

Nestedness structure of bird assemblages in a fragmented forest in Central Argentina: the role of selective extinction and colonization processes

S. Dardanelli, L. M. Bellis

Dardanelli, S., Bellis, L. M., 2021. Nestedness structure of bird assemblages in a fragmented forest in Central Argentina: the role of selective extinction and colonization processes. *Animal Biodiversity and Conservation*, 44.1: 17–29, Doi: <https://doi.org/10.32800/abc.2021.44.0017>

Abstract

Nestedness structure of bird assemblages in a fragmented forest in Central Argentina: the role of selective extinction and colonization processes. Nestedness analysis constitutes an important tool to understand the processes that shape wildlife communities. It also allows a quick first evaluation of species extinction proneness in fragmented landscapes. Here, we tested whether avian assemblages in the fragmented Espinal forest exhibited nested subset patterns. Furthermore, we examined whether selective extinction or selective colonization are driving nested subset patterns. We studied avian assemblages in 13 forest fragments in central Argentina during breeding and non-breeding seasons. We completed partial Spearman rank correlations to explore the relationship between nestedness rank order and habitat patch variables and species life history traits related to species extinction proneness and colonization rate. Bird species showed strong nestedness patterns, both for the total incidence matrix and for forest fragments and species separately. Nestedness patterns were similar during the breeding and non-breeding seasons. The nested rank order of forest fragments correlated with area and distance to nearest fragment, both of which are patch characteristics known to increase the probabilities of species extinction. The nested rank order of species was correlated with the minimum area of species requirement, trophic guild, and range size, traits that are linked to extinction risk. Selective extinction processes rather than selective colonization appear to be driving nestedness patterns of bird assemblages in fragmented Espinal forest. The most effective way to preserve forest bird species in the Espinal forest seems to be by protecting the larger fragments of this relictual forest.

Key words: Forest fragments, Avifauna, Community assembly, Seasonality, Species traits, Espinal forest

Resumen

Estructura anidada de ensamblajes de aves en un bosque fragmentado del centro de Argentina: el papel de los procesos de extinción y colonización selectivos. El análisis de anidamiento constituye una herramienta importante para comprender los procesos que dan forma a las comunidades de vida silvestre. También permite hacer una primera evaluación rápida de la propensión a la extinción de las especies en paisajes fragmentados. En el presente estudio, analizamos si los ensamblajes de aves en el bosque fragmentado del Espinal siguen un patrón de subconjuntos anidados. Además, examinamos si la extinción selectiva o la colonización selectiva están impulsando patrones de subconjuntos anidados. Estudiamos los ensamblajes de aves en 13 fragmentos de bosque del centro de Argentina durante las estaciones reproductiva y no reproductiva. Realizamos correlaciones parciales de rango de Spearman para analizar la relación entre el orden de rango de anidamiento y las variables de parche de hábitat y los rasgos de la historia de vida de las especies relacionados con la propensión a la extinción y la tasa de colonización de las especies. Las especies de aves mostraron marcados patrones de anidamiento, tanto en relación con toda la matriz de incidencias como con los fragmentos de bosque y las especies por separado. Los patrones de anidamiento fueron similares en la estación reproductiva y no reproductiva. El orden de rango de anidamiento de los fragmentos de bosque se correlacionó con la superficie y la distancia al fragmento más cercano, que son características del parche que aumentan la probabilidad de extinción de las especies. El orden de rango de anidamiento de las especies se correlacionó con el requerimiento mínimo de superficie de la especie, el gremio trófico y el tamaño del

rango, que son características vinculadas al riesgo de extinción. A diferencia de los procesos de colonización selectiva, los de extinción selectiva parecen estar impulsando los patrones de anidamiento de ensamblajes de aves en el bosque fragmentado del Espinal. La forma más eficaz de conservar las especies de aves del bosque del Espinal parece ser mediante la protección de los fragmentos más extensos de este bosque relictual del centro de Argentina.

Palabras clave: Fragmentos de bosque, Avifauna, Ensamblaje comunitario, Estacionalidad, Rasgos de especies, Bosque del Espinal

Received: 19 III 20; Conditional acceptance: 21 IV 20; Final acceptance: 27 VII 20

Sebastián Dardanelli, Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Paraná, Ruta 11 km 12.5, 3101 Oro Verde, Entre Ríos, Argentina.– Laura M. Bellis, Instituto de Altos Estudios Espaciales "Mario Gulich" (CONAE–UNC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina.

Corresponding author: S. Dardanelli. E–mail: sedardanelli@gmail.com

ORCID ID: S. Dardanelli: 0000-0003-4341-3879; Laura Bellis: 0000-0002-0725-5079

Introduction

Habitat loss and fragmentation are among the most important threats to biodiversity worldwide (Wilcove et al., 1998; Sala et al., 2000; Haddad et al., 2015). Broad-scale habitat fragmentation gives rise to archipelagos of natural habitat fragments or islands immersed in a matrix of anthropogenic open habitat (Matthews et al., 2015). Since species sensitivity to habitat fragmentation in a particular region is variable, species loss in those remaining habitat islands does not necessarily occur at random but may occur in a nested pattern (Patterson and Atmar, 1986; Atmar and Patterson, 1993, 1995). In nested assemblages, poorer communities constitute proper subsets of increasingly richer communities (Patterson and Atmar, 1986). Therefore, less widespread species occur on sites with relatively large species assemblages while poorer assemblages are mostly composed of ubiquitous species (Cutler, 1991; Soga and Koike, 2012). Consequently, in archipelagos with 'perfect' nestedness structure, it is possible to predict the order of disappearance of the less ubiquitous species from the poorer sites in response to environmental gradients (Atmar and Patterson, 1993) as the species that are present only in the richer fragments are more likely to become extinct as environmental disturbances increase (Nupp and Swihart, 2000).

Nestedness analysis is an important tool to understand the processes that shape communities and to reveal the ecological and evolutionary limits of the species. Furthermore, it has valuable implications for conservation (Wright et al., 1998; Martínez-Morales, 2005). Nestedness analysis is attractive because it allows a quick first evaluation of species extinction proneness in species assemblages of fragmented landscapes (Ganzhorn and Eisenbei, 2001). Although this approach alone is insufficient to evaluate strategies to preserve biodiversity in fragmented biotas (Cutler, 1994) it could be highly useful as predicting species loss can be used to make informed land-use decisions and to effectively protect species that will disappear first in a determined fragmentation scenario (Fleishman et al., 2007).

Four main processes have been proposed to explain nestedness patterns: (1) selective extinction of species with large spatial requirements in relation to fragment area (Wang et al., 2012; Matthews et al., 2015); (2) selective colonization of species with low dispersal ability in relation to fragments isolation (Kadmon, 1995); (3) random, passive sampling from a common species pool, which can result in a nested pattern if sites are more likely to be occupied by species that are regionally more abundant (Cook and Quinn, 1995; Wright et al., 1998); and (4) selective occupation of hierarchically nested habitats (Honnay et al., 1999). However, studies of the mechanisms explaining nestedness structure on archipelagos resulting from habitat fragmentation have found that, in most cases, nestedness structure is driven by selective extinction and, to a lesser extent, to selective colonization process (Watling and Donnelly, 2006; Matthews et al., 2015).

The selective extinction hypothesis is related to the concept of faunal 'relaxation' (Brown, 1978;

Wilcox et al., 1986). It states that fragment area is the main driver of communities' structure as species loss is predictable and follows gradients of species sensitivity to habitat size (Wright et al., 1998; Watling and Donnelly, 2006; Matthews et al., 2015). Under this mechanism animal species with large area requirements, high trophic guild (i.e. carnivorous and insectivorous), small range size and large body mass will be the first to become extinct when the area of the fragments is reduced (Matthews et al., 2015; Keinath et al., 2017; Li et al., 2019). On the other hand, the selective colonization hypothesis states that the habitat isolation would be the main mechanism behind nestedness structure of an assemblage (Watling and Donnelly, 2006; Meyer and Kalko, 2008). Under this mechanism, species with low dispersal ability—such as those with a low dispersal ratio or small body mass—will colonize only the less isolated fragments and will fail to colonize those that are more isolated (Loo et al., 2002; McAbendroth et al., 2005; Frick et al., 2009).

Although explanation of nestedness structure under selective extinction and selective colonization implies the combination of site variables with species traits (Ulrich et al., 2009), few studies have tried to analyze their roles in generating nestedness simultaneously (Wang et al., 2012; Li et al., 2019).

