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Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments

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Abstract Several factors, singly or in combination, have proven relevant in promoting nestedness in animal communities (area, isolation, habitat structure, etc.); however, little empirical evidence exists about the role of human disturbance. The goal of this paper was to assess whether human disturbance (pedestrians) may affect bird species composition in such a way as to generate a nested distributional pattern. The study was conducted in an urban fragmented landscape, the city of Madrid, where wooded parks were suitable fragments for many bird species, and had different levels of human visitation. At the community level, the distribution of species was significantly nested in two consecutive breeding seasons. Using two different procedures ("temperature" and "departures" methods) to analyse causality in nestedness, I found that pedestrian rate, fragment size and the diversity of stems were significantly correlated to the nested pattern. When analysed simultaneously, and controlling for their independent effects, these factors still accounted for nestedness. Pedestrian rate was the only factor significantly associated with changes in species composition between years. At the individual species level, 74 and 41% of species were significantly nested in relation to pedestrian rate in 1997 and 1998, respectively; however, these percentages were independent of foraging substrate and body size. Besides the classic area and habitat diversity effects, human disturbance can also promote nestedness: locally, by restraining the time and space of foraging and breeding opportunities, thus reducing fragment suitability, and regionally, by increasing extinction and decreasing colonization probabilities in highly disturbed fragments.

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Introduction

The analysis of community structure using species composition allows one to delve into the factors that shape communities in space and time (Patterson 1990; Worthen 1996). One metric of community structure is nestedness, whereby species inhabiting low species-richness locations are subsets of progressively species-richer ones (Patterson and Atmar 1986). What becomes relevant is not whether a community is nested, as long as nestedness appears to be a common phenomenon (Cook 1995; Boecklen 1997; Wright et al. 1998), but what mechanisms promote nestedness in communities with different phylogenetic and ecological attributes (Simberloff and Martin 1991; Lomolino 1996; Worthen and Rohde 1996; Hecnar and M'Closkey 1997; Wright et al. 1998).

Mechanisms promoting nestedness entail selective extinction (Patterson and Atmar 1986; Atmar and Patterson 1993; Lomolino and Davis 1997; Wright et al. 1998), selective colonization (Kadmon 1995; Lomolino 1996; Conroy et al. 1999), historical effects (Patterson 1990), nested habitats (Wright and Reeves 1992; Hecnar and M'Closkey 1997; Wright et al. 1998; Honnay et al. 1999), speciation (Cook and Quinn 1995) and differential reproductive success (Blake 1991). These factors may also affect species composition in combination, giving rise to interactive effects; namely, the probabilities of species occurrence decrease in more isolated and smaller fragments (Lomolino and Davis 1997; Lomolino 1999). Another factor that may also promote nestedness is disturbance (Worthen et al. 1998; Fleishman and Murphy 1999). For instance, Worthen et al. (1998) found out that desiccation stress produced a nested distributional pattern in mycophagous fly communities. Fleishman and Murphy (1999) suggested that human disturbance could affect nestedness in Great Basin butterfly communities. Nevertheless, little empirical evidence exists as to how disturbance may affect nestedness in vertebrate communities.

In a fragmented landscape, with different levels of human disturbance (e.g. ecotourism) and with species having different tolerance to disturbance, extinction would increase and colonization would decrease in highly disturbed fragments (Fernández-Juricic 2000a). These processes are expected to decrease the size of species subsets with increasing disturbance, giving rise to a nested pattern. Species composition is also expected to change in time, with highly disturbed sites having more species turnover, as a result of differential colonization and extinction (Fernández-Juricic, 2002). Moreover, individual species would distribute non-randomly, occupying fragments with low disturbance levels (Fernández-Juricic 2000a). However, the relative tolerance of individual species to disturbance may depend on certain biological traits. For instance, larger species and those feeding on the ground have been found to be more intolerant to human presence (Cooke 1980; Burger and Gochfeld 1991; Holmes et al. 1993; Knight and Cole 1995). Thus, a higher proportion of these species are expected to be affected by human visitation.

The goal of this paper was to assess whether human disturbance would affect bird species composition in such a way as to generate a nested distributional pattern at the community and individual species levels. To test this hypothesis, I studied bird species distributions in a fragmented landscape, the city of Madrid (Spain), in which wooded parks can be considered suitable fragments for bird species, surrounded by an unsuitable urban matrix (Fernández-Juricic 2000a, b, c). Wooded parks hold different levels of human disturbance (pedestrians) which affect locally and regionally the number of breeding species (Fernández-Juricic 2000a). However, human disturbance is likely to interact with other factors to promote nestedness, such as fragment size and habitat structure. Thus, given similar levels of human visitation, its negative effects are expected to decrease in larger and more structurally complex parks, for they provide a greater diversity of refuges against pedestrians (Fernández-Juricic 2000a).

