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Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects

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Summary

1. Afforestation with pines (*Pinus pinaster* and, to a lesser extent, *P. pinea* and *P. halepensis*) seems to be the most probable land-use change over large areas of dry cereal croplands in central Spain in the next 10–20 years. This will be encouraged by changes in the subsidy policies of the Common Agricultural Policy that aim to decrease food production and restore the environmental diversity previously lost through agricultural intensification. This study addresses the factors influencing the richness and composition of breeding bird communities in these pine plantations and evaluates the potential environmental benefits of the afforestation programmes.

2. The complement of bird species breeding in 88 plantations ranging in size from 0·1 to 6775 ha was determined. Plantations were characterized according to size, distance to the nearest large plantation, vegetation structure and geographical location (northern moist vs. southern xeric Iberian plateaux).

3. Plantation size alone accounted for 67–75% of the variation in species richness, and was also the main trait explaining the patterns of presence/absence of most individual bird species. Plantations smaller than 25 ha only maintained 50% of the regional pool of forest birds during breeding, whereas this proportion increased to 69–86% for plantations of 25–100 ha. Geographic location, degree of isolation and vegetation structure were also important. Bird species richness decreased with distance to a large plantation, and increased with prevalence of undergrowth shrubs and with plant species richness.

4. Both species richness and the incidence of individual species in plantations were affected by geographical location. They were greater in plantations of the northern plateau, reflecting a trend of increasing densities of most forest bird species in Spain in more northerly locations.

5. The results of this study suggest that re-afforestation of former arable land in the Spanish plateaux is unlikely to increase species richness in forest bird communities. Given the regional scarcity of many forest birds and the small scale of new plantations, re-afforestation schemes are unlikely to promote rich forest bird communities.

6. Since plantations are unsuitable habitats for the bird species breeding in Spanish dry cereal croplands, and such birds have a high conservation value because of their small and declining populations, the overall environmental benefits of large-scale afforestation programmes will not include increased diversity of birds.

Key-words: afforestation programmes, plantation size, regional abundance, species composition, species richness.

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Introduction

Dry cereal croplands now cover around 4 million hectares in Spain (i.e. around 20% of all cultivated land), mostly in the two plateaux that form the larger central part of the Iberian Peninsula. Productivity of these farming systems is very low because of the soil and climatic conditions; at present they are economically marginal and highly dependent on subsidies derived from the Common Agricultural Policy (CAP) (Suárez, Naveso & de Juana 1997 and references therein). This economic instability makes the long-term maintenance of these farming systems unlikely and strongly dependent on future trends in the CAP. Bearing in mind these trends, three main land-use changes have been proposed for dry cereal croplands in central Spain (Suárez, Naveso & de Juana 1997): local intensification in the more productive areas, and abandonment or afforestation in the more marginal ones. Afforestation seems to be the most likely land-use change over large areas of central Spain. The economic viability of afforestations is based on the financial support delivered by the Spanish government following EC Regulation 2080/92 (Castellano & Cifuentes 1994).

The evaluation of the effects of different land use and changes in use on animal and plant communities are of paramount importance since biodiversity criteria are expected to play an increasingly important role in driving CAP reforms and subsidies (Robson 1997). Changes in bird populations and communities have been used to evaluate the ecological value of European agricultural systems and the environmental impact of expected CAP reforms (Pain & Pienkowski 1997). Financial support appears to be given to afforestation programmes under the assumption that the new forest areas will have positive environmental effects that alleviate the damaging effects of agriculture (Robson 1997). This assumption arises from the fact that most of central Spain was covered by forests before widespread agriculture (Costa *et al.* 1990), and afforestation is viewed as an efficient way of recovering the original forest bird communities (Tellería 1992, 1993).

Such recovery, however, is strongly dependent on the way in which forest plantations are created and managed (reviewed by Avery & Leslie 1990 and Fuller, Gough & Marchant 1995). Appropriate design and implementation of afforestation programmes with explicit biodiversity standards is crucial (Spellerberg & Sawyer 1996). This depends on the availability of clear information on the relationships between the characteristics of plantations and animal and plant communities.

Extensive research in recent years has provided a good picture of the main characteristics of forests and forest plantations that affect bird populations and communities (reviewed by Avery & Leslie 1990; Tellería 1992 and Fuller 1995). Two main factors influence forest bird communities: variations in the spatial arrangement of forest patches within the landscape, and variations in the vegetation structure and floristic composition within such patches. The size and isolation of a forest patch influences the probability of it being occupied by birds (Wiens 1989). The structure and species composition of the tree, shrub and herb layers, which are closely dependent on forest management techniques (Avery & Leslie 1990), strongly influence the presence and abundance of forest birds (reviewed by Wiens 1989).

In addition, natural variation in the regional abundance of birds across their distribution range will affect the identity of species colonizing new plantations (van Dorp & Opdam 1987; Lawton 1993; Hinsley *et al.* 1996; Tellería & Santos 1997; Santos & Tellería 1997). For most forest birds this decreases southwards in the Iberian Peninsula, a fact that has been attributed to a general impoverishment of habitat towards the southern border of their range (Tellería & Santos 1994; reviewed by Brown 1995). Hence areas of afforestation will be expected to maintain less diverse bird communities the further south they are located.

This work aimed to provide information on the richness of breeding bird communities occurring in plantations on the Spanish plateaux, as well as identifying the characteristics of the plantations that determine such richness. The influence of geographical location, size, degree of isolation and vegetation structure of forest plantations on the richness and species composition of the breeding bird communities they support was analysed. This information will help to evaluate the potential environmental benefits of existing and future afforestation programmes on dry cereal croplands on the Spanish plateaux.

