles gundlachi</i>	Antillean nighthawk	*	*	*		
<i>Hirundo rustica</i>	Barn swallow	*	*	*	*	
<i>Setophaga ruticilla</i>	American redstart	*	*	*	*	*
<i>Xiphidiopicus percussus</i>	Cuban green woodpecker	*	*	*	*	
<i>Parkesia noveboracensis</i>	Northern waterthrush	*	*	*	*	*
<i>Thalasseus sandvicensis</i>	Sandwich tern	*	*	*		
<i>Egretta thula</i>	Snowy egret	*	*	*	*	
<i>Mniotilta varia</i>	Black-and-white warbler	*	*	*	*	*
<i>Geothlypis trichas</i>	Common yellowthroat	*	*	*	*	*

Table 2s. (Cont.)

Species/Cay		Anc	Cag	Gra	Cab	Bre
<i>Egretta caerulea</i>	Little blue heron	*	*			*
<i>Zenaida macroura</i>	Mourning dove		*			
<i>Calidris minutilla</i>	Least sandpiper	*	*	*	*	
<i>Platalea ajaja</i>	Roseate spoonbill	*	*	*		
<i>Rallus crepitans</i>	Clapper rail	*	*	*		*
<i>Setophaga americana</i>	Northern parula	*	*	*	*	*
<i>Actitis macularius</i>	Spotted sandpiper	*	*	*	*	
<i>Setophaga caerulescens</i>	Black-throated blue warbler	*	*	*	*	*
<i>Setophaga palmarum</i>	Palm warbler	*	*	*	*	
<i>Setophaga dominica</i>	Yellow-throated warbler		*	*	*	*
<i>Megaceryle alcyon</i>	Belted kingfisher	*	*	*	*	*
<i>Leucophaeus atricilla</i>	Laughing gull	*	*	*		
<i>Dumetella carolinensis</i>	Gray catbird	*	*	*	*	*
<i>Petrochelidon fulva</i>	Cave swallow	*		*	*	
<i>Coccyzus americanus</i>	Yellow-billed cuckoo	*		*		*
<i>Pluvialis squatarola</i>	Black-bellied plover	*	*	*	*	
<i>Seiurus aurocapilla</i>	Ovenbird	*	*	*		*
<i>Tringa semipalmata</i>	Willet	*		*	*	
<i>Sternula antillarum</i>	Least tern	*		*		
<i>Charadrius semipalmatus</i>	Semipalmated plover	*	*	*	*	
<i>Progne cryptoleuca</i>	Cuban martin	*	*	*	*	
<i>Setophaga tigrina</i>	Cape may warbler	*	*	*		
<i>Turdus plumbeus</i>	Red-legged thrush	*		*	*	
<i>Falco columbarius</i>	Merlin	*		*	*	
<i>Mimus polyglottos</i>	Northern mockingbird	*	*	*		
<i>Vireo olivaceus</i>	Red-eyed vireo	*	*	*		
<i>Himantopus mexicanus</i>	Black-necked stilt	*	*		*	
<i>Crotophaga ani</i>	Smooth-billed ani	*		*	*	
<i>Passerina cyanea</i>	Indigo bunting	*	*			*
<i>Nyctanassa violacea</i>	Yellow-crowned night-heron	*			*	
<i>Zenaida aurita</i>	Zenaida dove	*	*		*	
<i>Buteo jamaicensis</i>	Red-tailed hawk	*	*			
<i>Tringa melanoleuca</i>	Greater yellowlegs	*	*			
<i>Columbina passerina</i>	Common ground-dove		*		*	
<i>Falco peregrinus</i>	Peregrine falcon	*	*			
<i>Bubulcus ibis</i>	Cattle egret	*	*			
<i>Vireo griseus</i>	White-eyed vireo	*		*		
<i>Helmitheros vermivorum</i>	Worm-eating warbler	*		*		
<i>Patagioenas squamosa</i>	Scaly-naped pigeon	*				*
<i>Piranga olivacea</i>	Scarlet tanager		*	*		

Table 2s. (Cont.)

