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GEOGRAPHICAL, LANDSCAPE AND HABITAT EFFECTS ON BIRDS IN NORTHERN SPANISH FARMLANDS: IMPLICATIONS FOR CONSERVATION

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SUMMARY.—*Geographical, landscape and habitat effects on birds in northern Spanish farmlands: implications for conservation.*

Aims: Farmland habitats in northern Spain are local hotspots of bird richness, sustaining various increasingly rare species and housing huge numbers of migratory birds in winter. This makes them a key habitat for bird conservation. However, they are being negatively affected by conversion to tree plantations, urban developments and infrastructures.

Location: Bird communities in 67 farmland patches which were immersed in a matrix of shrublands and woodlands were studied. These were distributed along a 600 km-long stretch that runs parallel to the northern Spanish coast.

Methods: During June (2005) and January (2006) evaluation was carried out on the effect of farmland patch size, vegetation structure, elevation (a surrogate of climate harshness) and geographical location of farmlands on bird richness and abundance by means of 500 m long transects.

Results: Farmland patches with abundant tree and shrub cover scored the highest on abundance and species richness in spring. The size of farmland patch predicted the occurrence of many species in spring and winter, including some that are declining in Europe (e.g. *Lanius collurio*, *Passer montanus*, *Miliaria calandra*, *Alauda arvensis,* etc.). In winter, bird abundance increased at low elevation areas and decreased with increasing distance from the main gateway for European migrants entering the Iberian Peninsula at the western Pyrenees.

Conclusions: Results support the idea that easternmost farmlands are particularly important wintering grounds for European migrants and that the increasing deterioration or reduction of lowland farmland patches may affect bird populations. Because such negative effects are likely to increase in the near future, some general guidelines are suggested to apply the legal and budgetary resources of the European Union for better preserving farmland biodiversity in Northern Spain.

Key words: biodiversity, Common Agricultural Policy (CAP), land-use change.

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RESUMEN.—*Efectos geográficos, paisajísticos y de hábitat sobre las aves de las campiñas del norte de España: implicaciones conservacionistas*.

Objetivos: Las campiñas atlánticas del norte de España presentan una gran riqueza local de especies, mantienen aves que están rarificándose y albergan muchas aves migratorias durante el invierno, lo que las convierte en un hábitat importante desde una perspectiva conservacionista. Sin embargo, están siendo alteradas por la expansión de las plantaciones de árboles, así como por el desarrollo urbano y de diferentes infraestructuras.

Localidad: Para evaluar los efectos de estos cambios sobre las aves de las campiñas, se estudiaron 67 localidades distribuidas a lo largo de 600 Km. localizadas entre las montañas y las costas cantábricas.

Métodos: Durante junio de 2005 y enero de 2006 se evaluó, por medio de transectos de 500 m de largo, el efecto del tamaño de la campiña, la estructura de su vegetación, la altitud (un índice de la dureza climática) y la ubicación geográfica sobre la riqueza y abundancia de aves.

Resultados: Las campiñas con más cobertura de árboles y arbustos presentaron las mayores riquezas y abundancias de aves en primavera. El área de la campiña fue un buen indicador de la presencia de muchas especies en primavera e invierno, incluyendo algunas en declive a escala europea (e.g. *Lanius collurio*, *Passer montanus*, *Miliaria calandra*, *Alauda arvensis,* etc.). En invierno, la abundancia de aves aumentó en las campiñas ubicadas a bajas altitudes y disminuyó al aumentar la distancia al corredor migratorio pirenaico.

Conclusiones: Estos resultados, que apoyan la idea de que las campiñas orientales tienen una mayor importancia como áreas de invernada para las aves migratorias, son utilizados para predecir los efectos sobre las aves del deterioro y reducción superficial de las campiñas ubicadas a menores altitudes. Como es previsible que este deterioro aumente en el futuro, se sugerieren algunas líneas de acción para aplicar los recursos aportados por la Unión Europea para conservar la biodiversidad agraria en el norte de España.

*Palabras clave***:** biodiversidad, Política Agraria Comunitaria (PAC), cambios de uso.

INTRODUCTION

During the last decades, western European agriculture has undergone dramatic changes, which have impacted farmland biodiversity. For example, the abandonment of agricultural land has allowed woodlands and scrublands to spread at the expense of traditional farmland range. This has contributed to landscape homogenization and species loss. Also, ongoing agricultural intensification in the most productive areas is also threatening farmland biodiversity (Benton *et al.*, 2003). To stop this, the European Union (EU) has launched the Biodiversity Action Plan for Agriculture, which tries to encourage agricultural practices that are compatible with conservation (European Environmental Agency, 2006). The plan has a twofold goal, aiming to prevent further biodiversity loss where agriculture is already intensified, and to design sustainable farming where agriculture still has not been intensified. Representing the latter case, there is a general concern that some eastern European countries recently joined to the EU might lose farmland biodiversity if technological and economic incentives are aimed to just increase immediate productivity (Donald *et al.*, 2001; Báldi and Faragó, 2007; Herzon and O'Hara, 2007).

Population declines during the last decades are particularly worrying for farmland birds. They have become model species for the analysis of the effects of changing agricultural practices on farmland biodiversity (Donald *et al.*, 2001, 2007). As other organisms, birds have been affected by habitat loss and modification (for example hedgerow destruction), chemical contamination, or shortfall of various food sources (Benton *et al.*, 2003; Bradbury and Kirby, 2006). However, such negative effects on bird communities may vary between regions or types of landscape, and are also likely to