At the community level, I analysed: (1) the role of pedestrian rate, fragment size, and habitat structure as causal factors for nestedness; and (2) how these factors would affect variations in community composition between two breeding seasons. At the individual species level, I assessed: (3) how pedestrian rate, fragment size, and habitat structure would affect the degree of nestedness of species with different foraging substrates and body size. Analyses at the individual species level are highly informative in determining to what degree species contribute to the overall nested pattern (Simberloff and Martin 1991; Kadmon 1995).

Materials and methods

Wooded parks of Madrid were used as experimental plots because: (1) their habitat structure is similar to that of other natural forest areas (Fernández-Juricic 2000c); (2) they are inhabited by a large number of bird species also present in the regional pool of species (Fernández-Juricic 2000c); (3) they have footpaths similar to those of many reserves (Fernández-Juricic and Tellería 2000); and (4) they are subject to visitation patterns similar to those of other natural parks (Fernández-Juricic et al., 2001). Indeed, many authors have employed urban fragments as natural laboratories for ecological research (e.g. Crooks and Soulé 1999), mainly because ecological patterns and processes in urbanized areas are similar to those of other natural habitats (McDonnell and Pickett 1990; Fernández-Juricic and Jokimäki, 2001).

Twenty-seven parks, ranging from 0.4 to 100 ha, were surveyed in the city of Madrid during spring in 1997 and 1998 (for a complete description of parks, see Fernández-Juricic 2000a, c). Each park was sampled 4–5 times per year (April to June) in the morning from 0700 to 1100 hours to determine species composition and the abundance of individual species. Individuals seen or heard vocalizing in 100×50 m (0.5 ha) strip transects were recorded in parks >2 ha, moving at a steady speed (Järvinen and Väisänen 1977). The same transects were used for each visit after being located on a map. The number of transects per park was established according to a logarithmic scale of the size of each park. The mean number of transects per park-size category was: parks >30 ha, 89±5.66 transects (n=2); parks 10–29 ha, 24.43±6.72 transects (n=7); parks 2–9 ha, 7.67±3.49 transects (n=9); parks <2 ha, 1.67±0.23 transects (n=9). The number of individuals of each species within 0.5 ha was later used to calculate breeding densities, after averaging the number of birds in each transect across the visits (for a thorough description of survey procedures, see Fernández-Juricic 2000c). I included in the analyses only those species that were: (1) present in at least 25% of the visits; (2) observed on at least two consecutive visits; and (3) recorded when singing, building a nest or carrying food. These criteria allowed me to avoid analysing species that were not breeding in wooded parks and that used them as alternative habitats for feeding. Ducks and swifts were excluded from the analysis, for their distribution was mainly determined by water sources and breeding sites in buildings, respectively. Such resources were not homogeneously distributed over this urban landscape, and could have biased results. Moreover, house sparrows (*Passer domesticus*) and rock doves (*Columba livia*) were not included because they are widespread species in urban habitats, and are highly associated with human activities (Fernández-Juricic 2000b).

Pedestrian rate was determined following Fernández-Juricic (2000a). With a team of three observers, I recorded simultaneously the number of pedestrians, at morning and midday, in 3-min periods in the same locations of the line transects used to sample bird species. In parks <2 ha, a single observer was enough to cover the whole area. This procedure was repeated 3 times at each park with 25 day-intervals. Final figures were averaged and turned into pedestrians/min per 10 ha per park. Park areas were obtained from the official records of the Municipality of Madrid. The degree of isolation was not evaluated because previous studies showed that isolation did not affect bird species richness and composition in wooded parks of Madrid, mainly because of the low variation in isolation in this landscape (Fernández-Juricic 2000c).

The following 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: grass cover, shrub cover, coniferous cover, deciduous cover, number of stems <10 cm, 10–30, 30–50 and >50 cm dbh (diameter at breast height). The selection of traits followed Tellería and Santos (1995, 1997). The number of sample units per park was determined according to its size (log-transformed). Cover variables were visually estimated following Prodon and Lebreton (1981). I calculated a Shannon-Wiener diversity index with cover variables (H_{cover}), and with number of stems in different categories (H_{tree}). Diversity indices are useful for summarizing vegetation traits since they take into account not only their occurrence but also their relative abundance (Fox and Fox 2000).

