



Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain) Implications for local and regional bird conservation

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Abstract

Management strategies for the regional conservation of forest birds sometimes do not consider explicitly their applicability to areas with different degrees of urbanization. I studied the spatial and temporal distribution of forest passerines in wooded parks in the city of Madrid during two consecutive breeding seasons to identify factors relevant to local conservation, and compared these results to previous studies in rural-fragmented forests in central Spain to derive recommendations for local and regional management guidelines. Five independent factors were considered: park size, isolation, density of potential corridors, vegetation structure, and pedestrian rate as an indicator of human disturbance within parks. Species richness and species temporal persistence was positively influenced by park size, shrub and tree cover, number of shrub and tree species, number of thick tree trunks, and negatively by the number of thin tree trunks. Species turnover was negatively affected by park size, such that the temporal persistence of species was enhanced in large parks. The pattern of guild assembly was not random but nested (parks with few species were subsets of progressively richer parks); the accumulation of species being affected mainly by park size and human disturbance, and to a lesser degree by isolation and vegetation structure. With regard to the spatial distribution of individual species, park size and vegetation structure positively influenced five species each, whereas isolation and human disturbance negatively influenced two and one species, respectively. Fragment size and habitat structure were the most relevant factors affecting species richness of forest specialists in both rural and urban fragmented landscapes; therefore, regional conservation strategies to protect these species may also be applicable to urbanized areas in central Spain. However, some specific recommendations should be considered in urban and suburban landscapes: (1) habitat quality ought to be enhanced to meet specific habitat requirements, particularly in large parks; (2) the mechanisms and rates of dispersal of forest birds through the urban matrix should be further studied to improve the movements between regional and local populations; and (3) species-specific variations in tolerance to pedestrians and thresholds levels of human visitation within parks should be determined to minimize human disturbance effects.

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1. Introduction

Forest fragmentation and habitat attrition have been identified as key factors involved in the decline of several bird species (McGarigal and McComb, 1995; Trzcinski et al., 1999; Villard et al., 1999; Owens

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and Bennett, 2000). Forest passerines are particularly sensitive to fragmentation conditions, probably due to their high habitat specificity (Canaday, 1996; Tellería and Santos, 1997; Ford et al., 2001) and low vagility (Belisle et al., 2001; Sekercioglu et al., 2002). The study of the factors underlying the distribution of forest birds in natural landscapes has been of paramount importance in deriving general guidelines for large-scale conservation networks (e.g., state, provincial, national levels). However, relatively little is known as to whether or not these management recommendations can be also applicable to areas within the regional network that have considerable urban, suburban, and exurban development (Miller and Hobbs, 2002). This is an area of concern in conservation biology due to increasing rates of urban sprawl, which has contributed to further loss and fragmentation of forest habitats (Fernández-Juricic and Jokimäki, 2001; Marzluff, 2001; Marzluff and Ewing, 2001).

The spatially realistic theory of metapopulation ecology combines classic metapopulation theory with the dynamic theory of island biogeography (Hanski, 1999, 2001), and provides a comprehensive framework to understanding the local responses of forest passerines to urbanization. Urban populations can be considered as sets of semi-independent populations in an urban matrix connected by dispersal to themselves and to regional populations. If urban populations decline or go extinct from time to time, it is important to know whether individuals from regional populations would find the necessary environmental conditions to “rescue” urban populations. For instance, in central Spain, widespread agricultural activities have extensively fragmented forest habitats (reviewed in Santos and Tellería, 1998). Suitable habitat for forest birds is now restricted to scattered and small forest fragments of mainly original holm oaks (*Quercus ilex*) and reforested pines (*Pinus* sp.). Recent studies have shown that forest passerines are positively affected, among other things, by large fragment size, decreasing isolation between fragments, and an increase in the quality and quantity of specific vegetation substrates (Tellería and Santos, 1997, 1999; Díaz et al., 1998; Santos et al., 2002). Thus, it is necessary to determine the factors that affect the spatial and temporal distribution of forest passerines in urban fragmented landscapes. If there are differences in how fragmentation affects these species in urban habitats, new manage-

ment recommendations ought to be incorporated into large-scale conservation planning to enhance their representation in urban and suburban habitats, and as a result increase the persistence of metapopulations over regional scales.

Some processes have been often reported to affect birds in urban environments (see Bowman and Marzluff, 2001; Fernández-Juricic and Jokimäki, 2001; Marzluff, 2001; Marzluff and Ewing, 2001): habitat loss (reductions in the type and amount of suitable habitat), changes in the configuration of suitable habitats (decrease in fragment size and increase in isolation), lower connectivity (increase in the amount of urban matrix and reduction in the quality of wooded streets as potential corridors between fragments), and secondary fragmentation (decrease in habitat quality within fragments, sensu Soulé et al., 1992) brought about by human disturbance (e.g., visitors to wooded parks). All these processes (independently or in combination) are expected to reduce species richness and species persistence, and decrease the probabilities of fragment occupation by individual species. Moreover, the assembly of the guild of forest passerines could be affected by some of these processes through higher rates of extinction and lower rates of colonization per fragment, which would result in a nested distribution pattern (species present in low-species richness fragments would be subsets of those present in species-richer ones; Atmar and Patterson, 1993).

Previous studies on the effects of urbanization on breeding forest specialists have examined species richness or the probabilities of fragment occupation of individual species (e.g., Jokimäki, 1999; Natuhara & Imai, 1999; Mortberg, 2001). However, I took a more comprehensive approach by considering the effects of primary and secondary fragmentation on both spatial and temporal responses of a guild of forest passerines at different organization scales. Specifically, I assessed the role of wooded park size, isolation, wooded street density, vegetation structure, and human disturbance on (1) species richness, persistence, and turnover, (2) the assembly of the guild at the community level (whether the accumulation of species followed a nested or random pattern), and (3) the responses of individual species. Furthermore, the location of the study area (Madrid) allowed me to compare the relative importance of these factors

with two previous studies on similar species in rural-fragmented landscapes in central Spain (Díaz et al., 1998; Santos et al., 2002). This approach will help identify factors relevant to the conservation of forest specialists at local and regional scales.

