Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation

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This study intends to assess the influence of fragment age, size and isolation (from the regional species pool) on bird community composition patterns in urban parks in Madrid, and the role of local and regional factors on community structure. Park age was a good indicator of habitat complexity. Park age and area accounted for 62% of the variability in species richness, but two measures of isolation from the regional species pool were not included as significant factors. Species composition in urban parks showed a high degree of nestedness, which was associated with park age and area, but not with two measures of isolation from the regional species pool. The degree of nestedness increased with park age; the distribution of species varying from nested in old and mature parks to random in young parks. The incidence (% of species occurrence in parks) in young parks was correlated with regional densities, whereas in mature and old parks the incidence was correlated with local densities. In this urban landscape, species composition appears to be regulated by local factors (particularly in mature and old parks), such that species accumulate in an orderly (not random) fashion in relation to park age and area. Regional influences seem to be more pronounced only in young parks, which are mainly colonized by species from the regional species pool.

Key words: birds; fragmentation; isolation; nestedness; species composition; urban landscapes.

INTRODUCTION

Urban ecosystems have recently drawn the attention of ecologists, because they constitute interesting arenas for studying different patterns and processes of community assembly (Crooks & Soulé 1999; Niemelä 1999). Urban landscapes usually consist of a set of newly created fragments (different sized urban parks) isolated from one another by an urban matrix that may restrain wildlife movements (Soulé *et al.* 1988). Two issues of urban community structure remain little studied: (i) the patterns and processes of community composition (the identities of the species themselves in each urban park, Worthen 1996), and (ii) the relative importance of local and regional factors in the assembly of urban communities (Clergeau *et al.* 1998).

The analysis of patterns in species composition allows one to delve into the processes that shape communities in time and space (Patterson 1990). One measure of the degree of order in the structure of a community is nestedness (Patterson & Atmar 1986). Communities are nested subsets of one another when fragments with low species richness are subsets of fragments that are progressively richer in species composition (Patterson & Atmar 1986). Several mechanisms may bring about a nested pattern, including passive sampling, selective extinction, differential colonization, habitat/area requirements and speciation (Wright *et al.* 1998). One aspect that has received comparatively little consideration, however, is how species composition patterns, particularly nestedness, develop over time (but see Patterson 1990). Temporal patterns may be very important in urban landscapes because urban parks may be of different ages, providing a mosaic of stands with different habitat structures for community development.

Community composition patterns in urban landscapes may be affected by fragment size, age and isolation from the regional species pool

(Vizyová 1986; Soulé *et al.* 1988; Jokimäki *et al.* 1996). Fragments differing in size, age and isolation would yield a nested pattern (Wright *et al.* 1998). Larger parks should favor species establishment because of greater habitat/area availability (Hinsley *et al.* 1995). Isolation from the regional species pool may foster the rapid occupation of parks by highly agile species, while sedentary species may require more time to establish in suitable parks, having more restricted distributions (Patterson 1990; Lomolino 1996). Park age may determine the availability of suitable habitat for colonists owing to an increase in habitat complexity with age (May 1982; Schleck *et al.* 1995). Such temporal increases in the availability of habitats are expected to modify the degree of nestedness, which would increase with park age (species with specialized requirements would occupy progressively older urban parks). As a result, community structure in newly created parks would be particularly regulated by regional factors (e.g. dispersal from the regional species pool), whereas local factors (e.g. habitat complexity, park area) would mainly affect older parks (Cornell & Lawton 1992). This pattern can be detected by the influence of ecological densities on the ability of species to colonize fragments (Tellería & Santos 1999), such that species densities in the regional pool are expected to account for the incidence of species (% of fragments occupied) in younger rather than older fragments (Tellería & Santos 1999).

I analyzed (i) whether community structure followed a nested pattern, and how park age, size and isolation accounted for nestedness; (ii) how the degree of nestedness varied with park age; and (iii) the role of regional and local densities in the incidence (% of parks occupied) of young, mature and old urban parks.