Fragment size was log (x_{+1})-transformed for normalization. I used Pearson product moment correlations to determine (1) the relationship between species abundance and incidence (number of fragments occupied) so as to assess whether abundant species were widespread across this landscape (Atmar and Patterson 1993); and (2) the correlation between independent factors.

To analyse nestedness, I set up a presence/absence matrix in which species were arranged in columns by decreasing number of fragments occupied, whereas fragments were ordered by decreasing species richness. Many different metrics of nestedness have been put forward in the last two decades (reviewed in Wright et al. 1998; but see also Lomolino 1996; Brualdi and Sanderson 1999). A recent paper (Sfenthourakis et al. 1999) evaluated two of the most used procedures: the "temperature" method of Atmar and Patterson (1993, 1995; Kelt 1997), and the "departures" method of Lomolino (1996). Sfenthourakis et al. (1999) concluded that the former method is more suitable for evaluating the level of nestedness. Therefore, I first analysed the degree of nestedness with the "temperature" method, which estimates the maximum nestedness in a given matrix by re-arranging species and fragments in such a way as to minimize unexpected species occurrences (Atmar and Patterson 1993). The degree of order was calculated with the Nested Calculator software (Atmar and Patterson 1995), which yields an index called the temperature ($T°$) of the matrix, with a perfectly nested matrix having 0°, and a random one 100°.

I assessed causality of the nested matrices by means of both the "temperature" and the "departures" methods (Lomolino 1996; Patterson and Atmar 2000). Firstly, the influence of each factor (pedestrian rate, fragment size, H_{cover}, H_{trees}) on nestedness was analysed independently. With the "temperature" procedure, I correlated by means of Spearman Rank correlations, the ranking order of fragments in the final nested matrix with the order of fragments, after re-arranging the matrix in relation to the independent factors. This procedure has proven useful for indicating the possible mechanisms involved in a nested structure (Patterson and Atmar 2000): a significant correlation suggests that a community is packed in a predictable order owing to the influence of a given factor. With the "departures" method, matrices were sorted according to the independent factors, and then the unexpected presences of species (or departures) were 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 1,000 simulations with departure values less than or equal to that of the ordered matrices (Lomolino 1996). It is noteworthy that the "departures" procedure permits to test the causality in nestedness combining two factors at the same time; that is, it assesses the effect of one variable after controlling for the effect of the other (Lomolino 1996). For each departure in the matrix ordered by one variable, I counted the number of departures that can be accounted for by the relative change in the second variable (Lomolino 1996). For instance, when analysing fragment size and pedestrian rate, I determined the number of departures not explained by area that could be affected by human visitation: absent to present due to decreasing pedestrian rate. The significance of the departures combining two factors was evaluated with a binomial test. Those causal factors that were found to account for nestedness in either year were analysed in combinations to assess their relative contribution to the nested pattern in both years.

In determining how species composition changed between years in relation to pedestrian rate, fragment size, H_{cover} and H_{tree}, I calculated for each fragment the Sorenson index of similarity as $2*C/(\mathrm{TS97}+\mathrm{TS98})$, where C was the number of common species between years, and TS97 and TS98 were the overall species richness in 1997 and 1998, respectively. Lower values of this index indicated a high turnover in species composition. I performed a stepwise multiple regression analysis to relate similarity values to the four independent variables. The regression was obtained with forward selection procedures. Pedestrian rate was averaged between both years for this analysis.

At the species level, I used the Mann-Whitney test to determine the degree of nestedness of individual species (Schoener and Schoener 1983; Simberloff and Levin 1985; Simberloff and Martin 1991). This test yields the probability that the observed sequence of presences and absences differs from a random one (for the advantages of using this test, see Hecnar and M'Closkey 1997). For each species, I performed the test arranging the matrix as to every independent factor. Species occupying all the fragments and those with only one presence or one absence were excluded from the analyses, because such distributions do not provide any relevant information on nestedness (Simberloff and Martin 1991).

To assess whether the influence of foraging substrate (ground and tree foragers) and species size (species with less and more than 30 g) was related to the propensity to fit a nested pattern, I used a test for differences between proportions (StatSoft 1999). The P-level was computed based on the t-value for the comparison:

$$|t| = \sqrt{[(N1*N2)/(N1+N2)]} * \frac{|p1-p2|}{\sqrt{(p*q)}}$$

where $p1$ and $p2$ were the proportions in each sample, $N1$ and $N2$ were the sample sizes in each sample, $p=(p1*N1+p2*N2)/(N1+N2)$, and $q=1-p$. Degrees of freedom were computed as $N1+N2-2$ (StatSoft 1999). Even though I also recorded species belonging to other foraging substrates (e.g. bush), I took into account only ground and tree foragers, because of their larger sample size. Species were sorted into two size categories based on the binomial frequency distribution of body sizes (less and more than 30 g).