2. Methods

2.1. Study area

The study was conducted in the city of Madrid (about 18 km × 20 km), which has an extensive network of wooded parks that harbor many bird species (Fernández-Juricic, 2000a). Twenty-two parks (Fig. 1) were selected as representative of wooded areas in the city with high tree cover, composed of a mix of deciduous, coniferous and holm oak trees, introduced and native shrub species, and areas of watered grass. These parks included >80% of the green areas in the city of Madrid.

2.2. Breeding surveys

I recorded the presence of forest passerines and the number of individuals of each species seen in 100 m long and 50 m wide transects in parks >2 ha in size (Järvinen and Väisänen, 1977). I conducted four to five surveys within each wooded park every year during the springs of 1997 and 1998 (April to June). All parks were surveyed on weekday mornings (from 07:00 to 10:00). Transects were separated by 50–150 m, and the same transects were used for each of the four to five visits. The number of transects per wooded park was established as to a logarithmic scale of the size of each park. In parks <2 ha, I sampled the whole park employing a proportional amount of time to that used in line transects (see more details of the survey techniques in Fernández-Juricic, 2000a,b).

Previous studies conducted in Madrid have analysed various aspects of the spatial distribution of all breeding species; however, the present study was focused only on forest species. I studied small passerines that

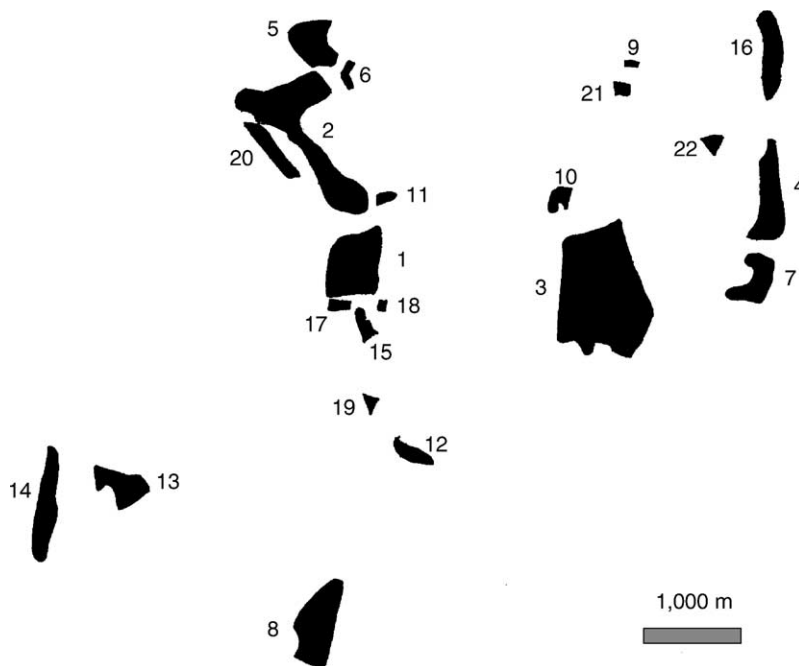


Fig. 1. Schematic representation of the 22 wooded parks in the city of Madrid (Spain) selected for this study. (1) Moro, (2) Oeste, (3) Retiro, (4) Fuente Berro, (5) Ciudad Universitaria, (6) Santander, (7) Roma, (8) Austria, (9) Joan Miró, (10) Descubrimiento, (11) España, (12) Arganzuelas, (13) Cerro Almodovar, (14) Aluche, (15) Vistillas, (16) Breogan, (17) Atenas, (18) Emir, (19) Concha Piquer, (20) Bombillas, (21) Picasso, and (22) Eva Perón.

depend on forests during the breeding season either for feeding or nesting (based on Cramp, 1992; Tellería et al., 1999), setting aside species that fed in wooded parks without forest cover (such as Blackbird *Turdus merula*, Magpie *Pica pica*, etc.). I only took into account individuals displaying continuous vocal and nesting behaviors and species seen on at least two visits in order to exclude occasional occurrences that may have not been related to breeding in wooded parks. The species included in the analyses were: Bonelli's Warbler (*Phylloscopus bonelli*, PBO), Coal Tit (*Parus ater*, PAT), Blue Tit (*Parus caeruleus*, PCA), Great Tit (*Parus major*, PMA), Long-tailed Tit (*Aegithalos caudatus*, ACA), Treecreeper (*Certhia brachydactyla*, CBR), Blackcap (*Sylvia atricapilla*, SAT), Orphean Warbler (*Sylvia hortensis*), Sardinian Warbler (*Sylvia melanocephala*), Robin (*Erithacus rubecula*, ERU), Wren (*Troglodytes troglodytes*), Great Spotted Woodpecker (*Dendrocopos major*), and Song Trush (*Turdus philomenos*).

2.3. Independent factors

Five independent factors were considered: park size, isolation, density of wooded streets, vegetation structure, and human disturbance. I did not consider other variables related to the degree of urbanization, as they influenced mostly species breeding in the urban matrix (e.g., House Sparrows *Passer domesticus*, Rock Doves *Columba livia*, Swallows) but not forest specialists (Fernández-Juricic, 2000c). Park size was taken from the last edition of the official catalogue of the Municipality of Madrid. Isolation was measured on a 1:10,000 scale map as the following distances (km) between parks: distance to the nearest park (D_1), distance to the nearest park harboring at least n_{+1} species (D_2), and distance to the "mainland forest" (Casa de Campo) (D_3), a 1722 ha forest stand located at the NW of Madrid. This forest fragment is considered representative of the regional pool of species in the province of Madrid (Fernández-Juricic, 2000a), and thus a possible source of colonizing species. These isolation measures proved relevant in previous studies in the same landscape (Fernández-Juricic, 2000a, 2002a). I also assessed the density of wooded streets, which may function as corridors (Fernández-Juricic, 2000c), by randomly choosing three 250 m radius sampling plots around each park and counting the

number of wooded streets on a 1:10,000 scale map. Samples were then averaged for each park.

