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/functio nal 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 (JRN P), 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 JRN P increases from the trophic guilds that include species dependent on the marine resources to the guilds composed by species consuming exclusively terrestrial items. Thus,
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 Spiritus 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 Croosopetalum 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
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; Al, aerial insectivore; G, granivore (Andraca, 2010); GCAF, ground–dwelling insectivore–frugivore; FIF, foliage insectivore–frugivore; P, predator; CAR, carnivore (Andraca, 2010); I, insectivore; G, granivore (Pizarro et al., 2012); CAR, carnivore (Pizarro et al., 2012).

| Species                  | Kirkconnell et al. (1992) | Andraca (2010) | Variant III | Pizarro et al. (2012) |
|--------------------------|----------------------------|----------------|-------------|-----------------------|
| Setophaga petechia       | FGI                        | TI             | I           |                       |
| Setophaga tigrina        | FGI                        | TI             | I           |                       |
| Setophaga americana      | FGI                        | TI             | I           |                       |
| Setophaga palmarum       |                           | TI             | I           |                       |
| Setophaga ruticilla      | AI                         | I              |             |                       |
| Seiurus aurocapilla      |                           | TI             | I           |                       |
| Parkesia noveboracensis  |                           | TI             | I           |                       |
| Bubulcus ibis            |                           | TI             | I           |                       |
| Charadrius vociferus     |                           | TI             | I           |                       |
| Oreothlypis peregrina    | FGI                        | TI             | I           |                       |
| Vireo olivaceus          | FGI                        | TI             | I           |                       |
| Vireo altiloquus         | FGI                        | TI             | I           |                       |
| Vireo griseus            | FGI                        | TI             | I           |                       |
| Sphyrapicus varius       |                           | TI             | I           |                       |
| Xiphidiopicus percussus  |                           | TI             | I           |                       |
| Mniotilta varia          |                           | TI             | I           |                       |
| Geothlypis trichas       |                           | TI             | I           |                       |
| Setophaga caerulescens   |                           | TI             | I           |                       |
| Setophaga dominica       |                           | TI             | I           |                       |
| Setophaga discolor       |                           | TI             | I           |                       |
| Chlorostilbon ricordii   |                           |                |             |                       |
| Contopus caribaeus       | ASI                        | Al             | I           |                       |
| Contopus virens          | ASI                        | Al             | I           |                       |
| Myiarchus sagrae         | ASI                        | Al             | I           |                       |
| Tyrannus dominicensis    | ASI                        | Al             | I           |                       |
| Tyrannus caudifasciatus  | ASI                        | Al             | I           |                       |
| Chordeiles gundlachii    | Al                         | I              |             |                       |
| Hirundo rustica          | Al                         | I              |             |                       |
| Progne cryptoleuca       | Al                         | I              |             |                       |
| Species                        | Kirkconnell et al. (1992) | Andraca (2010) Variant III | Pizarro et al. (2012) |
|-------------------------------|---------------------------|---------------------------|-----------------------|
| Petrochelidon fulva          | AI                        | I                         |                       |
| Chordeiles minor             | AI                        | I                         |                       |
| Zenaida asiatica             | GGG                       | Gₐ                        | Gₚ                    |
| Zenaida macroura             | GGG                       | Gₐ                        | Gₚ                    |
| Zenaida aurita               | GGG                       | Gₐ                        | Gₚ                    |
| Columbina passerina          | GGG                       | Gₐ                        | Gₚ                    |
| Geotrygon montana            | GGG                       | Gₐ                        | Gₚ                    |
| Tiaris olivaceus             | Gₐ                        | Gₚ                        |                       |
| Passerina caerulea           | Gₐ                        | Gₚ                        |                       |
| Passerina cyanea             | Gₐ                        | Gₚ                        |                       |
| Agelaius humeralis           | Gₐ                        | Gₚ                        |                       |
| Coccyzus americanus          | PGIF                      | GCIF                      | I                     |
| Coccyzus minor               | PGIF                      | GCIF                      | I                     |