Species/Cay		Anc	Cag	Gra	Cab	Bre
<i>Spatula discors</i>	Blue-winged teal	*	*			
<i>Calidris mauri</i>	Western sandpiper	*		*		
<i>Setophaga citrina</i>	Hooded warbler	*		*		
<i>Coccyzus minor</i>	Mangrove cuckoo	*				
<i>Protonotaria citrea</i>	Prothonotary warbler			*		
<i>Oreothlypis peregrina</i>	Tennessee warbler			*		
<i>Geotrygon montana</i>	Ruddy quail-dove	*				
<i>Tyto alba</i>	Barn owl					
<i>Chordeiles minor</i>	Common nighthawk	*				
<i>Mergus serrator</i>	Red-breasted merganser	*				
<i>Limnodromus griseus</i>	Short-billed dowitcher	*				
<i>Setophaga castanea</i>	Bay-breasted warbler			*		
<i>Setophaga fusca</i>	Blackburnian warbler		*			
<i>Numenius phaeopus</i>	Whimbrel	*				
<i>Catharus minimus</i>	Gray-cheeked thrush	*				
<i>Catharus fuscescens</i>	Veery	*				
<i>Sphyrapicus varius</i>	Yellow-bellied sapsucker		*			
<i>Sula leucogaster</i>	Brown booby					*
<i>Icteria virens</i>	Yellow-breasted chat			*		
<i>Tiaris olivaceus</i>	Yellow-faced grassquit	*				
<i>Piranga rubra</i>	Summer tanager			*		
<i>Charadrius vociferus</i>	Killdeer		*			
<i>Pheucticus ludovicianus</i>	Rose-breasted grosbeak					*
<i>Passerina caerulea</i>	Blue grosbeak	*				
<i>Contopus virens</i>	Eastern wood-pewee		*			
<i>Dolichonyx oryzivorus</i>	Bobolink	*				
<i>Hydroprogne caspia</i>	Caspian tern	*				
<i>Calidris alba</i>	Sanderling		*			
<i>Icterus galbula</i>	Baltimore oriole		*			
<i>Asio dominguensis</i>	Short-eared owl		*			
<i>Sula dactylatra</i>	Masked booby		*			
<i>Icterus melanopsis</i>	Cuban oriole		*			
<i>Catharus ustulatus</i>	Swainson's thrush			*		
Species's total		88	76	73	55	40

Table 2s. (Cont.)

CaE	Cin	Cru	Cac	BPP	BSe	BPC	BGr	Alc	JGr	Alz	BRI	Cam	Lar	Oo
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36	29	29	28	27	26	25	20	20	17	15	13	12	5	1

Table 3s. Mean \pm SD of nestedness degree ($CL_{lower} - CL_{upper}$ 95%) of avian trophic guilds (≥ 5 species) in 19 cays of the Jardines de la Reina National Park, southern Cuba. Grouping classifications were based on criteria of Kirkconnell et al. (1992), Andraca (2010) and Pizarro et al. (2012): NODF, nestedness metric based on overlap and decreasing fill; $NODF_{FF}$, null model 'Fixed-Fixed'; p , probability.

Trophic guilds	Matrix fill (%) / size (columns x rows)	$NODF_{obs}$	$NODF_{FF}$ N = 1000	p
Kirkconnell et al. (1992)				
Water-ambusher	58.6/19 x 7	78.79	79.58 \pm 0.97	0.18
Carnivore			(77.06–80.74)	
Water-plunger	41.4/19 x 7	69.18	69.33 \pm 1.38	0.28
Piscivore			(65.39–70.74)	
Shoreline-gleaner	28.3/19 x 8	42.12	41.96 \pm 0.65	0.50
Carnivore			(40.82–42.62)	
Shoreline-prober	16.8/19 x 5	13.44	13.55 \pm 0.53	0.38
Carnivore			(12.66–14.23)	
Ground-gleaner	31.6/19 x 5	54.42	55.97 \pm 0.36	0.01
Granivore			(55.06–56.54)	
Foliage-gleaner	33.8/19 x 7	69.79	69.79 \pm 0.15	0.50
Insectivore			(69.79–69.79)	
Air-sallier	52.6/19 x 5	49.62	49.68 \pm 0.54	0.50
Insectivore			(48.47–50.13)	
Pecker-gleaner	28.9/19 x 6	48.43	48.49 \pm 0.23	0.45
Insectivore-frugivore			(48.12–48.70)	
Foliage-gleaner	6.3/19 x 5	1.93	1.72 \pm 0.30	0.50
Insectivore-frugivore			(1.10–1.93)	

Tabla 3s. Media \pm DE ($LC_{inferior} - LC_{superior}$ 95%) del grado de anidamiento de los gremios tróficos de aves (≥ 5 especies) en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba. Las clasificaciones en grupos se basaron en los criterios de Kirkconnell et al. (1992), Andraca (2010) y Pizarro et al. (2012): NODF, índice de anidamiento basado en el relleno superpuesto y decreciente; $NODF_{FF}$ modelo nulo FF "Fijo-Fijo"; p , probabilidad.