Vegetation structure 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 (see also Fernández-Juricic, 2000a). The number of sample units per park was determined by its size (log-transformed). Cover and height variables were visually estimated following Prodon and Lebreton (1981). All cover variables corresponded to different vegetation substrates. The values for each vegetation trait measured at each transect (Table 1) were averaged for the whole park.

In determining human disturbance, I recorded the number of people per unit area and per unit time in 1997 and 1998, following Fernández-Juricic (2000b). Within each transect (0.5 ha), the number of pedestrians observed walking and sitting in 3 min periods were recorded with one to three observers at 08:00–09:00 and 13:00–14:00. Sampling was repeated three times at each park, at 20-day intervals, with final values converted into rates of pedestrians per minute per hectare. I have not considered the effects of cats and dogs, as previous studies in this landscape have found them not to affect significantly different population parameters (Fernández-Juricic and Tellería, 1999; Fernández-Juricic et al., 2003).

2.4. Statistical analyses

Throughout the statistical analyses certain variables were log-transformed ($\log_{10} x_{+1}$) to meet normality requirements: shrub cover, coniferous cover, park size, wooded street density, and pedestrian rate.

To reduce the number of vegetation variables on the averaged habitat structure data per park, I performed a principal component analysis on the correlation matrix. Only those factors with eigenvalues >1 were selected (Kaiser criterion), and factor loadings were rotated with a varimax raw transformation.

Pearson correlation was used to assess the relationships between species richness in 1997 and 1998, and between independent variables.

A decrease in the availability of breeding and foraging substrates has been associated with reduction in the area of forest fragments (Martin et al., 1995). However, it is not clear if that is the case in this urbanized landscape. I then analyzed the association between

Table 1

Factor loadings of the individual variables obtained by a principal components analysis (PCA) on the vegetation structure of 22 wooded parks in the city of Madrid, Spain

	PC1	PC2	PC3	PC4	PC5
GRASSC	−0.050	−0.026	−0.899*	0.078	−0.171
SHRUBC	0.798*	−0.071	−0.148	0.062	0.186
SPSHRUB	0.762*	0.182	0.116	−0.515	−0.039
HESHRUB	0.624	0.041	−0.498	0.070	0.461
CONIFTC	−0.048	−0.932*	−0.084	−0.115	0.070
DECIDTC	0.286	0.672	0.161	−0.375	0.471
OAKTC	0.776*	0.099	0.025	0.127	0.107
SPTREE	0.721*	0.086	0.416	0.068	−0.080
TREEHE	0.170	−0.099	0.097	0.088	0.897*
SDBH <10	−0.046	0.721*	−0.246	−0.179	−0.538
SDBH 10–30	−0.056	0.057	0.218	−0.818*	−0.060
SDBH 30–50	0.329	0.038	0.346	0.618	0.049
SDBH >50	0.716*	0.006	0.067	0.403	0.248
Eigen values	4.007	2.337	1.567	1.342	1.061
Explained variance	30.819	48.793	60.847	71.170	79.329

Abbreviations: GRASSC, grass cover; SHRUBC, shrub cover; SPSHRUB, number of shrub species; HESHRUB, shrub height; CONIFTC, coniferous cover; DECIDTC, deciduous cover; OAKTC, holm oak cover; SPTREE, number of tree species; TREEHE, tree height; SDBH <10 (number of stems <10 cm d.b.h.); SDBH 10–30 (number of stems 10–30 cm d.b.h.); SDBH 30–50 (number of stems 30–50 cm d.b.h.); and SDBH >50 (number of stems >50 cm d.b.h.). *, significant $P < 0.05$.

park size and vegetation structure with a three-tiered approach that considered the mean number of substrates, their distribution, and the quality and quantity of vegetation structure. First, I assessed the influence of park size on the mean number of vegetation substrates (grass, shrub, coniferous, deciduous, holm oak) per park with a linear regression, expecting larger parks to have more substrates. Second, I analyzed whether the presence/absence of vegetation substrates across the 22 wooded parks considered followed a random or nested distribution with the Nestedness Calculator software (see below for details). I later determined with a Spearman rank correlation whether this distribution was associated with park size (see below), the expectation being that vegetation structure would be nested in relation to the area of the park. Third, I determined whether the factors derived from the principal component analysis on vegetation structure, which reflected both habitat quality and quantity, would be associated with park size with Pearson correlations, with the expectation of positive relationships.

I evaluated the relationships between species richness and the five independent factors with multiple stepwise regression models (forward selection procedures) to characterize the spatial distribution of forest species within each breeding season. For the temporal

distribution, I assessed similar relationships with the same statistical analysis but considered two dependent variables. First, I calculated species turnover rate per park as the total number of local extinction and colonization events/total number of species observed in both years (Clark and Rosenzweig, 1994). Second, I calculated an indicator of species temporal persistence per park: the number of species that were present in a given park over the two consecutive breeding seasons.

Community assembly was studied in relation to the pattern of species accumulation (random or nested). To find out whether nestedness stemmed from an artifact of passive sampling (Fischer and Lindenmayer, 2002), I first evaluated the relationship between the mean number of species per transect (0.5 ha) and park size (following Herkert, 1994), including wooded parks with at least 3 ha so as to have enough transects. A non-significant relationship (slope = 0) would support the random sampling hypothesis (Haila et al., 1993), whereas a slope >0 would suggest a non-random pattern of species accumulation. I then proceeded to assess the degree of nestedness with the Nestedness Calculator (Atmar and Patterson, 1993, 1995), which compares the observed distribution of species to that expected under maximum nestedness and yields the “temperature” of the matrix. A

perfectly nested assemblage would have 0° , whereas one that is random would have 100° (see calculation details in Atmar and Patterson, 1995; Patterson and Atmar, 2000). I set up presence/absence matrices that included the species present in each park within each breeding season (Appendices A and B), and those species recorded in each park in both breeding seasons, as an indicator of species persistence.