| Crotophaga ani               | PGIF                      | GCIF                      | I                     |
| Dumetella carolinensis       | PGIF                      | GCIF                      | I                     |
| Mimus polyglottos            | PGIF                      | GCIF                      | I                     |
| Quiscalus niger              | PGIF                      | GCIF                      | I                     |
| Turdus plumbeus              | GCIF                      | I                         |                       |
| Piranga rubra                | FGIF                      | FIF                       | I                     |
| Piranga olivacea             | FGIF                      | FIF                       | I                     |
| Pheucticus ludovicianus      | FGIF                      | FIF                       | I                     |
| Icterus galbula              | FGIF                      | FIF                       | I                     |
| Icterus melanopsis           | FGIF                      | FIF                       | I                     |
| Falco columbarius            | D                         | CARₚ                      |                       |
| Falco peregrinus             | D                         | CARₚ                      |                       |
| Buteo jamaicensis            | D                         | CARₚ                      |                       |
| Tyto alba                    | D                         | CARₚ                      |                       |
| Asio dominguensis            | D                         | CARₚ                      |                       |
| Spatula discors              |                           | CARₚ                      |                       |
| Nyctanassa violacea          |                           | CARₚ                      |                       |
| Buteogallus gundlachii       |                           | CARₚ                      |                       |
| Ardea alba                   | WAC                       | CARₐ                      | CARₚ                  |
| Ardea herodias               | WAC                       | CARₐ                      | CARₚ                  |
| Butorides virescens          | WAC                       | CARₐ                      | CARₚ                  |
| Egretta tricolor             | WAC                       | CARₐ                      | CARₚ                  |
| Egretta rufescens            | WAC                       | CARₐ                      | CARₚ                  |
| Egretta caerulea             | WAC                       | CARₐ                      | CARₚ                  |
| Egretta thula                | WAC                       | CARₐ                      | CARₚ                  |
| Eudocimus albus              | CARₐ                      | CARₚ                      |                       |
| Platalea ajaja               |                           | CARₚ                      |                       |
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 (\( \text{NODF}_{\text{obs}} - \text{NODF}_{\text{exp}} / SD_{\text{exp}} \)).

### 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 (\( \text{Charadrius semipalmatus} \)), zenaida dove (\( \text{Zenaida aurita} \)), gray catbird (\( \text{Dumetella carolinensis} \)), common yellowthroat (\( \text{Geothlypis trichas} \)) and yellow–throated warbler (\( \text{Setophaga dominica} \)). Highest species numbers were documented in Anclitas (88), Caguama (76) and Grande (74). Species such as white–winged pigeon (\( \text{Zenaida asiatica} \)) and yellow warbler (\( \text{Setophaga petechia} \)) 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 1. (Cont.)

| Species                       | Kirkconnell et al. (1992) | Andraca (2010) Variant III | Pizarro et al. (2012) |
|-------------------------------|---------------------------|---------------------------|-----------------------|
| \( \text{Pelecanus occidentalis} \) | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Hydroprogne caspia} \) | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Thalasseus maximus} \) | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Stemula antillarum} \) | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Sula leucogaster} \)   | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Sula dactylatra} \)    | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Pandion haliaetus} \)   | WPP                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Leucophaeus atricilla} \) | CAR<sub>A</sub>         | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Charadrius wilsonia} \)  | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Charadrius semipalmatus} \) | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Actitis macularius} \)  | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Pluvialis squatarola} \) | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Calidris minutilla} \)  | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Calidris mauri} \)    | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Calidris alba} \)     | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Arenaria interpres} \) | SGC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Tringa melanoleuca} \) | SPC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Tringa semipalmata} \) | SPC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Himantopus mexicanus} \) | SPC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Limnodromus griseus} \) | SPC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Rallus crepitans} \)  | SPC                       | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Phalacrocorax auritus} \) | CAR<sub>A</sub>         | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
| \( \text{Megaceryle alcyon} \) | CAR<sub>A</sub>           | CAR<sub>A</sub>            | CAR<sub>P</sub>       |