The Espinal xerophytic forest in central Argentina provides a suitable scenario to address the effects of habitat fragmentation in species assemblage structure. Here, open forests historically used for cattle grazing have been converted to row crop production (Baldi and Paruelo, 2008). The expansion of cultivated land has been related to a combination of climate change (increasing precipitation), increasing global demand for agricultural products, national economic policies, and new technologies (genetically modified seeds, agrochemicals, machinery) (Grau and Aide, 2008; Zak et al., 2008).

At present, the Espinal xerophytic forest is an extremely degraded lowland forest with less than 5% of the original forest area (Dardanelli et al., 2006; Lewis et al., 2009; Morello et al., 2012; Noy-Meir et al., 2012). Because of this severe fragmentation and habitat loss, avian diversity has been negatively affected (Dardanelli and Nores, 2001; Dardanelli, 2006; Dardanelli et al., 2006). At least eight species appear to have become extinct in this forest in the province of Córdoba, Central Argentina, and another nine species are sensitive to fragmentation (Dardanelli et al., 2006). However, fragmentation effects on the species composition and nestedness structure of avian assemblages have not been assessed. Studying drivers behind nestedness structure of avian assemblages in fragmented Espinal forest would provide insights that could help avian conservation. The design of effective management plans in poorly studied and highly fragmented habitats, such as the Espinal forests of Córdoba, Argentina, could take advantage of nestedness analyses, especially in a place where there is no time or resources to undertake long-term studies and when decisions for conservation action are urgent (Ganzhorn and Eisenbei, 2001; Fleishman et

al., 2007). Here, we tested whether avian assemblages in the fragmented Espinal forest exhibit nestedness patterns for winter and summer assemblages. Furthermore, we examined the mechanisms underlying the nestedness structure, particularly focusing on whether selective extinction, selective colonization, or passive sampling are driving nestedness patterns for winter and summer assemblages.

Material and methods

Study area

Our study was conducted in the Espinal forest fragments in the eastern lowlands of Córdoba Province, Argentina (fig. 1). Forest fragments are located in private lands since there are no protected areas in the region. The mean annual precipitation of about 700–800 mm falls mostly in late–spring and summer, from October to March; the rest of the year is the dry season. The mean annual temperature is 16°C, with a maximum peak of 44°C and minimum temperature of –9°C (Morello et al., 2012). This region is regarded a semiarid environment because of the high potential of evapotranspiration that generates a water deficit for 11 months of the year (Morello et al., 2012).

The vegetation of forest fragments has a tree stratum of 5–10 m in height composed mainly of *Prosopis alba*, *Prosopis nigra*, *Celtis ehrenbergiana*, *Geoffroea decorticans*, and *Aspidosperma quebracho–blanco*. Common components of the understory (1 to 5 m height) are species in the genera *Acacia* and *Schinus*, also including *Porlieria microphylla* and *Jodina rhombifolia*. The herbaceous stratum (0–1 m height) includes herbs and grasses; common components of the stratum are species of the genera *Solanum* spp., *Eupatorium* spp., *Stipa* spp., *Setaria* spp., *Paspalum* spp., etc. (Cabrera, 1994; Morello et al., 2012).

All fragments in our study had three well–developed vegetation strata (tree, shrub, and herbaceous), were completely isolated (no corridors or rivers connecting any fragment, fig 1), and were embedded in a matrix of croplands, mostly soybean during the austral summer and wheat or fallow fields during the winter. Thus, we considered the contrast between forest fragments and the matrix to be high (Lindenmayer and Fischer, 2006) for forest birds.

Bird sampling

We surveyed bird species in 13 forest fragments (ranged from 0.25 to 217.4 ha). Nocturnal species (Strigidae and Caprimulgidae) and species that only flew over the fragments were not considered. Surveys were conducted during the austral winter (June–August 2001) and austral summer (December 2001–March 2002) seasons. One observer (SD) carried out all the surveys by intensive searches recording all bird species seen or heard while walking slowly through the whole fragment from pre–dawn to 11:00 and from 14:00 until sunset. We surveyed each fragment until no new species were added in 4–8 additional

sampling days (Dardanelli et al., 2006). To adjust for differences in species detectability we compared species richness among forest patches and between seasons using rarefaction curves. Rarefaction analysis calculates species richness after standardizing differences in abundance among samples by estimating the expected number of species of each sample if all samples are reduced to a standard size (Magurran, 2004). Rarefaction curves were performed using iNext (Chao et al., 2016).

We distinguished two types of birds occurring in the fragments: forest species (species that inhabit only xerophytic forests in the study area), and habitat generalists that use both forest and open areas (table 1s in supplementary material). Because the focus of this study is on patch level effects, we centred our investigation on species for which xerophytic forest is a primary habitat. Therefore, prior to analysis, we removed all species for which xerophytic forest is not considered primary habitat (Cook et al., 2002; Watson, 2003; table 1s in supplementary material). We also removed migratory species (Nores, 1996; Barnett and Pearman, 2001), considering only year–round residents as they necessarily colonize the fragments at the beginning of the breeding season and leave (disappear) at the end of the breeding season (Watson, 2003). However, we acknowledge the response of generalist and migratory bird species to fragmentation could have some relevance and would need to be considered when designing conservation measures at regional scales for the Espinal forests in Argentina. It is important to mention that most fragments and all species analyzed in this study persist in the study area (Verga et al., 2019; eBird, 2020). Thus, we consider that the results of our study could be applied to the current scenario, as both the fragmented forest and the bird species have remained constant.

The order of the families and the generic and specific names of bird species follow the South American Classification Committee (Renssen et al., 2020).

Species traits

To analyse the influence of extinction and the colonization process in structuring species occurrences, we selected species life history traits commonly associated with avian species extinction proneness or dispersal ability (table 2s in supplementary material). Geographic range size, trophic guild and natural abundance are life history traits related to extinction proneness (Davidar et al., 2002; Henle et al., 2004; Feeley et al., 2007; Wang et al., 2010). On the other hand, body mass and dispersal ratio area are life history traits that are usually linked to species ability to colonize new sites (Schoener and Schoener, 1984; Cook and Quinn, 1995; Henle et al., 2004; Jenkins et al., 2007).

We obtained distributional range size from Birdlife International species factsheets (BirdLife International, 2020). Trophic guild data were constructed by extracting data of local species diet (Zotta, 1940; Del Hoyo et al., 1992; Alessio et al., 2005; Salvador et al., 2017) and creating four categories: 1, herbivores; 2, omnivores; 3, insectivores, and 4, carnivores. Mini-