I evaluated the influence of park size, isolation, wooded street density, vegetation structure, and human disturbance on the degree of nestedness of the different matrices by correlating, with a Spearman rank correlation, the ranking order of parks in the observed matrix (arranged to maximize nestedness, Patterson and Atmar, 2000) with the order of parks after re-arranging the matrix in relation to the aforementioned factors. A significant correlation would indicate that species are packed in a predictable order owing to the influence of a given factor (Patterson and Atmar, 2000).

At the species level, I determined the effects of park size, isolation, wooded street density, vegetation structure, and human disturbance on the occurrence of individual species within parks by means of multiple stepwise logistic regressions (Hosmer and Lemeshow, 1989). Species occurring in less than five parks were not included in the analysis owing to low sample size (Hinsley et al., 1995a). Minimum area requirements for those species influenced by park size were estimated by the following two criteria. For species for which the probability of occupation was fairly constant above a certain threshold area, minimum area requirements were based on the change in the slope of the relationship (see Fahrig, 2002). For species for which the probability of occupation did not reach a plateau, minimum area requirements were estimated as the area at which the probability of occupation was $>50\%$.

One potential problem with using linear and logistic regression models to predict the distribution of species is that the relevant factors may vary between breeding seasons. To evaluate the robustness of the models, I calculated model consistency for overall species richness and for the occurrence of individual species as [(number of shared factors in the two models)/(total number of different factors in the two models)] $\times 100$ (following Gutzwiller and Barrow, 2001). Shared factors were those present in models in 1997 and 1998, with the same sign for the regression coefficient.

3. Results

3.1. Number of species

Eleven forest passerines were recorded in 1997, and 12 in 1998 (Appendices A and B). Only three species in 1997 (*P. ater*, *E. rubecula* and *S. atricapilla*), and two in 1998 (*P. ater*, *P. caeruleus*) were found in at least 50% of wooded parks. Species richness was highly correlated between 1997 and 1998 (Pearson correlation, $r = 0.85$, $P < 0.001$).

3.2. Vegetation structure

Five factors were selected from the principal component analysis accounting for 79% of the variability in vegetation structure (Table 1). The first factor (PC1) was positively correlated with shrub cover, number of shrub species, holm oak cover, number of tree species, and number of stems >50 cm d.b.h., reflecting the diversity of shrub and tree species, and the availability of shrubs, holm oaks, and thick tree trunks. The second factor (PC2) was positively correlated with number of stems <10 cm d.b.h. and negatively with coniferous cover, distinguishing between parks with thin tree trunks and those with high availability of coniferous trees. The third factor (PC3) was negatively correlated with grass cover, and the fourth factor (PC4) was also negatively correlated with the number of medium-sized tree trunks (number of stems 10–30 cm d.b.h.). Finally, the fifth factor (PC5) correlated positively with tree height.

3.3. Relationships between independent factors

The qualitative and quantitative variation in vegetation structure was not associated with park size. The mean number of vegetation substrates per park was not significantly influenced by park size (linear regression, $F_{1,20} = 1.32$, $P = 0.263$, $R^2 = 0.06$). The distribution of different vegetation substrates across the 22 wooded parks was nested ($T^\circ = 8.02$, random $T^\circ = 40.59$, S.D. = 10.16, $P < 0.001$); that is, parks with n substrates were subsets of parks with $n+1$ substrates. However, this nested distribution of vegetation substrates was not associated with park size (Spearman correlation, $R = 0.12$, $P = 0.586$). Finally, park size was not associated with any of the five factors

accounting for quality and quantity of vegetation structure (PC1, $r = 0.27$, $P = 0.227$; PC2, $r = 0.12$, $P = 0.582$; PC3, $r = -0.38$, $P = 0.08$; PC4, $r = 0.17$, $P = 0.441$; PC5, $r = 0.23$, $P = 0.311$).

The relationships between park size and isolation ($D1$, $r = -0.22$, $P = 0.326$; $D2$, $r = 0.33$, $P = 0.128$; $D3$, $r = -0.10$, $P = 0.646$), and park size and human disturbance (pedestrian rate 1997, $r = -0.41$, $P = 0.067$; pedestrian rate 1998, $r = -0.38$, $P = 0.081$) were not significant, and neither were the relationships between isolation factors (r varied between 0.17 and 0.41, $P > 0.05$). Wooded street density was not correlated with any of the other independent factors (r varied between -0.24 and 0.21 , $P > 0.05$). However, pedestrian rates were highly correlated between years ($r = 0.86$ and $P < 0.001$).

3.4. Spatial and temporal distribution of species

In 1997, species richness was positively related to park size and PC1, and negatively to PC2 ($F_{3,18} = 25.08$, $P < 0.001$, $R^2 = 0.81$, Table 2). In 1998, species richness was affected by the same factors ($F_{3,18} = 31.37$, $P < 0.001$, $R^2 = 0.84$, Table 2); thus, model consistency between years was 100%. Consequently, in each breeding season species occupied large parks with high diversity of shrubs and trees, and high availability of coniferous and holm oak substrates, and thick tree trunks.

As for the temporal distribution, species turnover was only accounted for by park size ($F_{1,20} =$

10.5 , $P < 0.01$, $R^2 = 0.34$, $SRTO = (0.87 - 0.13) \times \log$ park size), such that the relative number of extinction and colonization events was higher in small wooded parks. The number of species that were present in a given park in two consecutive breeding seasons was influenced positively by park size, PC1 and PC5, and negatively by PC2 ($F_{4,17} = 29.24$, $P < 0.001$, $R^2 = 0.87$, Table 2). Hence, park size as well as the diversity and availability of vegetation favored the persistence of forest species in the city of Madrid.