### Table 2. Mean ± 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.

| Trophic guilds | Matrix fill (%) / size (columns x rows) | NOFD_{obs} | NOFD_{pp} N = 1000 | p |
|----------------|------------------------------------------|------------|----------------------|---|
| **Kirkconnell et al. (1992)** | | | | |
| Water–ambusher | 58.6 / 19 x 7 | 78.79 | 77.10 ± 3.40 | 0.34 |
| Carnivore | | (69.44–82.86) | | |
| Water–plunger | 41.4 / 19 x 7 | 69.18 | 67.61 ± 5.78 | 0.44 |
| Piscivore | | (55.10–76.94) | | |
| Shoreline–gleaner | 28.3 / 19 x 8 | 42.12 | 40.00 ± 3.12 | 0.24 |
| Carnivore | | (34.20–46.44) | | |
| Shoreline–prober | 16.8 / 19 x 5 | 13.44 | 12.96 ± 1.66 | 0.40 |
| Carnivore | | (9.71–16.35) | | |
| Ground–gleaner | 31.6 / 19 x 5 | 54.42 | 54.28 ± 2.60 | 0.43 |
| Granivore | | (48.62–58.29) | | |
| Foliage–gleaner | 33.8 / 19 x 7 | 69.79 | 64.43 ± 4.43 | 0.09 |
| Insectivore | | (54.94–72.41) | | |
| Air–sallier | 52.6 / 19 x 5 | 49.62 | 49.05 ± 5.50 | 0.48 |
| Insectivore | | (39.17–60.09) | | |
| Pecker–gleaner | 28.9 / 19 x 6 | 48.43 | 49.11 ± 3.45 | 0.43 |
| Insectivore–frugivore | | (41.91–55.73) | | |
| Foliage–gleaner | 6.3 / 19 x 5 | 1.93 | 1.68 ± 0.39 | 0.50 |
| Insectivore–frugivore | | (1.10–2.21) | | |
| **Andraca (2010) (Variant III)** | | | | |
| Carnivore | 39.0 / 19 x 31 | 81.72 | 77.58 ± 2.42 | 0.03 |
| Predator | 9.5 / 19 x 5 | 2.76 | 3.80 ± 0.80 | 0.14 |
| Granivore | 28.7 / 19 x 9 | 61.07 | 59.19 ± 4.51 | 0.33 |
| Aerial Insectivore | 40.2 / 19 x 11 | 61.06 | 61.46 ± 3.87 | 0.48 |
| Foliage | 6.3 / 19 x 5 | 1.93 | 1.66 ± 0.41 | 0.50 |
| Insectivore–frugivore | | (1.10–2.21) | | |
| Ground–dwelling | 27.1 / 19 x 7 | 49.52 | 50.18 ± 3.68 | 0.44 |
| Insectivore–frugivore | | (43.39–57.36) | | |
| Terrestrial Insectivore | 29.1 / 19 x 19 | 81.32 | 70.50 ± 3.43 | 0.00 |
| | | (63.56–76.93) | | |
values according to the PP null model (NODF = 2.54; \( p = 0.01 \)). Results from FF null model (NODF = 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

| Trophic guilds | Matrix fill (%) / NOFD | NOFD_{obs} N = 1000 | p  |
|----------------|------------------------|----------------------|----|
| 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 |

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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### Supplementary material

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

| Kirkconnell et al. (1992)                      | Frugivore           | Frugivore–granivore | Ground–and foliage pecker–and–gleaner | Granivore–insectivore | Aerial Predator | Aerial nocturnal predator | Air–sallier nocturnal predator | Insectivore and small–vertebrate predator |
|------------------------------------------------|--------------------|---------------------|---------------------------------------|------------------------|-----------------|--------------------------|-----------------------------------|-------------------------------------|
| Bark–gleaner insectivore                       | BGI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Bark–excavator insectivore                     | BEI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Foliage–gleaner insectivore                   | FGI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Bark–and–foliage gleaner insectivore          | BFGI               |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–ambusher insectivore                    | GAI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–pecker insectivore                     | GPI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–and–water pecker insectivore           | GWPI               |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–and–bark–excavator insectivore         | GBEI               |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–and–foliage gleaner–pecker             | GFPGI              |                     |                                       |                        |                 |                          |                                    |                                     |
| Air–sallier lower–canopy–gleaner              | ASLCGI             |                     |                                       |                        |                 |                          |                                    |                                     |
| Air–sallier insectivore                       | ASI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Aerial nocturnal insectivore                   | ANI                |                     |                                       |                        |                 |                          |                                    |                                     |
| Air–sallier insectivore–frugivore             | ASIF               |                     |                                       |                        |                 |                          |                                    |                                     |
| Air–sallier–and–forager insectivore–frugivore | ASIF               |                     |                                       |                        |                 |                          |                                    |                                     |
| Foliage–gleaner insectivore–frugivore         | FGIF               |                     |                                       |                        |                 |                          |                                    |                                     |
| Pecker–gleaner insectivore–frugivore          | PGIF               |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–forager insectivore–frugivore          | GFIF               |                     |                                       |                        |                 |                          |                                    |                                     |
| Floral–hover–gleaner nectarivore–insectivore  | FHGNI              |                     |                                       |                        |                 |                          |                                    |                                     |
