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Effects of forest fragmentation on European birds: implications of regional differences in species richness

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Abstract

Aim In this paper, we adopted a large-scale approach to evaluate the effect of regional richness of forest birds on the number of bird species retained by forest fragments in several localities across Europe.

Location We studied bird assemblages in fourteen forest archipelagos embedded in agricultural matrices from southern Norway to central Spain. Tree composition varied from oak and beech forests of the northern localities to oak and pine xerophitic woodlands of the southern ones. The number of fragments in each forest archipelago ranged from eighteen to 211.

Methods We used the Gleason equation ($s = a + z \log A$; where s and A are, respectively, the species richness and size of forest fragments and z the rate of species loss) to estimate the species richness for 1- and 15-ha fragments in each archipelago. The regional richness of forest birds was estimated by modelling the geographical distribution of species richness in the European atlas of breeding birds.

Results The latitudinal distribution of regional richness displayed a convex form, with the highest values being in central Europe. Along this gradient, the number of species retained by fragments and the rate of species loss was positively related to regional richness. In addition, the percentage of the regional pool of species sampled by fragments decreased in the southern localities.

Main conclusions Relationships between regional richness of forest birds and richness in fragments seem to explain why fragments in central Europe shelter more species than their southern counterparts. The decreased ability of southern forest fragments to sample the regional richness of forest birds, could be explained as an effect of the low abundance of many species in the Mediterranean, which could depress their ability to prevent extinction in fragments by a rescue effect. Alternatively, high beta diversity in the Mediterranean could produce undersampling by fragments of the regional pool of species. These regional differences in the response of bird assemblages to forest fragmentation are used to discuss the usefulness of large-scale, biogeographical approaches in the design of conservation guidelines.

Keywords
Europe, forest birds, habitat fragmentation, geographical gradients, regional richness.

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INTRODUCTION

Habitat loss and fragmentation is one of the main causes of the world-wide depletion in biodiversity. The negative effect of these causes on species richness is primarily determined by processes operating on local scales, such as habitat destruction, the reduction and isolation of fragments or the pervasive interferences of peripheral habitats (Andrén, 1994; Harrison & Bruna, 1999; Fahrig, 2002). However, processes operating on larger spatial scales are likely to be important determinants of species richness in fragments resulting from this habitat modification. They will decide, for instance, the regional species pool from which local communities can be assembled and will set the upper limit of species richness in fragments (Collins & Glenn, 1991; Caley & Schluter, 1997).

Despite the potential of large-scale approaches in evaluating local effects of habitat loss and fragmentation, there are no empirical studies on the way regional richness affects the number of species retained by fragments. This may be due to a scarcity of local studies on the effects of habitat fragmentation along conspicuous gradients of regional richness. European forest birds appear to avoid, however, these restrictions given that the number of species seems to decrease from central Europe outwards (Mönkkönen, 1994), and there are a number of studies on the effects of forest fragmentation on bird assemblages throughout the continent (Table 1). In this paper, we approach this topic by exploring the continental distribution of forest bird richness and the ability of forest fragments to retain species using two complementary approaches:

(i) We study the continental patterns of bird richness as a prior step to analyse their effect on the number of species retained by fragments in different European localities. If central Europe has the highest regional richness, this may explain why the number of species in fragments of this region is higher than observed further outwards (e.g. Hinsley *et al.*, 1998; Santos *et al.*, 2002).

(ii) We analyse whether the geographical location of fragments is related to their capacity to sample species along the European gradient. There are two features in the distribution of European forests and their birds that suggests that Mediterranean fragments will undersample species from the regional pool compared with central European fragments. Populations of many common forest birds are increasingly scarce and fragmented in these southern areas (Tellería & Santos, 1993; Hagemeijer & Blair, 1997), a feature that will tend to prevent the 'rescue effect' as a way of avoiding extinction in fragments (Brown & Kodric-Brown, 1977). In addition, the patchy and diverse nature of Mediterranean forests (Ozenda *et al.*, 1979) can produce an interspersed geographical distribution of forest birds and a concomitant increase in beta diversity (Whittaker, 1970), which will decrease the capacity of forest fragments to sample the regional richness of forest birds.