Because of the high number of probability estimations, I conducted a correction to circumvent the effect of increasing the probability of type I error. Several types of corrections have been put forward (Wright 1992); however, many of them are so stringent that one risks increasing type II errors (decreasing the power of individual tests) (Chandler 1995). To overcome this problem, I followed a two-tiered approach. I first identified groups of related tests (following Chandler 1995), and then I performed a less conservative correction (Sidák correction, Wright 1992) over each of them. The groups of tests, along with the number of p-estimates, are as follows: relationship between independent factors (10 estimates); relationship between abundance and incidence (2 estimates); degree of nestedness (2 estimates); causality in nestedness (22 estimates); temporal variations in community composition (1 estimate); nestedness in relation to individual species: area (1997, 19 estimates; 1998, 22 estimates), human disturbance (1997, 19 estimates; 1998, 22 estimates), H_{cover} (1997, 19 estimates; 1998, 22 estimates), and H_{tree} (1997, 19 estimates; 1998, 22 estimates); and proportion of species with different foraging substrates and body size whose distribution was nested (4 estimates). P-values (p_{i}) were first ordered so that $p_1<p_2<....<p_{\mathrm{n}}$, and then each p_{i} was sequentially adjusted to $p_{\mathrm{i}\ (\mathrm{Sidák})}=1-(1-p_{\mathrm{i}})^{(n-\mathrm{i}+1)}$, n being the number of p-values in each group of tests (see Wright 1992).

Results

Twenty-five species were recorded in 1997, and 29 in 1998 (Appendices 1–3). The incidence of individual species was positively correlated with their density in both years (1997, $r=0.61$, $P<0.001$; 1998, $r=0.66$, $P<0.001$). Some independent variables were significantly correlated: fragment size and pedestrian rate in 1997 and 1998 (1997, $r=-0.52$, $P<0.05$; 1998, $r=-0.53$, $P<0.05$), and pedestrian rate in 1997 and 1998 ($r=0.69$, $P<0.05$). The other correlations were not significant (r varied from –0.26 to 0.42, $P>0.05$).

The distribution of species was significantly nested in both years (1997, $T°_{\mathrm{obs}}=5.76$, $T°_{\mathrm{rand}}=63.64$, SD=4.34, $P<0.001$; 1998, $T°_{\mathrm{obs}}=9.16$, $T°_{\mathrm{rand}}=64.52$, SD=4.18, $P<0.001$). Taking into account the "temperature" proce-

Table 1 Causality in nestedness. In the “temperature” procedure, Spearman R and its associated probability (*in parentheses*) are shown, indicating the correlation of the observed nested matrix with each independent factor. In the “departures” procedure, the number of departures in the ordered matrix and the proportion of random runs with fewer departures for 1,000 permutations (*in parentheses*) are shown for both years. Significant values, after Sidák correction

	“Temperature” method		“Departures” method	
	1997	1998	1997	1998
Area	0.87 (<0.001)	0.83 (<0.001)	69 (<0.001)	86 (0.12)
Pedestrian rate	–0.89 (<0.001)	–0.79 (<0.001)	65 (<0.001)	72 (<0.001)
H_{cover}	0.25 (0.99)	0.34 (0.81)	87 (0.73)	97 (0.89)
H_{tree}	0.41 (0.48)	0.47 (0.18)	82 (0.30)	84 (<0.05)

Table 2 Nestedness scores (Mann-Whitney Z-values) of individual bird species in relation to fragment size (log *Area*), pedestrian rate (*Ped rate*), vegetation cover diversity (H_{cover}) and stem diversity (H_{tree}) in 1997 and 1998 breeding seasons. Also shown is the body weight (g) and food substrate of individual species (following Fernández-Juricic 2000c). Significant values, after Sidák correction, are marked in **bold type**; – species occupying all the fragments and those with only one presence or one absence in a given year were excluded from the analyses