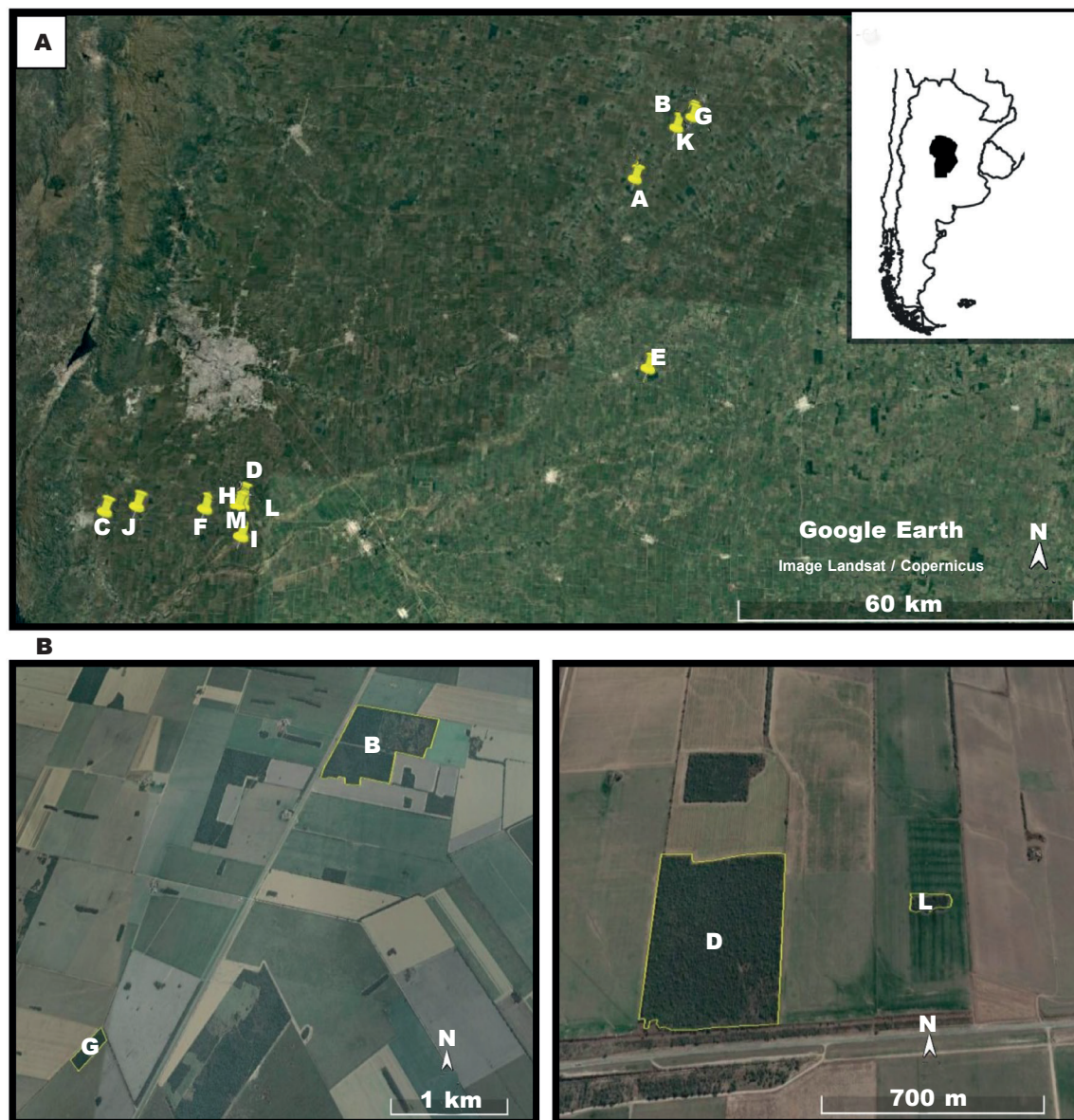


Fig. 1. A, study area showing the spatial distribution of the forest fragments of Espinal included in the study of nestedness of forest birds in central Argentina; B, examples of some of the studied forest fragments.

Fig. 1. A, área de estudio en la que se muestra la distribución espacial de los fragmentos de bosque del Espinal incluidos en el estudio del anidamiento de aves forestales en el centro de Argentina; B, ejemplos de algunos de los fragmentos de bosque estudiados.

mum area requirement was obtained from Dardanelli et al. (2006). Body mass data were obtained from Dunning (2008). The dispersal ratio was calculated by dividing each species mean wing length (mm) by the cube root of its mean mass in grams (Fischer and Lindenmayer, 2005; Li et al., 2019). The relationship of this ratio with dispersal ability is positive so that species with higher ratios will disperse longer distances and species with lower ratios will disperse shorter distances and will consequently be poor

dispersers (Fischer and Lindenmayer, 2005; Li et al., 2019). Species traits were not correlated among them (Pearson $r < 0.4$).

Site variables

We selected different landscape variables to characterize spatial configuration of the forest fragments: area (Area; ha), perimeter (m), two isolation variables: distance to the nearest fragment (DNF; meters) and

proximity index in a 2 km–buffer area (PI), and shape index (SI) (table 3s in supplementary material). Area, Perimeter and Isolation metrics were calculated using Quantum GIS (QGIS) software. We estimated shape index as $SI = P_m/P_c$, where P_m is the measured perimeter of the fragment and P_c is the perimeter of a circular fragment of the same area. This SI index was used in similar studies and has been found to be less correlated to the area than other shape indices (Hinsley et al., 1995; Santos et al., 2002; Watson et al., 2004). We found that the Perimeter and Shape index were highly correlated with Area (Pearson $r \geq 0.7$). For this reason, we excluded these variables, as they were dependent on area.

Data analysis

Matrices of presence–absence were assembled for both seasons. We used the metric based on overlap and decreasing fill 'NODF' to evaluate nestedness (Almeida–Neto et al., 2008). Through the online interface NeD (<http://ecosoft.alwaysdata.net/>) developed by Strona et al. (2014), nestedness can be calculated for the whole incidence matrix and independently for species (NODF between rows) and sites (NODF between columns). We ran five null models to estimate the significance level of nestedness: equiprobable row and column totals (EE), equiprobable row totals–Fixed column totals (EF), fixed row totals–equiprobable column totals (FE), and fixed–column and fixed–row totals (FF) algorithms. FF algorithm has shown to be highly restrictive and EE poorly restrictive (Ulrich and Gotelli, 2012; Strona and Fattorini, 2014; Matthews et al., 2015; Si et al., 2015). All these null models have strengths and weaknesses (Ulrich and Gotelli, 2012; Strona and Fattorini, 2014; Matthews et al., 2015; Si et al., 2015). However, PP and FF null models were described as less biased than the others (Ulrich and Gotelli, 2012). Furthermore, PP has been found to be the preferred model when research systems contain relatively small islands, when the scale of analysis is small, and because it is considered more ecologically meaningful (Ulrich and Gotelli, 2012; Strona and Fattorini, 2014; Matthews et al., 2015; Si et al., 2015). This model provides an unbiased proportional resampling of matrix incidences proportional to row and column totals (Almeida–Neto and Ulrich, 2011). Expected nestedness metrics and related parameters were generated for winter and summer assemblages by running 1,000 Monte Carlo simulations.

The passive sampling hypothesis can be tested using the Coleman's (Coleman, 1981; Coleman et al., 1982) random placement model (Calme and Desrochers, 1999; González–Oreja et al., 2012; Wang et al., 2012; Li et al., 2019). The random placement model was used to verify whether passive sampling from species abundance distributions was driving the nestedness structure of bird communities. Coleman et al. (1982) state that the number of species $\hat{s}_{(\alpha)}$ to be found residing in a given site depends on this site relative area, α (which equals the ratio of the area of a particular fragment to the summed area of all frag-

ments), and the overall abundances n_1, n_2, \dots, n_s of the S species represented in C , which is a collection of N individuals from S species (Coleman, 1981):

$$\hat{s}_{(\alpha)} = S - \sum_{i=1}^S (1 - \alpha)^{n_i}$$

The variance $\sigma^2 \hat{s}_{(\alpha)}$ is determined as

$$\sigma^2_{(\alpha)} = \sum_{i=1}^S (1 - \alpha)^{n_i} - \sum_{i=1}^S (1 - \alpha)^{2n_i}$$

If the hypothesis of random placement holds roughly two–thirds of the points should fall within the band bounded by \pm one standard deviation of the expected curve, or if less than two–thirds of the points fall within the bands, it should be rejected (Coleman et al., 1982).

To check for spatial autocorrelation in the data (i.e. figures of variables sampled at nearby locations tend to have more similar values than would be expected by chance) we fitted a semivariogram randomisation analysis based on 99 Monte Carlo permutations (Isaaks and Srivastava, 1989). Spatial autocorrelation in the response variable (species richness) violates the assumption of independently and identically distributed errors and hence inflates type I errors (Dormann, 2007).

The order in which sites and species are organized by NODF can be compared with several independent variables to evaluate their possible roles in producing nestedness (Patterson and Atmar 2000). To test the effects of forest fragment traits on nestedness, we performed Spearman rank correlations between the forest fragments rank orders in the maximally packed matrix and ranked traits of the forest fragments (table 3s in supplementary material). Similarly, to assess the role of species traits in driving nestedness patterns, we calculated Spearman rank correlations between the species rank orders in the maximally packed matrix and ranked species traits (table 2s in supplementary material). Statistical significance was established at $P < 0.05$.

Partial Spearman rank correlations and semivariograms were performed using R (R Development Core Team, 2016).