| Frugivore–nectarivore                         | FN                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–gleaner granivore                      | GGG                |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–and–foliage granivore                  | GFG                |                     |                                       |                        |                 |                          |                                    |                                     |
| Andraca (2010) (Variant III)                  | Terrestrial Insectivore |                   |                                       |                        |                 |                          |                                    |                                     |
| Terrestrial Insectivore                       | IT                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Aerial–insectivore                            | IAA                |                     |                                       |                        |                 |                          |                                    |                                     |
| Foliage insectivore–frugivore                 | FIF                |                     |                                       |                        |                 |                          |                                    |                                     |
| Ground–dwelling insectivore–frugivore         | GIF                |                     |                                       |                        |                 |                          |                                    |                                     |
| Nectarivore–insectivore                       | NI                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Frugivore                                     | FA                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Granivore                                     | G                  |                     |                                       |                        |                 |                          |                                    |                                     |
| Predator                                      | D                  |                     |                                       |                        |                 |                          |                                    |                                     |
| Insectivore                                   | GFGPI              |                     |                                       |                        |                 |                          |                                    |                                     |
| Insectivore                                   | ASLCGI             |                     |                                       |                        |                 |                          |                                    |                                     |
| Omnivore                                      | OA                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Scavenger                                     | SCAVA              |                     |                                       |                        |                 |                          |                                    |                                     |
| Carnivore–phytophage                          | CAR–S              |                     |                                       |                        |                 |                          |                                    |                                     |
| Scavenger                                     | SCAV               |                     |                                       |                        |                 |                          |                                    |                                     |
| Omnivore                                      | OP                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Piscivore                                     | PIS                |                     |                                       |                        |                 |                          |                                    |                                     |
| Crustaceovore                                 | CA                 |                     |                                       |                        |                 |                          |                                    |                                     |
| Molluscovore                                  | MA                 |                     |                                       |                        |                 |                          |                                    |                                     |
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 |
|----------------------------------|-----|-----|-----|-----|-----|
| Zenaida asiatica                |     |     |     |     |     |
| Setophaga petechia               | *   |     | *   |     | *   |
| Thalasseus maximus               |     | *   |     |     |     |
| Patagioenas leucocephala         |     |     | *   |     |     |
| Phalacrocorax auritus            |     | *   |     |     | *   |
| Ardea alba                       | *   |     |     | *   |     |
| Quiscalus niger                  |     | *   |     |     | *   |
| Pelecanus occidentalis           | *   |     |     |     | *   |
| Pandion haliaetus                |     | *   |     |     | *   |
| Tyrannus dominicensis            |     | *   |     |     | *   |
| Ardea herodias                   |     | *   |     |     | *   |
| Fregata magnificens              |     |     | *   |     | *   |
| Agelaius humeralis               |     |     | *   |     | *   |
| Vireo altiloquus                 | *   |     |     |     | *   |