Species	Food	Body weight	Area 97	Area 98	Ped rate 97	Ped rate 98	H_{cover} 97	H_{cover} 98	H_{tree} 97	H_{tree} 98
Troglodytes troglodytes	Bush	9.9	–2.04	**–2.55**	**–2.31**	–2.47	–2.13	–1.58	**–2.22**	–1.93
Serinus serinus	Ground	11.2	**–2.78**	**–2.92**	**–3.19**	**–3.03**	–1.34	–0.23	–0.85	–0.96
Carduelis carduelis	Ground	15.6	–	–1.48	–	–1.48	–	–1.07	–	–0.32
Erithacus rubecula	Ground	18.2	–1.63	–1.97	–0.75	–0.85	–1.41	–1.41	–1.13	–0.82
Motacilla alba	Ground	21	–1.02	–0.03	–1.30	–0.80	–0.42	–1.06	–0.19	–0.37
Passer montanus	Ground	22	**–2.55**	**–2.55**	**–2.55**	–2.47	–1.58	–1.58	–1.93	–1.93
Carduelis chloris	Ground	27.8	–1.64	–1.65	**–2.46**	**–3.03**	–0.20	–1.30	–1.23	–0.11
Coccothraustes coccothraustes	Ground	54	–	–1.94	–	–1.85	–	–0.97	–	–1.11
Upupa epops	Ground	61.4	**–2.13**	**–2.93**	–1.87	–2.43	–0.88	–0.19	–0.85	–1.59
Sturnus vulgaris	Ground	82.3	**–3.29**	**–3.45**	**–2.71**	**–3.75**	–0.08	–0.13	–1.31	–1.78
Psittacula krameri	Ground	116.5	–	–2.13	–	–1.76	–	–1.20	–	–1.85
Picus viridis	Ground	176	**–3.96**	**–3.66**	**–3.91**	**–3.77**	–0.41	–0.74	–1.62	–1.94
Pica pica	Ground	177.5	**–2.68**	–2.25	**–3.09**	–1.77	–0.88	–1.40	–1.08	–1.50
Columba oenas	Ground	291	**–3.62**	**–3.27**	**–3.27**	**–2.80**	–1.34	–1.58	–1.90	–2.39
Columba palumbus	Ground	490	**–2.78**	**–2.96**	**–4.06**	**–3.74**	–0.36	–0.22	–1.62	–1.97
Phylloscopus bonelli	Tree	7.5	–2.10	–1.59	–1.38	–1.44	–1.61	–0.81	**–2.38**	–1.09
Aegithalos caudatus	Tree	8.2	**–3.18**	–2.56	**–3.00**	–1.94	–1.59	–2.06	–1.97	**–2.68**
Certhia brachydactyla	Tree	8.5	**–3.62**	–2.68	**–3.27**	**–3.13**	–1.34	–1.14	–1.90	–1.62
Parus ater	Tree	9.1	**–2.96**	–2.21	**–2.71**	–1.96	–1.91	–1.99	–1.91	**–2.59**
Parus caeruleus	Tree	13.3	**–3.24**	**–3.38**	**–2.88**	**–3.21**	–1.90	–1.70	–1.85	**–2.42**
Sylvia atricapilla	Tree	15.5	–1.26	–1.77	–2.12	–1.65	–0.12	**–3.27**	–0.84	–2.19
Parus major	Tree	19	**–2.82**	–2.62	**–2.88**	**–2.86**	–0.80	–1.87	–1.19	–2.13

dure, in 1997 and 1998, pedestrian rate and fragment size accounted for the nested pattern (Table 1). With the “departures” method, I found that pedestrian rate significantly explained the departures in 1997 and 1998, fragment size in 1997 and H_{tree} in 1998 (Table 1). Species found in species-poor fragments were subsets of those found in species-rich fragments with lower pedestrian rate, larger size and higher tree diversity.

When analysed simultaneously, I found in both years that after controlling for the effects of fragment size, departures were significantly accounted for by pedestrian rates (1997, prop. of departures explained by pedestrian rate=0.72, P<0.001; 1998, prop. of departures explained by pedestrian rate=0.64, P<0.05). Considering fragment size and tree diversity, the latter factor was significant only in 1997 (1997, prop. of departures explained by H_{tree}=0.67, P<0.05; 1998, prop. of departures explained by H_{tree}=0.63, P=0.15). Moreover, tree diversity significantly accounted for departures in the matrix after partialling out the effects of pedestrian rate in both years (1997, prop. of departures explained by H_{tree}=0.71, P<0.01; 1998, prop. of departures explained by H_{tree}= 0.69, P<0.01).

Community similarity was only accounted for by mean pedestrian rate (Sorenson similarity index= 0.82–0.44*mean pedestrian rate, R^2=0.20, $F_{1,25}$=6.30, P<0.05), such that community similarity decreased (increasing species turnover) with increasing human visitation. None of the other independent factors was included in the final model.