Results

We recorded 43 forest resident species in the fragments (tables 2s, 4s, and 5s in supplementary material). Rarefaction analyses confirmed that all forest patches were adequately and comparatively sampled in both seasons (fig. 2). Four species were ubiquitous for both seasons, the stripe–crowned spinetail (*Crani-oleuca pyrrhophia*), the pearly–vented tody–tyrant (*Hemitriccus margaritaceiventer*), the golden–billed saltator (*Saltator aurantiirostris*), and the black–and–chestnut warbling–finch (*Poospiza whitii*) (tables 4s, 5s in supplementary material). Three other species had only one absence in winter, the great antshrike (*Taraba major*), the white–tipped plantcutter (*Phytotoma rutila*),

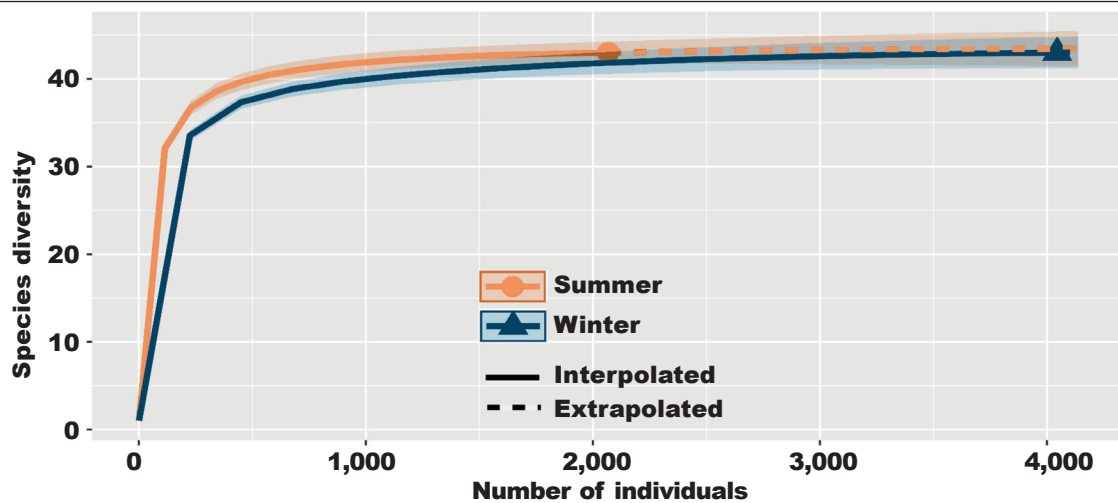


Fig. 2. Rarefaction curves for bird species richness for resident forest birds of forest fragments in the austral winter (blue) and austral summer (orange), in Córdoba, Argentina.

Fig. 2. Curvas de rarefacción de la riqueza de especies de aves forestales residentes en fragmentos de bosque en el invierno austral (azul) y el verano austral (naranja), en Córdoba (Argentina).

and the creamy-bellied thrush (*Turdus amaurochalinus*) (tables 4s and 5s in supplementary material); and one species had only one absence in summer, the brown cachalote (*Pseudoseisura lophotes*). All these species were common in the fragments. On the other hand, eight species: the sharp-shinned hawk (*Accipiter striatus erythronemius*), the spot-winged falconet (*Spizapteryx circumcinctus*), white-barred piculet (*Picumnus cirratus*), the scimitar-billed woodcreeper (*Drymornis bridgesii*), the narrow-billed woodcreeper (*Lepidocolaptes angustirostris*), the crested hornoro (*Furnarius cristatus*), the suiriri flycatcher (*Suiriri suiriri*) and the cinereous tyrant (*Knipolegus striaticeps*) occupied only the largest fragments (≥ 80 ha) and were all scarce. Some of these species occupied smaller fragments during winter (tables 4s and 5s in supplementary material).

The semivariogram did not show a significant association between the spatial distribution of the forest fragments and species richness in winter or summer (fig. 1s in supplementary material).

The bird assemblages were significantly nested in both seasons (table 1) for all null models except the very restrictive FF (fixed-fixed) model. Both NODF values and matrix structure were similar between seasons for resident birds (table 1). Our results show a high temporal constancy in the nested pattern for resident bird assemblages in Espinal forest fragments in Central Argentina.

Spearman's rank correlations showed that the remnant order that maximized nestedness in both winter and summer was correlated with remnants ordered according to the area and distance to the nearest fragment (table 2). The proximity index was not significantly correlated with remnant order.

Species order in matrices packed for maximum nestedness showed a significant relationship with minimum area requirement, trophic guild, and range size both in winter and summer, and with species distributional range size in summer (table 2). Species traits commonly related to colonization ability like body mass and dispersal ratio were not significantly correlated with the species order.

The nestedness of forest birds' assemblages was not caused by passive sampling in summer or winter assemblages. Only one data point in summer and four out of 13 in winter data points fell within ± 1 SD of the expected Coleman's species/relative area curves (fig. 3, 4), which means that it did not follow expectations from the random placement hypothesis.

Discussion

Bird assemblages in fragmented Espinal forest in Central Argentina showed a non-random structure, with species aggregation consistent with the nested subset model across seasons, for the whole matrix, and for columns (forest fragments) and rows (bird species) separately. This nested structure did not follow the random placement hypothesis (Coleman, 1981; Coleman et al., 1982).

The nestedness structure in our studied system showed a structure consistent with the selective extinction hypothesis as nestedness was related to fragment area and species traits associated with extinction proneness such as trophic guild, minimum area requirement and distributional range size. The correlation of fragment area and species traits with nested rank indicated that bird assemblages on

Table 1. Comparative analyses of nestedness for resident forest birds in forest fragments between seasons, in Córdoba, Argentina. Nestedness metrics and related parameters are provided for two seasons: winter and summer. *P*-values were generated by 1,000 Monte Carlo simulations: EE, equiprobable–equiprobable null model; PP, proportional–proportional null model; FF, fixed–fixed null model; SD, standard deviation; * significant nestedness ($P < 0.05$); matrix, nestedness estimator for the whole presence–absence matrix; species, row nestedness estimator among species (based on species incidence); fragments, column nestedness estimator among fragments (based on species composition).

*Tabla 1. Análisis comparativos del anidamiento de las aves residentes en fragmentos de bosque entre estaciones, en Córdoba (Argentina). Se proporcionan los valores de anidamiento y los parámetros relacionados para las dos estaciones: invierno y verano. Los valores P se generaron a partir de 1.000 simulaciones de Monte Carlo: EE, modelo nulo equiprobable–equiprobable; PP, modelo nulo proporcional–proporcional; FF, modelo nulo fijo–fijo; SD, desviación estándar; * anidamiento significativo ($P < 0,05$); matrix, estimador de anidamiento para toda la matriz de presencia–ausencia; species, estimador de anidamiento de fila entre especies (basado en la incidencia de especies); fragments, estimador de anidamiento de columna entre fragmentos (basado en la composición de especies).*

Season							
Extent	NODF _{obs}	NODF _{EE}	NODF _{EF}	NODF _{FE}	NODF _{PP}	NODF _{FF}	
Winter							
Matrix	84.51	57.95* (2.06)	73.03* (0.81)	62.00* (2.18)	66.77* (2.20)	85.07 (0.46)	
Species	84.19	57.87* (2.15)	73.23* (0.66)	61.43* (2.31)	66.70* (2.21)	84.83 (0.479)	
Fragments	88.29	58.81* (2.94)	70.72* (3.19)	68.54* (0.84)	67.57* (2.97)	87.93 (0.25)	
Summer							
Matrix	86.11	57.08* (2.12)	72.83* (0.87)	60.96* (2.16)	66.25* (2.24)	85.88 (0.49)	
Species	85.93	57.02* (2.21)	72.99* (0.72)	60.42* (2.28)	66.19* (2.97)	85.49 (0.54)	
Fragments	88.25	57.75* (2.91)	71.02* (3.94)	67.17* (0.84)	66.84* (3.05)	88.27 (0.25)	

smaller fragments were predictable subsets of richer faunas occurring on larger fragments. It also indicated that species requiring large areas have a restricted

distribution range and high trophic guild, are predictable subsets of species that do not need large areas, are broadly distributed, and are at low trophic guild.