| Chlorostilbon ricordii           | *   |     |     |     | *   |
| Charadrius wilsonia              | *   |     |     | *   |     |
| Tyrannus caudifasciatus          |     | *   |     |     | *   |
| Butorides virescens              | *   |     |     |     | *   |
| Cathartes aura                   | *   |     |     |     | *   |
| Anhinga anhinga                  |     | *   |     |     | *   |
| Buteogallus gundlachii           | *   |     |     | *   |     |
| Egretta tricolor                 | *   |     |     |     | *   |
| Egretta rufescens                | *   |     |     |     | *   |
| Contopus caribaeus               | *   |     |     |     | *   |
| Myiarchus sagae                  | *   |     |     |     | *   |
| Eudocimus albus                  |     | *   |     |     | *   |
| Setophaga discolor               | *   |     |     | *   |     |
| Arenaria interpres               |     | *   |     |     | *   |
| Chordeiles gundlachii            | *   |     |     | *   |     |
| Hirundo rustica                  | *   |     |     |     | *   |
| Setophaga ruticilla              | *   |     |     |     | *   |
| Xiphidiopicus percussus          | *   |     |     | *   |     |
| Parkesia noveboracensis          |     | *   |     |     | *   |
| Thalasseus sandvicensis          | *   |     |     | *   |     |
| Egretta thula                    | *   |     |     | *   |     |
| Mniotilta varia                  |     | *   |     | *   |     |
| Geothlypis trichas               |     |     | *   |     | *   |
| CaE | Cin | Cru | Cac | BPP | BSe | BPC | BGr | Alc | JGr | Alz | BRi | Cam | Lar | Oo |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 18 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 18 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 17 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 17 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 17 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 17 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 16 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 15 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 15 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 15 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 15 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 14 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 13 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 12 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 12 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 12 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 12 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 12 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 11 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 11 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 11 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 10 |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 9  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 9  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 8  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 8  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 7  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 7  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |

Table 2s. (Cont.)
Table 2s. (Cont.)

| Species/Cay                        | Anc | Cag | Gra | Cab | Bre |
|-----------------------------------|-----|-----|-----|-----|-----|
| *Egretta caerulea*                |     |     |     |     |     |
| *Zenaida macroura*                |     |     |     |     |     |
| *Calidris minutilla*              |     |     |     |     |     |
| *Platalea ajaja*                  |     |     |     |     |     |
| *Rallus crepitans*                |     |     |     |     |     |
| *Setophaga americana*             |     |     |     |     |     |
| *Actitis macularius*              |     |     |     |     |     |
| *Setophaga caerulescens*          |     |     |     |     |     |
| *Setophaga palmarum*              |     |     |     |     |     |
| *Setophaga dominica*              |     |     |     |     |     |
| *Megaceryle alcyon*               |     |     |     |     |     |
| *Leucophaeus atricilla*           |     |     |     |     |     |
| *Dumetella carolinensis*          |     |     |     |     |     |
| *Coccozus americanus*             |     |     |     |     |     |
| *Pluvialis squatarola*            |     |     |     |     |     |
| *Seiurus aurocapilla*             |     |     |     |     |     |
| *Tringa semipalmaris*             |     |     |     |     |     |
| *Sternula antillarum*             |     |     |     |     |     |
| *Charadrius semipalmatus*         |     |     |     |     |     |
| *Progne cryptoleuca*              |     |     |     |     |     |
| *Setophaga tigrina*               |     |     |     |     |     |
| *Turdus plumbeus*                 |     |     |     |     |     |
| *Falco columbarius*               |     |     |     |     |     |
| *Mimus polyglottos*               |     |     |     |     |     |
| *Vireo olivaceus*                 |     |     |     |     |     |
| *Himantopus mexicanus*            |     |     |     |     |     |
| *Crotaphaga ani*                  |     |     |     |     |     |
| *Passerina cyanea*                |     |     |     |     |     |
| *Nyctanassa violacea*             |     |     |     |     |     |
| *Zenaida ainfoa*                  |     |     |     |     |     |
| *Buteo jamaicensis*               |     |     |     |     |     |
| *Tringa melanoleuca*              |     |     |     |     |     |
| *Columbina passerina*             |     |     |     |     |     |
| *Falco peregrinus*                |     |     |     |     |     |
| *Bubulcus ibis*                   |     |     |     |     |     |
| *Vireo griseus*                   |     |     |     |     |     |
| *Helmitheros vermivorum*          |     |     |     |     |     |
| *Piranga olivacea*                |     |     |     |     |     |

*Table showing species and their Cay species names with respective abbreviations for Anc, Cag, Gra, Cab, Bre.*
Table 2s. (Cont.)