With regard to individual species, in 1997, of the 19 species analysed, 13 (68%) were significantly nested with respect to fragment size, 14 (74%) with respect to pedestrian rate, 2 (11%) with respect to H_{tree}, and none with respect to H_{cover} (Table 2). In 1998, of the 22 species analysed, 9 (41%) were nested in relation to area, 9 (41%) in relation to pedestrian rate, 3 (14%) in relation to H_{tree}, and 1 (5%) in relation to H_{cover} (Table 2). The proportion of species affected by pedestrian rate was independent of foraging substrate (1997, tree=0.71, ground 0.73, P=0.99; 1998, tree=0.43, ground=0.43, P=0.86) and body mass (1997, <30 g=0.69, >30 g=0.83, P=0.46; 1998, <30 g=0.36, >30 g=0.5, P=0.25) in both years.

Discussion

Community structure, along with the distribution of individual species, in urban wooded fragments follows a nested rather than a random distributional pattern. At the community level, species accumulate orderly in species-rich fragments. At the individual species level, species tend to occupy species-rich fragments, and avoid species-poor fragments. Such a nested pattern is correlated with fragment size, human disturbance and habitat diversity. Although human disturbance was found to be correlated to fragment size, there are grounds for believing that its independent effects are important at the community level (see also Fernández-Juricic 2000a) to account for nestedness; because after controlling for area effects, pedestrian rate was still correlated to the nested pattern.

Fragment size had an important influence on nestedness at the community and individual species levels. Nearly 55% of the species, on average, tended to occupy larger than smaller fragments in both years. Fragment size may affect species accumulation by increasing the availability of resources (Burke and Nol 1998; Zanette et al. 2000), and by providing greater habitat diversity (Martin et al. 1995), such that the specific requirements of certain species are only met in large fragments (Faaborg et al. 1995; Hinsley et al. 1995a; Tellería and Santos 1995, 1997; Debinski and Holt 2000; Fernández-Juricic 2000c). Furthermore, some species would prefer to occupy interior areas, thus avoiding small fragments because of the high proportion of edge habitat (Murcia 1995; McCollin 1998). In Madrid, species with special habitat requirements (mainly forest specialists) increase their breeding densities at interiors of large wooded parks (Fernández-Juricic, 2001). Finally, area-related extinction stochastic processes may also affect the accumulation of species (Hinsley et al. 1995b; Bellamy et al. 1996; Tellería and Santos 1997; Jokimäki et al. 2000). There is evidence that, in Madrid, large parks support larger populations, which are less prone to extinction during yearly fluctuations (E. Fernández-Juricic and J. Jokimäki, unpublished data).

Habitat diversity affected community composition patterns as well. Species accumulated in fragments with increasing diversity of stems. That was particularly the case with many insectivorous birds (*Parus* sp., *Troglodytes troglodytes*, *Aegithalos caudatus* and *Phylloscopus bonelli*, Table 2), which relied upon forest substrates to cope with their food requirements (Fernández-Juricic 2000c). This pattern suggests that resources may also be nested (Fleishman and Murphy 1999; Honnay et al. 1999). Even though resource distribution was not measured directly, wooded parks in Madrid are quite heterogeneous, with species colonizing parks as the amount of specific habitat resources accrues (Fernández-Juricic 2000c). Therefore, high-quality fragments are expected to support more specialized species than low-quality ones (Hinsley et al. 1995a; Bellamy et al. 1996; Jokimäki 1999).

Human disturbance effects upon species composition were found at the community and individual species levels, underscoring the importance of human visitation levels on the assembly of this community, as has already been suggested based on analyses of species richness (Fernández-Juricic 2000a). Similar negative effects of human disturbance on community assembly were also found in mammals (Dunstan and Fox 1996). The mechanism implicated may include processes at local (within-fragments) and regional (between-fragments) scales (Fernández-Juricic 2000a). Locally, individual birds reduce their time spent foraging and their intake rates when pedestrians are near resource patches (Burger and Gochfeld 1998; Fernández-Juricic and Tellería 2000). With greater disturbance levels, individuals usually stop their foraging activities and hide in protective cover or move to other patches (Miller et al. 1998; Fernández-Juricic 2000a; Fernández-Juricic and Tellería 2000). If human visitation increases further, individuals would face a sheer decrease in the temporal and spatial availability of resource patches (Fernández-Juricic 2000a). Regionally, this local response against pedestrians may decrease the chances of fragment occupation, while increasing extinction probabilities of low-tolerant species (Fernández-Juricic 2000a; Fernández-Juricic et al., 2001). Therefore, human disturbance may be regarded as an environmental filter (sensu Tonn et al. 1990) by which species distribute in fragments according to disturbance levels and species-specific tolerance levels to disturbance.