Table 2. Results of Spearman Rank correlations of forest fragments nestedness rank order with fragment traits; and bird species nestedness rank order with bird life history traits, for the maximally packed nested matrix: DNF, distance to nearest fragment; PI, proximity index in 2 km buffer; MAR, minimum area requirement; RS, distribution range size; TG, trophic guild; BM, body mass; DR, dispersal ratio. (Level of significance: ** $P < 0.01$, * $P < 0.05$)

*Tabla 2. Resultados de las correlaciones de rango de Spearman entre el orden de rango de anidamiento de los fragmentos de bosque con los rasgos de los fragmentos, por un lado, y entre el orden de rango de anidamiento de las especies de aves con los rasgos de la historia de la vida de las aves, por otro, para la matriz anidada empaquetada al máximo: DNF, distancia al fragmento más cercano; PI, índice de proximidad en la zona de amortiguación de 2 km; MAR, requerimiento mínimo de superficie; RS, tamaño del área de distribución; TG, gremio trófico; BM, masa corporal; DR, índice de dispersión. (Nivel de significancia: ** $P < 0,01$, * $P < 0,05$).*

	Fragment traits			Species life–history traits				
	Area	DNF	PI	MAR	TG	RS	BM	DR
Winter	0.60*	0.63*	0.42	0.75**	0.35*	0.20	0.10	0.11
Summer	0.78**	0.59*	0.53	0.78**	0.41**	0.33*	0.04	0.25

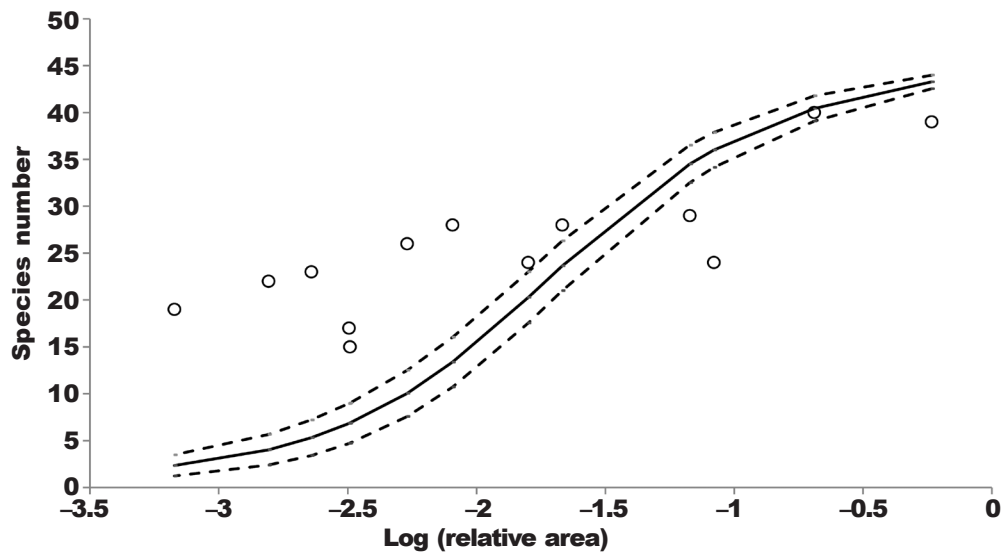


Fig. 3. Comparison of observed data to expected values under the random placement model for resident forest birds in forest fragments in the austral summer, in Córdoba, Argentina. Expected values (solid line) and associated standard deviations (± 1 SD; dashed lines) are shown. Open circles represent observed species richness.

Fig. 3. Comparación de los datos observados y esperados según el modelo de ubicación aleatoria para aves forestales residentes en fragmentos de bosque en el verano austral, en Córdoba (Argentina). Las líneas continuas representan los valores esperados y las líneas discontinuas representan las desviaciones estándar asociadas (± 1 DE; líneas discontinuas). Los círculos representan la riqueza de especies observada.

These results are in agreement with similar studies in fragmented habitats where selective extinction arises as the most common driver of nestedness structure (Wright et al., 1998; Matthews et al., 2015; García-Quintas and Parada, 2017; De la Hera, 2019). The importance of extinction driven processes in shaping community assembly has been found in many fragmented landscapes (Martinez-Morales, 2005). It has been suggested that the trigger for this kind of patterns is a faunal relaxation process, which is characteristic of highly fragmented or relic-tual forest ecosystems (Brooks et al., 1999; Ferraz et al., 2007).

The prevalence of colonization driven patterns is less frequent in fragmented terrestrial habitats (Wright et al., 1998; Watling and Donnelly, 2006), and it appears to be an important driver for other isolated habitats such as mountaintops, land-bridge islands and oceanic islands (Cook and Quinn, 1995; Wright et al., 1998; Watling and Donnelly, 2006; Meyer and Kalko, 2008; García-Quintas and Parada, 2017). Our results showed that selective colonization seems to have some influence on community assembly as distance to nearest fragment was correlated with fragments nested order. However, species traits commonly associated with dispersal ability such as body mass and dispersal ratio were not related to species order. In this regard, it is possible that dispersal ratio and body mass were not good indicators

of dispersal ability for birds in this study. The other possibility is that because colonization has marginal importance in driving nestedness structure in our system, it does not express any significant relationship with our dispersal ability proxies. Consequently, we could venture to say that the selective colonization hypothesis only partially explains birds' nestedness structure in Espinal forest of Central Argentina. One possible explanation for the low influence of selective colonization is that species with low dispersal ability have already become extinct in the study area. We documented this in a previous study in the same area where, for example, most large birds have disappeared from fragmented forests (Dardanelli et al., 2006). Moreover, as has been demonstrated in other studies (Watling and Donnelly, 2006; Matthews et al., 2015), it is very difficult to find biologically meaningful isolation effects on assemblage structure. In the case of bird communities in South America, it is even more challenging considering knowledge of colonization ability or dispersal rate of species is scarce (Faaborq et al., 2010; Jahn et al., 2017). It is therefore challenging to assess the role of selective colonization hypothesis in the assemblage structure of Espinal forest birds. Nevertheless, it seems to have secondary importance as a driver of nestedness aggregation. This highly fragmented forest has almost disappeared from this region and the few remaining fragments have undergone faunal relaxation for many years, giving

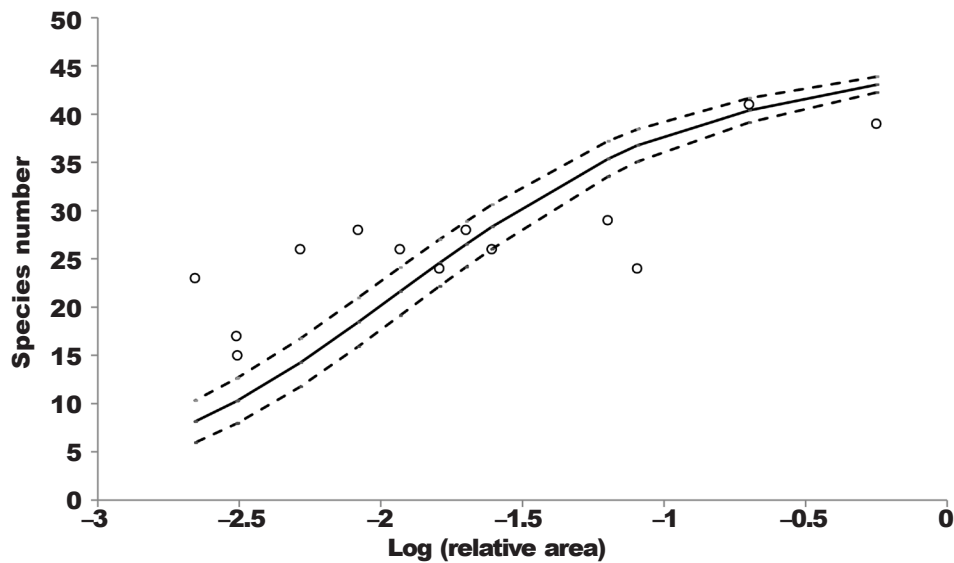


Fig. 4. Comparison of observed data to expected values under the random placement model for resident forest birds of forest fragments in the austral winter, in Córdoba, Argentina. Solid lines represent expected values and dashed lines represent associated standard deviations (± 1 SD; dashed lines). Open circles represent observed species richness.

Fig. 4. Comparación de los datos observados y esperados según el modelo de ubicación aleatoria para las aves forestales residentes en fragmentos de bosque en el invierno austral, en Córdoba (Argentina). Las líneas continuas representan los valores esperados y las líneas discontinuas representan las desviaciones estándar asociadas (± 1 DE; líneas discontinuas). Los círculos representan la riqueza de especies observada.

rise to extinction driven biotas. Consequently, we did not find any relationship between proximity indexes or any species trait related to dispersal ability with nestedness order.

Nestedness structure did not vary between seasons. Consequently, seasonality does not seem to influence nestedness in our system. These results are consistent with the results of Seoane et al. (2013), García-Quintas and Parada (2014), Zhou et al. (2014) and De la Hera (2019) who found no seasonality effects on nestedness structure of birds in isolated woodlots in Spain and birds of urban parks in Hong Kong and Spain. Our results, however, contradict the results of Murgui (2010) who found small but significant differences in nestedness structure and species–area relationships between seasons in urban parks in Spain. This author ruled out an increase in mortality outside the breeding seasons as they have mild winters. He considered that the use of alternative habitats outside of parks during autumn and winter is the most likely explanation for the observed patterns. The winters in the Espinal forest fragments in Central Argentina are mild and bird species are probably less prone to use alternative habitats than birds in urban parks. Another difference is that specialist birds analyzed in our system are generally more sensitive to disturbances and less adaptable than generalist species in urban parks in Spain.