METHODS

Study areas and species

We reviewed the available literature on the effects of fragmentation on bird assemblages in forests located in agricultural matrices. Our main source was the review in Hinsley *et al.* (1998), which was enlarged with additional data from Poland and Spain (Table 1; Fig. 1a; see also Santos *et al.*, 2002). We did not include, however, the temporal pseudoreplica from British forests used in Hinsley *et al.* (1998) nor studies where data on bird richness per fragment were not available. The species included in these studies were restricted to diurnal birds that nest and feed within woodlands. Species that use nest sites in forests but mainly feed in the surrounding agricultural open landscape were excluded. The final set of sixty-seven species accounted for studying the distribution of species richness across Europe is listed in Appendix. The set of these species recorded in each forest archipelago ranged from thirteen to thirty-three (Table 1).

We also recorded from the reviewed papers the forest cover in the area occupied by the study forest archipelagos to

Table 1 Main features of the fourteen forest archipelagos considered in this study. *n*, Number of forest fragments

	Latitude	*n*	Local forest cover (%)	Forest type	Local pool of species	Gleason algorithm	R^2	Sources
1	39.33	36	15	*Pinus pinaster, P. pinea*	13	$s = 0.82 + 2.20 \log A$	58.1	Díaz *et al.* (1998)
2	39.75	66	7.2	*Quercus ilex*	13	$s = 1.62 + 1.76 \log A$	37.1	Santos & Tellería (1998)
3	41.25	32	15	*Pinus pinaster, P. pinea*	18	$s = 1.82 + 2.74 \log A$	23.0	Díaz *et al.* (1998)
4	42.17	103	7.6	*Quercus ilex*	24	$s = 2.76 + 2.88 \log A$	69.0	Santos & Tellería (1998)
5	42.58	29	16.9	*Quercus pyrenaica*	22	$s = 1.82 + 1.60 \log A$	56.7	Santos & Tellería (1998)
6	42.92	18	10.9	*Quercus faginea, Acer campestris*	20	$s = 7.07 + 5.00 \log A$	86.0	Santos & Tellería (1998)
7	51.70	211	10	*Quercus robur, Fagus sylvatica*	33	$s = 12.5 + 7.55 \log A$	62.4	Van Dorp & Opdam (1987)
8	51.90	20	9	*Quercus robur, Fagus sylvatica*	24	$s = 10.2 + 7.68 \log A$	77.3	Ford (1987)
9	51.95	28	22.2	*Pinus sylvestris, Quercus robur*	19	$s = 5.67 + 6.82 \log A$	81.7	Cieslak & Dombrowski (1993)
10	52.17	22	23.6	*Pinus sylvestris, Quercus robur*	23	$s = 6.96 + 7.15 \log A$	86.7	Cieslak & Dombrowski (1993)
11	52.40	149	1	*Quercus robur, Fagus sylvatica*	24	$s = 7.95 + 6.52 \log A$	71.4	Hinsley *et al.* (1995)
12	53.90	16	4	*Quercus robur, Fagus sylvatica*	24	$s = 9.72 + 6.67 \log A$	54.8	McCollin (1993)
13	56.30	39	15	*Quercus robur, Fagus sylvatica*	19	$s = 6.59 + 5.11 \log A$	58.9	Komdeur & Gabrielsen (1995)
14	59.70	200	25	*Quercus robur, Fagus sylvatica*	19	$s = 3.27 + 2.01 \log A$	44.7	Borch & Ystad (1991)