Materials and methods

STUDY AREA

Field work was carried out in two study areas located near Carpio del Campo in the northern Spanish plateau (Valladolid province; 41°13′N, 5°5′W, 770–790 m a.s.l.) and San Clemente in the southern plateau (Cuenca-Albacete provinces; 39°24′N, 2°27′W, 710–730 m a.s.l.). They are flat areas mainly devoted to extensive cereal cultivation, in which the former holm oak *Quercus ilex* L. forest has been almost completely eliminated. Re-afforestation with pines (mainly *Pinus pinaster* Ait. and, to a lesser extent, *P. pinea* L. in the north and *P. halepensis* Mill. in the south) on former arable land has taken place in both areas, so that pine plantations of a variety of sizes are now found among cereal fields. The size distribution of plantations is strongly skewed towards stands smaller than 2 ha, although most of the area re-afforested (which comprises around 15% of the study areas) is accounted for by a few large plantations (Table 1).

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Table 1. Number of plantations studied according to plantation size. The average (± SD) size of plantations (in ha), the average (± SD) number of 3-min samples carried out to determine the complement of breeding bird species, and the average (± SD) number of samples for measurements of vegetation structure are also shown. The individual sizes, the length of line transects censused to determine regional bird densities, and the exact number of vegetation samples and 3-min samples are given for the plantations of each study area larger than 100 ha in size. In addition, the size distribution of all plantations found in each study area (both according to their numbers and to the area covered by them) is also provided. See text for further details

	Size range (ha)	*n*	Average plantation size (ha)	Average no. 3-min samples	Average no. vegetation samples	Plantations available (%)	
						By number	By area
Northern study area							
	0·1–2·0	20	1·05 ± 0·47	5·85 ± 1·95	2·35 ± 0·67	63·4	1·7
	2·1–10·0	11	4·79 ± 2·18	10·55 ± 3·78	3·91 ± 0·70	30·2	3·6
	10·1–100·0	6	37·21 ± 21·08	23·00 ± 11·54	9·17 ± 2·40	4·7	5·5
	> 100 ha	1	136	2·5 km	18		
		1	137	4·0 km	18	1·7	89·2
		1	6775	10·9 km	30		
						n = 232	8029·2 ha
Southern study area							
	0·1–2·0	22	0·77 ± 0·49	4·86 ± 1·55	1·68 ± 0·48	75·3	3·6
	2·1–10·0	12	3·48 ± 1·61	9·25 ± 4·14	3·75 ± 0·75	15·3	3·8
	10·1–100·0	11	39·00 ± 23·03	18·55 ± 6·61	10·00 ± 3·32	7·6	21·0
	> 100 ha	1	230	3·6 km	32		
		1	610	31 samples	42	1·8	71·7
		1	842	5·0 km	49		
						n = 170	2346·8 ha

The majority of plantations in both study areas are mature stands planted some 50 years ago, whose management consists of selective thinning and light grazing by sheep. Current tree density varies between 400 and 1600 trees ha^{-1}, and canopy closure varies between 55% and 95%. Plantation edges are usually sharp and almost shrubless, partly because of the effect of sheep grazing and partly because the surrounding arable lands are ploughed as close to tree trunks as possible in most cases. The main understorey shrub species are *Q. coccifera* L. and *Genista scorpius* (L.) DC in San Clemente and *Retama sphaerocarpa* (L.) Boiss. in Carpio del Campo, together with saplings of pines and, less frequently, holm oaks. The northern area is colder and wetter than the southern area (Font 1983).

BIRD CENSUSES

We sampled 40 plantations in the northern plateau and 48 in the southern plateau, ranging in size from 0·1 to 6775 ha (Table 1). We selected a number of plantations representative of the range of plantation sizes available in each study area, as measured on recent aerial photographs (Table 1). All large plantations (> 100 ha) were included, whereas the smaller ones were chosen randomly after excluding some plantations because of difficult access or unusual use (i.e. recreation or waste disposal). The size of each plantation, as well as distance to the nearest plantation larger than 100 ha (which could act as 'sources' of dispersing individuals), was measured on aerial photographs. The distances measured were the linear distances between the nearest edges of each pair of plantations.

We ascertained the species composition of bird populations in each plantation during the 1994 breeding season (April–June). We recorded the presence/absence of each bird species during two to three visits to each plantation on average, evenly distributed throughout the study period (e.g. Hinsley *et al.* 1996 and Tellería & Santos 1997 for similar procedures). Some small plantations were visited more than three times to confirm the breeding status of the birds found there, while the largest plantations (> 100 ha), because of time constraints, were censused only once after the arrival of the latest long-distance migrants had been confirmed. We did not attempt to measure the abundance of breeding birds because comparisons of abundance estimates between habitat patches of widely differing sizes are misleading (reviewed by Haila 1988 and Opdam 1991).

Censuses were made early in the morning, with some additional late afternoon visits to small plantations. We noted the presence of every bird species as well as any indication of breeding activity within the plantation (singing males, territorial behaviour, nest construction or provisioning, occupied nests, etc.). Small- to medium-sized plantations (0·1–80 ha), plus one plantation larger than 100 ha, were searched by walking a route that was established to get to within 100 m of every point in the plantation in each visit (Sutherland 1996). Routes comprised a number of consecutive 3-min long samples. The number of samples per visit was established according to a logarithmic scale of the size of each plantation, and results obtained in each visit were pooled together. The three largest plantations (> 100 ha) found in the northern study area and two of the three found in the southern area were censused by means of line transects to obtain, in addition to presence/absence data, an estimate of the regional abundance (number of birds per km) of each bird species in each geographical location (for a similar procedure see Tellería & Santos 1997). Both routes and line transects were established to sample the edges and the interior of each plantation.

In order to ascertain whether the list of species obtained for each plantation was complete, we plotted the cumulative number of species against the number of 3-min samples performed in each plantation. For transect counts, we examined the rarefaction curves (James & Rathburn 1981) relating the number of species with the number of individuals detected. These curves reached asymptotic values for all plantations, thus indicating that all lists were complete (i.e. few or no new species would have been found by increasing sampling effort).