Protecting the larger and less isolated forest fragments would be the most effective way to preserve resident birds in this relictual Espinal forests. The preservation of large and less isolated fragments would help to protect resident birds with large area requirements, small distribution range size, and high trophic guilds (i.e. carnivorous and insectivorous species). For example, by protecting the two largest forest fragments it is possible to maintain most species (97.7% in summer; 95.3% in winter) of forest birds in the dataset. As mentioned by other authors, nestedness analysis can be used in combination with other approaches to provide valuable recommendations for decision-making when long-term data are not available. Based on the results of the present study, future landscape management of Espinal forest should ensure the protection of large fragments as they preserve the largest populations of resident forest species throughout the year.

Acknowledgements

We thank G. and M. Esmóris, R. Parra, A. Varselotti and F. Mansilla for providing access to their properties. We also thank D. A. Serra and M. Nores for assistance with the bird surveys. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) provided partial funding.

References

- Alessio, V. G., Beltzer, A. H., Lajmanovich, R. C., Quiroga, M. A., 2005. Ecología alimentaria de algunas especies de Passeriformes (Furnariidae, Tyrannidae, Icteridae y Emberizidae): consideraciones sobre algunos aspectos del nicho ecológico. *Insugeo, Miscelánea*, 14: 441–482.
- Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., 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., 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*, 26: 173–178.
- Atmar, W., Patterson, B. D., 1995. *Nested temperature calculator: a visual basic program, including 294 presence absence matrices*. The Field Museum, Chicago, IL.
- 1993. The Measure of Order and Disorder in the Distribution of Species in Fragmented Habitat. *Oecologia*, 96: 373–382.
- Baldi, G., Paruelo, J. M., 2008. Land-use and land cover dynamics in South American temperate grasslands. *Ecology and Society*, 13: 6.
- Barnett, J. M., Pearman, M., 2001. *Lista comentada de las aves argentinas: Annotated checklist of the birds of Argentina*. Lynx, Barcelona, Spain.
- BirdLife International, 2020. *IUCN Red List for birds* [WWW Document], 2020. URL <http://datazone.birdlife.org/home> [Accessed 3 May 2020].
- Brooks, T. M., Pimm, S. L., Kapos, V., Ravilious, C., 1999. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology*, 68: 1061–1078.
- Brown, J. H., 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs*, 2: 209–227.
- Cabrera, A. L., 1994. *Enciclopedia Argentina de agricultura y jardinería, Tomo II, Fascículo 1: regiones fitogeográficas Argentinas*. ACME, Buenos Aires.
- Calme, S., Desrochers, A., 1999. Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia*, 118: 361–370.
- Chao, A., Ma, K. H., Hsieh, T. C., 2016. *iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity*. Program and User's Guide, http://chao.stat.nthu.edu.tw/wordpress/software_download/ [Accessed on June 17th 2020]
- Coleman, B. D., 1981. On random placement and species-area relations. *Mathematical Biosciences*, 54: 191–215.
- Coleman, B. D., Mares, M. A., Willig, M. R., Hsieh, Y.-H., 1982. Randomness, Area, and Species Richness. *Ecology*, 63: 1121–1133.
- Cook, W. M., Lane, K. T., Foster, B. L., Holt, R. D., 2002. Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, 5: 619–623.
- Cook, R. R., Quinn, J. F., 1995. The Influence of Colonization in Nested Species Subsets. *Oecologia*, 102: 413–424.
- Cutler, A. H., 1991. Nested Faunas and Extinction in Fragmented Habitats. *Conservation Biology*, 5: 496–504.
- 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape and Urban Planning*, 28: 73–82.
- Dardanelli, S., 2006. Dinámica de comunidades de aves en fragmentos de bosque de la Provincia de Córdoba. Tesis doctoral, Universidad Nacional de Córdoba.
- Dardanelli, S., Nores, M., 2001. Extinción y colonización de aves en fragmentos de bosque de la Provincia de Córdoba, Argentina. *Boletín de la Academia Nacional de Ciencias*, 66: 55–60.
- Dardanelli, S., Nores, M. L., Nores, M., 2006. Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. *Diversity and Distributions*, 12: 687–693.
- Davidar, P., Yoganand, K., Ganesh, T., Devy, S., 2002. Distributions of forest birds and butterflies in the Andaman Islands, Bay of Bengal: nested patterns and processes. *Ecography*, 25: 5–16.
- De la Hera, I., 2019. Seasonality affects avian species distribution but not diversity and nestedness patterns in the urban parks of Vitoria-Gasteiz (Spain). *Animal Biodiversity and Conservation*, 42: 279–291, Doi: <https://doi.org/10.32800/abc.2019.42.0279>
- Del Hoyo, J., Elliott, A., Sargatal, J., 1992. *Handbook of the birds of the world*. Lynx Edicions, Barcelona, Spain.
- Dormann, C. F., 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16: 129–138.
- Dunning, J., 2008. *CRC handbook of avian body masses, 2nd edition*. CRC Press, Boca Raton FL, USA.
- eBird, 2020. *eBird: An online database of bird distribution and abundance* [web application]. eBird, Cornell Lab of Ornithology, Ithaca, New York. Available online at: <http://www.ebird.org> [Accessed on June 17th 2020].
- Faaborq, J., Holmes, R. T., Anders, A. D., Bildstein, K. L., Dugger, K. M., Gauthreaux Jr., S. A., Heglund, P., Hobson, K. A., Jahn, A.E., Johnson, D. H., Latta, S. C., Levey, D. J., Marra, P. P., Merkord, C. L., Erica, N. O. L., Rothstein, S. I., Sherry, T. W., Scott Sillett, T., Thompson III, F. R., Warnock, N., 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*, 80: 3–48.
- Feeley, K. J., Gillespie, T. W., Lebbin, D. J., Walter, H. S., 2007. Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. *Animal Conservation*, 10: 493–501.
- Ferraz, G., Nichols, J. D., Hines, J. E., Stouffer, P. C., Bierregaard, R. O., Lovejoy, T. E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science*, 315: 238–241.
- Fischer, J., Lindenmayer, D. B., 2005. The sensitivity