3.5. Community assembly

Species richness per unit area (0.5 ha) increased with park size in both years, with the slopes of both relationships significantly >0 (Fig. 2). The pattern of species occurrence was not random but nested: parks with few species were subsets of progressively richer parks. This pattern was significant in both years (1997, $T^\circ = 12.36$, random $T^\circ = 51.8$, S.D. = 7.11, $P < 0.001$; 1998, $T^\circ = 10.82$, random $T^\circ = 50.69$, S.D. = 7.5, $P < 0.001$). Moreover, the distribution of species occupying a given park in two consecutive breeding seasons was also significantly nested ($T^\circ = 10.82$, random $T^\circ = 50.69$, S.D. = 7.5 and $P < 0.001$).

The ordered accumulation of species was affected mainly by park size and human disturbance, and to a lesser degree by vegetation structure and isolation. Wooded street density did not affect significantly this pattern ($P > 0.05$). In 1997, the order of species distribution was positively correlated with park size ($R = 0.70$, $P < 0.001$), and negatively with distance to the nearest park ($R = -0.46$, $P < 0.05$) and human disturbance ($R = -0.55$, $P < 0.01$). In 1998, besides park size ($R = 0.72$, $P < 0.001$) and human disturbance ($R = -0.55$, $P < 0.01$), PC1 affected positively the order of species distribution ($R = 0.46$, $P < 0.05$). Finally, park size ($R = 0.82$, $P < 0.001$) and human disturbance ($R = -0.75$, $P < 0.001$) affected the distribution of species occupying a given park in two consecutive breeding seasons. Consequently, species tended to accumulate orderly in wooded parks with large size, low human disturbance, low degree of isolation, and high diversity shrub and tree species, and high availability of holm oaks and thick tree trunks.

Table 2

Factors affecting species richness of forest passerines in 1997 (SR 1997) and 1998 (SR 1998), and total number of species that occupied wooded parks in both breeding seasons (SR 1997–1998) in Madrid, Spain

	SR 1997	SR 1998	SR 1997–1998
Model intercept	0.27	0.32	-0.29
log park size	1.56 (57.1%)	1.52 (51.2%)	1.31 (54.8%)
PC1	1.07 (14.9%)	1.12 (17.8%)	1.15 (18.2%)
PC2	-0.82 (8.6%)	-1.14 (15%)	-0.80 (9.7%)
PC5			0.56 (4.4%)

Results are from stepwise multiple regression analyses. Shown are the coefficients and the amount of variance explained (in parentheses) by each factor.

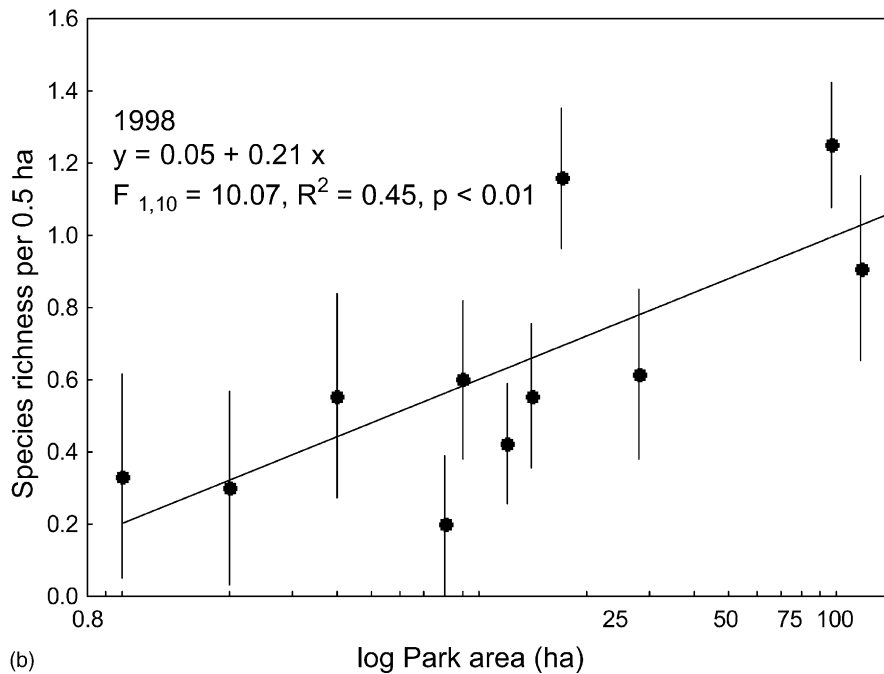
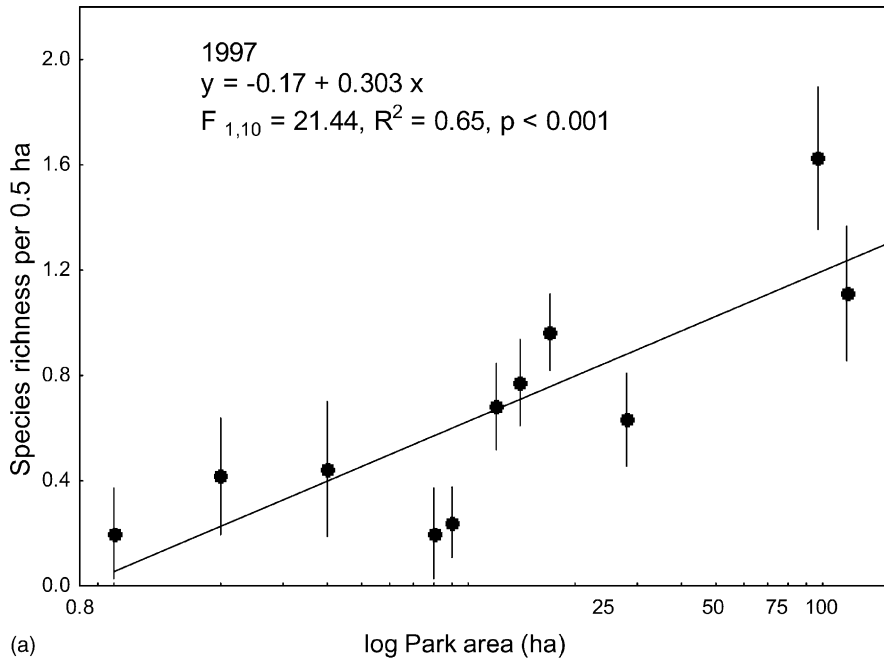


Fig. 2. Relationship between park size and the mean number of forest bird species found in 0.5 ha per park in the city of Madrid (Spain) during the 1997 (a) and 1998 (b) breeding seasons.