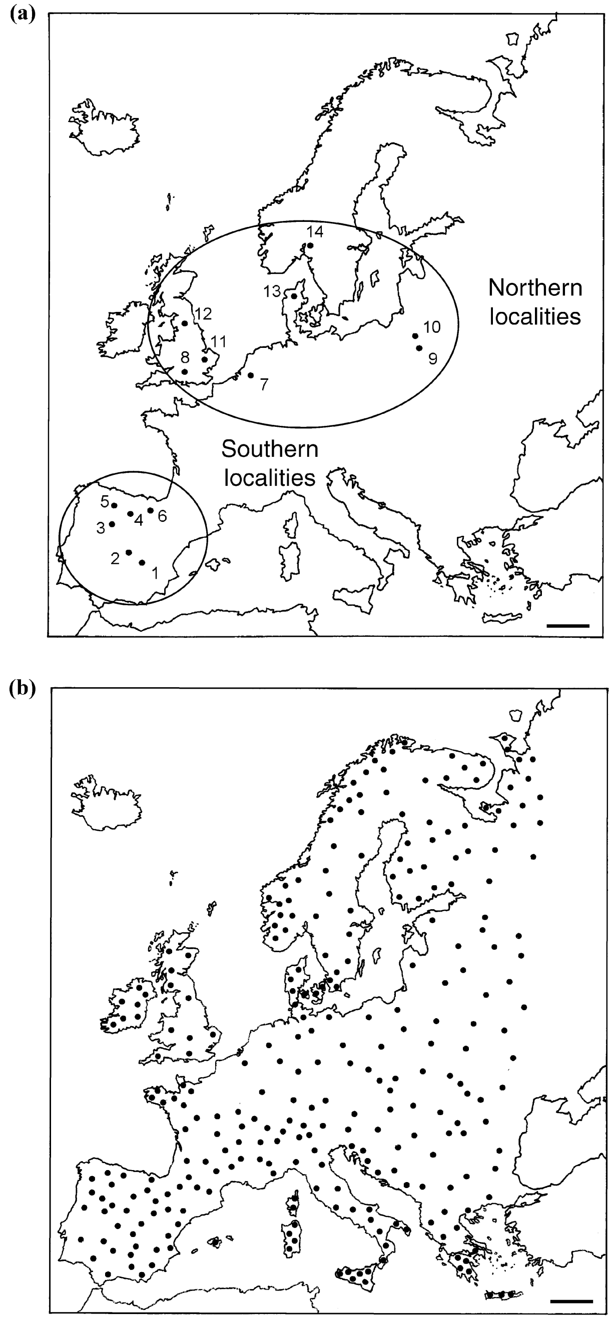

Figure 1 (a) Distribution of the fourteen forest archipelagos considered in this study. (b) Distribution of sampling points ($n = 280$) throughout Europe.

evaluate the effect of habitat loss on species richness in fragments (Table 1). It has been suggested that habitat loss and fragmentation are not identical processes and that, under a given local cover of habitat, the ability of many vertebrates to maintain presence in fragments drops independently of the size and spatial arrangement of fragments (Andrén, 1994; Fahrig, 2002).

Fragment and regional species richness

Each one of the studies we reviewed employs the Gleason equation ($s = a + z \log A$) to describe richness (s) according to fragment size (A in ha) or provides data to calculate it. From this equation, we calculated local richness for 1-ha fragments (s_1; the intercept in equations of Table 1) and 15-ha fragments (s_{15}) although in the latter case Norwegian forests (site 14) were excluded (the largest fragment was 2 ha). As slopes were strongly correlated to intercepts ($r = 0.91$, $P < 0.001$) in the set of study localities, we can acept that z values are a proper way of describing the rate of species loss as fragment size decreases (Gould, 1979; see Brown & Lomolino, 1998 for review).

A main methodological problem when comparing local and regional richness is that as regional area increases, localities sample a decreasing proportion of the regional pool of species (Caley & Schluter, 1997; Srivastava, 1999). To avoid this, it is important to fix the size of regional and local areas for all estimates of species richness. We fixed local areas at 1 and 15-ha forest fragments (see above). However, the forest archipelagos where the studies were carried out varied in area from several hundred to several thousand km^2 (see Hinsley *et al.*, 1998; Santos *et al.*, 2002). To cope with this problem, we modelled the geographical distribution of species richness in 280 50×50-km sampling plots distributed in Europe (Fig. 1b; Iceland and islands smaller than Mallorca were not considered). At each sampling point, the number of species of the sixty-seven breeding forest birds in the Appendix was recorded from Hagemeijer & Blair (1997). Each sampling point was assigned to one latitudinal (LAT) and longitudinal (LON) position (Lambert projection). We carried out multiple regression analysis to explore the latitudinal and longitudinal variation of regional richness (S) from the matrix of two-dimensional geographical co-ordinates (LAT and LON) by generating all terms for a cubic trend surface regression (Legendre, 1990). These terms describe linear gradient as well as more complex features, such as patches or gaps, which require the quadratic and cubic terms of the co-ordinates and their interactions to be described accurately (Borcard *et al.*, 1992; see Baquero & Tellería, 2001 for further details). The resulting model was used to calculate regional richness (S) at the co-ordinates of the central point in each forest archipelago studied.

Analyses

The role of regional richness (S) and local cover of forests (covariates) in determining the number of bird species in fragments (s) were assessed by means of a two-way ANCOVA (effects: fragment size, 1 vs. 15 ha; and geographical location: northern vs. southern localities in Fig. 1a). A similar statistical approach (ANCOVA) was carried out to assess the effect of geographical location (northern vs. southern localities) and covariates (regional richness and local cover of forests) on the rate of species loss (z).