If the aforementioned mechanism holds, then increasing levels of disturbance would affect inter-annual patterns of species composition (Villa et al. 1992). In Madrid, breeding-species composition varied between two consecutive breeding seasons, with less turnover in less visited parks. Low-disturbed parks may have higher-quality territories, enhancing site-fidelity (Willard et al. 1995), and increasing breeding densities (Fernández-Juricic 2000a; Fernández-Juricic and Tellería 2000). Despite these community patterns, the proportion of species following a nested occurrence pattern with respect to disturbance was independent of foraging substrate and body size, contrary to previous evidence (Cooke 1980; Burger and Gochfeld 1991; Holmes et al. 1993; Knight and Cole 1995; but see Gutzwiller et al. 1998). This may be the result of the limited range of species studied, which makes comparisons difficult. Alternatively, the behavioural processes affecting tolerance may not be apparent at the community level. Species may show nonlinear patterns in relation to disturbance (e.g. inversely “U’’ shaped, Blair 1996), which would prevent detection with the analyses employed. In any case, the only trait that appears to increase persistence probabilities in this landscape is species density (Fernández-Juricic, 2002). As the distribution of abundant species is more widespread, then local extinctions from some fragments due to disturbance could be offset by rapid re-colonization (Williamson 1989).

Besides the classic area and habitat diversity effects (Hecnar and M’Closkey 1997; Wright et al. 1998; Honnay et al. 1999), human disturbance can promote nestedness in bird communities. Even though the results of this study cannot be generalized to landscapes with different levels of disturbance, some conservation implications can be drawn for areas with increasing human visitation. First, the increase in local levels of human disturbance can affect community structure at the landscape scale, decreasing the suitability and availability of fragments for reproduction. This must be evaluated in areas with increasing levels of ecotourists due to the popularity of wildlife recreational activities, such as national parks, natural reserves, etc. Second, human disturbance could increase the convergence of communities to nested subsets (Patterson and Atmar 1986), leading to areas dominated by widespread species with high tolerance to people. If so, rare or low-tolerant species could be restraining their breeding to low-disturbed and large fragments only. Third, area may be interacting with human disturbance in such a way as to become a sort of buffer against which pedestrian effects may be reduced (Fox and Fox 2000). Since small fragments have higher edge/area ratios than large fragments, similar visitation levels would further decrease the proportion of suitable area on small fragments. If human visitation were to be increased temporarily, then large fragments would be the appropriate target spots due to this buffering effect. Therefore, at least in highly disturbed landscapes, the implementation of single large, instead of several small, areas (Doak and Scott Mills 1994) seems to be a more sensible strategy.

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Appendix 1

Bird species found in 27 wooded parks in the city of Madrid (Spain) during the springs of 1997 and 1998. This table presents the common and scientific names of the species, abbreviations, and the number of parks occupied in each year

Common name	Scientific name	Abbreviation	1997	1998
Blackbird	*Turdus merula*	TUME	27	26
Song thrush	*Turdus philomenos*	TUPH	1	1
Mistle thrush	*Turdus viscivorus*	TUVI		1
Goldfinch	*Carduelis carduelis*	CACA	1	2
Greenfinch	*Carduelis chloris*	CACH	23	19
Hawfinch	*Coccothraustes coccothraustes*	COCO		2
Stock dove	*Columba oenas*	COOE	6	6
Woodpigeon	*Columba palumbus*	COPA	18	13
Jackdaw	*Corvus monedula*	COMO	1	1
Robin	*Erithacus rubecula*	ERRU	10	8
White wagtail	*Motacilla alba*	MOAL	2	8
Green parakeet	*Myopsitta monachus*	MYMO		1
Treecreeper	*Certhia brachydactyla*	CEBR	6	8
Long-tailed tit	*Aegithalos caudatus*	AECA	5	5
Coal tit	*Parus ater*	PAAT	17	17
Blue tit	*Parus caeruleus*	PACA	9	11
Great tit	*Parus major*	PAMA	7	6
Bonelli’s warbler	*Phylloscopus bonelli*	PHBO	7	5
Tree sparrow	*Passer montanus*	PAMO	3	3
Magpie	*Pica pica*	PIPI	21	23
Green woodpecker	*Picus viridis*	PIVI	9	8
Great spotted woodpecker	*Dendrocopos major*	DEMA		1
Ring-necked parakeet	*Psittacula krameri*	PSKR	1	2
Serin	*Serinus serinus*	SESE	18	21
Spotless starling	*Sturnus unicolor*	STUN	17	18
Blackcap	*Sylvia atricapilla*	SYAT	11	9
Orphean warbler	*Sylvia hortensis*	SYHO	1	
Sardinian warbler	*Sylvia melanocephala*	SYME		1
Wren	*Troglodytes troglodytes*	TRTR	2	3
Hoopoe	*Upupa epops*	UPEP	6	5