- of lizards to elevation: A case study from south-eastern Australia. *Diversity and Distributions*, 11: 225–233.
- Fleishman, E., Donnelly, R., Fay, J. P., Reeves, R., 2007. Applications of nestedness analyses to biodiversity conservation in developing landscapes. *Landscape and Urban Planning*, 81: 271–281.
- Frick, W. F., Hayes, J. P., Heady III, P. A., 2009. Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes. *Oecologia*, 158: 687–697.
- Ganzhorn, J. U., Eisenbei, B., 2001. The the concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. *Basic and Applied Ecology*, 2: 87–99.
- 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: 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: 7–16, <https://doi.org/10.32800/abc.2017.40.0007>
- González-Oreja, J. A., De La Fuente-Díaz, A. A., Hernández-Santín, L., Bonache-Regidor, C., Buzo-Franco, D., 2012. Can human disturbance promote nestedness? Songbirds and noise in urban parks as a case study. *Landscape and Urban Planning*, 104: 9–18.
- Grau, H. R., Aide, M., 2008. Globalization and land-use transitions in Latin America. *Ecology and society*, 13.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, 1: e1500052.
- Henle, K., Lindenmayer, D. B., Margules, C. R., Saunders, D. A., Wissel, C., 2004. Species survival in fragmented landscapes: where are we now? *Biodiversity and Conservation*, 13: 1–8.
- Hinsley, S. A., Bellamy, P. E., Newton, I., 1995. Bird species turnover and stochastic extinction in woodland fragments. *Ecography*, 18: 41–50.
- Honnay, O., Endels, P., Vereecken, H., Hermy, M., 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. *Diversity and Distributions*, 5: 129–141.
- Isaaks, E. H., Srivastava R. M., 1989. *Applied geostatistics*. Oxford University Press, New York, USA.
- Jahn, A.E., Bejarano, V., Cueto, V. R., Di Giacomo, A. S., Fontana, C. S., 2017. Movement ecology research to advance conservation of South America's grassland migratory birds. *Perspectives in Ecology and Conservation*, 15: 209–215.
- Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., Lyon, B. N., Metzger, G. A., Olandese, M. L., 2007. Does size matter for dispersal distance? *Global Ecology and Biogeography*, 16: 415–425.
- Kadmon, R., 1995. Nested Species Subsets and Geographic Isolation – a Case-Study. *Ecology*, 76: 458–465.
- Keinath, D. A., Doak, D. F., Hodges, K. E., Prugh, L. R., Fagan, W., Sekercioglu, C. H., Buchart, S. H. M., Kauffman, M., 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. *Global Ecology and Biogeography*, 26: 115–127.
- Lewis, J. P., Noetinger, S., Prado, D. E., Barberis, I. M., 2009. Woody vegetation structure and composition of the last relicts of Espinal vegetation in subtropical Argentina. *Biodiversity and Conservation*, 18: 3615–3628.
- Li, C., Zhao, B., Wang, Y., 2019. Nestedness of waterbird assemblages in the subsidence wetlands recently created by underground coal mining. *Current Zoology*, 65: 155–163.
- Lindenmayer, D. B., Fischer, J., 2006. *Habitat fragmentation and landscape change*. CSIRO Publishing, Collingwood VIC, Australia.
- Loo, S. E., Mac Nally, R., Quinn, G. P., 2002. An experimental examination of colonization as a generator of biotic nestedness. *Oecologia*, 132: 118–124.
- Magurran, A., 2004. *Measuring biological diversity*. Blackwell, Oxford.
- Martinez-Morales, M. A., 2005. Nested species assemblages as a tool to detect sensitivity to forest fragmentation: the case of cloud forest birds. *Oikos*, 108: 634–642.
- Matthews, T. J., Cottee-Jones, H. E. W., Whittaker, R. J., 2015. Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. *Diversity and Distributions*, 21: 392–404.
- McAbendroth, L., Foggo, A., Rundle, S. D., Bilton, D. T., 2005. Unravelling nestedness and spatial pattern in pond assemblages. *Journal of Animal Ecology*, 74: 41–49.
- Meyer, C. F., Kalko, E. K., 2008. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Diversity and Distributions*, 14: 644–654.
- Morello, J., Matteucci, S. D., Rodríguez, A. F. S., 2012. Ecorregiones y complejos ecosistémicos argentinos, FADU. ed. FADU, Buenos Aires, Argentina.
- Murgui, E., 2010. Seasonal patterns of bird crop use in traditional irrigated land (The Huerta of Valencia, Spain). *Ardeola*, 57: 87–102.
- Nores, M., 1996. Avifauna de la provincia de Córdoba. In: *Biodiversidad de la Provincia de Córdoba: 255–337* (E. di Tada, E. H. Bucher, Eds.). Universidad Nacional de Río Cuarto, Córdoba, Argentina.
- Noy-Meir, I., Mascó, M., Giorgis, M. A., Gurchich, D. E., Perazzolo, D., Ruiz, G., 2012. Estructura y diversidad de dos fragmentos del bosque de espinal en Córdoba, un ecosistema amenazado. *Boletín de la Sociedad Argentina de Botánica*, 47: 119–133.
- Nupp, T. E., Swihart, R. K., 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, 81: 512–526.
- Patterson, B. D., Atmar, H., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28: 65–82.

- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>
- Remsen, J. V. J., Areta, J. I., Cadena, C. D., Jaramillo, A., Nores, M., Pacheco, J. F., Pérez-Emán, J., Robbins, C. S., Stiles, F. G., Stotz, D. F., Zimmer, K. J., 2020. *A classification of the birds species of South America* [WWW Document]. URL <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm>
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. *Science*, 287: 1770–1774.
- Salvador, S. A., Salvador, L., Ferrari, C., 2017. *Aves de la provincia de Córdoba, Argentina. Distribución e historia natural*. Docuprint, Buenos Aires, Argentina.
- Santos, T., Tellería, J. L., Carbonell, R., 2002. Bird conservation in fragmented Mediterranean forests of Spain: Effects of geographical location, habitat and landscape degradation. *Biological Conservation*, 105: 113–125.
- Schoener, A., Schoener, T. W., 1984. Experiments on dispersal: short-term floatation of insular anoles, with a review of similar abilities in other terrestrial animals. *Oecologia*, 63: 289–294.
- Seoane, J., Villén-Pérez, S., Carrascal, L. M., 2013. Environmental determinants of seasonal changes in bird diversity of Mediterranean Oakwoods. *Ecological Research*, 28: 435–445.
- Si, X., Baselga, A., Ding, P., 2015. Revealing beta-diversity patterns of breeding bird and lizard communities on inundated land-bridge islands by separating the turnover and nestedness components. *PLoS one*, 10: e0127692.
- Soga, M., Koike, S., 2012. Relative Importance of Quantity, Quality and Isolation of Patches for Butterfly Diversity in Fragmented Urban Forests. *Ecological Research*, 27: 265–271.
- Strona, G., Fattorini, S., 2014. On the methods to assess significance in nestedness analyses. *Theory in Biosciences*, 133: 179–186.
- Strona, G., Galli, P., Seveso, D., Montano, S., Fattorini, S., others, 2014. Nestedness for Dummies (NeD): a user friendly web interface for exploratory nestedness analysis. *Journal of Statistical Software*, 59: 1–9.
- 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.
- Verga, E. G., Hümöller, H. L. S., Vergara-Tabares, D. L., Galetto, L., Peluc, S. I., 2019. Importancia para la conservación de las aves de un relicto de bosque en la región fitogeográfica del Espinal, Argentina. *Neotropical Biology and Conservation*, 14: 241–256.
- Wang, Y., Bao, Y., Yu, M., Xu, G., Ding, P., 2010. Nestedness for different reasons: The distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions*, 16: 862–873.
- Wang, Y., Wang, X., Ding, P., 2012. Nestedness of snake assemblages on islands of an inundated lake. *Current Zoology*, 58: 828–36.
- Watling, J. I., Donnelly, M. A., 2006. Fragments as Islands: a Synthesis of Faunal Responses to Habitat Patchiness. *Conservation Biology*, 20: 1016–1025.
- Watson, D. M., 2003. Long-term consequences of habitat fragmentation – Highland birds in Oaxaca, Mexico. *Biological Conservation*, 111: 283–303.
- Watson, J. E. M., Whittaker, R. J., Dawson, T. P., 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of southeastern Madagascar. *Journal of Biogeography*, 31: 1791–1807.
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience*, 48: 607–615.
- Wilcox, B.A., Murphy, D. D., Elrich, P. R., Austin, G. T., 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals. *Oecologia*, 69: 188–194.
- 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.
- Zak, M. R., Cabido, M., Cáceres, D., Díaz, S., 2008. What drives accelerated land cover change in central Argentina? Synergistic consequences of climatic, socioeconomic, and technological factors. *Environmental Management*, 42: 181–189.
- Zhou, D., Chu, L.M., 2014. Do avian communities vary with season in highly urbanized Hong Kong? *The Wilson Journal of Ornithology*, 126: 69–80.
- Zotta, A., 1940. Lista sobre el contenido estomacal de las aves argentinas. *Hornero*, 7: 402–411.

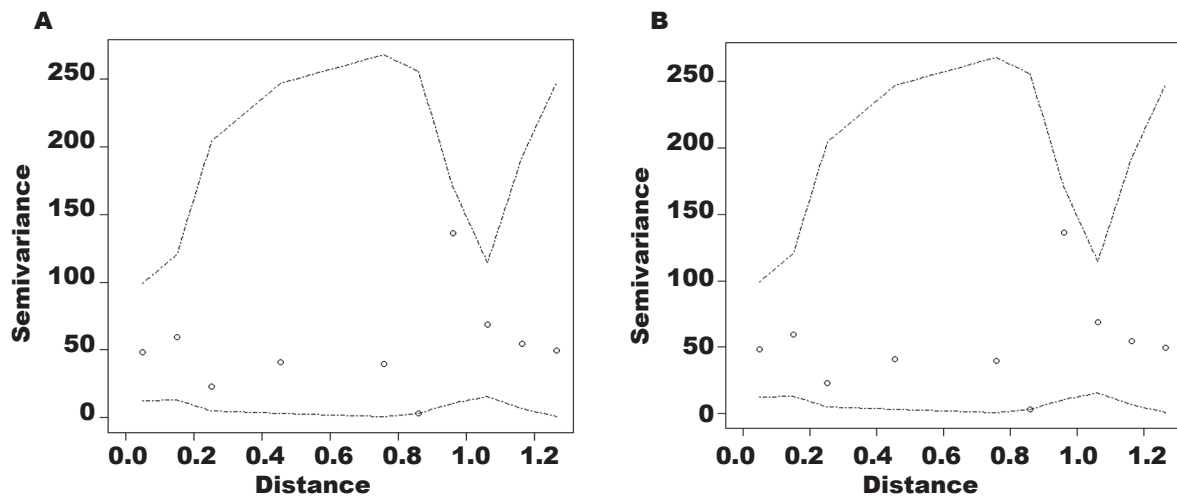
Supplementary material

Fig. 1s. Spatial autocorrelation of the response variable shown by the semi-variogram of the species richness of forest resident birds of forest fragments in the austral summer (A) and winter (B), in Córdoba, Argentina. Dotted lines indicate the 95% confidence envelope based on Monte Carlo permutations. Points outside the simulation envelope indicate significant spatial autocorrelation.