Some records were excluded from the lists of breeding species according to the following criteria. (i) Raptors and owls were not detected reliably with our census technique, so they were not considered. (ii) Some of the species detected did not breed at all in the plantations studied, either because they nested in open areas and visited forests only occasionally (stone curlew *Burhinus oedicnemus* L.) or because they were late-season migrants that did not breed in the study areas (Bonelli's warbler *Phylloscopus bonelli* Vieillot, spotted flycatcher *Muscicapa striata* Pallas and pied flycatcher *Ficedula hypoleuca* Pallas, which were detected in April June but did not breed, as ascertained by means of systematic searches in July). (iii) Some species records obtained for the smallest plantations (< 1 ha) could have come from transient individuals breeding in some other plantation nearby (Hinsley *et al.* 1995). To avoid this potential bias, such records were considered only when we obtained direct evidence for breeding in the plantation (e.g. nest construction or provisioning behaviour, occupied nests) or when we detected the species on at least two different visits (out of 3–5).

We classified the species found into three groups according to their dependency on forest habitats during breeding. (i) Ubiquitous species, such as pigeons, shrikes, sparrows and some finches, are able to nest and feed in other habitat types apart from forest (e.g. isolated shrubs, field margins or even croplands). (ii) Forest generalists, such as thrushes, some corvids and most finches, breed in forests but can also exploit the agricultural matrix surrounding them. Most forest generalist species are tree- or shrub-nesters and ground-feeders. (iii) Forest specialists, such as *Sylvia* warblers and pariforms (tits and allies), are restricted to forests habitats both for nesting and feeding. They place nests on trees and shrubs, and forage in tree and shrub canopies as well as on tree trunks and branches (see Møller 1987; van Dorp & Opdam 1987; Harms & Opdam 1990; McCollin 1993 for a full discussion of criteria for species' groupings in studies of forest fragmentation). We classified the *Sylvia* warblers typical of shrublands and open woodlands (e.g. *S. undata* Boddaert and *S. hortensis* Gmelin) as forest specialists since they are only found in the woodlots and plantations of the Spanish plateaux. This is due to the almost complete absence of any woody vegetation outside such forest patches.

VEGETATION STRUCTURE

The vegetation structure of plantations was characterized immediately after bird censuses were completed. We measured a number of variables on circular sample units of 25-m radius, which were uniformly distributed across each plantation. The number of sample units per plantation was established according to a logarithmic scale of its size. Variables were selected following Morrison, Marcot & Mannan (1992) and Tellería & Santos (1997) (Table 2). Cover variables, as well as the average height of trees and shrubs, were estimated visually by the same observer in order to avoid interpersonal errors (Prodon & Lebreton 1981).

The original number of vegetation variables was summarized into a few independent factors by means of a principal component analysis carried out on the average values of each variable for each plantation. Variables were normalized prior to analysis by angular (covers) or logarithmic transformations (Zar 1984). This procedure was established to reduce multicolinearity in the multivariate analysis of bird responses to plantation traits (see below and Hinsley *et al.* 1995).

DATA ANALYSIS

The dependency of the species richness of breeding birds on the geographical location, size, distance to the nearest large plantation and vegetation structure of plantations was analysed by means of step-wise multiple regressions (Neter, Wasserman & Kutner 1985). We performed separate analyses for total species richness, richness of forest species (both generalists and specialists) and of forest specialists only. The location of the study area (northern or southern plateau) was included in the regression model as a dummy variable. The size of the plantations (in ha) and their distance to the nearest plantation larger than 100 ha (in m) were normalized by means of logarithmic transformations. Vegetation structure of each plantation

Table 2. Variables describing the structure of the vegetation in the plantations studied, and factor loadings of each individual variable in the two first factors obtained in the principal component analysis of the vegetation structure of plantations

Variable	Description	PC1	PC2
BARECOV	Cover of bare ground (%)	0·393**	0·224*
HERBCOV	Cover of herbaceous plants (%)	−0·800***	0·091
SSHRCOV	Cover of shrubs less than 50 cm tall (%)	0·807***	0·297**
LSHRCOV	Cover of shrubs more than 50 cm tall (%)	0·850***	0·177
SHRHEIGHT	Average height of shrubs (cm)	0·763***	0·167
TREECOV	Cover of trees (%)	−0·203	−0·801***
TREEHEIGHT	Average height of trees (m)	−0·392***	0·186
NTREE1	Number of trunks less than 10 cm d.b.h. (no. ha^{-1})	0·795***	−0·018
NTREE2	Number of trunks between 10 and 30 cm d.b.h. (no. ha^{-1})	0·000	−0·757***
NTREE3	Number of trunks between 30 and 50 cm d.b.h. (no. ha^{-1})	−0·559***	0·204
NTREE4	Number of trunks more than 50 cm d.b.h. (no. ha^{-1})	0·009	0·298**
PINCOV	Cover of pines *Pinus* spp. (%)	−0·168	−0·794***
OAKCOV	Cover of holm oaks *Quercus ilex* (%)	0·500***	0·395***
TREESPP	Number of tree species	0·466***	0·354***
SHRSPP	Number of shrub species	0·808***	0·244*
	Eigenvalue	5·04	2·56
	% variance	33·6	17·0

***$P < 0·001$, **$P < 0·01$, *$P < 0·05$, $n = 88$.

was measured as the factor scores in the first two principal components obtained in the multivariate analysis of vegetation traits described above.

The distribution of individual bird species in plantations was modelled by means of step-wise logistic regressions. This technique estimates the dependency of a binary variable from a set of independent or predictor variables, which can be either discrete or continuous (Hosmer & Lemeshow 1989; see Hinsley *et al.* 1995 for a similar approach). In our case, we estimated the probability of occupancy of plantations of each breeding bird species (scored as 1 if occupied and 0 if unoccupied) from the location of the plantations (scored as 1 for the northern plateau and 0 for the southern plateau), the size of the plantations (log-transformed), their distance to the nearest large plantation (log-transformed), and their vegetation structure as measured by the first two principal components of vegetation traits. All species occurring in less than 10 plantations were excluded because of low sample size. This latter criterion was relaxed to less than five plantations in the case of forest specialists because of their particular interest (see Hinsley *et al.* 1995 for a similar procedure).

The relationship between the changes in the patterns of occupancy and the changes in regional densities between the two study areas was analysed by means of a linear regression between the differences in regional density between the northern and southern study areas (independent variable) and the differences in the proportion of plantations occupied by each bird species between such study areas (dependent variable). All species whose relative abundance could not be measured in either study area were excluded. Differences among species groups were tested by means of an ANCOVA (Neter, Wasserman & Kutner 1985). Normality of variables was checked before analyses by means of the Kolmogorov–Smirnov test (Zar 1984).