| Species          | CaE | Cin | Cru | Cac | BPP | BSe | BPC | BGr | Alc | JGr | Alz | BRI | Cam | Lar | Oo |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|
| Egretta caerulea |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
| Zenaida macroura |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
| Calidris minutilla |   |   |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
| Platalea ajaja   |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 6  |
| Rallus crepitans |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Setophaga americana | | |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Actitis macularius | | |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Setophaga caerulescens | | |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Setophaga palmarum |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Setophaga dominica |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Megaceryle alcyon |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Leucophaeus atricilla | | |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Dumetella carolinensis | | |     |     |     |     |     |     |     |     |     |     |     |     | 5  |
| Petrochelidon fulva | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Coccyzus americanus | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Pluvialis squatarola | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Seiurus aurocapilla | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Tringa semipalmata | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Sternula antillarum | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Charadrius semipalmatus | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Progne cryptoleuca | | |     |     |     |     |     |     |     |     |     |     |     |     | 4  |
| Setophaga tigrina | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Turdus plumbeus | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Falco columbarius | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Mimus polyglottos | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Vireo olivaceus | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Himantopus mexicanus | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Crotophaga ani | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Passerina cyanea | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Nyctanassa violacea | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Zenaida aurita | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Buteo jamaicensis | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Tringa melanoleuca | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Columbina passerina | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Falco peregrinus | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Bubulcus ibis | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Vireo griseus | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Helmitheros vermivorum | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Patagioenas squamosa | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Piranga olivacea | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Table 2s. (Cont.) | | |     |     |     |     |     |     |     |     |     |     |     |     | 3  |
| Species/Cay               | Anc      | Cag | Gra | Cab | Bre |
|--------------------------|----------|-----|-----|-----|-----|
| Spatula discors          | Blue–winged teal |     |     |     |     |
| Calidris mauri           | Western sandpiper | *  |     |     |     |
| Setophaga citrina        | Hooded warbler |     | *  |     |     |
| Coccyzus minor           | Mangrove cuckoo | *  |     |     |     |
| Protonotaria citrea      | Prothonotary warbler | *  |     |     |     |
| Oreothlypis peregrina    | Tennessee warbler | *  |     |     |     |
| Geotrygon montana        | Ruddy quail–dove | *  |     |     |     |
| Tyto alba                | Barn owl |     |     |     |     |
| Chordeiles minor         | Common nighthawk |     |     | *  |     |
| Mergus serrator          | Red–breasted merganser |     |     | *  |     |
| Limnodromus griseus      | Short–billed dowitcher | *  |     |     |     |
| Setophaga castanea       | Bay–breasted warbler | *  |     |     |     |
| Setophaga fusca          | Blackburnian warbler | *  |     |     |     |
| Numenius phaeopus        | Whimbrel |     |     |     | *  |
| Catharus minimus         | Gray–cheeked thrush | *  |     |     |     |
| Catharus fuscescens      | Veery |     |     |     | *  |
| Sphyrapicus varius       | Yellow–bellied sapsucker | *  |     |     |     |
| Sula leucogaster         | Brown booby | *  |     |     |     |
| Icteria virens           | Yellow–breasted chat |     |     | *  |     |
| Tiaris olivaceus         | Yellow–faced grassquit |     | *  |     |     |
| Piranga rubra            | Summer tanager | *  |     |     |     |
| Charadrius vociferus     | Killdeer |     |     |     | *  |
| Pheucticus ludovicianus  | Rose–breasted grosbeak | *  |     |     |     |
| Passerina caerulea       | Blue grosbeak | *  |     |     |     |
| Contopus virens          | Eastern wood–pewee | *  |     |     |     |
| Dolichonyx oryzivorus    | Bobolink | *  |     |     |     |