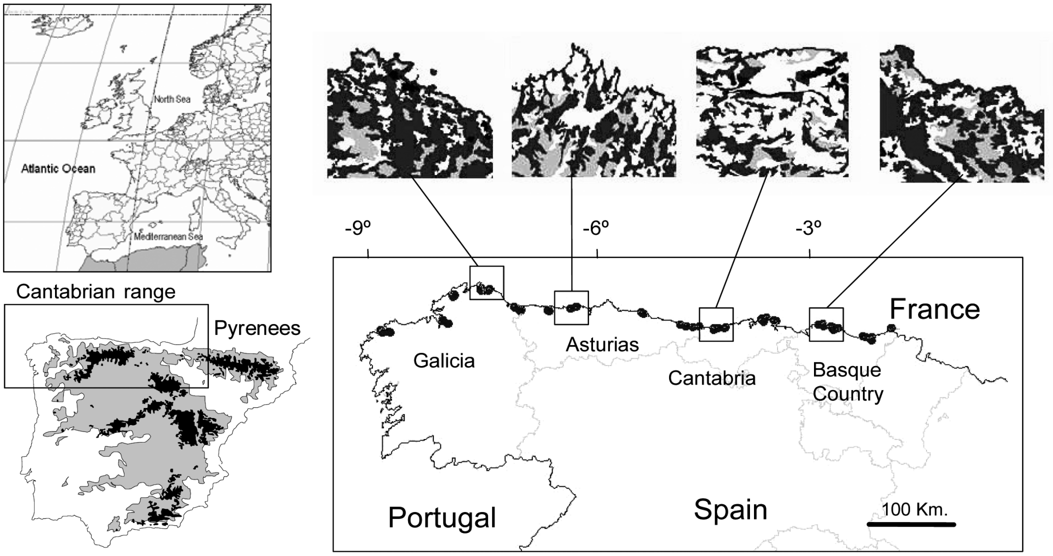

FIG. 1.—Left, location of the study area in Europe (above) and a detailed map (below) of the major topographic features of the Iberian Peninsula (grey and black shading represents areas above 500 and 1000 m, respectively). Right, distribution of study sites within the four administrative sectors considered, with selected sketches to better visualize their landscape structure (farmlands are in white, and grey and black areas refer to scrub and woodlands, respectively).
[Izquierda, ubicación del área estudio en Europa (arriba) y mapa detallado (debajo) de los principales rasgos geográficos de la península Ibérica (el sombreado gris y negro representa altitudes por encima de los 500 y 1.000 m). Derecha, distribución de los lugares de estudio dentro de las cuatro unidades administrativas consideradas, con ampliaciones parciales para visualizar mejor la estructura del paisaje (las campiñas figuran en blanco mientras que en gris y negro figuran las zonas cubiertas por vegetación arbustiva y arbórea.]

be dependent on local agricultural practices. Therefore, considering geographic, landscape and habitat determinants of bird distribution may be important to identify ongoing conservation problems at different scales (Concepción *et al*., 2008). In turn, exploring the interplay of geographic, landscape and habitat effects as determinants of farmland biodiversity may be pivotal to correctly applying the agro-environmental schemes sponsored by the EU Common Agricultural Policy (CAP).

Geographical, landscape and habitat effects on the structure of farmland bird communities across a lowland corridor that ranges from East to West in northern Spain were explored, these were bounded to south by the Cantabrian Mountains and to North by the Atlantic coast (fig. 1). Northern Spanish farmlands, the southernmost Atlantic *bocage* in Europe, are mostly devoted to hay production and cattle grazing, forming a mosaic of meadows, grazed pastures, edges and woodland, which scores the highest bird species richness among all habitats in the region (Tellería and Galarza, 1990) and attracts rare or declining species in Europe (such as *Lanius collurio* or *Miliaria calandra*). In addition, long-term monitoring of common bird species in Spain (the SACRE programme coordinated by the Spanish Ornithological Society, http://www.seo.org) is revealing the population decline of several farmland bird species, some of which already qualify as endangered in Europe (Donald *et al.*, 2001). These patterns, together with the large numbers of central and northern European migratory birds that winter in northern Spanish farmlands (Santos *et al.*, 1990), make the *bocage* farmland system an interesting habitat for conservation.

Administratively, the area encompasses four autonomous regions located by the coast of the Cantabrian Sea (Galicia, Asturias, Cantabria and Basque Country; fig. 1). The whole region is undergoing intense landscape modification due to agricultural abandonment which is affecting farmland landscapes in three major ways. First, the farmland mosaic has been substituted by homogeneous plantations of exotic trees, primarily eucalyptus and pines. Second, agricultural intensification in the remaining farmlands has removed hedgerows, or increased contamination due to fertilisers among other threats. Third, farmlands are becoming smaller and increasingly fragmented due to urban and industrial expansion, which comes together with an increasing demand for infrastructures (motorways, railways, etc.; European Environmental Agency, 2006; Observatorio de la Sostenibilidad en España, 2005). Therefore, although farmland still accounts for 30 % of land in the region, they are affected by an ongoing process of intense modification and fragmentation, particularly in some overpopulated, coastal sectors (Observatorio de la Sostenibilidad de España, 2005).

The distribution of bird richness and abundance in northern Spanish farmlands during spring and winter was modelled; this being based on geographic, landscape and habitat variables. The distribution of each bird species was also studied in order to identify which farmland features are important for the conservation of the most endangered species. This approach considered farmland patches as units which were evaluated, according to a multiscale approach (Donald and Evans, 2006): the potential effects on birds of habitat structure, landscape configuration, local climate and geographical location.

Habitat structure

The association between the structure of bird assemblages and the physiognomy and floristic traits of vegetation is a cornerstone of theoretical and applied bird population studies (Wiens, 1989). In the case of farmland birds, both species richness and abundance increase with the cover of hedgerow (Carrascal and Tellería, 1985; Hinsley and Bellamy, 2000). In addition, bird assemblages may be influenced by the existence of small orchards and ploughed fields typical of northern Spanish farmlands, because these habitat features may be important for larks, finches, buntings and other granivorous species that track seed abundance in winter (Robinson *et al.*, 2001).

Landscape configuration

Northern Spanish farmlands are located in valleys or mountain slopes, where they make up gaps of open habitat surrounded by extensive tree plantations or, less typically, by natural forests. As a consequence, many of the processes that affect bird communities in fragmented landscapes may operate similarly in northern Spanish farmlands (Ioffe *et al.*, 2004; Donald and Evans, 2006). In particular, large habitat patches usually have more species in fragmented habitats, an effect that may be generalised to most ecological contexts (Rosenzweig, 1995). Therefore, variation in farmland size might contribute to explain the distribution of species richness.