METHODS

Study area and bird surveys

This work was carried out in the city of Madrid (Spain) during the spring of 1998 (May to July). Madrid was selected for three reasons: (i) urban parks have been created there since the eighteenth century, and there is enough documentation to determine their age accurately; (ii) most of the

parks have a heterogeneous habitat structure, allowing me to appraise how bird species track habitat differences; and (iii) the parks have different degrees of isolation in relation to the regional species pool, permitting me to evaluate the role of colonization. Moreover, the influence of local and regional factors can be studied relatively easily in urban settings due to the differences in community composition between urban (local) and rural (regional) areas (Clergeau *et al.* 1998).

Madrid has an extensive network of wooded urban parks. Twenty-five parks were selected for study, ranging from 1 to 100 ha in area, 8–367 years in age and 0.56–6.3 km in distance from the regional species pool (Table 1, Fig. 1). To evaluate community changes along a temporal sequence, urban parks were considered to be a chronosequence of fragments differing in their time of creation (for a similar approach see Shankar Raman *et al.* 1998).

Measurements of park area, along with the dates of creation, were obtained from official records of the Municipality of Madrid (Table 1). A preliminary study was conducted during spring 1997 in order to determine a minimum number of visits to each urban park. Ten randomly selected parks were visited on 15 occasions to record species richness. With cumulative species richness curves (rarefaction method), I concluded that four visits would be necessary to detect nearly 95% of bird species.
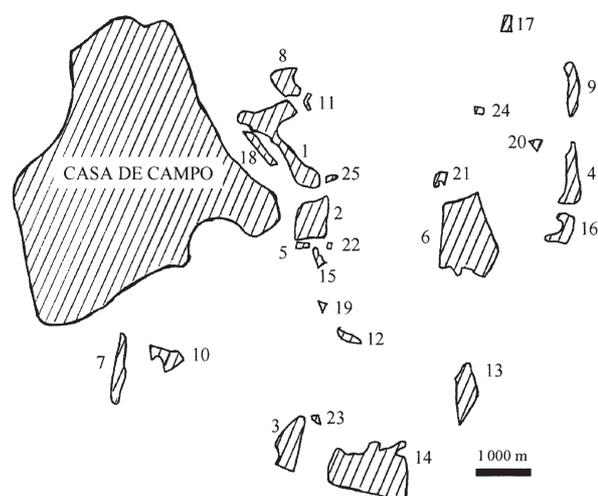

Fig. 1. Schematic representation of the 25 urban parks in the city of Madrid (Spain) selected for the study and Casa de Campo, considered the mainland. Park numbers as in Table 1.

Table 1   Characteristics of urban parks in Madrid selected for this study

Park	Age (years)	Area (ha)	Distance to the regional species pool #1*	#2**	No. species
1 Oeste	99	98.60	0.70	0.46	24
2 Moro	264	18.86	0.72	0.20	24
3 Emp. Austria	38	29.39	4.16	3.60	19
4 Fuente del Berro	103	13.50	5.70	3.56	16
5 Atenas	27	5.73	0.80	0.40	15
6 Retiro	367	118.2	3.46	2.50	15
7 Aluche	25	10.25	1.00	0.58	14
8 Ciudad Universitaria	88	15.51	1.48	1.20	14
9 Breogan	29	2.24	6.30	5.90	13
10 Cerro Almodóvar	15	9.13	1.14	0.96	11
11 Santander	25	3.2	2.76	2.04	11
12 Arganzuelas	69	7.99	3.10	2.86	11
13 TiernoGalván	9	44.25	4.40	4.40	10
14 Pradolongo	17	64.90	4.5	4.44	10
15 Vistillas	18	2.24	1.2	0.98	10
16 Roma	18	13.85	5.40	4.90	10
17 Berlin	31	3.63	5.40	4.42	10
18 Bombillas	8	10.05	0.56	0.40	9
19 Concha Piquer	23	1.24	2.80	2.06	8
20 Eva Perón	22	2.99	5.26	5.02	7
21 Descubrimiento	26	1.82	3.40	3.00	7
22 Emir	27	1.00	1.18	0.38	7
23 Olaf Palme	11	3.66	3.92	3.58	6
24 Picasso	18	1.16	4.28	3.80	6
25 España	27	2.70	1.44	0.41	6
Mean	56.16	19.44	3.00	2.48	11.72
Range	359	117.20	5.74	5.70	18

*Straight-line distance to the regional pool; **distance to the regional pool taking into account the urban matrix only.

