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The importance of northern Spanish farmland for wintering migratory passerines: a quantitative assessment

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Summary

Migratory birds are critically dependent on adequate wintering habitats for their long-term survival. Cantabrian farmland, a mixed agricultural landscape extending across the coastal lowlands of northern Spain, constitutes an important wintering area for many short-distance migrants coming from central-western and northern Europe. Unfortunately, the Common Agricultural Policy of the European Union and national afforestation schemes have resulted in a massive replacement of farmland by pine *Pinus* spp. and eucalypt *Eucalyptus* sp. plantations. This work assesses the importance of Cantabrian farmland as wintering grounds for short-distance European migrants and for wintering species that originate in nearby woodlands. We examined the seasonal changes in passerine bird populations in the Cantabrian region and used winter ringing recoveries obtained in the area to evaluate the contribution made by European migrants to winter populations. Bird communities were surveyed along 299 500-m long transects distributed between 67 farmland patches, 67 lowland forests and 14 upland forests. Winter assemblages were more diverse and species more abundant in farmland than in lowland or upland forests, whereas these differences were smaller in the spring. Bird numbers in farmland tripled in winter, numbers increasing by about 6.9 million birds compared to breeding populations. Most of this increase was accounted for by species that also bred in the region and that considerably increased their abundance (65.6% of all wintering birds, with the Chaffinch *Fringilla coelebs* responsible for 31.4% of the total increase) and by five exclusively wintering species (34.4%, with the Meadow Pipit *Anthus pratensis* accounting for 25.2% of the total increase). The main bulk of this increase is caused by the influx of European migrants. The importance of halting the current spread of eucalypt plantations (which increased over 400% over the past 30 years) and of applying more effective agri-environment schemes to achieve appropriate farmland conservation is discussed.

Resumen

La supervivencia de las aves migrantes depende críticamente de hábitats de invernada adecuados. La campiña cantábrica, un paisaje agrícola mixto que se extiende a través de las tierras costeras del norte de España, es un área de invernada importante para muchos migrantes procedentes del centro, oeste y norte de Europa. Desgraciadamente, la Política Agrícola Comunitaria de la Unión Europea y los planes nacionales de repoblación han producido una sustitución masiva de campiña por plantaciones de pinos *Pinus* spp. y eucaliptos *Eucalyptus* sp. En este trabajo se evalúa la importancia de la campiña cantábrica como área de invernada para migrantes europeos de corta distancia y para invernantes procedentes de los bosques próximos. Para ello, examinamos los cambios estacionales en las poblaciones de pájaros de la región cantábrica y usamos las recuperaciones invernales (de aves anilladas) obtenidas en el área para estimar la contribución de los migrantes europeos a la poblaciones invernantes. Se censaron las comunidades de aves en 299 transectos lineales de 500 m de longitud, distribuidos entre 67 campiñas, 67 bosques bajos y 14 bosques altos. Las comunidades invernales fueron más diversas y las especies más abundantes en las campiñas que en bosques altos y bajos, mientras que las diferencias fueron menores en primavera. El número de pájaros se triplicó en invierno en las campiñas, incrementándose en unos 6.9 millones de aves con respecto a las poblaciones reproductoras. La mayoría de este incremento se debió a especies que también crían en la región y que aumentaron considerablemente su abundancia (un 65.6% de todos los pájaros invernantes; el Pinzón Vulgar *Fringilla coelebs* fue responsable del 31.4% del incremento total) y a cinco especies exclusivamente invernantes (34.4%, con la Bisbita Común *Anthus pratensis* sumando el 25.2% del incremento total). La mayor parte de este incremento es causado por la entrada de migrantes europeos. Se discute la importancia de detener la extensión de las plantaciones de eucaliptos (que aumentaron más de un 400% en los últimos 30 años) y de aplicar esquemas agro-ambientales más efectivos para lograr una conservación adecuada de las campiñas.

Introduction

Land use changes are producing dramatic transformations in European landscapes, such that the environment is subjected to increasingly harmful pressures (EEA 2004, 2007). Thus, populations of many birds and other species that inhabit the changing habitats are declining (EEA 2010). Since farming extends over almost 50% of the territory of the 27 member states of the European Union, and a large number of wildlife species and habitats are highly dependent on management of agricultural land, changes in the agricultural sector are of conservation concern (Donald *et al.* 2006, EEA 2010). Migratory birds are particularly vulnerable to these changes since they require suitable breeding, wintering and stopover habitats to complete the migratory cycle (Webster *et al.* 2002, Galarza and Tellería 2003, Dänhardt *et al.* 2010). Thus, migratory populations that depend on scarce habitats at any stage of their year-round cycle may be extremely vulnerable to habitat loss or change (Robbins *et al.* 1993, Bibby 2003).

European short-distance migrants that breed to the north and west winter in the mild areas of the Mediterranean basin and North Africa, but also in coastal sectors of western Europe, from the Netherlands and southern British Isles to northwestern Iberia (Bernis 1966, Moreau 1972, Gillings *et al.* 2008). The latter include the Cantabrian coastlands, a belt of mixed agricultural and wooded landscape extending across northernmost Spain from the lower reaches of the Cantabrian range (Bernis 1966, Santos *et al.* 1990, Tellería *et al.* 2008). Several studies have shown that Cantabrian farmland is a habitat supporting large numbers of wintering birds (Tellería and Galarza 1990, Tellería *et al.* 2008).