Elevation

Climate harshness affects bird distribution in temperate regions because birds tend to avoid habitats that compromise their ability to secure and maintain body reserves (Blem, 1990). Such effects may be particularly important in winter, forcing birds to avoid colder areas (Root, 1988; Carrascal and Díaz, 2006). The study area is climatically simple on a geographic scale and most variation in temperature is due to elevation, particularly during winter (Ninyerola *et al.*, 2005). Therefore, lowland farmlands might be more important habitats for wintering birds than farmlands located at higher elevations.

Geographical location

Finally, it was explored how the geographical location of farmland areas across the study region affected bird distribution. It was hypothesised that it may determine both breeding and wintering communities through two different processes. First, northern Spanish farmlands are distributed along the east-to-west corridor through which some elements of the European biota probably colonised the north of the Iberian Peninsula. For example, species richness of forest birds decreases westwards along such Atlantic corridor (Ramírez and Tellería, 2003). That similar biogeographical constraints might influence the pattern of species loss in northern Spanish farmlands was explored. Second, migratory birds seem to face greater transport cost as they have to move further from their major migratory pathways before their arrival to wintering grounds. Such effect may make western farmlands less likely to attract European migratory birds moving to winter in the Iberian Peninsula, which they access mainly through the western Pyrenees (Galarza and Tellería, 2003; Tellería *et al.*, 2008).

MATERIAL AND METHODS

Study area

The study area spans a 600 km-long belt located between the Atlantic coast and the northern slopes of the Cantabrian Mountains (fig. 1). It is a rough and rainy sector (over 1,000 mm of annual precipitation; Ninyerola *et al.*, 2005) in which the lowland countryside is occupied by farmlands, pine and eucalyptus plantations (*Pinus radiata*, *Pinus pinaster*, *Eucalyptus globulus*) and small villages, while highland areas (over 600 m) are covered by pasturelands and broadleaved forests (*Fagus sylvatica, Quercus petraea,* etc.). Climate conditions are deeply affected by the influence of mountains, which create altitudinal variation in temperature. Thus, while mountain tops are covered with snow during winter, lowlands show mild winters, particularly by the coast where mean temperatures in January range between 7 and 9 ºC (Ninyerola *et al.*, 2005).

A selection was made of 67 farmland patches (farmland areas surrounded by shrublands and woodlands with different sizes, vegetation structures and elevation) distributed from East to West along northern Spain (fig. 2), using satellite images provided by SIGPAC (a GIS facility for CAP information sponsored by the Spanish Ministry of Agriculture, http://sigpac.mapa.es/fega/visor/). The distance was measured from each farmland patch to the western Pyrenees (more precisely to the French-Spanish border by the Atlantic coast). In the field, farmland patches were located by means of GPS devices and maps.

Bird counts and vegetation structure

Samples of one to six 500 m line-transects were carried out throughout each farmland patch, depending on the size of each patch (they ranged from 2.5 to 374 ha; see fig. 2). Different teams of observers sampled birds in the first half of June 2005 (two or three teams at a time), measuring the abundance of each species (number of birds per transect). The sampling was repeated in mid January 2006 to assess the abundance of wintering birds in exactly the same transects, which were located using GPS devices. These data were used to

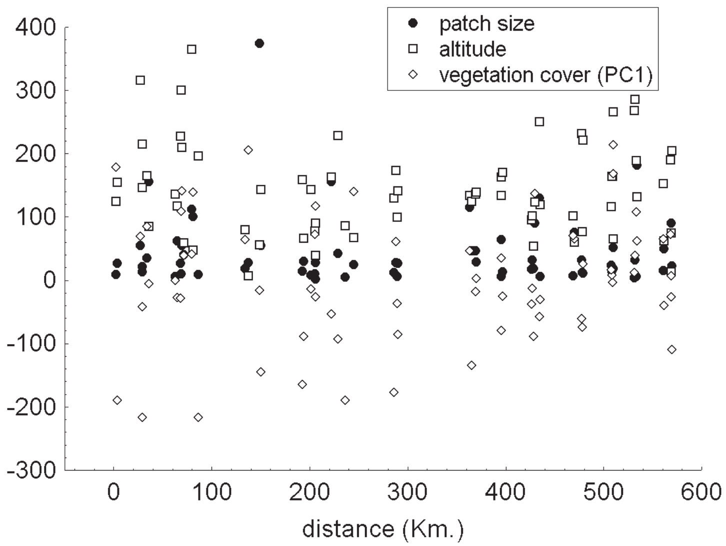

FIG. 2.—Variation in patch area, altitude and vegetation cover (as determined by factor scores in PC1; see text) of the study farmlands along the geographical gradient brought about by the location of sites at increasing distance westwards from the western Pyrenees (distance = 0 at the Spanish-French border by the Atlantic coast).

[Variación en el tamaño, altitud y cobertura vegetal (determinada por la ubicación de cada muestra en PC1, ver texto) de las campiñas estudiadas a lo largo del gradiente geográfico definido por la distancia a los Pirineos occidentales (la distancia 0 se sitúa en la frontera hispano-francesa).]

evaluate the mean number of individuals and species detected per transect in each farmland patch. In the case of larger patches, the accumulated number of species recorded in all transects within each patch were used to assess the total number of species.

The structure of vegetation in farmlands was measured by means of two 25 m radius circles distributed at 200 m intervals along each transect. In each circle, shrub cover (vegetation below 2-m height) and tree cover (vegetation above 2 m height) were estimated visually, the number of shrub and tree species counted, and the average height of the tree canopy estimated. The scores of the two sampling circles to characterize each line transect were averaged. The presence or absence of small orchards or other ploughed fields were also recorded to asses their potential role in bird distribution. Each farmland was finally characterised by averaging bird abundance and habitat characteristics measured in each transect.

Statistical analyses

A Principal Component Analysis (PCA) was conducted to reduce the number of variables used to describe vegetation structure. The PCA retained a single principal component (PC1), which explained 68.01% of variance in the correlation matrix and was interpreted as a gradient of increasing vegetation cover and tree and shrub species richness (factor loadings for number of shrub species: 0.71; shrub cover: 0.71; tree cover: 0.88; mean tree height: 0.87; number of shrub and tree species: 0.92; eigenvalue: 3.40). Farmland size, vegetation cover (as determined by PC1), elevation and distance to Western Pyrenees changed along the study sectors (fig. 2) and were not correlated with one another (all Spearman r < 0.15, *P* > 0.05, *n* = 67).