However, I conducted 6–7 surveys in each park in 1998 in order to get the best estimates of species richness and their breeding densities. All parks were surveyed in the morning (from 07.00 to 11.00 hours). The number of individuals seen and vocalizing in 100 m long and 50 m wide fixed transects were recorded in parks >2 ha, moving at a steady speed (Järvinen & Väisänen 1975; Seber 1982). Individuals out to 25 m at each side of the observer were recorded separately to individuals beyond the main belt. By this method, I assessed the number of individuals of each species within 0.5 ha, which was later used to calculate breeding densities after averaging the number of birds in each fixed transect throughout all visits. Transects were separated by 50–150 m to ensure their independence. In parks <2 ha, I sampled the whole park, employing a proportional amount of time to that used in line transects (for similar survey procedures see Tellería & Santos 1995).

Bird surveys conducted in 1999 (3–4 visits to each park) yielded similar results to the 1998 breeding season surveys. Species richness within parks was correlated significantly between years ($r = 0.87$, $P < 0.001$). The Sorenson index ($2 \times$ number of species recorded in both years / number of species in 1998 + number of species in 1999) ranged between 0.69 and 0.92, which underscores that species composition within each park remained alike. Thus, the results of the 1998

breeding season can be regarded as representative of the species composition in Madrid urban parks during at least two years.

Two dependent variables were calculated for each species: (i) incidence, the percentage of occupied parks; and (ii) density, the number of individuals in 10 ha. Species were classified according to feeding (ground, bush, tree) and nesting substrates (tree hole, open tree, bush, building) following Cramp (1992) (Table 2). This classification criterion was intended to include the fact that the distribution of some species (particularly tree foragers and hole nesters) is constrained by the availability of specific resources and fragment size (Tellería & Santos 1995). Waterfowl (Anatidae) and swifts (Apodidae) were excluded from analyses, as their distribution is mainly determined by water sources and breeding sites in buildings, respectively. Such resources were not homogeneously distributed over the urban landscape and may have biased the results.

Regional species pool

Casa de Campo, a 1722 ha forest fragment immediately north-west of the city of Madrid, was regarded as the most representative stand of the regional species pool (Fig. 1). It is located 1.3 km from Monte El Pardo and 0.85 km from Dehesa de la Villa, sharing with them structural similarities, particularly in the type of regional vegetation found in the province of Madrid (coniferous forests and *Quercus* sp. stands with a savannah appearance; Santos *et al.* 1985). Casa de Campo has 17 times the area of the largest urban park of the city and harbors all the species recorded in urban parks as well as about 10 more species. The vegetation structure of Casa de Campo differs significantly from that of the urban parks (discriminant function analysis, $F_{6,49} = 14.89$, $P < 0.001$, Wilk's Lambda $= 0.35$) in the following traits: number of tree species, number of trees > 50 cm d.b.h., tree height, and deciduous, coniferous and grass cover (E. Fernández-Juricic, unpublished data).

Casa de Campo was sampled in the same manner and season as the other urban parks, obtaining two estimators of bird abundance based on 67 fixed transects: (i) the density of individuals/10 ha, and (ii) and the percentage of transects occupied per species. Both measures correlated significantly with published estimates of regional abundance in the province of Madrid (Díaz *et al.* 1994) (sample units = bird species, % of occupied regional patches *vs* Casa de Campo density, Pearson correlation, $r = 0.407$, $P < 0.01$; % of occupied regional patches *vs* % of occupied transects in Casa de Campo, $r = 0.433$, $P < 0.001$).