It is assumed that the winter increase in bird abundance on Cantabrian farmland is mainly due to the arrival of migrants originating in central and northern Europe, from the British Isles and France to Scandinavia and Russia (Santos *et al.* 1990, Galarza and Tellería 2003, Tellería *et al.* 2009). This is obvious for species that are exclusively winter visitors to the Iberian Peninsula, such as the Redwing *Turdus iliacus* and the Meadow Pipit *Anthus pratensis*, but the possibility that a significant proportion of these wintering populations originates from local movements of birds breeding in nearby forests has not yet been comprehensively studied. In fact, the upland forests of northern Spain undergo a dramatic loss of their breeding bird populations during the winter (Álvarez and Purroy 1993, Santos *et al.* 2010). Cantabrian woodlands extend throughout the coastal sectors and the northern slopes of the region, covering nearly 1.3 million hectares (MAPA 2006). Given that 45% of this wooded area is above 400 m altitude, and that it loses a significant proportion of its breeding populations in winter (Santos *et al.* 2010), it is feasible that many birds move to winter in nearby lowland farmland. We do not know, however, whether the winter increases in bird populations in Cantabrian farmland are mostly due to the arrival of extra-Iberian migrants or whether they are also related to such regional shifts in bird distribution.

Changes in land use have affected the capacity of the Cantabrian region to support migratory landbirds in winter. Abandonment of rural areas in the 1950s and 1960s, and the later incentives from the 1992 Common Agricultural Policy reform, greatly encouraged the afforestation of Cantabrian lowlands (MAPA 2006). This has resulted in the massive substitution of farmland by exotic tree plantations (*Pinus radiata* and *Eucalyptus* sp.) that today account for 60% of the forest area in the region (MFE50 2007). Since most afforestation occurs at low altitudes (75.5% below 400 m; MFE50 2007), where it replaces farmland (Tellería *et al.* 2008), the capacity of the traditional farming landscape as a wintering ground for migratory birds has rapidly declined. So, in the period 1994–2005 over 10,000 ha were afforested annually in the region, with the loss of farmland area occurring mainly in the east (Observatorio de la Sostenibilidad en España 2005, MAPA 2006). In addition, farmland located at the lowest altitudes is subject to encroachment by urban areas and infrastructure, which affect the ability of the most suitable sites to accommodate migratory birds (Tellería *et al.* 2008).

This study examines the breeding and wintering passerine bird assemblages in the farmland and woodlands of the Cantabrian region. The main goal was to evaluate the importance of Cantabrian farmland as a wintering ground for short-distance European migrants and for local birds originating in nearby woodlands. To this end, we first appraised the seasonal changes in passerine populations breeding in the farmland and wooded habitats of the region; previous studies have shown significant changes within farmland and high altitude woodland assemblages (Tellería *et al.* 2008, Santos *et al.* 2010), but there remains a lack information on the dynamics of bird populations in the lowland forests (below 400 m) that now comprise nearly 40% of the regional area. Secondly, we used local ringing recoveries to assess the relative importance of short-distance, extra-Iberian migrants in the bird populations supported by farmland in winter. We therefore use estimates of population change to evaluate the role of farmland as a wintering area while taking account of the movements of European birds and also of those that originate from the lowland and upland forests of the region.

Methods

Study area

The study area extends over 30,000 km² along a 600-km long belt in northern Spain, between the Atlantic coast and the northern slopes of the Cantabrian Mountains (Figure 1). Upland areas (above 500 m asl) are covered by pastures and extensive broadleaved natural forests (beech *Fagus sylvatica,* oak *Quercus petraea,* etc.) and pine plantations, while lowlands are covered by a patchwork landscape of farmland and forests: mainly pine *Pinus radiata* and *P. pinaster* and eucalypt *Eucalyptus globulus* plantations; remnants of natural forests (mainly oaks *Quercus robur*) are very scarce in the lowlands. The farmland is a mosaic of habitats mostly comprising pastures and orchards accompanied by a network of tree-shrub hedges and small copses; farmland is mostly devoted to hay production and cattle grazing, although the intensity of use is decreasing by the progressive abandonment of farming practices. The region is rainy, with over 1,000 mm of annual precipitation (Ninyerola *et al.* 2005), and climatic conditions are severely affected by the influence of the nearby mountains. Thus, there is a sharp altitudinal variation in temperature, with mountain tops covered with snow during winter, whereas coastal lowlands experience mild winters, with mean temperatures of 7–9 °C in January (Ninyerola *et al.* 2005).