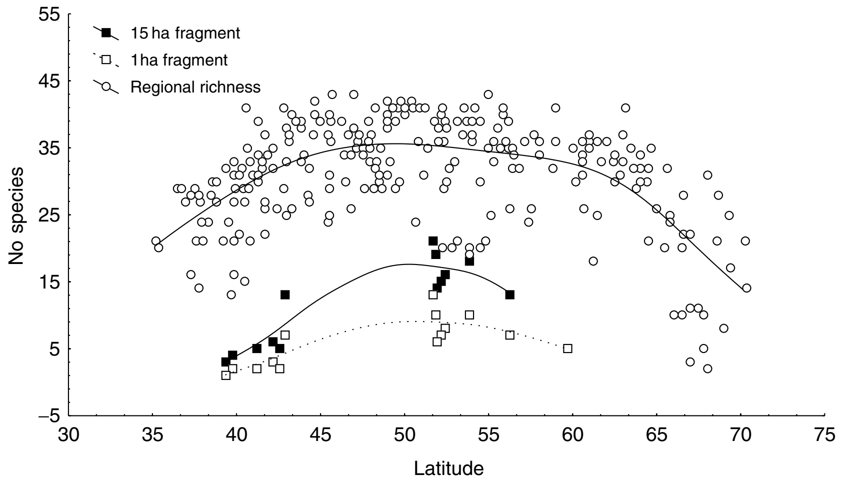

Figure 2 Latitudinal distribution of the regional richness of European forest birds and the richness of forest birds in 1- and 15-ha fragments. Lines have been fitted according to the distance-weighted least squares smoothing procedure.

Table 2 Differences between northern and southern localities in the number of bird species and in the rate of species loss as fragment size decreases (results of one-way ANOVA comparing localities are also shown)

	Northern localities (mean ± SE)	Southern localities (mean ± SE)	$F_{1,12}$	P
Regional richness	34.86 ± 1.16	30.59 ± 0.83	7.92	0.016
15-ha Fragments	16.57 ± 2.09	6.00 ± 1.46	32.83	<0.001
1-ha Fragments	8.25 ± 0.92	2.83 ± 0.87	22.91	<0.001
Species loss (z)	6.19 ± 0.66	2.90 ± 0.46	14.57	0.002
Forest cover	13.73 ± 3.25	12.10 ± 1.69	0.005	0.944

RESULTS

The model carried out to describe the geographical distribution of species richness explained a large amount of the variance in the distribution of this variable throughout the western Palearctic ($S = -38.78 - 54.44\ \mathrm{LAT}^2 - 56.17\ \mathrm{LAT\ LON}^2 + 14.23\ \mathrm{LON}^3 - 3.95\ \mathrm{LON}^2 + 25.71\ \mathrm{LAT}^2\ \mathrm{LON}$, $R^2 = 0.63$, $P < 0.0001$, $n = 280$). It described a pattern of richness in which the highest scores occurred in central Europe (Fig. 2). Thus, we used this model to calculate the regional richness (S) on which to evaluate the ability of fragments to retain species on local scales.

Northern localities had higher scores in regional richness and in the number of the species retained by 1- and 15-ha fragments (Table 2). Richness of forest birds in fragments followed a similar pattern that the latitudinal distribution of regional richness, supporting the predicted role of large-scale patterns in the effects of fragmentation on local scales (Fig. 3a). In addition to fragment size, geographical location also affected the number of species retained by fragments (Table 3) supporting the depressed ability of southern fragments to retain species of the regional pool of forest birds (Table 2). After controlling for the effects of the rest of variables, local cover of forest was negatively correlated to bird richness in fragments. This suggests that the higher availability of forests was related to lower ability of fragment archipelagos to sample regional richness.

The rate of species loss (z) was higher in the northern localities than in the southern ones (Table 2), and was correlated to regional richness and local cover of forests (Fig. 3b). However, after controlling for the effect of covariates, there was not any specific effect of the geographical location on the rate of species loss (Table 3). In this case, local cover of forests was negatively correlated to z suggesting that the rates of species loss decreased in archipelagos with high forest cover.