Results

SAMPLING EFFORT AND NUMBER OF SPECIES OF BREEDING BIRDS

Overall we found 46 species of birds breeding in the plantations, 44 in the northern and 35 in the southern study areas (Table 3). Out of these, 23 (52·57%) and 19 (54·29%), respectively, were ubiquitous species; 11 (25·00%) and 10 (28·57%) were forest generalists; and only 10 (22·73%) and six (17·14%) were forest specialists. These proportions did not differ among study areas ($\chi^2_2 = 0·409$, $P = 0·815$).

VEGETATION STRUCTURE

The first two factors derived from the principal component analysis of vegetation structure accounted for 50·6% of the variance of the original data set. The first factor (PC1; 33·6% of the original variance of the data set) was positively correlated with cover of shrubs, oaks and small trees, with shrub height, and with the number of tree and shrub species, and negatively correlated with cover of herbs and large trees as well as with tree height (Table 2). It separated shrubby plantations with high plant diversity from plantations dominated by large trees with an open understorey. The second factor (PC2; 17·0% of variance) was positively correlated with the amount of bare ground, shrubs and oak, and with the number of species of trees and shrubs, and negatively with the proportion of medium-sized trees (which are the most frequent size class of planted pines) and pines. It separated tree

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Table 3. The bird species found breeding in pine plantations in the two study areas. Species were classified as ubiquitous (U), forest generalist (G) and forest specialist (S) according to their dependency on forest habitats during breeding (see text for further details). The number of plantations occupied in each study area (out of 40 and 48 for the northern and southern plateau, respectively), the area of the smallest plantation occupied in each plateau (in ha), and the regional densities (no. birds km^{-1}, as measured on line transects covering 17·4 and 8·6 km in the northern and southern plateau, respectively) are also shown for each bird species

		No. plantations occupied		Smallest plantation		Regional density	
Bird species	Group	North	South	North	South	North	South
Alectoris rufa (*Alru*) Red-legged partridge	U	2	5	1·76	1·00	–	0·20
Columba oenas (*Cooe*) Stock dove	U	1	2	6775·00	26·80	0·09	–
C. palumbus (*Copa*) Wood pigeon	U	30	42	0·80	0·20	3·79	2·33
Streptopelia turtur (*Sttu*) Turtle dove	U	12	21	1·24	0·50	0·43	0·34
Clamator glandarius (*Clgl*) Great spotted cuckoo	U	6	2	1·16	2·30	–	0·14
Cuculus canorus (*Cuca*) Common cuckoo	U	4	4	27·28	7·80	0·10	0·20
Caprimulgus europaeus (*Caeu*) European nightjar	U	3	0	32·00			
C. ruficollis (*Caru*) Red-necked nightjar	U	1	3	62·00	1·00	–	0·20
Upupa epops (*Upep*) Hoopoe	U	26	12	1·04	2·00	0·67	–
Picus viridis (*Pivi*) Green woodpecker	U	7	14	1·76	1·00	0·26	0·54
Dendrocopos major (*Dema*) Great spotted woodpecker	S	11	4	1·16	26·30	1·78	0·38
Galerida theklae (*Gath*) Thekla lark	U	1	0	5·84	–	–	–
Lullula arborea (*Luar*) Wood lark	G	16	12	1·16	0·20	2·55	0·58
Erithacus rubecula (*Erru*) Robin	G	1	0	137·00	–	0·25	
Luscinia megarhynchos (*Lume*) Nightingale	G	0	4	–	2·00	–	0·14
Turdus merula (*Tume*) Blackbird	G	12	14	1·24	1·00	0·63	2·87
T. viscivorus (*Tuvi*) Mistle thrush	G	14	7	1·24	5·10	1·95	0·82
Sylvia undata (*Syun*) Dartford warbler	S	0	5	–	1·80	–	0·90
S. cantillans (*Syca*) Subalpine warbler	S	9	13	1·04	2·80	0·40	0·82
S. hortensis (*Syho*) Orphean warbler	S	2	6	26·00	13·20	0·09	1·36
Aegithalos caudatus (*Aeca*) Long-tailed tit	S	5	11	26·00	2·30	0·70	1·04
Parus ater (*Paat*) Coal tit	S	5	0	26·00	–	2·43	–
P. cristatus (*Pacr*) Crested tit	S	1	0	6775·00		1·01	
P. caeruleus (*Paca*) Blue tit	S	10	0	1·04	–	1·24	–
P. major (*Pama*) Great tit	S	13	15	1·04	2·00	0·97	4·18
Regulus ignicapillus (*Reig*) Firecrest	S	1	0	6775·00	–	0·09	–
Certhia brachydactyla (*Cebr*) Short-toed treecreeper	S	17	0	1·04	–	3·01	–
Oriolus oriolus (*Oror*) Golden oriole	G	8	6	4·12	26·30	0·33	
Lanius excubitor (*Laex*) Great grey shrike	U	3	0	1·16	–	–	–
L. senator (*Lase*) Woodchat shrike	U	21	4	1·04	4·80	1·26	0·28
Garrulus glandarius (*Gagl*) Jay	G	1	3	32·00	230·00	–	0·24
Cyanopica cyana (*Cycy*) Azure-winged magpie	G	15	0	0·40	–	1·79	–
Pica pica (*Pipi*) Magpie	U	4	11	0·80	0·40	–	0·14
Corvus corone (*Cvco*) Carrion crow	U	13	11	1·16	2·00	0·34	2·18
C. corax (*Crcx*) Raven	U	2	0	4·40	–	–	–
Sturnus unicolour (*Stun*) Spotless starling	U	17	3	1·16	7·80	0·14	
Passer domesticus (*Pado*) House sparrow	U	2	3	1·76	7·80	–	–
P. montanus (*Pamo*) Tree sparrow	U	16	1	0·40	1·90	1·30	–
Petronia petronia (*Pepe*) Rock sparrow	U	7	6	0·76	1·00	2·28	
Fringilla coelebs (*Frco*) Chaffinch	G	30	24	0·40	0·80	4·53	5·54
Serinus serinus (*Sese*) Serin	G	19	15	0·76	1·00	4·17	1·16
Carduelis chloris (*Cach*) Greenfinch	G	14	8	1·04	16·60	1·44	1·64
C. carduelis (*Cacd*) Goldfinch	U	17	21	0·76	1·00	1·19	2·01
C. cannabina (*Cacn*) Linnet	U	9	19	1·04	0·20	0·29	2·47
Coccothraustes coccothraustes (*Cccc*) Hawfinch	G	13	2	1·04	4·80	3·46	–
Emberiza cirlus (*Emci*) Cirl bunting	U	2	1	4·12	26·80	–	–