We counted wintering and breeding birds in 67 discrete farmland patches (these varied in size and were surrounded by non-farmland habitat), and 67 nearby lowland forests, mainly afforested areas (44 eucalypt plantations, 15 pine plantations and eight deciduous woodlands dominated by oak and chestnut *Castanea* spp). We also surveyed 14 extensive upland forests: nine natural deciduous forests mainly of oak and beech, and five pine plantations. The sites were regularly distributed across the study area (Figure 1) and were selected using cartography provided by the SIGPAC facility (http://sigpac.mapa.es/fega/visor/). Mean altitudes were 143 m for farmland

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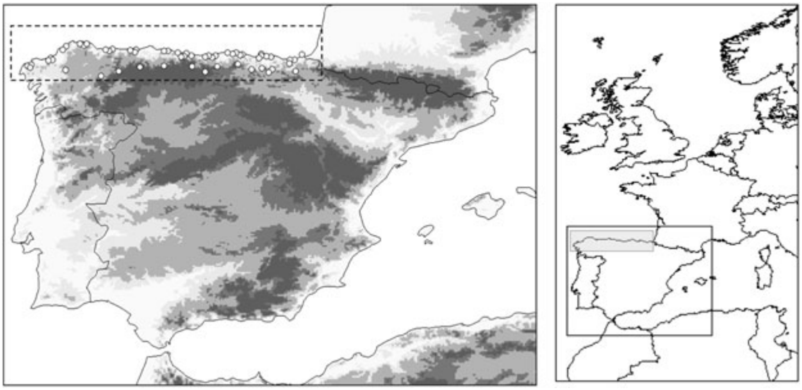

Figure 1. Location of the study area in Europe (right) and map (left) showing location of the Cantabrian region with the distribution of the study localities and the major topographic features of the Iberian Peninsula (grey and black shading represent areas above 500 m and 1000 m, respectively).

localities, and 175 m and 800 m for lowland and upland forests respectively. Farmlands and lowland forests are rather small patches of a few tens of hectares (rarely larger than 100 ha), while upland forests are extensive woodlands of hundreds to thousands of hectares (Tellería *et al.* 2008, Santos *et al.* 2010).

Bird counts, bird population estimates, and incidence of northern migrants

Between one and six 500-m long line transects were carried out in each farmland patch, giving a total of 127 transects in the 67 farmland patches. Each lowland forest patch was censused by a single 500-m transect (n = 67 woodlands). Three to 12 line transects were carried out in each of the 14 upland forests (105 transects in all). Transects were chosen for convenience, taking advantage of paths and rural roads, and in order to take a representative sample of each farmland patch and extensive forest. Birds were sampled in the first half of June 2005 and January 2006. All birds seen or heard were counted within and outside a 50-m wide belt (the near and far belts, respectively, see Bibby *et al.* 2000), a method that allows estimation of relative or absolute densities (Bibby *et al.* 2000). For an overall appraisal of seasonal changes, we used the mean number of species (richness) and individuals (relative density or abundance) per transect in the 50-m belt, whereas population changes were estimated from absolute densities (see below). Data analyses were restricted to passerines, excluding corvids. Bird species wintering in farmland were classified as ground or tree/shrub feeders according to their preferred feeding substrates (Carrascal and Tellería 1985, pers. obs.).

In order to estimate population changes, habitat areas were calculated from the digital forest map of Spain scale 1:50,000 (MFE50 2007); we only considered those forests with trees above 8 m in height. For the calculation of farmland areas we considered grasslands, meadows and crop mosaics with tree or shrub edges. Bird populations of individual species were separately estimated from their spring and winter absolute densities and the surface areas of each habitat in the studied area. Absolute densities per transect were estimated from the proportion of contacts detected within a threshold distance (25 m in our transects), using the method proposed by Carrascal *et al.* (2010). To estimate population sizes, we applied a random replacement procedure and generated 1,000 datasets from which average absolute densities +/- 95% confidence intervals were calculated. Estimates were carried out using Pop Tools 3.0 (http://www.cse.csiro.au/poptools/) in Microsoft Excel. Final estimates of population sizes and their confidence limits in each habitat and season

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were obtained by multiplying the estimated average densities by the area covered by each habitat. Estimates were calculated for 34 of 38 species wintering in farmland; the four excluded species were uncommon and accounted for just 0.28% of the birds recorded in winter (*Motacilla cinerea*, *Sylvia melanocephala*, *Cettia cetti* and *Fringilla montifringilla*).

Differences between spring and winter populations provided estimates of population changes in each habitat. The potential role of lowland and upland forests as sources of wintering birds for farmland was estimated for each species by the difference in bird numbers between spring and winter seasons (bird outflow: breeding minus wintering populations), whereas the converse was calculated for farmland (bird influx: wintering minus breeding populations).

The number of winter recoveries (December–February) in the study area of migrants originating in other European countries (i.e. birds ringed outside Iberia) was used to assess the importance of visitor populations as a potential source of wintering birds in farmland. We considered all available recoveries obtained up to 2009 by the Spanish Ringing Scheme (Ministerio de Medio Ambiente, Rural y Marino).

Data analysis

Differences in bird richness and abundance between habitats (lowland and upland forests and farmland) and seasons (spring and winter) were analysed using repeated measures ANOVAs.

Regression models (GRM; StatSoft 2007) were used to analyse the effects of population movements on winter increases in farmland at regional (occurring within the study area) and greater scales (long-distance movements, originating north of the area), by using the difference between winter and spring populations in farmland as a response variable (bird influx). Differences between spring and winter populations (bird outflow) in lowland and upland forests were used as predictor variables (indicators of potential local effects), while long-distance effects were controlled using the number of winter recoveries as a third predictor. Variables that were log-transformed to fulfil the requirements of parametric tests are mentioned in each analysis.