General regression models (GRM; StatSoft, 2002) were used to study how local and regional features affect bird abundance and richness. The models were obtained by means of stepwise regression, using distance, vegetation cover (PC1), farmland size and elevation as independent variables. As the abundance of local breeders may affect bird abundance and richness in winter, these variables were included in a second test with the above mentioned variables to study the features affecting the structure of bird communities in winter. Both forward and backward stepwise procedures were used, which allowed assessment of the robustness of the final models. In addition, to explore the role of ploughed fields on bird distribution, ANCOVA was conducted with the occurrence of ploughed fields as a factor and the retained variables in the GRM analyses as covariates. Finally, Discriminant Function Analyses (DFA) were conducted with forward and backward stepwise procedures to explore the factors affecting the occurrence of each species in farmlands.

RESULTS

Species composition

A total of 64 bird species were detected during the two study periods (appendix 1). The presence of swifts (*Apus apus*) and swallows (*Hirundo rustica*, *Delichon urbica*) flying over the study areas was not considered because, although they were using the farmlands during aerial feeding, it was unclear if they were actually linked to the site in which they were observed. Large birds, such as raptors (*Buteo buteo*, *Accipiter gentilis*, *Milvus milvus, Falco tinnunculus*, etc.) and gulls (*Larus michahellis*, *Larus ridibundus*) were also excluded because their large home range may include several farmland patches. Finally, two species pairs (starlings: *Sturnus unicolor* and *Sturnus vulgaris,* and chiffchaffs: *Phylloscopus collybita* and *Phylloscopus ibericus*) occurring in the area were considered as single species, because distinguishing between the two species was difficult in many cases.

In spring, bird communities were dominated by woodland species (*Turdus merula*, *Erithacus rubecula*, *Fringilla coelebs*, etc), but species typical of tree-covered farmlands were also frequent (*Carduelis carduelis*, *Carduelis chloris*, *Emberiza cirlus, Pica pica*, etc.) and species related to open fields (*Alauda arvensis, Miliaria calandra, Coturnix coturnix*) were more scarce (appendix 1).

The seasonal turnover of species involved seven wintering species replacing eight summer visitors (appendix 1). Such parity in species numbers led to a weak yet statistically significant increase in the total number of species per farmland from spring to winter (spring: 13.78 ± 0.74 species; winter: 14.96 ± 0.73 species; t-test for dependent samples, t_{66} = 2.05, *P* = 0.044). Similarly, the increase from spring to winter in the mean number of species per transect was close to statistical significance (spring: 10.26 ± 0.42 species per transect; winter: 11.14 ± 0.41 species per transect; t_{66} = 1.82, *P* = 0.074). Unlike species richness, bird numbers dramatically increased from spring to winter (spring: 23.54 ± 1.31 birds per transect; winter: 62.34 ± 4.21 birds per transect; t_{66} = 9.30, *P* < 0.001; fig. 3). Such increase was due to the arrival of wintering chaffinches (*Fringilla coelebs*), meadow pipits (*Anthus pratensis*), thrushes (*Turdus philomelos* and *Turdus iliacus*) and other migratory birds (appendix 1).

Factors affecting bird communities

During the breeding period, both abundance and richness of birds increased in farmlands with more vegetation cover, as well as in

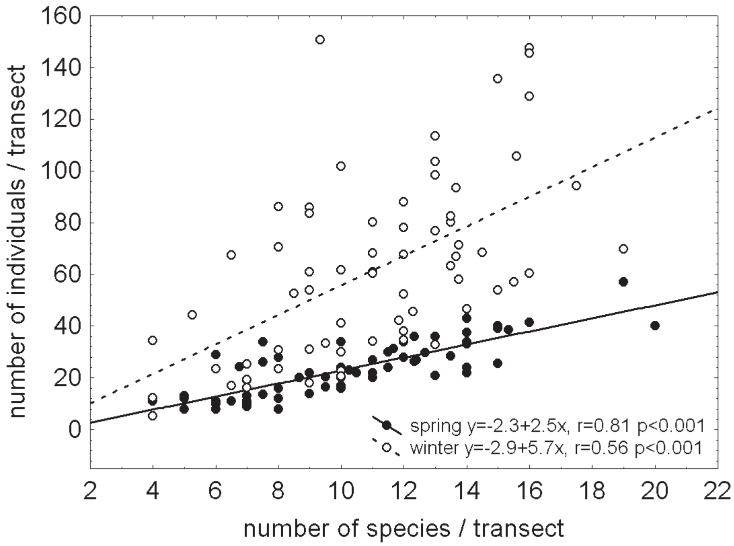

FIG. 3.—Relationships between the mean species richness (number of species per transect) and abundance of birds (number of individuals per transect) in northern Spanish farmlands, both in spring and in winter (n = 67 farmlands).
[Relaciones entre el número medio de especies (número de especies por transecto) y la abundancia de aves en las campiñas del norte de España en primavera e invierno (n = 67 campiñas).]

large farmland patches (table 1). Against predictions, species richness increased westwards, which appeared to be related to the frequent occurrence of some species in the westernmost farmlands (for example, *Carduelis chloris*, *Corvus corone*, *Emberiza cia*, *Emberiza cirlus* or *Prunella modularis*, appendix 1). Controlling for the effect of vegetation cover (table 1), the mean species richness of birds per transect was significantly higher in farmlands with ploughed fields ($F_{1,64} = 4.20$, $P = 0.045$). It was not possible to identify any influence of the occurrence of orchards on the structure of breeding bird communities.

In winter, both species richness and bird abundance increased in farmlands located at low elevation, as well as in large farmland patches. Distance also explained variation in mean abundance and species richness, with more birds wintering in eastern sectors (table 1). Controlling for the effect of spring abundance and richness, the abundance and species richness of wintering birds remained best explained by farmland size, elevation and distance to the western Pyrenées (table 1, fig. 4).

Factors affecting individual species

Size of farmland patch was the most frequently retained explanatory variable in models of individual species (20 out of 64 species were negatively affected by decreasing farmland size; appendix 1). Distance was also important, followed by vegetation cover and elevation.