plantations dominated by pines from those including other plant species and bare ground. Hence PC2 can be interpreted as an inverse gradient of pine and tree dominance, whereas PC1 can be interpreted as an inverse gradient of the intensity of management (grazing, thinning and/or understorey removal) or, less likely, the relative age of plantations within the range covered (nearly all plantations appeared in the first aerial photographs of the study areas taken 50 years ago).

CORRELATES OF BIRD SPECIES RICHNESS

The breeding bird diversity maintained by plantations was significantly related to geographical location (northern or southern plateau), size, and vegetation structure of plantations. Species richness was higher in the plantations of the northern plateau, and increased with the size of plantations as well as with the cover of plant species other than pines (inverse of PC2) (Table 4). However, these trends changed when ubiquitous species were deleted from the analysis. The richness of forest species (both generalist and specialist) was not affected by the vegetation structure of plantations. Richness was larger in the northern plateau than in the southern, it decreased as the isolation of plantations increased, and it was strongly affected by the size of plantations (Table 4). In fact, plantation size alone accounted for 67–75% of the variation in species richness among plantations for each study area, irrespective of species groups (Table 4 and Fig. 1).

RESPONSES OF INDIVIDUAL BIRD SPECIES

We were able to derive logistic regression models for the patterns of presence/absence of 30 bird species out of the 46 detected (see the Appendix). All models were highly significant ($P < 0{\cdot}001$) and accurate (78–97% of plantations were correctly classified as either occupied or unoccupied). Patterns of presence/absence were mostly explained by the size of plantations. The probability of occupancy increased with plantation size for most species (87%), whereas the probability of occupancy for the remaining four species was not affected by plantation size but by the vegetation structure, the degree of isolation and/or the geographical location of plantations. Plantation size was the only trait related to the probability of occupancy of plantations for seven species, whereas the remaining 19 were also affected by vegetation structure, degree of isolation and/or geographical location of plantations (see the Appendix). Overall, the probability of occupancy increased as the size and floristic diversity of plantations increased, and younger/less intensively managed plantations were more readily occupied by breeding bird species. The probability of occupancy was larger for plantations located close to large reafforestation in the northern plateau, although there were some species that showed opposite trends relative to the geographical location and isolation of plantations (see the Appendix).

The differences in the patterns of occupancy of plantations between the two study areas were related to between-area differences in regional densities (Fig. 2). This relationship did not differ among ubiquitous species, forest generalists and forest specialists ($F_{2,36} = 0{\cdot}249$, $P = 0{\cdot}781$; ANCOVA with species group as the classification factor and differences in regional densities as the covariate; $F_{1,36} = 11{\cdot}887$, $P = 0{\cdot}002$ for the covariate, and $F_{2,36} = 0{\cdot}237$, $P = 0{\cdot}790$ for the interaction term). Out of the 40 species included in the analysis, 18 (45%) were more abundant and distributed in the northern study area, whereas 12 (30%) were more abundant and distributed in the southern study area, and 10 (25%) showed inverse abundance–distribution relationships (Fig. 2). Hence more species showed decreasing abundance and distribution among study areas in a southwards rather than in a northwards direction ($\chi^2_1 = 8{\cdot}187$, $P = 0{\cdot}004$).

Table 4. Step-wise multiple regression models (F-to-enter = 4·0; F-to-remove = 2·0; Neter, Wasserman & Kutner 1985) for the dependence of the richness of breeding birds on the geographical location of plantations, their size, their distance to the nearest forest larger than 100 ha, and the structure of the vegetation ($n = 88$ plantations). Results are shown separately for all bird species, for forest species (both generalist and specialist), and only for forest specialists (Table 3). See text for further details

Independent variable	Coefficient	SE	% variance	P
All species				
Constant	3·234	0·518		< 0·0001
Plantation size	6·589	0·437	75·04	< 0·0001
Geographic location	3·566	0·691	4·50	< 0·0001
PC2	1·518	0·392	2·89	0·0002
Model			82·43	< 0·0001
Forest species (both generalist and specialist)				
Constant	4·818	1·252		0·0002
Plantation size	3·648	0·366	70·53	< 0·0001
Geographic location	1·771	0·495	4·67	0·0005
Distance to the nearest large forest	−1·157	0·331	2·90	0·0007
Model			78·10	< 0·0001
Forest specialists only				
Constant	1·705	0·616		0·0070
Plantation size	1·575	0·180	67·34	< 0·0001
Distance to the nearest large forest	−0·450	0·163	3·19	0·0070
Geographic location	0·505	0·244	1·10	0·0414
Model			71·63	< 0·0001