This urban landscape has three structurally and functionally different elements: the urban matrix, wooded streets and urban parks. Wooded streets appear to function as corridors increasing the general connectivity of the landscape (Fernández-Juricic, in press). I then determined the degree of regional isolation on a 1 : 20 000 map by means of two measures: (i) the straight-line distance between each park and Casa de Campo (distance to the regional pool [DRP] 1), and (ii) the distance between each park and Casa de Campo (DRP 2) but considering only the urban matrix irrespective of the other landscape elements (parks and corridors with trees at least 4 m high) that may have enhanced landscape connectivity (Fernández-Juricic, in press). I did not take into account other measures of local isolation (e.g. distance to the nearest park), because they have no effect on community structure in this urban landscape (Fernández-Juricic, in press).

Vegetation structure and park age

Park age was used as an indicator of habitat complexity in urban parks of Madrid. Several vegetation traits were measured in 25 m radius circular plots distributed at 30 m intervals along transects in parks > 2 ha, and randomly in parks < 2 ha. The number of sample units per park was determined as to its size (log transformed). Cover and height variables were visually estimated following Prodon & Lebreton (1981). Vegetation traits included: grass cover, shrub cover, coniferous cover, deciduous cover, number of shrub and tree species, shrub and tree height, and the number of stems < 10, 10–30, 30–50, and > 50 cm d.b.h. I calculated a Shannon–Wiener diversity index with cover variables, number of stems in different categories, and number of shrub and tree species. Park age (log transformed) correlated significantly with cover diversity ($r = 0.46$, $P < 0.02$), stem diversity ($r = 0.47$, $P < 0.02$), shrub height ($r = 0.62$, $P < 0.001$),

Table 2 Bird species found in 25 urban parks in Madrid during spring 1998

Scientific name	Common name	F	N	I
Passer domesticus	House Sparrow	G	T*Bd	25
Turdus merula	Blackbird	G	T	24
Pica pica	Magpie	G	T	22
Serinus serinus	Serin	G	T	22
Columba livia	Rock Dove	G	Bd	21
Sturnus unicolor	Starling	G	T*	19
Carduelis chloris	Greenfinch	G	T	17
Parus ater	Coal Tit	T	T*	15
Columba palumbus	Woodpigeon	G	T	11
Parus caeruleus	Blue Tit	T	T*	10
Sylvia atricapilla	Blackcap	T	T	9
Erithacus rubecula	Robin	G	G	8
Certhia brachydactyla	Treecreeper	T	T*	8
Picus viridis	Green Woodpecker	G	T*	8
Motacilla alba	White Wagtail	G	R	6
Upupa epops	Hoopoe	G	T*	6
Parus major	Great Tit	T	T*	6
Columba oenas	Stock Dove	G	T*	6
Phylloscopus bonelli	Bonelli's Warbler	T	G	5
Troglodytes troglodytes	Wren	B	B	3
Carduelis carduelis	Goldfinch	T	G	3
Aegithalos caudauts	Long-tailed Tit	T	T	2
Passer montanus	Tree Sparrow	G	T*	2
Corvus monedula	Jackdaw	G	T*	2
Myopsitta monachus	Monk Parakeet	T	T	2
Psittacula krameri	Ring-necked Parakeet	G	T*	1
Coccothraustes coccothraustes	Hawfinch	G	T	1
Turdus philomenos	Song Thrush	G	T	1
Dendrocopos major	Great Spotted Woodpecker	T	T*	1
Galerida cristata	Crested Lark	G	G	1
Sylvia melanocephala	Sardinian Warbler	B	B	1
Turdus viscivorus	Mistle Thrush	G	T	1

F, feeding substrate; N, nesting substrate (based on Cramp 1992); I, incidence (no. parks occupied). Feeding substrates: G, ground; B, bush; T, tree. Nesting substrates: T*, tree hole; T, open tree; B, bush; R, rock; Bd, building. Park numbers are as given in Table 1.

and tree height ($r=0.51$, $P<0.01$), but not with shrub and tree species diversity ($r=0.24$, $P<0.25$). Of these habitat variables, only one correlated significantly with park area (shrub height, $r=0.50$, $P<0.01$), the other four showed no correlation at all (cover diversity, $r=0.28$, $P=0.18$; stem diversity, $r=0.31$, $P=0.14$; shrub and tree species diversity, $r=0.34$, $P=0.1$; tree height, $r=0.1$, $P=0.62$).