Results

Bird species composition was rather similar in lowland and upland forests and clearly different from that found in farmland habitat (Table 1). The bird assemblages of the two woodland habitats were dominated by tits and other small insectivores (such as Wrens *Troglodytes troglodytes*, Robins *Erithacus rubecula* and warblers) in both seasons, although the former were noticeably more prevalent in winter and the latter in the nesting season. Thus, tits *sensu amplio* (including genus *Regulus* and the Long-tailed Tit *Aegithalos caudatus*) accounted for 37.4% and 27.9% of breeding birds in upland and lowland forests respectively, but they increased to 59.9% and 57% in winter. In contrast, Robins, Wrens and Blackcaps *Sylvia atricapilla* together reached 35.1% and 54.2% in spring but decreased to 9.7% and 21.8% of wintering birds in the two forest types. Farmland showed the lowest numbers of tits and 'small insectivores' (up to 7.9% and 19.9% respectively in spring), and comparatively high numbers of finches and buntings (these granivores accounted for 19.7% of all farmland birds in spring and 30.5% in winter, excluding the Bullfinch *Pyrrhula pyrrhula*) and thrushes (15% and 16.7% of all farmland birds in spring and winter, respectively). Farmland also differed by the presence of two exclusive and prominent groups: House Sparrows *Passer domesticus* (22.9% and 11.4% of birds in spring and winter) and meadow winterers (skylarks *Alauda arvensis*, meadow pipits *Anthus pratensis* and wagtails *Motacilla* spp., which accounted for 19.9% of wintering birds).

Seasonal dynamics of bird communities

Species richness changed between spring and winter (repeated measures ANOVA of log-trasformed species-richness, $F_{1,145} = 12.072$, $P < 0.001$) and between habitats ($F_{2,145} = 16.245$, $P < 0.001$),

Table 1. Bird species composition in the three studied habitats in the breeding and winter seasons. The percentages of individuals recorded in 500 x 50 m transects (2.5 hectares) are given; percentages ≥ 5% in bold type; number of transects in parentheses.

	Farmland (127)		Upland forests (105)		Lowland forests (67)	
	% spring	% winter	% spring	% winter	% spring	% winter
Alauda arvensis	-	0.57	-	-	-	-
Anthus pratensis	-	**18.61**	-	-	-	-
Anthus trivialis	0.45	-	0.07	-	-	-
Motacilla alba	1.87	1.58	-	-	-	-
Motacilla cinerea	-	0.03	0.14	0.19	-	0.16
Troglodytes troglodytes	**7.03**	2.22	**8.51**	**6.33**	**29.75**	**11.50**
Prunella modularis	2.06	1.05	1.96	0.19	0.17	1.26
Erithacus rubecula	**6.06**	**6.90**	**14.72**	**6.72**	**16.03**	**9.29**
Phoenicurus ochruros	0.80	0.19	-	-	-	-
Saxicola torquata	3.66	1.30	0.07	-	-	-
Turdus philomelos	1.11	4.72	2.70	0.77	0.83	2.83
Turdus iliacus	-	**6.50**	-	1.15	-	2.83
Turdus viscivorus	0.35	0.39	0.47	0.77	-	-
Turdus merula	**14.13**	**7.17**	**6.08**	**6.53**	3.31	**5.98**
Sylvia borin	0.03	-	1.35	-	0.17	-
Sylvia atricapilla	2.95	0.88	**11.21**	0.19	**11.40**	1.57
Sylvia melanocephala	-	0.11	-	-	-	-
Sylvia undata	0.13	-	0.41	-	0.33	0.16
Cisticola juncidis	0.59	0.10	-	-	-	-
Cettia cetti	0.13	0.02	-	-	-	-
Hippolais polyglotta	2.43	-	-	-	-	-
Phylloscopus bonelli	-	-	0.34	-		
Phylloscopus collybita	-	0.67	0.34	0.19	0.50	2.83
Phylloscopus ibericus	-	-	0.27	-	0.33	-
Regulus regulus	-	-	0.34	-	-	0.31
Regulus ignicapillus	0.67	0.76	4.32	**10.56**	**8.76**	**15.43**
Muscicapa striata	0.19	-	0.07	-	-	-
Parus major	**5.12**	1.68	3.58	4.80	2.48	**6.30**
Periparus ater	0.37	0.27	**9.52**	**9.40**	**9.92**	**19.69**
Cyanistes caeruleus	0.06	0.48	**5.54**	**8.45**	0.99	3.62
Lophophanes cristatus	0.25	0.08	**5.40**	**7.49**	1.98	3.94
Poecile palustris	-	0.08	1.35	**6.33**	-	0.94
Aegithalos caudatus	0.13	0.10	2.03	**9.98**	0.66	**5.67**
Sitta europaea	-	-	3.78	**7.29**	0.33	0.16
Certhia familiaris	-	-	-	0.96	-	-
Certhia brachydactyla	-	-	2.57	4.80	1.65	1.42
Lanius collurio	1.13	-	-	-	-	-
Lanius meridionalis	0.13	-	-	-	-	-
Sturnus vulgaris/unicolor	2.84	4.44	-	-	-	-
Passer domesticus	**22.91**	**11.39**	-	-	-	-
Passer montanus	1.10	0.13	-	-	-	-
Fringilla coelebs	4.31	**20.67**	**9.59**	0.58	4.13	1.73
Fringilla montifringilla	-	0.12	-	-	-	-
Carduelis cannabina	1.53	0.16	0.07	-	-	-
Carduelis carduelis	**5.38**	3.48	0.14	-	1.32	0.16
Carduelis chloris	3.68	1.21	0.20	-	0.17	-
Carduelis spinus	-	0.90	0.07	2.11	-	1.26
Serinus serinus	3.52	0.05	1.01	-	1.16	-
Pyrrhula pyrrhula	0.72	0.04	1.22	3.84	2.81	0.79

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Table 1. Continued.