DISCUSSION

General features of northern Spanish farmlands

Agricultural landscapes are usually characterised by a mosaic of land uses, where crops,

TABLE 1

Results of general regression models (GRM) in which species richness and abundance of farmland birds are analysed in function of farmland size, vegetation cover (PC1 scores), elevation and distance to the western Pyrenees. The winter model 2 takes into account also the effect of spring abundance and richness. All models with $n = 67$.
[Resultados de un "modelo de regresión general (GRM) en el que la riqueza de especies y la abundancia de aves son analizados en función del tamaño de la campiña, la cobertura de vegetación (PC1), la altitud y la distancia a los Pirineos occidentales. El modelo 2 para el invierno tiene en cuenta el efecto de la abundancia y riqueza primaveral.]

	Total bird richness		**Mean bird richness**		**Mean bird abundance**	
Spring model:	β	*P*	β	*P*	β	*P*
Farmland size	0.65	< 0.001	—	—	0.31	0.006
Vegetation cover	0.21	0.022	0.27	0.029	0.32	0.005
Elevation	—	—	—	—	—	—
Distance	0.19	0.032	—	—	—	—
Model	$R^2 = 0.53$	< 0.001	$R^2 = 0.07$	0.029	$R^2 = 0.23$	< 0.001
Winter model 1:	β	*P*	β	*P*	β	*P*
Farmland size	0.75	<0.001	0.27	0.016	0.24	0.042
Vegetation cover	—	—	—	—	—	—
Elevation	-0.23	0.004	-0.31	0.006	—	—
Distance	—	—	-0.27	0.015	-0.32	0.007
Model	$R^2 = 0.63$	<0.001	$R^2 = 0.25$	< 0.001	$R^2 = 0.17$	0.002
Winter model 2:	β	*P*	β	*P*	β	*P*
Farmland size	0.50	<0.001	—	—	0.24	0.042
Vegetation cover	—	—	—	—	—	—
Elevation	-0.26	< 0.001	-0.38	< 0.001	—	—
Distance	—	—	-0.35	< 0.001	-0.32	0.007
Spring scores	0.38	< 0.001	0.43	< 0.001	—	—
Model	$R^2 = 0.71$	< 0.001	$R^2 = 0.36$	< 0.001	$R^2 = 0.17$	0.002

meadows, tree plantations and pastures are interspersed with towns and roads. Such a landscape mosaic offers an array of opportunities for species, some of which prefer natural or semi-natural habitat elements, while others thrive using anthropogenic elements such as crops, farms or urban areas. In this context, tree-covered farmlands surrounded by forests have been considered the paradigm of diverse agricultural landscapes in Europe, because they represent the closest equivalent to early practice of forest clearing for farming (Hoogeveen *et al*., 2001).

The Atlantic farmlands in northern Spain, with their abundant meadows and hedgerows interspersed with woodlands, are particularly suitable for birds associated with edge or open habitats (the main components of farmland bird communities; appendix 1). In fact, farmlands score the highest richness of bird species among all habitat types in the region (tree plantations, broadleaved forests and mountain pastures), and lodge many exclusive species at the regional scale (Tellería and Galarza, 1990). In addition, these tree-covered agricultural habitats sustain large numbers of some forest birds dur-

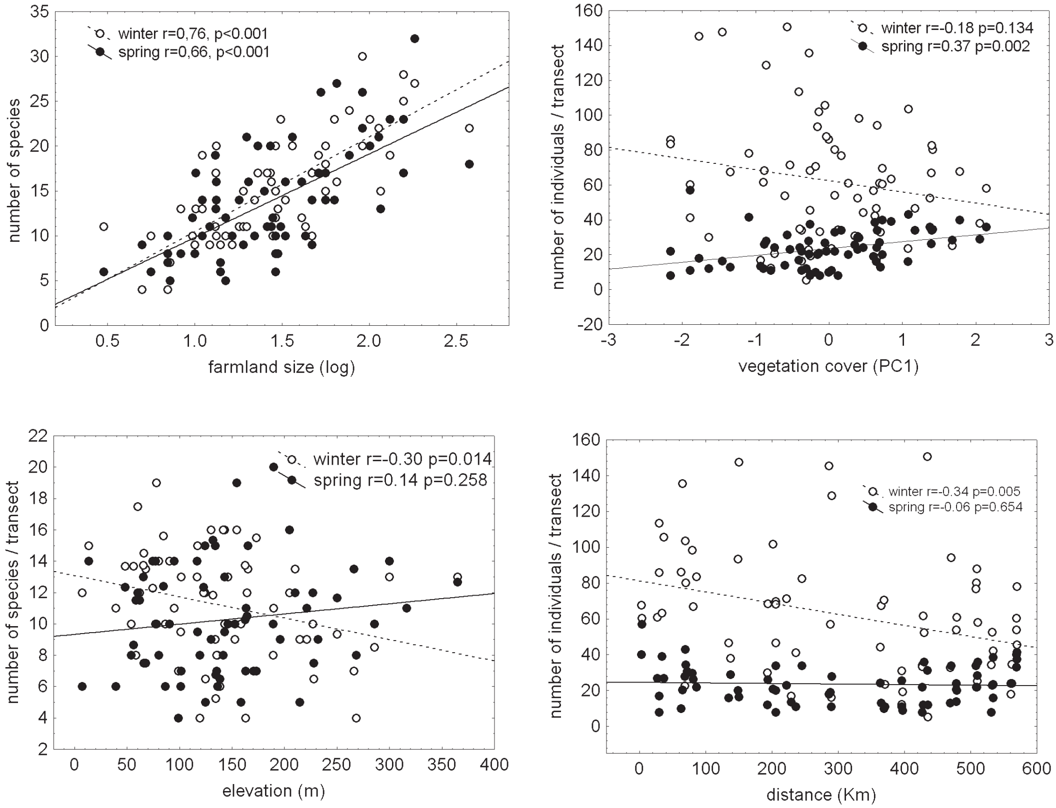

FIG. 4.—Relationships between the study features of northern Spanish Atlantic farmlands and the structure of bird communities. See text for further details.
[Relaciones entre los rasgos estudiados en las campiñas y la estructura de las comunidades de aves. Véase el texto para más detalles.]

ing winter (e.g. *Fringilla coelebs*, *Erithacus rubecula*, etc.), which together with the arrival of some migratory birds associated to meadows (e.g. *Anthus pratensis, Turdus iliacus*, etc.), make farmlands one of the most important habitats for wintering birds in Spain (Santos *et al.*, 1990; Tellería *et al.*, 1999).