Statistical analyses

Of the four independent variables, park area and age, and DRP 1 and DRP 2 were significantly correlated (area *vs* age, $r=0.62$, $P<0.001$; DRP 1 *vs* DRP 2, $r=0.95$, $P<0.001$). To determine which of these variables better accounted for species richness, controlling for their covariation (Soulé *et al.* 1988), I employed a multiple regression analysis, with forward-stepwise selection procedures.

To evaluate the degree of nestedness throughout this study, a presence/absence matrix was constructed, with parks (rows) rank ordered in relation to decreasing number of species, and species (columns) rank ordered in relation to decreasing number of sites occupied (Table 2) (Atmar & Patterson 1993). Nestedness was assessed with the Nestedness Temperature Calculator, a program proposed by Atmar and Patterson (1993, 1995) as an improvement on RANDOM0 and RANDOM1 algorithms (Patterson & Atmar 1986). The new metric (T°) allows the measurement of the degree of order/disorder in a matrix by assessing the 'temperature' of the system; the temperature of a perfectly nested matrix being 0° and that of a random matrix, 100°. The Nestedness Calculator corrects many flaws from previous methods, such as the insensitivity to rare events, the unequal emphasis on presence more than on absence, and matrix size dependence (Atmar & Patterson 1995; Kelt 1997). The temperature of the observed systems was contrasted with an expected T° of a matrix of similar rank generated at random (which can be considered to be a null model of the passive sampling model, Wright *et al.* 1998), thereby obtaining a z-score and its probability value; that is, the likelihood of randomly producing a matrix more nested that the observed one.

I evaluated the role of park area, age and isolation upon nestedness first by correlating the ranking order of fragments in the final nested matrix with the order of fragments after rearranging the matrix in relation to area, age and DRP 1 and DRP 2. This procedure has proven useful for indicating the possible mechanisms involved in a nested structure (Kadmon 1995; Honnay *et al.* 1999; Patterson & Atmar 2000). A significant correlation would underscore that bird communities accumulate in a predictable (not random) order owing to the influence of a given factor; for instance, that species accumulate in an orderly fashion in parks increasingly closer to the regional species pool. For those factors that were significantly associated with the nested pattern, I also employed the 'departures' method of Lomolino (1996). With this procedure, matrices can be sorted according to the independent factors, and then the unexpected presence of species (or departures) may be determined (Lomolino 1996). The statistical significance was attained by means of comparing the observed number of departures to that of randomly generated matrices, finally expressed as the proportion of 1000 simulations with departure values less than or equal to that of the ordered matrices (Lomolino 1996). It is noteworthy that the departures procedure allows for testing the causality in nestedness combining two factors at the same time; that is, it assess the effects of one variable after controlling for the effects of the other (Lomolino 1996). Thus, significantly correlated causal factors were analyzed in combination to assess their relative contribution to the nested pattern. The significance of the departures caused by one factor (after controlling the effects of the other) was evaluated with a binomial test (Lomolino 1996).

In assessing the temporal variation in nestedness, I sorted parks into three age classes based on habitat structure: (i) young (<25 years, 10 parks), (ii) mature (between 25 and 75 years, 10 parks), and (iii) old (>75 years, 5 parks). The degree of nestedness was then calculated for each age class. Because the difference in the number of parks may have biased T° estimates (Wright *et al.* 1998), especially with such a low sample size, I used five parks for each category. I assessed the degree of nestedness in 10 matrices of young parks, and 10 matrices of mature parks by means of selecting randomly (in each run) five parks, but excluding those with similar ages to avoid pseudoreplication

within each age class. For example, if the random algorithm selected the following five mature parks for one run Santander (25 years), Descubrimiento (26 years), Berlín (31 years), España (27 years) and Emir (27 years), I omitted the last park and proceeded selecting another park with a different age.