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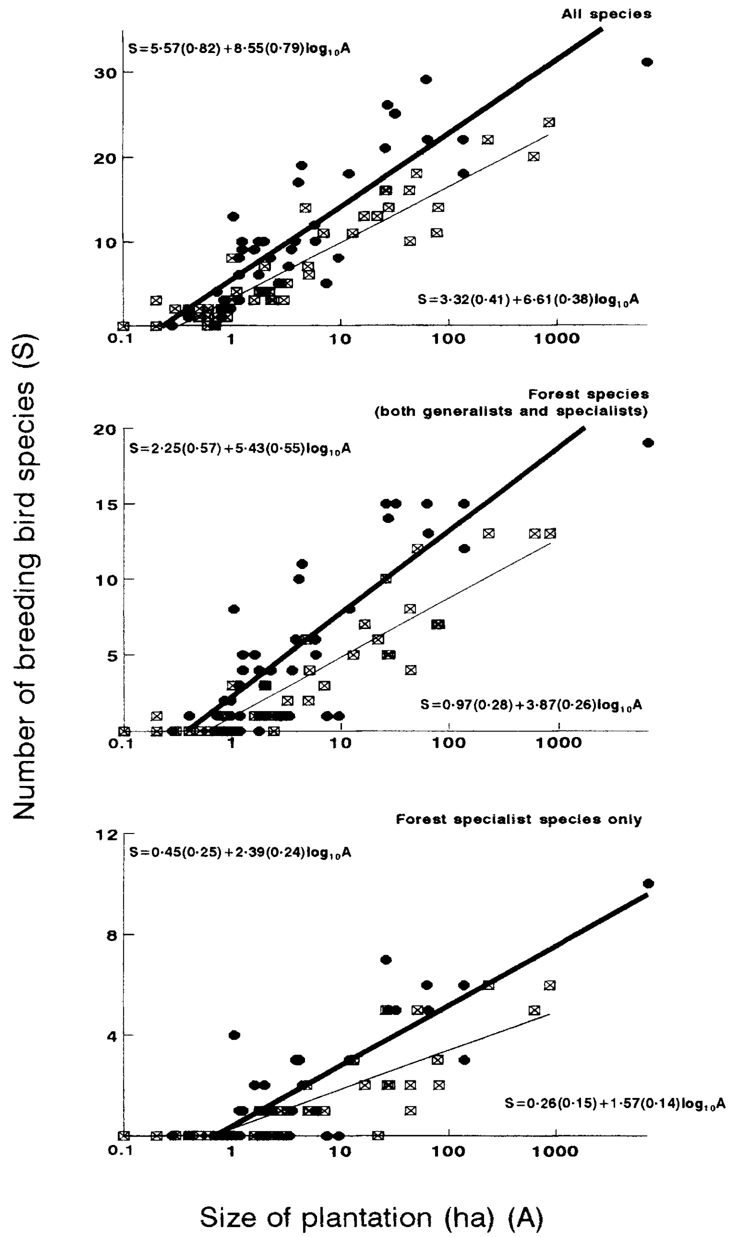

Fig. 1. Species–area relationships for the bird communities breeding in plantations in both the northern Spanish plateau (thick line, dots) and in the southern plateau (thin line, crossed squares). The statistical models shown in the upper left inside axes of the graphs describe the species–area relationships for the northern plateau, whereas those shown in the lower right inside axes describe the corresponding relationships for the southern plateau. Figures in parentheses are the standard errors of the estimates of model parameters. Results for the whole set of species, for forest species (both generalists and specialist) and for forest specialists only are shown separately (see text and Table 3 for further details).

Discussion

The breeding bird communities within pine plantations on former arable land in the Spanish plateaux were significantly affected by management factors (landscape and vegetation traits) and factors acting at broad biogeographical scales (i.e. changes in regional bird abundances).

Landscape traits, especially plantation size, were the main correlates of breeding bird diversity between plantations. In fact, plantation size explained most of the between-plantation variation in bird species richness irrespective of geographical location or the birds' dependence on forest habitats for nesting and/or foraging. Further, plantation size was also the main, and even the only, trait associated with the presence/absence of most individual bird species in plantations. Small plantations supported poorer breeding bird communities, and the probability of being occupied by particular bird species also decreased with decreasing size. The degree of isolation of plantations had an additional negative effect on the richness of both generalist and specialist forest bird species (but not ubiquitous species), as well as on the

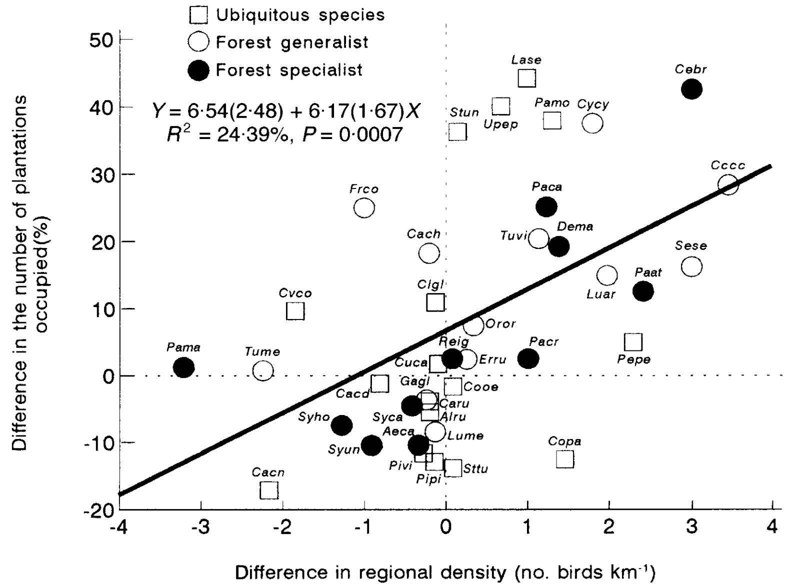

Fig. 2. Relationships between the differences in regional density between study areas and the differences in the proportions of plantations occupied by each bird species ($n = 40$, since the remaining six species were not detected within line transects in either study area; see Table 3). Figures in parentheses in the regression model are the standard errors of the estimates of model parameters. Negative values indicate larger densities or proportions of plantations occupied in the southern plateau compared with the northern one, while positive values show the opposite.

probability of occupancy by some species. All these findings closely resemble the patterns found in fragmented natural forests, and the processes underlying them are probably similar in the case of re-afforestation. Large forest tracts are able to support rare species, provide a larger diversity of habitats, and are less affected by edge effects compared to small tracts. On the other hand, distant woodlots are less likely to be colonized by dispersing individuals than woodlots located near large forest tracts (e.g. Howe 1984; Blake & Karr 1987; van Dorp & Opdam 1987; Bellamy, Hinsley & Newton 1996).