| Hydroprogne caspia       | Caspian tern | *  |     |     |     |
| Calidris alba            | Sanderling |     |     | *  |     |
| Icterus galbula          | Baltimore oriole | *  |     |     |     |
| Asio dominguenensis      | Short–eared owl | *  |     |     |     |
| Sula dactylatra          | Masked booby | *  |     |     |     |
| Icterus melanopsis       | Cuban oriole | *  |     |     |     |
| Catharus ustulatus       | 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 |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |
|     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1  |

| 36 | 29 | 29 | 28 | 27 | 26 | 25 | 20 | 20 | 17 | 15 | 13 | 12 | 5  |
Table 3s. Mean ± 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) | NOFD_{obs} | NOFD_{FF} N = 1000 | p         |
|-------------------------------|----------------------------------------|------------|---------------------|-----------|
| Kirkconnell et al. (1992)     |                                        |            |                     |           |
| Water–ambusher                | 58.6 / 19 x 7                          | 78.79      | 79.58 ± 0.97        | 0.18      |
| Carnivore                     |                                        |            | (77.06–80.74)       |           |
| Water–plunger                 | 41.4 / 19 x 7                          | 69.18      | 69.33 ± 1.38        | 0.28      |
| Piscivore                     |                                        |            | (65.39–70.74)       |           |
| Shoreline–gleaner             | 28.3 / 19 x 8                          | 42.12      | 41.96 ± 0.65        | 0.50      |
| Carnivore                     |                                        |            | (40.82–42.62)       |           |
| Shoreline–prober              | 16.8 / 19 x 5                          | 13.44      | 13.55 ± 0.53        | 0.38      |
| Carnivore                     |                                        |            | (12.66–14.23)       |           |
| Ground–gleaner                | 31.6 / 19 x 5                          | 54.42      | 55.97 ± 0.36        | 0.01      |
| Granivore                     |                                        |            | (55.06–56.54)       |           |
| Foliage–gleaner               | 33.8 / 19 x 7                          | 69.79      | 69.79 ± 0.15        | 0.50      |
| Insectivore                   |                                        |            | (69.79–69.79)       |           |
| Air–sallier                   | 52.6 / 19 x 5                          | 49.62      | 49.68 ± 0.54        | 0.50      |
| Insectivore                   |                                        |            | (48.47–50.13)       |           |
| Pecker–gleaner                | 28.9 / 19 x 6                          | 48.43      | 48.49 ± 0.23        | 0.45      |
| Insectivore–frugivore         |                                        |            | (48.12–48.70)       |           |
| Foliage–gleaner               | 6.3 / 19 x 5                           | 1.93       | 1.72 ± 0.30         | 0.50      |
| Insectivore–frugivore         |                                        |            | (1.10–1.93)         |           |
Tabla 3s. Media ± 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) | NOFD_{obs} N = 1000 | p            |
|-----------------------------|----------------------------------------|----------------------|--------------|
| Andraca (2010) (Variant III) |                                        |                      |              |
| Carnivore                   | 39.0/19 x 31                           | 81.72                | 81.94 ± 0.75 | 0.32         |
|                             |                                        |                      | (80.13–82.99)|              |
| Predator                    | 9.5/19 x 5                             | 2.76                 | 3.81 ± 0.68 | 0.11         |
|                             |                                        |                      | (2.21–4.97) |              |
| Granivore                   | 28.7/19 x 9                            | 61.07                | 62.10 ± 0.86| 0.12         |
|                             |                                        |                      | (60.06–63.33)|              |
| Aerial                      | 40.2/19 x 11                           | 61.06                | 61.40 ± 1.07| 0.31         |
| Insectivore                 |                                        |                      | (58.76–62.86)|              |
| Foliage                     | 6.3/19 x 5                             | 1.93                 | 1.72 ± 0.30 | 0.50         |
| Insectivore–frugivore       |                                        |                      | (1.10–1.93) |              |
| Ground–dwelling             | 27.1/19 x 7                            | 49.52                | 49.65 ± 0.17| 0.19         |
| Insectivore–frugivore       |                                        |                      | (49.22–49.96)|              |
| Terrestrial                 | 29.1/19 x 19                           | 81.32                | 81.21 ± 0.49| 0.48         |
| Insectivore                 |                                        |                      | (80.15–81.87)|              |