To analyze the influence of regional density of individual species on their incidence in parks with different ages, I assessed the density and incidence of species in each age class: young, mature, and old parks. Using species as sample units, I correlated regional densities (Casa de Campo) against local incidence to evaluate the role of the former on bird species distribution in young, mature, and old parks, respectively (following Tellería & Santos 1999). The relationship between local density and local incidence was analyzed similarly.

Throughout the statistical analyses, a few variables were log transformed ($\log_{10} x + 1$) to meet the statistical requirements of normality and homoscedasticity. Transformed variables included park age, park area, regional density and local density.

RESULTS

The multiple regression model first selected park age, which accounted for 46% of the variability in species richness; and then included park area, which explained another 16% of the variability [species richness = $-1.19 + 2.58 \times$ (log) park age $+ 1.83 \times$ (log) park area; $F_{2,22} = 17.40$; $R^2 = 0.61$; $P < 0.001$]. Neither DRP 1 nor DRP 2 was selected as a significant factor to account for species richness.

Species composition in urban parks showed a high degree of nestedness ($T^\circ_{observed} = 16.26$, $T^\circ_{random} = 64.05$, SD = 4.05, $P < 0.001$, Table 2), highlighting a predictable sequence of species addition. Assuming that species with a high number of occupied fragments have lower extinction probabilities, then species position within the nested matrix could indicate their probabilities of persistence in the landscape (Table 2) (Atmar & Patterson 1995; Patterson & Atmar 2000). Of those species occupying >10 parks ($n = 10$), 80% were ground foragers and 20% were tree foragers; 50% of these species nested in trees, 30% in tree holes, and 20% in tree holes and buildings (species

highly associated with human activities, house sparrows and rock doves). Species occupying 5–9 urban parks ($n = 9$) included 55% ground foragers and 45% tree foragers; 22% nested on the ground, 11% on rocks, 11% on trees and 56% in tree holes. Finally, those species that occupied <5 urban parks ($n = 13$) included 62% ground foragers, 23% tree foragers and 15% shrub foragers; 8% of these nested on the ground, 15% on bushes, 46% on trees and 31% in tree holes.

Park age and area correlated significantly with the order of the nested matrix (Spearman's rank correlation: park area, $r = 0.68$, $P < 0.001$; park age, $r = 0.62$, $P < 0.001$), such that species appeared to accumulate in an orderly fashion in increasingly older and larger urban parks. However, DRP 1 and DRP 2 were not correlated with the nested order of species distribution (DRP 1, $r = 0.17$, $P = 0.41$; DRP 2, $r = 0.25$, $P = 0.23$). Park age and area also accounted for nestedness when analyzed by the departures method (number of departures in the matrix ordered by age = 78, $P < 0.001$; number of departures in the matrix ordered by area = 88, $P < 0.05$). When analyzed simultaneously, and after controlling age effects, park area also accounted for nestedness (binomial test, proportion of departures in the age ordered matrix explained by increasing area = 0.64, z = 2.38, $P < 0.01$).

Regarding the temporal development of nestedness, the temperature of the matrices decreased (increasing the degree of order) with park age. The distribution of species in old parks was nested ($T^\circ_{observed} = 22.27$, $T^\circ_{random} = 39.91$, SD = 8.51, $P < 0.02$). Species also followed a nested distribution in five out of 10 matrices corresponding to mature parks (Table 3), with the mean $T^\circ_{observed} = 23.18 \pm 8.66$. Species distribution in young parks yielded a random pattern in all runs (Table 3), with the mean $T^\circ_{observed} = 33.91 \pm 2.32$.