From these findings, it is suggested that plantations should be as large as possible if the build-up and maintenance of rich bird communities is among the goals of re-afforestation. However, it seems clear that this is not the case for current re-afforestation schemes in Spain. The size distribution of plantations in the two Spanish plateaux was strongly skewed towards very small stands (0·1–2 ha; Table 1) and these small plantations only maintained 6–14% of the forest bird species breeding in plantations (Table 5). This size distribution of plantations did not fit the size distribution of landholdings, which is dominated by medium-sized farms (15%, 38%, 40% and 7% of the landholdings are in the size classes of < 2, 2–10, 10–100 and > 100 ha, respectively; $n = 303803$ landholdings in Castilla-La Mancha, Castilla-León and Madrid regions; Instituto Nacional de Estadística 1993). These figures show that landowners allocate only part of their lands to re-afforestation, a trend that is encouraged in Spain by the policy of paying higher re-afforestation subsidies (on a per hectare basis) for plantations smaller than 25 ha (Castellano & Cifuentes 1994).

Bearing in mind the generality of mixed land-uses and the rarity of large landholdings, it seems unrealistic to expect that re-afforestation schemes would promote plantations large enough to support all forest bird species breeding in plantations of central Spain (Table 5). However, plantations smaller than 25 ha only maintained 50% of the regional pools of forest species during breeding, whereas this proportion increased to 69–86% for plantations of 25–100 ha (Table 5). In order to enhance bird diversity, plantations larger rather than smaller than 25 ha should be promoted. Additionally, the location of new plantations should take into account the isolation effects documented here. The landscape configuration of such plantations should aim to minimize the distances between new stands and large forests that could act as sources of colonizing individuals.

Vegetation traits within plantations also influenced the distribution patterns of breeding birds, although these effects were much less strong than the effects of landscape traits. Re-afforestation with denser shrub undergrowth and more plant species supported richer bird communities, as obtained in other European pine re-afforestation (Cieslak 1985) as well as in studies carried out in fragmented natural forests and woodlots (Howe 1984; Lynch & Whigham 1984; Opdam, Rijsdijk & Hustings 1985; Ford 1987).

The minor role of vegetation traits compared to landscape traits could arise from the relative structural and floristic homogeneity of plantations that are representative of managed plantations on the Spanish

Table 5. Percentage of breeding species of forest birds (generalist and specialists species combined), maintained by plantations of different size in each study area (out of 21 and 16 bird species, respectively; the number of plantations according to size class and study area are shown in parentheses). A bird species was considered to be maintained by the corresponding size class of plantations if more than 20% of plantations within such size class (that is, at least one out of five) were occupied

	Size class (ha)			
	0·1–2·0	2·1–25·0	25·1–100·0	> 100·0
Northern study area	14·3	52·4	85·7	95·2
	(20)	(12)	(5)	(3)
Southern study area	6·3	50·0	68·8	100·0
	(22)	(15)	(8)	(3)

plateaux. It is known that early stages of development of pine plantations support different bird species in relation to their changing vegetation characteristics (Helle & Mönkkönen 1985; Potti 1985; Carrascal & Tellería 1990), although such early stages are extremely transient compared to the mature, productive stage (10–15 years for the full development of plantations compared to tens and hundreds of years under thinning and light grazing exploitation regimes; Castellano & Cifuentes 1994 and references therein). Alternative exploitation regimes such as the introduction of secondary tree species, the maintenance of old and dead trees, etc., might improve the breeding bird communities supported by pine plantations through their effects on habitat traits (Tellería 1992; López & Moro 1997). However, the potential benefits of these alternative regimes for the breeding bird communities cannot be evaluated since no such regimes have been established to date.

The range of vegetation traits and bird responses could also be broadened by comparison of pine plantations with plantations of other tree species, but no such plantations exist in Spain at comparable spatial scales (Ministerio de Agricultura 1994). Preliminary comparisons with a fragmented holm oak forest located near Lerma in the northern plateau (Burgos province; 42 05′N, 3 45′W; 800–850 m a.s.l.; Tellería 1992) appear to indicate that patches of the original holm oak forest could maintain richer breeding bird communities than plantations of the same size, although such differences appear to be slight [the species–area relationship for such forests is: no. forest species $= 3{\cdot}56 + 5{\cdot}6 \log_{10}(\text{area})$ (Tellería 1992), indicating that oak forests maintain one to two more species than pine plantations of the same size]. However, it should be borne in mind that oak forest remnants in the Spanish plateaux present a shrubby structure due to intensive use (e.g. the mean tree height in Lerma's oak forests is 4·5 m compared to 8–9 m in pine plantations) so that fuller comparisons between pine and holm oak forests, including isolation, vegetation structure and location effects, will be needed to support this conclusion.

The richness of bird species breeding in plantations was also affected by the geographical location of plantations, which maintained richer bird communities in the northern area. This may be interpreted according to the observed relationships between the regional densities of species and their ability to occur in fragments (Lawton 1993). Higher regional densities tend to produce higher rates of fragment occupation and hence higher numbers of species per fragment. Since regional densities of most forest birds tend to decrease southwards in the Iberian Peninsula (Tellería & Santos 1994), the patterns observed in the plantations studied could have been caused by such differences in regional abundances. Significant relationships between geographical differences in regional abundances and the ability of species to occupy fragments have been also suggested for fragmented natural forests at a continental scale, as supported by the higher rates of fragment colonization in England compared to Spain (Santos & Tellería 1997). Comparisons between our results and those obtained in Polish pine plantations on former arable land (Cieslak 1985) also support the generality of this pattern, since Polish plantations maintain 5–7 and 6–11 more species than Spanish plantations of 1 and 10 ha, respectively. In short, the biogeographic trends shown by the regional densities of birds, which are caused by broad biogeographic processes not susceptible to direct management (Brown 1995), act to restrict the potential importance of the pine plantations for forest bird communities in the Spanish plateaux.

In summary, it seems that re-afforestation on former arable land in the Spanish plateaux has little scope for building-up and maintaining rich forest bird communities. This is mainly due to the marginal location of the Iberian Peninsula within the distribution ranges of most forest birds, as well as the socio-economic restrictions on the size of new plantations. These limitations could be alleviated somewhat by reducing the isolation of small plantations, and by managing vegetation structure within plantations to increase their suitability for forest birds.