	Farmland (127)		Upland forests (105)		Lowland forests (67)	
	% spring	% winter	% spring	% winter	% spring	% winter
Coccothraustes coccothraustes	-	-	-	-	-	0.16
Loxia curvirostra	-	-	-	0.38	-	-
Emberiza cirlus	1.77	0.44	-	-	-	-
Miliaria calandra	0.21	-	-	-	-	-
Emberiza cia	0.19	0.49	0.61	-	0.50	-

and was higher in farmland during winter and in upland forests during spring (interaction season x habitat: $F_{2,145} = 30.600$, $P < 0.001$); seasonal change was negligible in the case of lowland forests (Table 2). A similar pattern was detected in bird abundance, with sharp differences between seasons ($F_{1,145} = 9.210$, $P < 0.001$) and habitats ($F_{2,145} = 47.153$, $P < 0.001$; interaction: $F_{2,145} = 40.778$, $P < 0.001$). Bird abundance thus increased dramatically in farmland during winter, while it declined in upland forests and remained rather stable in lowland forests (Table 1). The results are substantially the same if House Sparrows (exclusive to farmland, where they reach high densities and are closely associated with buildings) are excluded.

Farmland as a wintering ground. Origins of wintering bird populations

Farmland is the major wintering habitat for migratory passerines in the Cantabrian region. Bird density in farmland increased three-fold in winter (Table 2), such that wintering numbers increased by 6.9 million individuals over breeding numbers (Table 3). Most of this increase was accounted for by species that only occurred in winter, and by resident species that increased exceptionally their breeding populations during winter (Table 4). Exclusive winterers, mainly the Meadow Pipit (73.2% of that category) and the Redwing *Turdus iliacus* (20.4%) comprised 34.4% of the increase in wintering bird numbers. In the resident group (65.6% of the increase) the Chaffinch *Fringilla coelebs*, whose density increased over 16-fold, contributed 2.2 million new individuals (31.4% of the total winter increase); another important bird was the Song Thrush *Turdus philomelos*, which showed a 14-fold increase and added 385,000 new birds (5.6%) to the farmland wintering population. The remaining population increases, such as those of small insectivores (e.g. tits) and even of sparrows and Starlings *Sturnus* spp. (Table 4) may be explained by the local recruitment that occurred in the breeding season.

The winter influxes of birds recorded in farmland were positively associated with the numbers of winter recoveries (Figure 2), whereas birds originating from upland and lowland forests had no effect on the winter increase in bird numbers in farmland, even when the exclusively wintering species were excluded (Table 5). Therefore, the winter increases reported in farmland (Table 4) are mainly accounted for by the arrival of European migrants.

The majority of birds wintering in farmland fed on the ground; 22 of 34 species and 91.3% of estimated bird numbers used the ground as their preferred feeding substrate. The Chaffinch and

Table 2. Bird species richness and bird abundance by 500 x 50 m transects (2.5 ha) in the three studied habitats in the breeding and winter seasons (mean ± SE); number of study sites in parentheses.

	Species richness		Bird abundance	
	Spring	Winter	Spring	Winter
Farmland (67)	5.94 ± 0.33	8.03 ± 0.32	12.32 ± 0.80	37.10 ± 2.99
Lowland forests (67)	4.99 ± 0.28	5.03 ± 0.35	9.34 ± 0.60	9.91 ± 0.90
Upland forests (14)	7.60 ± 0.44	3.05 ± 0.42	14.09 ± 0.95	5.73 ± 1.00

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the Meadow Pipit, the two most abundant birds and typical ground feeders in winter, accounted for 41.5% of all wintering birds in farmland (Table 4).

Discussion

Seasonal dynamics of bird communities in the Cantabrian region

This study augments the information provided by previous regional surveys on the seasonal changes in bird communities in farmland and upland forests of the Cantabrian region. In those studies we showed the marked influence of altitude on the winter changes in bird abundance, resulting in very large declines in bird numbers in the forests (Santos *et al.* 2010) and the concentration of populations within the lowest, coastal, sectors of farmland (Tellería *et al.* 2008). In addition, local studies have demonstrated the importance of open agricultural habitats, and in particular pastures, in supporting the greater part of the wintering populations, whereas habitats with high cover of woody vegetation are scarcely used (Carrascal and Tellería 1985, Fernández and Galarza 1986). Extensive tree cover is very scarce in Cantabrian farmland (< 10%; authors' data), where orchards and especially grassland pastures comprise nearly 90% of the habitat. Over 90% of wintering birds search for food on the ground, so the significance of the Cantabrian farmland as a wintering habitat is explained by their combination of a southern location in the European continent within an important migratory flyway, the mild climate due to low altitude and proximity to the sea and the high availability of grassland (Santos and Tellería 1985, Tellería *et al.* 2008, 2009).