Table 3

Logistic regression models for those species that occupied at least five wooded parks in the city of Madrid, Spain

Species	χ^2	d.f.	<i>P</i>	% CC	Const	Area	<i>D1</i>	<i>D2</i>	<i>F1</i>	<i>F2</i>	<i>F3</i>	<i>F5</i>	HD
CBR 97	22.3	1	***	91	−52.5	19.6							
CBR 98	10.6	1	**	73	−4.1	1.8							
PMA 97	8.8	1	**	91	−4.2	1.5							
PMA 98	9.1	2	*	91	−2.8	1.2	−3.9						
PAT 97	3.9	1	*	77	2.9								−0.9
PAT 98	13.7	3	**	86	8.3				4.9	−3.2			−2.7
SAT 98	10.6	2	**	86	−0.4				1.9	−1.1			
PCA 97	14.1	2	***	77	−4.3	2.6		−1.7					
PCA 98	22.4	3	***	86	−8.6	4.2					−2.3	5.5	
ACA 97	22.3	1	***	91	−52.4	19.6							
ACA 98	10.6	1	**	73	−4.1	1.8							
PBO 97	15.9	2	***	82	−12.6	4.5					5.6		
PBO 98	7.1	2	*	91	−3.5	0.8				−1.6			
ERU 97	6.2	1	*	73	0.1				1.4				

The table depicts the factors and their *b*-coefficients, the χ^2 statistic, its probability, and the percentage of wooded parks correctly classified as occupied or unoccupied (% CC). Significance levels, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Abbreviations: *Phylloscopus bonelli*, PBO; *Parus ater*, PAT; *Parus caeruleus*, PCA; *Parus major*, PMA; *Aegithalos caudatus*, ACA; *Certhia brachydactyla*, CBR; *Sylvia atricapilla*, SAT; and *Erithacus rubecula*, ERU; and HD, human disturbance (pedestrian rate/min per 10 ha).

3.6. Individual species

Fourteen models corresponding to eight species were obtained (Table 3). Park size positively influenced the probabilities of occupation of five species, whose area requirements in the city of Madrid were estimated as (Fig. 3): *C. brachydactyla*, 30–40 ha; *P. major*, 20–50 ha; *P. caeruleus*, 30–45 ha; *A. caudatus*, 40–90 ha; and *P. bonelli*, 40–90 ha. Isolation (*D1* and *D2*) decreased the occurrence of two species (*P. major* and *P. caeruleus*). PC1 affected two species (*P. ater* and *S. atricapilla*), PC2, three species (*P. ater*, *S. atricapilla* and *P. bonelli*), PC3, two species (*P. caeruleus* and *P. bonelli*), and PC5, one species (*P. caeruleus*). The negative influence of pedestrian rate was limited to only one species (*P. ater*). Wooded street density did not affect any species. Mean model consistency was 56.9% ($n = 6$ species), with values ranging from 25 to 100%. The two variables that were found to be consistent between years for some species were: park size and pedestrian rate (Table 3).

4. Discussion

Several factors influenced the spatial and temporal distribution of forest specialists at the community and

individual species levels in wooded parks in the city of Madrid. The main results were that: (a) park size and the availability and diversity of shrub and tree substrates were the most important factors increasing the suitability of wooded parks for forest passerines and their probabilities of persistence between breeding seasons, (b) the nested spatial and temporal assembly of the guild was positively affected by park size and vegetation structure, and negatively by the distance between parks and the degree of human disturbance within parks, and (c) responses to park size, habitat structure, isolation and human disturbance were species-specific and varied between breeding seasons.

Models were highly consistent in the factors affecting species richness and explained a great deal of the variability (81–87%). A recent study suggested that such consistent factors may indicate crucial needs to which species would generally respond (Gutzwiller and Barrow, 2001), increasing the confidence of managers to incorporate them into management strategies. The degree of consistency was substantially reduced when considering the occurrence of individual species. This may be related to the specific responses of individual species to unmeasured local conditions, changes in the availability of breeding territories, and delayed responses to environmental conditions due to site fidelity, intra- or inter-specific competition, etc.