Regional densities were correlated with local incidence of young parks only (Pearson correlation, $r = 0.48$, $P < 0.05$, Fig. 2). Neither mature nor old park local incidence was correlated with regional densities (mature parks, $r = 0.12$, $P = 0.62$; old parks, $r = 0.04$, $P = 0.86$), so their densities were combined to ascertain their influence on local incidence in young parks, and mature and old parks combined, respectively. Local incidence in young parks was not affected by the combined density of mature and old parks ($r = 0.22$, $P = 0.35$); however,

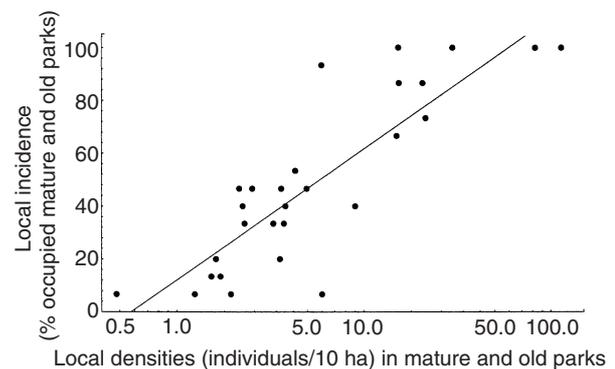**Table 3**   Degree of nestedness of mature (between 25 and 75 years) and young (<25 years) parks

Park age class	Run*	$T°_{observed}$[†]	$T°_{random}$[‡]	SD	P	Distribution of species
Mature	1	15.01	38.99	8.72	0.003	Nested
Mature	2	15.87	38.51	9.03	0.007	Nested
Mature	3	13.80	38.48	9.11	0.003	Nested
Mature	4	41.21	36.50	9.99	0.618	Random
Mature	5	26.33	40.15	10.62	0.097	Random
Mature	6	30.59	36.61	10.26	0.279	Random
Mature	7	25.89	40.59	10.55	0.082	Random
Mature	8	16.20	39.90	9.52	0.006	Nested
Mature	9	20.25	38.75	10.85	0.044	Nested
Mature	10	26.65	41.58	10.04	0.069	Random
Young	1	35.04	35.84	9.78	0.467	Random
Young	2	33.45	35.12	11.38	0.441	Random
Young	3	32.07	37.20	9.77	0.300	Random
Young	4	32.86	36.06	10.71	0.382	Random
Young	5	33.31	34.97	10.16	0.435	Random
Young	6	35.66	37.61	9.96	0.422	Random
Young	7	36.55	38.80	9.27	0.425	Random
Young	8	31.44	36.81	9.32	0.283	Random
Young	9	30.81	36.01	10.67	0.313	Random
Young	10	37.94	36.46	11.42	0.540	Random

*Each run is composed of five out of 10 parks with different ages, selected randomly; [†]T° of the observed matrix (an indicator of the disorder of the community); [‡]T° of the random matrix.
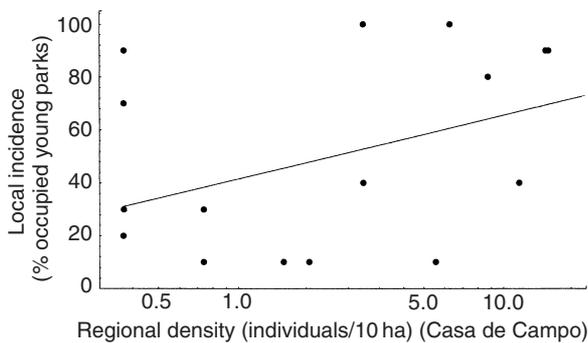
Fig. 2. Relationships between regional densities of species and their local incidence (percent of fragments occupied) in young urban parks (<25 years) in Madrid (Pearson correlation, $r = 0.48$; $P < 0.05$). Each point represents a species.

Fig. 3. Relationship between local densities of species and their local incidence in mature (between 25 and 75 years) and old parks (>75 years) in Madrid (Pearson correlation, $r = 0.63$; $P < 0.001$). Each point represents a species.

this combined density did account for the incidence of mature and old parks ($r = 0.63$, $P < 0.001$, Fig. 3). Although the relationships between local density and local incidence were not completely independent, they served to underscore the regional influences on young parks, and the lack of such influences on mature and old parks.