DISCUSSION

Regional patterns of species richness

The observed distribution of bird richness supports the existence of an optimal area for forest birds in Central Europe (Mönkkönen, 1994). This large-scale pattern has been interpreted as the outcome of Paleo-environmental fluctuations experienced in the Western Palearctic from the Quaternary (Blondel & Mouver-Chauviré, 1998). Throughout the late Pleistocene, forests seemed to be concentrated in the mild Mediterranean peninsulas but, as global warming progressed, they shifted northwards following the displacement of the optimum for forest growth (Huntley, 1993). In the Mediterranean, the depletion of this optimum was coupled with severe and ancient human pressures that favoured heliophytic, schlerophyllous or pyrophytic trees and shrublands (Costa *et al.*, 1990; Blondel & Vigne, 1993). The relative fragility of Mediterranean forests compared to central European ones, where man also used and modified vegetation, is accounted for by several factors, including low or irregular levels of precipitation, hot and dry summers and the

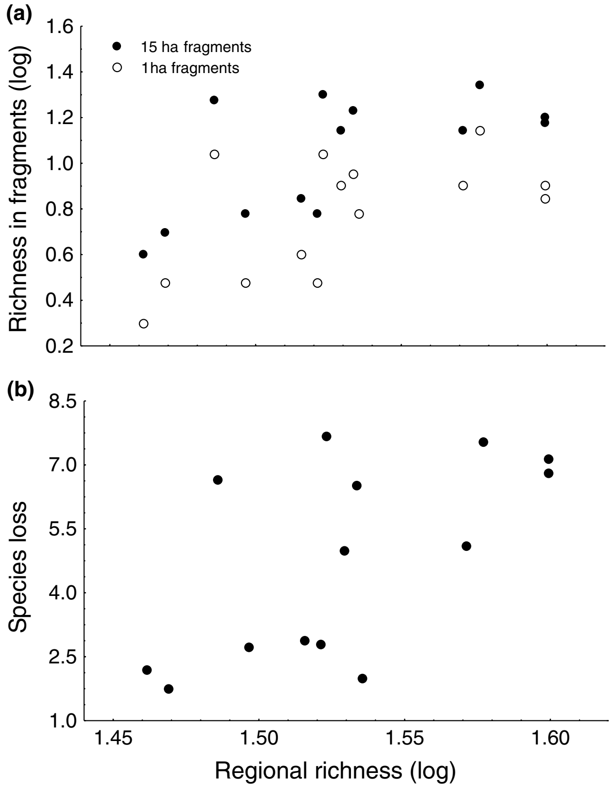

Figure 3 (a) Relationships between the regional richness of species and the number of species in 1- and 15-ha fragments. (b) Relationship between the rate of species loss in fragments and the regional richness along the study gradient.

concomitant inability of vegetation to growth up in these conditions (Blondel & Aronson, 1999; see Soulé *et al.*, 1988 for a discussion in the context of forest fragmentation). As a consequence, these forests are today regarded as suboptimal habitats for many common forest birds (review in Dias, 1996). These changes seem to be related to the retreat of many birds, which today conform the bulk of European bird communities (e.g. *Erithacus rubecula*, *Sylvia atricapilla*, *Phylloscopus collybita*, *Prunella modularis*, *Sylvia borin*, *Troglodytes troglodytes*, *Turdus philomelos*), to the moister forests of the Mediterranean region (river banks, moist slopes, some rainy coastal sectors, etc.) where tend to show a patchy distribution (Hagemeijer & Blair, 1997; see Tellería & Santos, 1993, for details on the scale of the Iberian Peninsula). This retreat has been hardly compensated by the existence of a small number of species endemic to the Mediterranean that are adapted to the dry, open woodlands of this region (e.g. *Sylvia cantillans*, *S. hortensis*, *S. undata*, *Phylloscopus bonelli*, *Serinus serinus*, *Emberiza cia*, *Cyanopica cyana*).