However, various features of the Spanish Atlantic farmlands may limit their suitability to some bird species that are common in other European areas (appendix 1). First, lowland natural forests surrounding northern Spanish farmlands, and particularly oak forests (*Quercus robur*), have been historically destroyed to enlarge agricultural and urban areas (García *et al.,* 2005). Although farmland abandonment has produced the recovery of tree cover in lowlands throughout the expansion of pine and eucalyptus plantations, such reforestations have failed to restore habitat suitability for many forest birds. Consequently, some species have become relatively scarce in the region (*Dendrocopos minor*, *Sitta europaea*, *Parus palustris*, etc.; Martí and Del Moral, 2003), which may affect the local composition of farmland bird assemblages (Tellería and Galarza, 1990). Second, most northern Spanish farmlands are located on the slopes of a rough landscape that lacks marshland patches suitable for some water-dependent birds which are common in other European agricultural areas (Bradbury and Kirby, 2006). Finally, northern Spanish farmlands are nearly exclusively devoted to hay production or grazing, which are favoured at the expense of crops, stubbles or other feeding substrata used by granivorous birds. This mode of land use explains the dominance of common species related to hedgerows (*Erithacus rubecula*, *Turdus merula*, *Troglodytes troglodytes*, etc.; appendix 1) and insectivorous birds associated with grasslands (e.g. *Anthus pratensis*), as well as the scarcity of farmland specialists dependent on arable fields that are today endangered in Europe (skylarks, buntings, finches, etc., Robinson *et al.*, 2001; Piha *et al.*, 2003). The latter species are more abundant in cereal fields of the dry Mediterranean highlands located at the southern slopes of the Cantabrian Mountains (Tellería and Santos, 1985).

Effects of farmland size and vegetation cover

Farmland size was a major determinant of species richness and abundance of birds during the breeding period, with large farmland patches having more species than small ones. Arguably, larger habitat patches may increase environmental heterogeneity, which should favour the local occurrence of specialist species. In addition, large habitat patches may sustain small populations of species with low ecological densities (Connor and McCoy, 1979). In fact, farmland size best explained the occurrence of the scarcest species in the study area (appendix 1). Preserving large farmland patches should attenuate the pervasive effect of habitat homogenisation. In the study area, such an effect may be critical in spring when meadows with tall vegetation often cover the smallest farmland patches, preventing the occurrence of ground-feeding birds that hardly ever feed in tall-grass fields (Buckingham *et al.*, 2004). However, large farmland patches often show a patchy distribution of harvested and un-harvested meadows, which allows birds to sequentially exploit a mosaic of feeding substrata. In addition, most ground-nesters typical of open habitats avoid the forest edge and are absent from small farmland patches (Piha *et al.*, 2003).

Apart from the size of farmlands, the cover of trees and shrubs also explained variation in species richness and abundance of breeding birds, supporting the view that large and more covered farmlands were the best breeding habitat for most farmland bird species. A close relationship between farmland bird abundance and vegetation cover has also been observed in previous studies, both in northern Spain and in other European farmland areas (Carrascal and Tellería, 1985; Hinsley and Bellamy, 2000; Wretenberg *et al.*, 2007). Such an effect of habitat structure seems to be associated with the fact that the bulk of species occurring in these farmlands prefer forested habitats, and many open-habitat species, such as shrikes and chats, benefit from small patches of trees and shrubs within open farmlands.

In winter, farmland size remained the best predictor of species richness and abundance of birds. In principle, this pattern can be explained with the same arguments that are applied to breeding bird communities, with a particularly important role of the requirements of ground-feeding flocking birds dominant in winter (finches, pipits, some thrushes, etc., table 1). In winter, many birds move free of nesting requirements in search of food, which may explain the importance of patch size because large areas allow flocking birds to move between suitable feeding sites within the same farmland patch if disrupted (e.g. human or predator disturbance).

Effects of elevation and geographical location

Both species richness and abundance of wintering bird communities decreased in farmlands located at high elevation (table 1), despite sampling which spanned a restricted elevational range. Such circumstance has also been observed in other regions, including southern Spanish wintering grounds where climate conditions are improved by latitude and the oceanic influence (Tellería *et al.*, 2005). Although work was carried out on lowland farmlands, the highest altitude sampling sites are likely to be affected by colder conditions than the lowest sites, particularly in winter (Ninyerola *et al.*, 2005). Negative relationships between temperature and bird numbers are usually associated to low thermal inertia caused by the high surface-to-volume ratio, which compromises energy balance in small passerine birds (Calder and King, 1974; Blem, 1990). Such environmental pressure is particularly strong in winter, when behavioural strategies aimed to reduce the metabolic cost of thermoregulation enhance survival (Carrascal *et al.,* 2001). Because of energetic constraints, birds inhabiting cold regions will be more willing to move toward warmer sites during winter (Huertas and Díaz, 2001; Carrascal and Díaz, 2006).

Apart from an effect of elevation, the results given here show a westwards increase of species richness of breeding birds, which does not support the predicted decrease in bird species richness with increasing distance from the assumed colonization route of the Iberian forest avifauna (Ramírez and Tellería, 2003). This unexpected result is remarkable because it stands against the distribution of the whole avifauna (all bird species) across Spain, where species density (birds/100 km^2) decreases in the western sectors of the Cantabrian range (Carrascal and Lobo, 2003). In this study, despite the distribution of some species (e.g. *Lanius collurio*, appendix 1), both species richness and the abundance of a group of species increased westwards during the breeding period. The results here may be related to the large-scale patterns of distribution of the Iberian avifauna. The existence of a lowland corridor into the northern Spanish range located along the Atlantic coast in the western edge of the Cantabrian Mountains (fig. 1) seems to us the best explanation for the increased abundance of many Mediterranean species in the westernmost farmlands (Martí and del Moral, 2003; González-Taboada *et al.*, 2007).