Appendix 2

Breeding-bird species composition in wooded parks in Madrid in 1997. Species' abbreviations as in Appendix 1

Park	TUME	CACH	PIPI	COPA	SESE	PAAT	STUN	SYAT	ERRU	PACA	PIVI	PAMA	PHBO	UPEP	CEBR	COOE	AECA	PAMO	TRTR	MOAL	PSKR	SYHO	COMO	CACA	TUPH
Oeste	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1						1
Moro	1	1	1	1	1	1	1	1		1	1	1	1		1	1	1	1	1		1	1			
Retiro	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1								
Austria	1	1	1	1	1		1		1		1	1		1	1	1		1							
Complutense	1	1	1	1	1	1	1			1	1	1		1	1	1	1								
Fte Berro	1	1	1	1	1	1	1	1	1	1	1				1	1	1								
Roma	1	1	1	1	1	1	1	1		1	1	1													
Bombillas	1	1	1	1	1		1	1			1			1						1			1		
Co Almodovar	1	1	1	1	1	1	1		1	1														1	
Atenas	1	1	1	1	1	1	1			1	1			1											
Santander	1	1	1	1	1	1	1	1	1				1												
Aluche	1	1	1	1	1	1			1				1							1					
Vistillas	1	1	1	1	1	1	1		1					1											
Arganzuelas	1	1	1	1		1	1		1				1												
Breogan	1	1	1	1	1	1		1																	
España	1		1			1	1		1	1															
Descubrimiento	1		1			1	1	1	1																
Emir	1	1	1	1			1	1																	
Joan Miro	1	1		1		1		1				1													
Concha Piquer	1	1	1		1								1												
Pl. Toros	1	1	1	1	1																				
Olaf Palme	1	1			1		1																		
Parr. Sanchez	1	1			1																				
Eva Peron	1	1																							
Picasso	1		1																						
Peñuelas	1	1																							
Arq. Ribera	1																								

Appendix 3

Breeding-bird species composition in wooded parks in Madrid in 1998. Species' abbreviations as in Appendix 1

Park	TUME	PIPI	SESE	CACH	STUN	PAAT	COPA	PACA	SYAT	CEBR	MOAL	ERRU	PIVI	PAMA	COOE	UPEP	AECA	PHBO	TRTR	PAMO	PSKR	CACA	COCO	COMO	TUPH	MYMO	DEMA	SYME	TUVI
Moro	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1		1			1		1	
Oeste	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1		1			1		1		
Austria	1	1	1	1	1	1	1	1		1	1		1		1	1	1		1	1			1						
Fte Berro	1	1	1	1	1	1	1	1	1	1		1	1	1	1														
Atenas	1	1	1	1	1	1	1	1		1			1			1	1	1											
Retiro	1	1	1		1	1	1	1	1				1	1	1	1					1								
Aluche	1	1	1	1	1	1		1	1		1	1					1	1											
Complutense	1	1	1	1	1	1	1			1			1	1		1		1											
Breogan	1	1	1	1	1	1	1		1	1	1							1											
Santander	1	1	1		1	1	1				1	1																	1
Arganzuelas	1	1	1	1	1	1				1		1			1														
Co Almodo	1	1	1	1	1			1	1			1										1							
Vistillas	1	1	1	1	1	1	1	1																					
Bombillas	1	1	1	1	1		1						1											1					
Roma	1	1	1	1	1	1	1	1																					
Joan Miro	1	1	1	1		1			1		1																		
Concha Piquer	1	1	1	1	1									1															
Emir	1	1			1	1	1																						
Descubrimiento	1	1	1								1	1																	
Eva Peron	1		1	1	1			1																					
Picasso	1	1				1					1																		
España	1	1				1			1																				
Olaf Palme	1	1	1	1																									
Arq. Ribera	1	1	1																										
Parr. Sanchez	1			1																									
Pl. Toros	1			1																									
Peñuelas																													

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