Lowland forests, which are studied here for the first time at a regional scale, maintain rather numerically stable bird communities without relevant seasonal changes, in contrast to the dramatic winter increases and decreases in numbers that occur in farmland and upland forests respectively (Table 1). Since pine and eucalypt plantations comprised most of the sample of lowland forests (59 of 67 localities), the numerical stability of their bird communities may be related to the presence of year-round foliage on the dominant tree species (pines and eucalypts; see Murakami 2002) and to their location at low altitudes (Santos *et al.* 2010). Lowland plantations thus maintain many small passerines that glean insects off foliage during the winter period, and these form the majority of their bird communities (over 70% of birds) across the huge areas that such forests currently occupy in the Cantabrian region. These results are supported by earlier local studies carried out in the eastern sector of the region (Fernández and Galarza 1986, Tellería and Galarza 1990). However, eucalypt plantations (44 of 67 localities and including the more extensive forests) seem to have the lowest breeding densities among the lowland forests (see Bongiorno 1982, authors' data), so another possible explanation is that these forests can only sustain very low bird densities, even in the breeding season.

Origins of wintering bird populations

A vast regional rearrangement of bird assemblages occurs in the Cantabrian area in winter. Since a large number of the wintering birds are only present during that season, a proper interpretation

Table 3. Estimated inter-seasonal numerical changes in bird populations in the three studied habitats (pooled estimates for 34 species with wintering populations in farmland).

Habitat	Area (hectares)	Total spring numbers (mean ± 1.96 sd)	Total winter numbers (mean ± 1.96 sd)	Mean bird input (winter less spring)
Farmland	572,330	2,843,927 ± 882,915	9,768,000 ± 3,748,255	6,924,073
Upland forests	535,220	2,580,324 ± 1,003,008	1,160,825 ± 840,447	-1,419,499
Lowland forests	710,170	2,836,022 ± 710,803	3,042,076 ± 1,185,648	206,054

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Table 4. Mean absolute population sizes (± 95% confidence limits) estimated for 34 passerine birds: 29 resident species and five winter visitors in the Cantabrian farmland; R (residents): species present in both the breeding and winter seasons; W (winter visitors): species exclusively recorded in winter. Population estimates obtained in lowland and upland forests for the same species are given for comparison. Feeding substrates: feeding mostly on the ground (G, ground feeders) or on arboreal and shrubby vegetation (T-S, tree-shrub feeders). Recoveries: number of extra-Iberian winter recoveries (December–February) obtained in the study area up to 2009.

		Farmland		Lowland forests		Upland forests	
	Recoveries	Spring	Winter	Spring	Winter	Spring	Winter
A. arvensis (G, W)	18	0[1]	38,623 (86,959-0)	-	-	-	-
A. pratensis (G, W)	59	-	1,746,575 (2,234,937-1,258,213)	-	-	-	-
M. alba (G, R)	8	53,074 (71,346-34,802)	159,043 (208,900-109,187)	-	-	-	-
T. troglodytes (T-S, R)	7	230,051 (278,529-181,574)	205,895 (258,047-153,743)	748,314	329,020	220,471	56,474
P. modularis (G, R)	29	57,850 (83,783-31,917)	93,045 (126,152-59,939)	14,883	56,153	73,254	3,376
E. rubecula (G, R)	67	212,328 (261,072-163,584)	607,926 (699,345-516,508)	473,656	291,915	402,531	53,771
P. ochruros (G, R)	1	21,073 (33,177-8,968)	20,219 (36,832-3,606)	-	-	-	-
S. torquata (G, R)	2	115,006 (151,824-78,188)	129,803 (178,141-81,465)	-	-	1,332	-
T. philomelos (G, R)	159	30,004 (47,752-12,255)	414,952 (540,629-289,275)	26,002	72,287	73,923	9,233
T. iliacus (G, W)	107	-	487,160 (867,280-107,039)	-	61,021	-	38,761
T. viscivorus (G, R)	2	12,090 (19,695-4,485)	28,827 (44,381-13,273)	-	-	12,761	13,540
T. merula (G, R)	101	384,154 (449,242-319,066)	698,237 (808,906-587,569)	136,302	170,752	181,195	79,649
S. atricapilla (T-S, R)	14	124,201 (158,988-89,413)	76,907 (112,485-41,329)	316,099	42,747	281,676	1,806
C. juncidis (G, R)	0	14,884 (21,633-8,135)	7,973 (25,051-0)	-	-	-	-
P. collybita (T-S, R)	43	5,177 (8,886-1,469)	77,871 (110,080-45,661)	8,165	73,344	7,163	1,739
R. ignicapilla (T-S, R)	4	23,944 (37,055-10,832)	87,506 (133,369-41,644)	252,732	578,447	146,385	214,011
P. major (T-S, R)	31	148,419 (189,381-107,456)	177,751 (226,457-129,045)	83,423	154,965	87,090	42,933
P. ater (T-S, R)	0	9,686 (17,499-1,872)	22,940 (35,470-10,409)	324,360	587,728	297,736	147,374
C. caeruleus (T-S, R)	19	13,904 (25,081-2,727)	58,870 (85,841-31,899)	32,567	107,656	172,279	95,500
L. cristatus (T-S, R)	0	9,637 (18,156-1,119)	10,844 (21,506-181)	80,109	122,415	162,377	97,894
P. palustris (T-S, W)	0	-	10,804 (23,108-0)	-	28,101	36,550	93,541
A. caudatus (T-S, R)	7	18,958 (34,259-3,657)	11,013 (23,718-0)	18,753	155,546	62,684	119,622
S. vulgaris/unicolor (G, R)	28	83,056 (122,700-43,413)	441,932 (668,826-215,038)	-	-	-	-
P. domesticus (G, R)	4	654,801 (852,765-456,837)	1140,383 (1532,560-748,207)	-	-	-	-
P. montanus (G, R)	0	32,097 (55,666-8,528)	25,069 (48,784-1,355)	-	-	-	-
F. coelebs (G, R)	25	141,177 (184,350-98,003)	2,312,004 (3,341,242-1,282,766)	151,044	133,891	274,186	27,355
C. cannabina (G, R)	14	33,707 (57,325-10,089)	20,933 (41,639-227)	-	-	1,328	-