In winter, both species richness and abundance of birds decreased westwards, a result which supports the view that the regional patterns of bird abundance are influenced by the layout of birds' migratory pathways, independently of the local environmental conditions birds realise in different parts of their northern Spanish wintering range (Galarza and Tellería, 2003). The result has been related to greater costs of transport faced by migrating birds, as they move further from their main migratory gateway into the Iberian Peninsula (Galarza and Tellería, 2003). Ringing recoveries of pipits, chaffinches and other abundant wintering birds support the same pattern (authors' unpublished data), which may be thus considered as a large-scale geographical effect on the ability of farmlands to attract European migratory birds (Tellería *et al*., 2008).

Conservation implications

Preserving and restoring biodiversity in agricultural landscapes is central to current conservation policies, because the future of many species depends on landscape use in manmade habitats (Bennet *et al.*, 2006). However, agricultural landscapes are seldom defined by one particular farming practice making the analysis of farmland biodiversity hardly understandable unless a multi-scale approach is used (Donald and Evans, 2006). It has been shown here that the distribution of birds in northern Spanish farmlands defines major biogeographical patterns, while it still remains affected by local management in the form of variable size and vegetation structure of individual farmlands. From this perspective, farmland patches are viewed as management units, an approach which may help to improve conservation of farmland birds in northern Spain for two main reasons.

Firstly, an approach focused of farmland patches may bring this habitat type to the attention of conservationists and managers, who usually perceive northern Spanish farmlands as an extended and rather continuous matrix. This view is reinforced by the EC Habitat directive (Council Directive 92/43/EEC) that is mainly focused to the conservation of natural habitats. Such perception has its roots in the evidence that the farmland range has been historically expanded by humans to cover much of northern Spain (Observatorio de la Sostenibilidad en España, 2005). As a consequence, farmlands have been left out of the Natura 2000 network of important habitats proposed for the Spanish Atlantic region, which is dominated by marshlands and natural forests (EU Notification nº 20004-4032 in application of the Directive 92/43/EEC). However, the real situation is that Spanish Atlantic farmlands are being progressively reduced, particularly to the east where the Basque Country and Cantabria have respectively lost 1.1 and 2.0 % of their former farmland range between 1987 and 2000 (Observatorio de la Sostenibilidad de España, 2005). According to the present results, losing farmland range may be critical for bird conservation. In the first place because farmland loss is particularly severe in coastal and lowland sectors, where the largest urban and industrial pressures are concentrated (Observatorio de la Sostenibilidad de España, 2006). Taking into account the importance of lowland farmlands for birds, and the increasing number of extra-Iberian wintering individuals in eastern sectors of the Cantabrian range, the ongoing and largely neglected loss of farmlands becomes of particular conservation concern.

Second, if farmland patches are treated as conservation units, with their particular species composition and environmental and geographical features, such units will be easily identified by administrators and developers during landscape planning. Therefore, if farmlands are viewed as habitat to be protected, they may be explicitly considered in environmental impact assessments, and be proposed as candidate habitats for conservation measures (Morris and Therivel, 2001). These results help to identify farmland conservation priorities by regional administrations in northern Spain, stressing for the importance of large lowland farmlands as habitats for both the richest bird communities and the most endangered species.

In conclusion, large lowland farmlands should be declared priority sites to apply the agri-environmental schemes sponsored by the CAP. Because subsidy receivers are legally obliged to keep their land in good agricultural and environmental shape from 2005 onwards (Council Regulation 1782/2003 and Commission Regulation 796/2004), they may be advised to carry out specific management actions to improve the habitat according to the preferences of endangered birds. However, agri-environment measures are still in the earliest stage of design because of the complexity brought about by the many interacting features of farmland habitat (Buckingham *et al.*, 2004; Donald *et al.*, 2007; Whitthingham, 2007). For example, it is important to discuss the potential conflict raised by other EU environmental policies that may negatively affect farmland biodiversity in northern Spain, such as funding for afforestation directed to reduce the greenhouse effect and to protect soils (Ministerio de Agricultura, Pesca y Alimentación, 2006).

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APPENDIX 1 *[Apéndice 1]*

Occurrence and abundance of birds breeding and wintering in northern Spanish farmlands. The number of farmland patches occupied by each species (*n*) and the mean number of individuals recorded per transect are reported. The results of discriminant analyses evaluating the positive (+) or negative (-) effect of farmland size (SIZE), elevation (ELEV), distance from the western Pyrenées (DIST) and vegetation cover (COV) on bird occurrence are also shown (*$P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$).

*[Presencia y abundancia de las especies de aves reproductoras e invernantes en las campiñas del norte de España. Se detalla el número de campiñas ocupadas por cada especie (n) y el número medio de individuos observados por transecto. Los resultados de un análisis discriminante han evaluado el efecto positivo (+) o negativo (-) del tamaño de la campiña (SIZE), su altitud (ELEV), distancia a los Pirineos occidentales (DIST) y cobertura vegetal (COV) sobre la presencia de las aves (*P < 0.05, ** P < 0.01 y *** P < 0.001)]*