Effects on fragment richness

Richness in fragments showed a positive association with regional richness, a fair demonstration of the effects of processes operating on larger spatial scales on the capacity of forest fragments to retain species. The decreased number of species in southern fragments is congruent with the biogeographical scenario described above, where regional richness and abundance of forest birds decreased from the core forest biome in central Europe. But, as we predicted in the Introduction, we have detected a decreased ability of southern fragments to retain species with regard to northern fragments. This can be explained again by some biogeographical differences in the distribution of central and southern European forest birds. It has been suggested that the well-being of populations decreases towards the border of species range causing a concomitant decrease in both abundance and fitness (Brown, 1984; Lawton, 1993; Hoffmann & Blows, 1994). As a consequence, species along the border of their ranges will tend to be scarce and will occur in a lower percentage of sites than in core areas. In this way, birds in fragments will be more prone to extinction near the edges of their range (Kattan *et al.*, 1994; Tellería & Santos, 1999). A second approach refers to the increased *beta diversity* of Mediterranean landscapes compared to central Europe. The high topographical, climatic and pedological diversity characteristic of the landscape in southern Europe produces a patchy, non-overlapping distribution of forest types (Ozenda *et al.*, 1979) and birds with particular habitat preferences (Blondel & Aronson, 1999; see Cody, 1986, for a review of beta diversity in other Mediterranean areas around the world). In this way, forest fragments in agriculture matrices of the Mediterranean will hardly sample some bird species restricted to moist forests in river banks or rainy mountain slopes (see above).

Table 3 Results of ANCOVA comparing the number of species retained in fragments and the rate of species loss in northern and southern localities controlling for the effect of fragment size (in the case of richness), regional richness and forest cover. Beta scores of covariates are in parentheses

	No. of species in fragments		Species loss (z)	
Source of variation	$F_{1,21}$	P	$F_{1,10}$	P
Effects				
Geographical location	16.11	<0.001	2.09	0.1795
Fragment size	30.40	<0.001	–	–
Location × size	0.005	0.943	–	–
Covariates				
Regional richness	8.25 (0.61)	0.009	6.23 (0.63)	0.032
Forest cover	10.75 (−0.69)	0.004	6.05 (−0.66)	0.034

Results in this paper concerning to the effect of forests availability on the ability of fragments to sample regional richness are confusing given that, according to our hypothesis (see 'Introduction'), habitat loss will strongly depress the ability of species to maintain in fragmented landscapes (Fahrig, 2002; see also Andrén, 1994). The decreased ability of fragments to sample regional richness as forest cover increases could be interpreted, however, as a result of the increasing crowding of birds in fragments of intensively deforested areas. This crowding has been observed in other areas and seems to be the related to the increase of edge effect, benefical for some forest generalists, as habitat loss progresses (McGarigal & McComb, 1995; Trzcinski *et al.*, 1999; Villard *et al.*, 1999; see Fahrig, 2002 for review). Nevertheless, we agree that further investigation is needed for a full understanding of this pattern.

Relationships between forest cover and species loss (z) adjusted well to the basic prediction of multiple-patch or landscape-scale approaches on the effects of habitat loss and fragmentation (Bascompte & Solé, 1996; Hanski *et al.*, 1996): high forest cover in the area, and the related large bird populations, will prevent extinction in fragments by rescue effects from large regional populations. Low z values in the Mediterranean can be interpreted, however, as a result of the degraded situation of forests in this region and not as a result of any particular ability of Mediterranean forests to prevent losses (after controlling for the effect of regional richness, no significant effect of the geographical location was detected). Low z values have been related to recently fragmented habitats (when many species still remain in fragments) or to extremely degraded situations in which accumulated extinction have depleted species along the full range of sizes (Soulé *et al.*, 1988). According to the history of the Mediterranean forest avifauna (see above), this seems to be the case of the Spanish fragments. However, forest fragments in central Europe seem to adjust to an intermediate situation (higher z values), in which large fragments are still diverse but small ones show depleted richness through accumulative effects of fragmentation. Similar conclusions have been drawn for European plant species which show low rates of extinction in Mediterranean areas where human implantation is most ancient and early extinction of the more vulnerable species is assumed (Greuter, 1995).

CONCLUSIONS

Agriculture is one of the main rural land uses in Europe (it accounts for 44% of the total area) and there is an increasing concern for integrating biodiversity retained in these managed landscapes (e.g. forest remnants, marshlands, etc.) in current networks of protected sites (e.g. Natura 2000 Network; see Ostermann, 1998). This aim must be supported, however, by criteria directed to evaluate the conservation priority of extant and potential protected sites at the scale of Europe, as well as their resilience to possible habitat alterations (e.g. Council of Europe, 1996). Large-scale approaches can contribute to both needs. The description of species distribution across large areas is, for instance, useful to evaluate the best places for conserving biodiversity (e.g. Williams *et al.*, 1998). In addition, similar large-scale approaches have been used to highlight functional differences in the way local assemblages face harmful processes affecting biodiversity (Caley & Schluter, 1997). Consequently, some descriptive and functional approaches in this paper could be useful in the design of plans to protect biological diversity of European forest fragments.