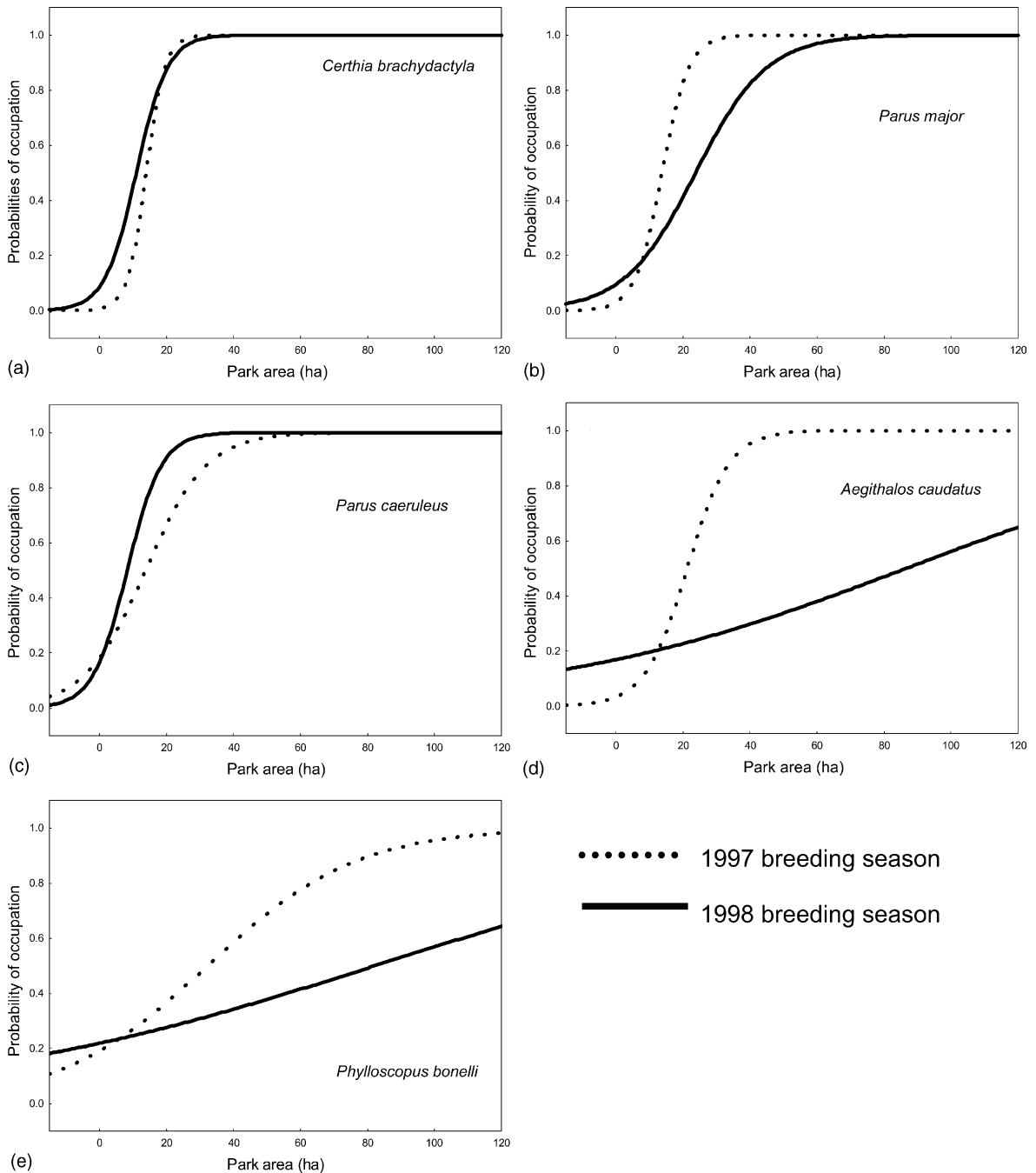


Fig. 3. Probabilities of occupation of wooded parks in Madrid of five forest species in two consecutive breeding seasons: (a) *C. brachydactyla*, (b) *P. major*, (c) *P. caeruleus*, (d) *A. caudatus*, and (e) *P. bonelli*. Park area was transformed in the analyses, but is shown here without transformation for the sake of clarity.

(Newton, 1998). Nevertheless, certain patterns are worth mentioning.

Contrary to previous suggestions (e.g., Patterson and Brown, 1991), the nested distribution of vegetation substrates was not affected by the size of fragments; likely because the high degree of human manipulation for recreational purposes makes them less variable in terms of vegetation structure. Hence, the influence of park size is independent of habitat structure and floristic composition in this landscape. Moreover, the increase in the number of forest birds in large parks appears not to be determined by the higher probabilities of randomly encountering individuals in large habitat areas (random sample hypothesis). The significant increase in species richness per unit area in large parks (Fig. 2) and the role of park size in the spatial and temporal nested assembly of this guild suggest that forest birds would colonize wooded parks that fulfill certain size requirements (between 20 and 90 ha depending on the species). Edge effects in urbanized landscapes are expected to reduce the availability of interior habitats in increasingly small wooded parks due to the influence of the urban matrix (Fernández-Juricic, 2001). In this landscape, edge effects include both an increase in noise levels and a reduction of available habitat due to the physical presence of people (Fernández-Juricic, 2001). This could have reduced the abundance of some species, and hence diminished their probabilities of colonization and increased their chances of local extinction in small parks (Fahrig, 2002).

The effects of park size on temporal distribution patterns agree with the predictions of metapopulation theory (Hanski, 1999), such that small parks favored species turnover, whereas large parks enhanced species persistence. This pattern may have to do with a greater effect of environmental fluctuations in medium to small-sized parks because population sizes are smaller (Newton, 1998). Similar temporal patterns have been found in rural fragmented landscapes (Hinsley et al., 1995b; Bellamy et al., 1996; Mason, 2001).

Vegetation structure, isolation, and human disturbance modified the spatial and temporal distribution of forest passerines as well, but to a lesser extent. Species selected parks with a high amount and diversity of shrubs and trees, probably to ensure the availability of food, nest, and protective cover during the breeding season. This habitat selection pattern may be tied

to the requirements of individual species (Freemark and Merriam, 1986; Andrén, 1994). For instance, hole nesters, such as *P. major*, were particularly influenced by the number of thick and tall coniferous trees, which provide substrates for feeding and nesting; whereas *E. rubecula* was positively influenced by the diversity and cover of shrubs, a substrate it uses for protective cover and nesting.