Table 4. Continued.

	Recoveries	Farmland		Lowland forests		Upland forests	
		Spring	Winter	Spring	Winter	Spring	Winter
C. carduelis (G, R)	16	148,750 (184,688-112,813)	335,325 (473,553-197,097)	42,264	10,559	10,305	-
C. chloris (G, R)	7	83,971 (111,603-56,339)	110,749 (172,206-49,292)	12,880	-	3,362	-
C. spinus (T-S, W)	28	-	101,498 (153,991-49,004)	-	37,149	2,039	10,734
S. serinus (G, R)	2	105,415 (129,514-81,316)	7,932 (17,441-0)	27,596	-	21,600	-
P. pyrrhula (T-S, R)	2	18,996 (34,536-3,457)	7,684 (14,189-1,180)	73,068	24,463	29,650	48,120
E. cirlus (G, R)	1	50,654 (73,324-27,984)	47,225 (82,786-11,665)	-	-	-	-
E. cia (G, R)	0	6,863 (13,013-714)	44,481 (81,443-7,520)	7,758	-	18,449	-

[1]One bird detected outside the 50m belt in spring.

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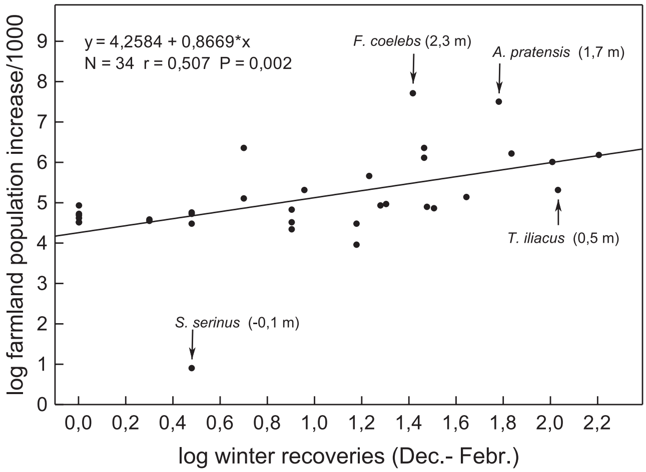

Figure 2. Relationships between the winter increases of bird populations occurring in the farmland and the number of winter recoveries for 34 bird species in the Cantabrian region.

of this process requires not only the consideration of the regional populations concerned, but also the potential role of extra-Iberian migratory populations.

Farmland bird populations were 3.4 times greater in winter than in spring, accounting for an estimated increase of 6.9 million birds in the available farmland habitat. Admittedly, a part of this increase is due to reproductive recruitment of many local nesting species (such as tits, other small insectivores and sparrows; Tables 3 and 4), but most was accounted for by birds of different origin. Our results indicate that this winter increase hardly involves forest birds performing regional movements from upland woodlands during the winter, whereas it is strongly correlated with the arrival of extra-Iberian birds, as evidenced by ring recoveries. In fact, the largest part of the population increase (69.2%) was due to four species with very high ring recovery rates. Two are exclusively wintering birds in the area: the Meadow Pipit and the Redwing (responsible for 25.2% and 7.0% of the increase, respectively), and two are resident species that are joined by large numbers of northern European conspecific migrants, the Chaffinch and the Song Thrush (31.4% and 5.6% of the increase). The relationship between the bird influxes in farmland and ring recoveries remains even when only the species with resident populations in the Cantabrian

Table 5. Results of the two general regression models (GRM) carried out on the increase in winter populations in farmland (bird influxes: winter minus spring abundances). Winter decreases in forests were calculated as spring minus winter abundances (bird outflows). Note that the GRM run with 'all species' includes resident species and birds present in the study area exclusively as wintering species. All variables were log-transformed.

Predictors	Winter increases in farmland					
	Only resident species (*n* = 29)			All species (*n* = 34)		
	parameter	*F*	*P*	parameter	*F*	*P*
Intercept	-0.067	1.108	0.303	-0.081	1.458	0.237
Winter recoveries	0.160	6.490	0.017	0.225	14.073	< 0.001
Winter decreases in upland forests	0.434	2.312	0.141	0.205	0.485	0.492
Winter decreases in lowland forests	0.001	0.00004	0.995	-0.019	0.032	0.858
Whole model	$R^2_{3,25}$ = 35.2	4.531	0.011	$R^2_{3,30}$ = 36.5	5,737	0.003

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area were considered in the analysis (Table 3). Therefore, it may be concluded that our results indicate that migratory, extra-Iberian birds make the major numerical contribution to the bird communities of the most important wintering habitat of Northern Spain. This finding is also supported by traditional analyses of ringing recoveries, which show the Cantabrian coast to be an important area for the passage of many migrant species from northern and central-western Europe (Santos *et al.* 1990, Asensio 1985, Cantos 1992, Bueno 1998), whereas its importance as a wintering ground is restricted to a rather small number of species. This is the case for such species as the Robin and the Blackcap, whose European populations supply a large migratory flux during the autumn passage, but which are rather scarce (Robin) or very rare (Blackcap) winter visitors, a common pattern among small insectivores (Cantos 1992, Bueno 1998).