DISCUSSION

This study supports new evidence for (i) a nested distribution of urban birds explained by park age and size, and (ii) the influence of local rather than regional factors in the distribution of species in mature and old urban parks.

In this fragmented landscape composed of a set of urban parks with different ages, the main factors affecting species richness and community composition are park age and size. Bird species appear to follow the changes in vegetation structure brought about by a temporal increase in habitat complexity (Schleck *et al.* 1995) as well as by the greater area and availability of habitats in large parks (Martin & Lepart 1989; Andrén 1994). Species accumulate in an orderly fashion in relation to park age and area; small and young fragments are subsets of larger and older ones.

The two measures of isolation from the regional species pool do not appear to exert any significant influence on species richness or on community assembly. In a landscape with newly created fragments, it could be expected that colonists from the regional pool would have settled as to the degree of isolation of the fragments (Patterson 1990). However, the lack of isolation effects appears to characterize the composition of many communities (Wright *et al.* 1998 and references therein). Wright *et al.* (1998) suggest that this pattern stems from the low variation of isolation distances in the landscape as well as from the large range of dispersal abilities of the colonizing species. This may be the case with urban parks in Madrid, which are mainly colonized by highly agile species (mostly ground foragers), and whose range of isolation from the regional pool is relatively low (approximately 5.75 km). Moreover, the increase in connectivity brought about by the presence of wooded streets acting as corridors may also reduce the degree of regional isolation (Fernández-Juricic, 2000).

The increase in the degree of nestedness with park age is a finding that is in opposition to other studies in which later colonization and extinction reduced nestedness (Patterson 1990 and references therein). My findings can be interpreted as the result of changes in habitat complexity with park age and the correlation between park age and area. Temporal changes in vegetation structure and the increase in park area would bring about a higher availability of feeding and nesting substrates. Colonizing species may have settled in fragments by occupying positions outside the niche space of residents, because of the greater availability of the new substrates (Blondel *et al.* 1988; Bersier & Meyer 1994; Table 2). For example, as park age

increases, so does the percentage of species with more specific habitat requirements (bush and foliage eaters along with species nesting in tree holes). Therefore, the fulfillment of habitat requirements can be suggested as an important mechanism by which the effects of park age and area support a nested pattern of species composition and allow the settlement of new colonizers (Martin & Lepart 1989; Patterson & Brown 1991; Andrén 1994).

The increase in nestedness with park age is supported by the influence of regional densities on the probability of park occupation. Regional densities only affected species incidence in young parks, where community structure corresponded to a random pattern that may result from the high variability in species occupation (Table 2), lack of foraging specialization of many species and low habitat availability (May 1982; Patterson 1990; Haila *et al.* 1993). Young parks appear to be affected by the continuous colonization of species from the regional pool, whose variability would influence the turnover of local species. Conversely, species incidence in mature and old parks was associated only with their local densities. Species persistence in mature and old parks would be regulated largely by internal processes, modified to some degree by the colonization of migrants from other sources (such as a regional species pool). The high incidence of local rather than regional factors in shaping urban communities has also been found in several other cities throughout North America and Europe (see Clergeau *et al.* 1998 for references).

Taking into account that this urban community is highly shaped by local factors, it can be considered to be a reservoir of native bird species, making it a relevant spot for conservation. Its nested structure, influenced by park age and size, underscores the order of appearance and disappearance of species. It follows that not only larger but also older parks deserve conservation priority, to ensure the persistence of rare species. Previous studies have also emphasized the role of old fragments in the conservation of bird communities (see references in Shankar Raman *et al.* 1998). A conclusion that emerges from this study is that conservation efforts within fragmented landscapes need to include a temporal perspective (particularly in secondary successional habitats) that considers the

role of local and regional factors on the functioning of fragments of different ages.

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