	Spring						Winter					
	n	Mean ± se	SIZE	ELEV	DIST	COV	n	Mean ± se	SIZE	ELEV	DIST	COV
Aegithalos caudatus	4	0.21±0.11	-	-	-	-	3	0.07±0.05	-	-	-	-
Alauda arvensis	1	0.02±0.02	-	-	-	-	6	0.49±0.34	***(+)	-	-	*(-)
Anthus pratensis	0	-	-	-	-	-	61	12.45±1.79	-	-	-	-
Anthus trivialis	9	0.24±0.07	-	-	-	-	0	-	-	-	-	-
Carduelis cannabina	14	1.02±0.24	***(+)	-	-	-	6	0.38±0.2	-	*(-)	-	-
Carduelis carduelis	45	3.44±0.37	**(+)	-	-	-	35	2.99±0.94	***(+)	-	-	-
Carduelis chloris	35	2.1±0.25	*(+)	-	**(+)	-	21	1.13±0.42	***(+)	***(-)	-	-
Carduelis spinus	0	0±0	-	-	-	-	24	0.87±0.29	*(+)	-	-	*(+)
Certhia brachydactyla	1	0.02±0.02	-	-	-	*(+)	3	0.03±0.02	-	-	-	-
Cettia cetti	4	0.19±0.11	-	**(-)	*(-)	-	3	0.02±0.02	-	-	*(-)	*(+)
Cisticola juncidis	20	0.82±0.13	***(+)	*(-)	-	-	4	0.07±0.03	-	-	-	-
Columba palumbus	13	0.39±0.13	-	-	**(+)	-	6	0.1±0.07	-	-	-	-
Corvus corone	28	2.04±0.34	***(+)	-	***(+)	-	38	0.61±0.18	***(+)	-	-	-
Coturnix coturnix	2	0.03±0.02	-	-	-	*(-)	0	-	-	-	-	-
Cuculus canorus	5	0.1±0.04	-	-	-	-	0	-	-	-	-	-
Cyanistes caeruleus	5	0.08±0.04	*(+)	-	-	*(+)	21	0.34±0.07	*(+)	-	-	-
Dendrocopos major	4	0.06±0.03	**(+)	-	-	-	8	0.05±0.03	-	-	-	-
Dendrocopos minor	0	-	-	-	-	-	1	0.02±0.02	-	-	-	-
Emberiza cia	5	0.08±0.04	-	-	**(+)	-	9	0.37±0.12	-	-	***(+)	-
Emberiza cirlus	20	0.82±0.15	*(+)	-	***(+)	-	15	0.51±0.17	***(+)	-	***(+)	-
Emberiza citrinella	2	0.03±0.02	-	**(+)	-	*(+)	0	-	-	-	-	-
Erithacus rubecula	51	3.3±0.32	-	-	-	*(+)	64	5.18±0.41	-	-	-	-
Fringilla coelebs	41	2.85±0.33	**(+)	-	-	-	63	16.57±3.58	-	-	-	-

Fringilla montrifringilla	0	-	-	-	-	-	2	0.25±0.25	-	-	-	-
Garrulus glandarius	10	0.28±0.09	-	-	-	-	24	0.07±0.05	-	-	*(-)	-
Hippolais polyglotta	37	1.53±0.2	*(+)	-	-	*(-)	0	-	-	-	-	-
Jynx torquilla	4	0.1±0.05	-	-	**(-)	-	0	-	-	-	-	-
Lanius collurio	15	0.42±0.11	*(+)	-	*(-)	-	0	-	-	-	-	-
Lanius excubitor	1	0.02±0.02	-	-	-	-	0	-	-	-	-	-
Miliaria calandra	6	0.27±0.09	***(+)	-	-	-	0	-	-	-	-	-
Motacilla alba	30	0.9±0.14	**(+)	-	-	-	40	1.47±0.2	***(+)	-	-	-
Motacilla cinerea	0	-	-	-	-	-	4	0.03±0.02	-	-	-	-
Muscicapa striata	2	0.03±0.02	-	-	*(-)	-	0	-	-	-	-	-
Oriolus oriolus	1	0.02±0.02	-	-	-	-	0	-	-	-	-	-
Parus ater	8	0.21±0.08	-	-	*(+)	*(+)	11	0.18±0.06	-	-	-	-
Parus cristatus	5	0.14±0.09	-	-	-	**(+)	4	0.03±0.03	-	-	-	-
Parus major	43	1.96±0.24	-	-	**(-)	-	42	1.26±0.22	-	-	***(-)	-
Parus palustris	0	-	-	-	-	-	3	0.03±0.02	-	-	-	-
Passer domesticus	42	14.96±1.72	***(+)	-	-	-	36	11.03±1.81	***(+)	-	-	-
Passer montanus	10	0.62±0.19	*(+)	-	-	-	4	0.28±0.16	***(+)	-	-	-
Phoenicurus ochruros	14	0.4±0.09	**(+)	-	-	-	9	0.18±0.06	***(+)	-	***(+)	-
Phylloscopus collybita	11	0.18±0.06	-	-	*(-)		27	0.54±0.12	***(+)	***(-)	-	-
Pica pica	14	0.82±0.22	***(+)	-	-	-	18	0.41±0.11	***(+)	-	-	-
Picus viridis	13	0.25±0.07	-	-	-	-	13	0.08±0.04	-	-	-	*(+)
Prunella modularis	21	0.71±0.15	*(+)	-	***(+)	-	30	0.91±0.14	*(+)	-	-	-
Pyrrhula pyrrhula	9	0.22±0.07	-	-	-	-	6	0.05±0.03	*(+)	-	-	-
Rallus aquaticus	0	-	-	-	-	-	1	-	-	-	-	-
Regulus ignicapillus	11	0.27±0.08	-	-	-	-	16	0.53±0.13	***(+)	*(-)	-	-
Saxicola torquata	29	1.36±0.19	***(+)	-	-	-	30	1.02±0.17	***(+)	-	-	*(-)
Serinus serinus	49	3.34±0.3	-	-	*(+)	-	6	0.1±0.07	***(+)	-	-	-
Streptopelia decaocto	5	0.22±0.11	***(+)	-	-	-	2	-	-	-	-	-
Streptopelia turtur	6	0.16±0.06	**(+)	-	**(-)	-	0	-	-	-	-	-
Sturnus unicolor/vul	25	3.78±0.67	**(+)	-	***(-)	-	30	1.87±0.67	*(+)	-	***(+)	-
Sylvia atricapilla	43	2.23±0.24	*(+)	-	*(-)	-	24	0.59±0.13	-	-	-	-
Sylvia borin	1	0.02±0.02	-	-	-	-	0	-	-	-	-	-
Sylvia melanocephala	0	-	-	-	-	-	4	0.07±0.03	-	-	-	*(+)
Sylvia undata	2	0.03±0.02	-	-	-	-	1	0±0	-	-	-	-
Troglodytes troglodytes	56	4.42±0.36	-	-	-	-	49	1.54±0.19	*(+)	-	-	-
Turdus iliacus	0	-	-	-	-	-	33	3.78±1.66	***(+)	-	-	-
Turdus merula	64	6.68±0.5	-	-	-	**(-)	63	5.37±0.44	-	-	-	-
Turdus philomelos	17	1.02±0.22	-	-	-	-	53	3±0.46	-	-	-	-
Turdus pilaris	0	-	-	-	-	-	2	0±0	*(+)	-	-	-
Turdus viscivorus	14	0.33±0.08	-	*(+)	**(+)	-	16	0.32±0.1	-	-	***(+)	-