However, it should be noted that plantations also have negative effects on the conservation of bird communities since they exclude those species typical of the dry cereal croplands that they replace. Hardly any of these species enter plantations, and there is no information about the area around plantations that may be affected. Bearing in mind the high conservation value of dry grassland bird communities (Suárez, Naveso & de Juana 1997) and the limited scope for re-afforestation to support species-rich forest bird communities, this change in land use cannot be recommended as a means to protect the regional diversity of birds on the Spanish plateaux. A full analysis is needed to evaluate the overall environmental benefits of large-scale afforestation programmes.

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Appendix

Step-wise logistic regression models (P-to-enter = 0·05, P-to-remove = 0·10) for the probability of occupancy of plantations by each bird species as a function of the location (LOCATION: 1, northern plateau; 0, southern plateau), the size (SIZE, in ha, log-transformed), the distance to the nearest plantation larger than 100 ha (DISTANCE, in m, log-transformed) and the two multivariate gradients of vegetation structure (PC1 and PC2) of plantations. Models are of the form: P(occupancy) = $1/(1 + e^{a+b_1X_1+b_2X_2+b_3X_3+b_4X_4})$. The standard errors of the model's coefficients are given in parentheses. The percentage of plantations correctly classified as occupied [P(occupancy) > 0·5] or unoccupied [P(occupancy) < 0·5], as well as the significance level for the whole model, are also shown. See Table 3 for species abbreviations

Bird species	Model	Overall model classification (%)	χ^2	d.f.	*P*
Copa	1·37(0·43) + 1·20(0·47)LOCATION + 5·74(1·66)SIZE	88·64	39·79	2	< 0·0001
Sttu	–1·57(0·36) + 1·73(0·40)SIZE	80·68	30·18	1	< 0·0001
Upep	–5·99(1·68) – 1·77(0·42)LOCATION + 2·13(0·59)SIZE + 1·42(0·44)DISTANCE + 1·22(0·44)PC2	84·09	53·73	4	< 0·0001
Pivi	–2·41(0·46) + 1·59(0·38)SIZE	81·82	25·18	1	< 0·0001
Dema	–4·32(1·00) + 2·61(0·69)SIZE – 1·53(0·54)PC1	87·50	32·76	2	< 0·0001
Luar	–2·25(0·46) + 2·11(0·47)SIZE – 0·67(0·30)PC1	78·41	34·89	2	< 0·0001
Tume	–2·85(0·56) + 2·70(0·56)SIZE	85·23	48·81	1	< 0·0001
Tuvi	2·50(2·06) + 2·48(0·75)SIZE – 1·94(0·70)DISTANCE – 1·14(0·47)PC1	92·05	52·35	3	< 0·0001
Syun	–3·07(2·08) – 1·81(0·77)DISTANCE + 4·96(2·45)PC1	96·59	24·95	2	< 0·0001
Syca	1·18(1·71) + 1·39(0·47)SIZE – 1·11(0·52)DISTANCE	85·23	36·37	2	< 0·0001
Syho	–5·46(1·36) + 2·53(0·77)SIZE	95·45	26·02	1	< 0·0001
Aeca	–4·52(0·99) + 2·97(0·71)SIZE	92·05	44·28	1	< 0·0001
Paat	–10·76(25·70) – 5·85(25·62)LOCATION + 2·71(1·08)SIZE	95·45	23·16	2	< 0·0001
Paca	–9·14(26·71) – 6·33(26·69)LOCATION + 2·24(0·74)SIZE	95·45	33·56	2	< 0·0001
Pama	–3·05(0·61) + 3·29(0·69)SIZE	88·64	58·38	1	< 0·0001
Cebr	–7·34(17·17) – 6·07(17·16)LOCATION + 1·74(0·64)SIZE	84·09	43·65	2	< 0·0001
Oror	–3·72(0·74) + 2·09(0·52)SIZE	86·36	29·73	1	< 0·0001
Lase	–2·67(0·70) – 2·42(0·62)LOCATION + 1·39(0·58)SIZE + 1·54(0·58)PC2	85·23	52·71	3	< 0·0001
Cycy	–8·30(16·09) – 6·41(16·07)LOCATION + 2·34(0·78)SIZE	88·64	44·61	2	< 0·0001
Pipi	–2·05(0·41) + 1·28(0·43)PC1	85·23	12·95	1	0·0003
Crco	–7·01(1·86) + 3·17(0·72)SIZE + 1·15(0·43)DISTANCE – 0·94(0·35)PC1	82·95	39·90	3	< 0·0001
Stun	–2·69(0·62) – 0·63(0·51)LOCATION + 1·36(0·45)SIZE – 1·10(0·54)PC1	84·09	29·53	3	< 0·0001
Pamo	–0·15(0·98) – 1·77(0·56)LOCATION – 0·71(0·33)DISTANCE	82·95	27·98	2	< 0·0001
Pepe	–2·23(0·42) + 1·29(0·40)PC2	85·23	14·29	1	0·0002
Frco	3·25(1·85) + 2·47(0·65)SIZE – 1·11(0·54)DISTANCE – 0·76(0·31)PC1	87·50	44·05	3	< 0·0001
Sese	5·82(2·12) + 2·92(0·74)SIZE – 2·50(0·71)DISTANCE	88·64	67·85	2	< 0·0001
Cach	5·20(2·80) + 5·33(1·70)SIZE – 3·71(1·24)DISTANCE – 2·50(0·94)PC1	94·32	73·19	3	< 0·0001
Cacd	2·63(1·63) + 1·90(0·51)SIZE – 1·21(0·49)DISTANCE	85·23	43·87	2	< 0·0001
Cacn	–2·33(0·46) + 0·65(0·32)LOCATION + 2·16(0·47)SIZE	89·77	41·46	2	< 0·0001
Cccc	–3·47(0·76) – 1·67(0·53)LOCATION + 1·62(0·50)SIZE	89·77	29·06	2	< 0·0001