Our results do not support the occurrence of significant seasonal movements between wooded habitats and farmland, specifically from upland forests, whose bird populations declined by almost 60% in winter (Tables 1 and 2). Firstly, although the most parsimonious explanation of the winter population changes is to propose an ample movement from upland forests to nearby farmland, the number of birds that supposedly move does not match the increases estimated for resident populations in farmland. Secondly, decreases in bird density are common in all mountain and upland areas in the Spanish interior (Álvarez and Purroy 1993, Tellería *et al.* 2001, Ramírez 2004), suggesting that there are significant altitudinal migratory movements, but these remain poorly known because of the negligible ringing effort conducted in upland areas. Nevertheless, recent studies combining abundance and morphological data (Tellería *et al.* 2001, Pérez-Tris and Tellería, 2002) have shown that the populations of many bird species that breed in the highly seasonal environments of Northern Spain are migratory, moving to lowlands and/or more southern areas in winter. These species include such passerines as the Robin, the Blackcap, the Firecrest *Regulus ignicapillus*, the Blue Tit *Cyanistes caeruleus* and the Great Tit *Parus major*, all with important populations in the studied forests (Tables 3 and 4). On the other hand, the combination of ringing recoveries and biometric data obtained in the Gibraltar region during the autumn migration has shown a strong passage of Spanish finches towards Africa (Asensio 1984, 1985). Hence, most birds that leave the upland forests in winter have to move variable distances south of the Cantabrian mountains.

Conclusions and implications for conservation

Cantabrian farmland offers a traditional agricultural system that maintains in winter the highest levels of passerine bird richness and abundance in Northern Spain. Mild winters, together with an open habitat structure dominated by grasslands, and their geographical situation on the migratory flyway of many bird species, lend this farmland a special role as a wintering ground for their resident birds and for millions of migrant birds coming from northern European breeding areas. However, long-term past losses and some ongoing threats may gravely damage the future suitability of Cantabrian farmland for sustaining bird populations and, more specifically, its role as a wintering ground for European migrants. Today, afforestation with pines and eucalypts in areas below 400 m covers an area similar to that occupied by traditional farmland and comprises nearly 90% of the forest area (MFE50 2007). Another perceptible, concomitant development is the increasing abandonment of farming practices, resulting in declines in livestock and reductions in mowing and the scarce winter stubbles, with the ensuing loss of suitable habitat for birds that depend on grasslands (Moreira *et al.* 2005, Butler *et al.* 2010). This trend appears to be rather general in Cantabrian farmlands, but data are insufficient to make an accurate assessment of it. Moreover, it appears that the optimal management for bird conservation is an extensive use, intermediate between abandonment and intensive management (Vickery *et al.* 2001, Atkinson *et al.* 2005, Nikolov 2010). The landscape heterogeneity of Cantabrian farmland, including the mosaic of wooded patches and hedgerows in a matrix of pasturelands that is maintained by traditional agricultural usage, is the key feature explaining its high avian diversity as well as the mix of forest and grassland birds (see Benton *et al.* 2003, Wuczyński *et al.* 2011 and references therein). Hence, its adequate conservation requires that the slow but progressive loss of farmland area and the trend towards its abandonment be curbed, as well as the increasing encroachment of eucalypt plantations, which have particularly expanded in recent times (GV 2005) but have the lowest richness and abundance of birds in the Cantabrian lowlands (Bongiorno 1982, Tellería and Galarza 1990).

Farmland is not included in the Natura 2000 network (Council Directive 92/43/EEC; Tellería *et al.* 2008). Hence conservation and restoration measures should be managed through the agri-environment schemes (AES), encouraging those farming and forestry practices that are compatible with the preservation of natural values, and specifically those that make farmland a valuable winter habitat for grassland birds. However, the effectiveness of AES crucially depends on adequate funding allocation among the 27 Member States of the EU, which is just the opposite of the actual distribution of Axis 2 funds (for improving the environment and the countryside) provided by the CAP (Butler *et al.* 2010), as well as the appropriate distribution of funds within every member state. Thus, although Spain is the country with the highest diversity of farmland birds, it has the second lowest funding rate (Butler *et al.* 2010). At the same time, fund allocation among rural development measures is clearly biased in Spain towards Axes 1 and 3 (improvement of competitiveness and diversification of the rural economy, respectively), and to Natura 2000 areas within Axis 2 (MARM 2010; see also Llusia and Oñate 2005 and Moreno *et al.* 2010 for failures in AES application). Thus, additional funding and an adequate re-allocation of existing funds appears essential to a satisfactory implementation of AES targets in Spain, and is a further objective towards ensuring the conservation of the Cantabrian grasslands.

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