| Pizarro et al. (2012)       |                                        |                      |              |
| Carnivore                   | 33.2/19 x 38                           | 77.08                | 78.33 ± 0.80| 0.08         |
|                             |                                        |                      | (76.48–79.50)|              |
| Granivore                   | 28.7/19 x 9                            | 61.07                | 62.08 ± 0.85| 0.12         |
|                             |                                        |                      | (60.14–63.33)|              |
| Insectivore                 | 29.9/19 x 43                           | 80.04                | 80.05 ± 0.65| 0.41         |
|                             |                                        |                      | (78.58–80.93)|              |
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 |
|--------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|
| Setophaga petechia                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Quiscalus niger                      | *   | *   | *   | *   | *   | *   | *   | *   |
| Tyrannus dominicensis                | *   | *   | *   | *   | *   | *   | *   | *   |
| Chlorostilbon ricordii               | *   | *   | *   | *   | *   | *   | *   | *   |
| Vireo altilogus                      | *   | *   | *   | *   | *   | *   | *   | *   |
| Tyrannus caudifasciatus              | *   | *   | *   | *   | *   | *   | *   | *   |
| Myiarchus sagrae                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Contopus caribaeus                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga discolor                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Chordeiles gundlachii                | *   | *   | *   | *   | *   | *   | *   | *   |
| Xiphidiopicus percussus              | *   | *   | *   | *   | *   | *   | *   | *   |
| Hirundo rustica                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga ruticilla                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Parkesia noveboracensis              | *   | *   | *   | *   | *   | *   | *   | *   |
| Mniotilta varia                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Geothlypis trichas                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga caerulescens               | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga palmarum                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga dominica                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga americana                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Dumetella carolinensis               | *   | *   | *   | *   | *   | *   | *   | *   |
| Seiurus aurocapilla                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Petrochelidon fulva                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Coccyzus americanus                 | *   | *   | *   | *   | *   | *   | *   | *   |
| Progne cryptoleuca                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Mimus polyglottos                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Vireo olivaceus                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Setophaga tigrina                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Turdus plumbeus                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Crotophaga ani                      | *   | *   | *   | *   | *   | *   | *   | *   |
| Vireo griseus                       | *   | *   | *   | *   | *   | *   | *   | *   |
| Bubulcus ibis                       | *   | *   | *   | *   | *   | *   | *   | *   |
| Piranga olivacea                    | *   | *   | *   | *   | *   | *   | *   | *   |
| Oreothlypis peregrina                | *   | *   | *   | *   | *   | *   | *   | *   |
| Charadrius vociferus                | *   | *   | *   | *   | *   | *   | *   | *   |
| Sphyrapicus varius                  | *   | *   | *   | *   | *   | *   | *   | *   |
| Chordeiles minor                    | *   | *   | *   | *   | *   | *   | *   | *   |
| Coelocichla minor                   | *   | *   | *   | *   | *   | *   | *   | *   |
| Icterus galbula                     | *   | *   | *   | *   | *   | *   | *   | *   |
| Icterus melanopsis                 | *   | *   | *   | *   | *   | *   | *   | *   |
| Contopus virginianus                | *   | *   | *   | *   | *   | *   | *   | *   |
| Piranga rubra                       | *   | *   | *   | *   | *   | *   | *   | *   |
| Pheucticus ludovicianus              | *   | *   | *   | *   | *   | *   | *   | *   |
| 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  |
| *   | *   | *   | *   | 12  |
| *   | *   | *   | 11  |
| *   | *   | *   | 10  |
| *   | *   | 9   |
| *   | 8   |
| *   | 8   |
|   | 7   |
|   | 6   |
|   | 6   |
|   | 5   |
|   | 5   |
|   | 5   |
|   | 4   |
|   | 4   |
|   | 4   |
|   | 3   |
|   | 3   |
|   | 3   |
|   | 3   |
|   | 2   |
|   | 2   |
|   | 2   |
|   | 1   |
|   | 1   |
|   | 1   |
|   | 1   |
| 10 | 9   | 9   | 8   | 7   | 6   | 6   | 6   | 3   | 3   | 0   |

Species's total 34 33 33 24 20 13 10 10 10 9 9 8 7 6 6 6 3 3 0