The descriptive approach refers to the decrease of the regional richness of forest birds from central Europe southwards, and the concomitant decrease in the number of species retained by forest fragments of southern sectors. This pattern suggests additional complications for conserving diverse forest bird communities in agricultural matrices given that fragment size needs to be greatly increased to retain the same number of species found in small forest fragments of central Europe (Fig. 2). For instance, while beech *Fagus sylvatica* and oak *Quercus robur* 10-ha fragments in the UK account for sixteen to seventeen bird species, a similar evergreen oak *Quercus ilex* in Spain will account for three to six species (see Gleason equation in Table 1 for further comparisons; see also Santos *et al.*, 2002). Even so, it will be impossible to attain this richness in many cases because some birds common to European forests are very scarce or extinct in the south. This situation, resulting from large-scale temporal and spatial events (see above), is difficult to handle in the short term (Landres, 1992) and will inevitably constraint our management purposes in the south. However, it is important to remember at this point that richness, the focal parameter in this study, does not evaluate other features of bird assemblages in a given area, as the rarity, endemicity or complementarity, which could considerably enlarge our scope on the conservation interest of forest remnants (see Williams *et al.*, 1998 for review). Southern forests contain, for instance, some species endemic to the Mediterranean, some of which are needed from specific management guidelines (Tucker & Evans, 1997). From this follows the convenience of designing specific plans to assign conservation priority to forest remnants at the proper scale, avoiding pan-European standards resulting from a mere comparison of the richness retained by fragments.

The functional approach refers to the different ability of bird communities to sample regional richness in central and southern Europe. The design of management guidelines to approach this issue implies, however, further investigations. It seems particularly interesting to investigate the relative contribution of regional (e.g. changes in the abundance of species across the continent) and local features (forest cover and landscape configuration) in this process. Our results support, for instance, the positive role of local cover of forest in preventing species loss as fragment size decreases, a good evidence that patch size and regional richness are not sufficient for predicting populations persistence in fragmented landscapes.

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APPENDIX

Pool of forest birds included in the continental study of species richness. The pool is restricted to those birds that nest and feed within woodland (see text). Asterisks show those species that were recorded in the study forest archipelagos.

*Accipiter gentilis**, *Accipiter nisus**, *Aegithalos caudatus**, *Bombycilla garrulus*, *Carduelis spinus*, *Certhia brachydactyla**, *Certhia familiaris**, *Coccothraustes coccothraustes**, *Cyanopica cyana**, *Dendrocopos major**, *Dendrocopos minor**, *Dryocopus martius**, *Emberiza cia**, *Erithacus rubecula**, *Ficedula albicollis*, *Ficedula hypoleuca**, *Ficedula parva*, *Ficedula semitorquata*, *Fringilla coelebs**, *Fringilla montifringilla**, *Garrulus glandarius**, *Loxia curvirostra*, *Loxia leucoptera*, *Loxia pytyopsittacus*, *Loxia scotica*, *Luscinia luscinia**, *Luscinia megarhynchos**, *Muscicapa striata**, *Nucifraga caryocatactes*, *Oriolus oriolus**, *Parus ater**, *Parus caeruleus**, *Parus cinctus*, *Parus cristatus**, *Parus cyanus*, *Parus lugubris*, *Parus major**, *Parus montanus**, *Parus palustris**, *Perisoreus infaustus*, *Phylloscopus bonelli**, *Phylloscopus borealis*, *Phylloscopus collybita**, *Phylloscopus sibilatrix**, *Phylloscopus trochiloides*, *Phylloscopus trochilus**, *Pinicola enucleator*, *Prunella modularis**, *Pyrrhula pyrrhula**, *Regulus ignicapillus**, *Regulus regulus**, *Remiz pendulinus*, *Serinus serinus**, *Sitta europaea**, *Sylvia atricapilla**, *Sylvia borin**, *Sylvia cantillans**, *Sylvia hortensis**, *Sylvia melanocephala**, *Sylvia rueppelli*, *Sylvia sarda*, *Sylvia undata**, *Tarsiger cyanurus*, *Troglodytes troglodytes**, *Turdus iliacus*, *Turdus merula**, *Turdus philomelos**.