Isolation and human disturbance reduced the overall suitability of wooded parks and the chances of park occupation. Recent evidence reveals that movements of forest species are constrained when traveling through deforested areas and fragmented landscapes (e.g., Belisle et al., 2001). Colonization could then be limited by the distance separating parks surrounded by a low-quality urban matrix. Crossing this type of matrix would increase the risks of dispersal for species with low perceptual ranges and reluctant to move through an unsuitable matrix, such as habitat specialists (Opdam, 1991; Keitt et al., 1997; Fernández-Juricic, 2000c). The negative effects of human disturbance within wooded parks could be explained by the relationship between the frequency of human visitation (number of pedestrian per unit time per unit area) and the frequency of resource use (number of times per unit time per unit area birds make use of foraging, breeding, or roosting resources; Fernández-Juricic, 2000b, 2002b; Fernández-Juricic et al., 2003). Correlational and experimental evidence corroborates that high visitation levels within parks decrease the temporal and spatial availability of foraging and breeding resources throughout the breeding season (Fernández-Juricic et al., 2003). As human visitation becomes widespread in time and space within parks, the probabilities of extinction would increase and the chances of colonization would decrease (Fernández-Juricic, 2002b).

4.1. Conservation implications

The conservation of forest passerines in urbanized landscapes is important on two grounds. First, it would enhance the aesthetic value of urban parks and promote public awareness about wildlife (Savard et al., 2000). Second, if populations can be established in urban and suburban areas, the chances of species extinction at the regional level would decrease. The reason is because further reductions in the quality of regional populations due to fragmentation could eventually

Table 4

Factors affecting species richness (SR) of forest passerines in fragmented landscapes in central Spain

Factor ^a	SR holm oak forests	SR coniferous forests	SR mixed forests
(+) Fragment size	•	•	•
(+) Tree cover	•		•
(+) Shrub cover	•		•
(–) Tree height	•		
(–) Bare ground cover	•		
(–) Distance to the nearest wooded fragment	•	•	
(+) Number of shrub species			•
(+) Number of tree species			•
(–) Number of stems <10 cm d.b.h.			•
(+) Number of stems >50 cm d.b.h.			•

The comparison includes holm oak forests (Santos et al., 2002), coniferous forests (Díaz et al., 1998), and mixed forests (this study). Included are the results of models that studied similar forest species.

^a Shown in parentheses is the sign of the relationship. This summary does not include the influence of regional factors, such as the geographic location (Northern or Southern Plateau) of the forests.

turn some urban populations inhabiting high quality habitats (e.g., large forests tracts) into population sources (Fernández-Juricic and Tellería, 1999).

Can management recommendations for the protection of forest passerines in rural-fragmented habitats in central Spain be applied to this urban landscape? In comparison with two previous studies in holm oak and pine fragmented forests (Díaz et al., 1998; Santos et al., 2002), which analyzed many of the same species as in the present study, the factors affecting forest species richness are somewhat similar (Table 4). Although these comparisons should be taken with care because of differences among studies in scale, type of forest fragments and surrounding matrices, some conclusions can be drawn on the basis of qualitative patterns (Table 4). Fragment size was the foremost factor in the three studies, explaining more of the variability in species richness in rural-fragmented habitats (67–70%) than in Madrid (51–57%). Vegetation structure factors that favored species richness in holm oak forests were rather similar to those in mixed forests in Madrid: high shrub and tree cover. Other similarities were also found at the individual species level (see Díaz et al., 1998; Santos et al., 2002), which suggests that some forest birds have similar responses to fragmentation in both types of habitats. Distance to the nearest forest fragment decreased species richness in both rural-fragmented habitats, but had no effect in Madrid. Possibly, the lack of linear structures connecting fragments in farming landscapes may play some role (Santos et al., 2002). In Madrid, wooded

streets may function as corridors, but their use by forest species is still debatable (Fernández-Juricic, 2000c). Overall, this comparison underscores that regional conservation strategies to protect forest birds in central Spain may also be applicable to urbanized areas; but some specific issues related to park management deserve mention.

First, habitat quality within parks should be enhanced to meet some minimum habitats requirements for forest passerines. For instance, increasing the availability and diversity of shrub and tree substrates could raise colonization rates of species with low abundance; such as *T. troglodytes*, *T. philomenos*, *S. hortensis*, *S. melanocephala*, and *D. major*. Habitat restoration should also focus on large parks, since the nested pattern indicates that they harbor a set of rare species not present in small parks. However, the role of small parks could be important to facilitate dispersal.

Second, the extent to which forest passerines move through the urban matrix is not known. Previous studies indicate that these species avoid the urban matrix and use high quality wooded streets only occasionally (Fernández-Juricic, 2000c). Therefore, it is necessary to determine the process by which forest specialists move between parks (e.g., linear or stepping-stone movements, type of habitats used for movements, etc.) and the rate of such movement in order to estimate the probabilities of dispersal between regional and urban populations.

Third, the role of secondary fragmentation (habitat quality deterioration within parks by human

Appendix B

Matrix depicting the distribution of forest passerines in 22 wooded parks in the city of Madrid (Spain) during, 1998 breeding season. Species were arranged in columns by decreasing incidence, and parks in rows by decreasing species richness.

“1” denotes species presence. *Abbreviations: P. bonelli* (PBO), *P. ater* (PAT), *P. caeruleus* (PCA), *P. major* (PMA), *A. caudatus* (ACA), *C. brachydactyla* (CBR), *S. atricapilla* (SAT), *S. melanocephala* (SME), *E. rubecula* (ERU), *T. troglodytes* (TRT), *T. philomenos* (TPH), and *D. major* (DMA).

Wooded park	PAT	PCA	SAT	CBR	ERU	PMA	ACA	PBO	TRT	TPH	DMA	SME
Oeste	1	1	1	1	1	1	1	1	1	1	1	
Moro	1	1	1	1	1	1	1		1			1
Aluche	1	1	1		1		1	1				
Fte Berro	1	1	1	1	1	1						
Atenas	1	1		1			1	1				
Austria	1	1		1			1		1			
Retiro	1	1	1	1		1						
Breogan	1		1	1				1				
C. University	1			1		1		1				
Arganzuela	1			1	1							
Co Almod.		1	1		1							
Joan Miró	1		1									
Vistillas	1	1										
España	1		1									
Santander	1				1							
Roma	1	1										
Emir	1											
Picasso	1											
C. Piquer						1						
Descubrimiento					1							
Eva Perón		1										
Bombillas												

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