Trophic guilds	Matrix fill (%) / size (columns x rows)	$NODF_{obs}$	$NODF_{FF}$ N = 1000	p
Andraca (2010) (Variant III)				
Carnivore	39.0/19 x 31	81.72	81.94 \pm 0.75 (80.13–82.99)	0.32
Predator	9.5/19 x 5	2.76	3.81 \pm 0.68 (2.21–4.97)	0.11
Granivore	28.7/19 x 9	61.07	62.10 \pm 0.86 (60.06–63.33)	0.12
Aerial	40.2/19 x 11	61.06	61.40 \pm 1.07 (58.76–62.86)	0.31
Insectivore				
Foliage	6.3/19 x 5	1.93	1.72 \pm 0.30 (1.10–1.93)	0.50
Insectivore–frugivore				
Ground–dwelling	27.1/19 x 7	49.52	49.65 \pm 0.17 (49.22–49.96)	0.19
Insectivore–frugivore				
Terrestrial	29.1/19 x 19	81.32	81.21 \pm 0.49 (80.15–81.87)	0.48
Insectivore				
Pizarro et al. (2012)				
Carnivore	33.2/19 x 38	77.08	78.33 \pm 0.80 (76.48–79.50)	0.08
Granivore	28.7/19 x 9	61.07	62.08 \pm 0.85 (60.14–63.33)	0.12
Insectivore	29.9/19 x 43	80.04	80.05 \pm 0.65 (78.58–80.93)	0.41

Table 4s. Incidence matrix of 43 insectivore bird species found in 19 cays of the Jardines de la Reina National Park, southern Cuba: * presence; blank, not recorded; Oo, overall occurrence. Matrix contains species grouped in the trophic guilds Terrestrial Insectivore (Andraca, 2010) and Insectivore (Pizarro et al., 2012).

Species / Cay	Gra	Anc	Cag	Cab	Bre	CaE	Cac	BPC
<i>Setophaga petechia</i>	*	*	*	*	*	*	**	*
<i>Quiscalus niger</i>	*	*	*	*	*	*	*	*
<i>Tyrannus dominicensis</i>	*	*	*	*	*	*	**	*
<i>Chlorostilbon ricordii</i>	*	*	*	*	*			*
<i>Vireo altiloquus</i>	*	*	*	*	*		*	*
<i>Tyrannus caudifasciatus</i>	*	*	*	*	*	*	*	*
<i>Myiarchus sagrae</i>	*	*	*	*	*	*	*	*
<i>Contopus caribaeus</i>	*	*	*	*	*	*		
<i>Setophaga discolor</i>	*	*	*	*	*	*	**	
<i>Chordeiles gundlachii</i>	*	*	*				**	*
<i>Xiphidiopicus percussus</i>	*	*	*	*		*		*
<i>Hirundo rustica</i>	*	*	*	*		*	**	
<i>Setophaga ruticilla</i>	*	*	*	*	*	*		*
<i>Parkesia noveboracensis</i>	*	*	*	*	*	*		*
<i>Mniotilta varia</i>	*	*	*	*	*	*		
<i>Geothlypis trichas</i>	*	*	*	*	*			*
<i>Setophaga caerulea</i>	*	*	*	*	*			
<i>Setophaga palmarum</i>	*	*	*	*				
<i>Setophaga dominica</i>	*		*	*	*	*		
<i>Setophaga americana</i>	*	*	*	*	*			
<i>Dumetella carolinensis</i>	*	*	*	*	*			
<i>Seiurus aurocapilla</i>	*	*	*		*			
<i>Petrochelidon fulva</i>	*	*		*				
<i>Coccyzus americanus</i>	*	*			*		*	
<i>Progne cryptoleuca</i>	*	*	*	*				
<i>Mimus polyglottos</i>	*	*	*					
<i>Vireo olivaceus</i>	*	*	*					
<i>Setophaga tigrina</i>	*	*	*					
<i>Turdus plumbeus</i>	*	*		*				
<i>Crotophaga ani</i>	*	*		*				
<i>Vireo griseus</i>	*	*						
<i>Bubulcus ibis</i>		*	*					
<i>Piranga olivacea</i>	*		*					
<i>Oreothlypis peregrina</i>	*							
<i>Charadrius vociferus</i>			*					
<i>Sphyrapicus varius</i>			*					
<i>Chordeiles minor</i>		*						
<i>Coccyzus minor</i>		*						
<i>Icterus galbula</i>			*					
<i>Icterus melanopsis</i>			*					
<i>Contopus virens</i>			*					
<i>Piranga rubra</i>	*							
<i>Pheucticus ludovicianus</i>					*			
Species's total	34	33	33	24	20	13	10	10

Tabla 4s. Matriz de incidencia de 43 especies de aves insectívoras encontradas en 19 cayos del Parque Nacional Jardines de la Reina, en el sur de Cuba: * presencia; vacío, no registrada; Oo, presencia generalizada. La matriz contiene las especies agrupadas en los gremios tróficos Insectívoro Terrestre (Andraca, 2010) e Insectívoro (Pizarro et al., 2012).

Cru	BPP	Alc	Cin	BSe	JGr	BGr	Alz	Cam	BRi	Lar	Oo
*	*	*	*	*	*	*	*	*		18	
*	*	*	*	*	*	*	*	*		17	
*	*	*	*	*		*				15	
*	*	*	*	*		*			*		13
	*	*	*		*	*	*			13	
*	*			*		*				12	
*	*				*					11	
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10	9	9	8	7	6	6	6	3	3	0	