Fig. 1s. Autocorrelación espacial de la variable de respuesta representada por el semivariograma de la riqueza de especies de aves forestales residentes en fragmentos de bosque en el verano austral (A) y en el invierno austral (B), en Córdoba (Argentina). Las líneas punteadas indican el límite de confianza del 95% basado en las permutaciones de Monte Carlo. Los puntos fuera del límite de confianza indican una autocorrelación espacial significativa.

Table 1s. List of 31 generalist and open areas bird species recorded in the matrix (field crops) surrounding the 13 forest fragments, in Córdoba, Argentina.

Tabla 1s. Lista de las 31 especies de aves generalistas y de zonas abiertas registradas en la matriz (cultivos) alrededor de los 13 fragmentos de bosque, en Córdoba (Argentina).

Bird species	Bird species
<i>Nothura maculosa</i>	<i>Melanopareia maximiliani</i>
<i>Coragyps atratus</i>	<i>Xolmis irupero</i>
<i>Rupornis magnirostris</i>	<i>Machetornis rixosa</i>
<i>Milvago chimango</i>	<i>Pitangus sulphuratus</i>
<i>Caracara plancus</i>	<i>Troglodytes aedon</i>
<i>Falco femoralis</i>	<i>Mimus saturninus</i>
<i>Falco sparverius</i>	<i>Mimus triurus</i>
<i>Patagioenas maculosa</i>	<i>Embernagra platensis</i>
<i>Patagioenas picazuro</i>	<i>Sicalis luteola</i>
<i>Zenaida auriculata</i>	<i>Ammodramus humeralis</i>
<i>Columbina picui</i>	<i>Zonotrichia capensis</i>
<i>Myiopsitta monachus</i>	<i>Molothrus bonariensis</i>
<i>Guira guira</i>	<i>Molothrus rufoaxillaris</i>
<i>Colaptes campestris</i>	<i>Agelaioides badius</i>
<i>Furnarius rufus</i>	<i>Spinus magellanicus</i>
<i>Coryphistera alaudina</i>	

Table 2s. Traits of bird species for 43 forest resident species in Córdoba, Argentina: MAR, minimum area requirement; RS, distribution range size; TG, trophic guild (1, herbivores; 2, omnivores; 3, insectivores; 4, carnivores); BM, body mass; DR, dispersal ratio.

Tabla 2s. Rasgos de las 43 especies de aves forestales residentes, en Córdoba (Argentina): MAR, requerimiento mínimo de superficie; RS, tamaño de rango de distribución; TG, gremio trófico (1, herbívoros; 2, omnívoros; 3, insectívoros; 4, carnívoros); BM, masa corporal; DR, índice de dispersión.

Bird species	MAR (ha)	RS (km ²)	TG*	BM (gr)	DR
<i>Crypturellus tataupa</i>	2	4,860,000	2	237	19.39
<i>Nothoprocta cinerascens</i>	2	1,210,000	2	573	21.67
<i>Nothoprocta pentlandii</i>	2	613,000	2	266	21.32
<i>Accipiter striatus</i>	220	11,300,000	4	125	32.8
<i>Spizapteryx circumcincta</i>	80	1,420,000	4	196	29.95
<i>Leptotila verreauxi</i>	1	15,500,000	1	161	28.12
<i>Nystalus maculatus</i>	3	3,580,000	3	42	23.02
<i>Picumnus cirratus</i>	1	1,400,000	3	10.2	24.43
<i>Melanerpes cactorum</i>	80	924,000	3	37.8	29.80
<i>Dryobates mixtus</i>	1	3,640,000	3	30.6	26.22
<i>Colaptes melanochloros</i>	1	7,050,000	3	129	30.68
<i>Tarphonomus certhioides</i>	1	1,270,000	3	22.5	29.76
<i>Furnarius cristatus</i>	80	680,000	3	25.5	26.50
<i>Leptasthenura platensis</i>	8	2,010,000	3	10.6	27.31
<i>Cranioleuca pyrrhophia</i>	1	2,030,000	3	14.9	25.20
<i>Asthenes baeri</i>	1	1,730,000	3	17.8	22.98
<i>Phacellodomus sibilatrix</i>	2	967,000	3	15.5	24.06
<i>Pseudoseisura lophotes</i>	1	1,310,000	3	76	28.33
<i>Drymornis bridgesii</i>	80	1,210,000	3	110	28.38
<i>Lepidocolaptes angustirostris</i>	8	6,580,000	3	27.8	32.35
<i>Taraba major</i>	1	12,900,000	3	59.2	23.09
<i>Thamnophilus caerulescens</i>	1	3,970,000	3	21.1	23.88
<i>Rhinocrypta lanceolata</i>	2	1,010,000	3	61.9	20.43
<i>Suiriri suiriri</i>	80	2,050,000	3	15.3	27.39
<i>Stigmatura budytoides</i>	1	1,480,000	3	11.7	24.67
<i>Hemitriccus margaritaceiventer</i>	1	5,590,000	3	8.4	22.14
<i>Knipolegus striaticeps</i>	80	946,000	3	11	24.73
<i>Knipolegus aterrimus</i>	1	1,540,000	3	20.2	35.24
<i>Phytotoma rutila</i>	1	1,760,000	1	40.5	24.46
<i>Cyclarhis gujanensis</i>	1	13,500,000	3	28.8	28.55
<i>Polioptila dumicola</i>	1	3,680,000	3	7	26.66
<i>Turdus amaurochalinus</i>	1	3,770,000	2	57.9	28.69
<i>Pipraeidea bonariensis</i>	1	2,580,000	2	36	24.83
<i>Rhynchospiza strigiceps</i>	1	664,000	1	22.2	21.35
<i>Poospiza whitii</i>	1	962,000	1	17	25.16
<i>Microspingus torquata</i>	1	956,000	1	11	26.98
<i>Microspingus melanoleuca</i>	1	1,480,000	1	13.1	24.60
<i>Sicalis flaveola</i>	1	6,640,000	1	15.4	28.14
<i>Saltatricula multicolor</i>	2	1,110,000	1	22.2	24.91
<i>Coryphospingus cucullatus</i>	1	4,040,000	1	13.7	27.17
<i>Saltator aurantirostris</i>	1	2,470,000	1	45	23.90
<i>Cyanoloxia brissonii</i>	2	5,850,000	1	27.5	27.17
<i>Icterus pyrrhopterus</i>	8	8,120,000	3	29.7	25.83

Table 3s. Fragment traits for 13 forest fragments, in Córdoba, Argentina.

Tabla 3s. Rasgos de los 13 fragmentos de bosque, en Córdoba (Argentina).

Fragment	Area (ha)	SI	DNF (m)	Perimeter (m)	Proximity Index
A	217.4	0.62	31	8,584	7.57
B	76.7	0.76	125	4,090	4.68
C	31.5	0.81	209	2,670	0.45
D	24.4	0.89	196	2,050	0.89
E	7.5	0.71	246	1,370	5.71
F	6.2	0.86	624	1,026	1.53
G	3.3	0.80	211	810	7.73
H	2.0	0.82	196	608	7.23
I	1.21	0.88	570	440	0.16
J	1.19	0.83	632	470	0.70
K	0.85	0.88	103	370	21.87
L	0.58	0.78	449	347	1.50
M	0.25	0.76	430	232	0.92

