

Species traits explaining long-term abundance changes of breeding birds in farmland areas in Álava (N Spain).

Los rasgos de las especies explican los cambios a largo plazo en la abundancia de aves nidificantes en medios agrícolas en Álava (Norte de España).

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Abstract

In recent decades, the populations of many common bird species have greatly declined in Europe, particularly in farmland habitats. However, this decline has not affected every species, and to understand the mechanisms behind this interspecific variability, its relationship with several species-specific traits has been studied repeatedly. We used this approach to analyse long-term changes in the abundance of breeding passerines in farmland areas in northern Spain. Abundance changes were quantified in 2015 and 2016 by repeating the same line transects conducted in 1988/89 in three agricultural habitats located along a steep Atlantic-Mediterranean gradient in the province of Álava. We found that total bird abundance did not decline, as most species not closely linked to farmland habitats showed positive population changes, while the number of increasing and decreasing farmland specialists was similar. Specific traits explained a substantial proportion of the variability in abundance change, as warm-dwelling species and those occupying habitats with a complex vegetation structure showed more positive changes than those preferring colder conditions and more open habitats. These patterns can be explained by climate warming and by the increase in hedge and forest cover in the study area. Although we did not find a long-term decline in the overall abundance of the studied bird community nor in that of

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farmland specialists, open habitat species associated with a cool climate should be the focus of particular concern.

Key words: Agriculture, climate change, land-use change, passerines, population trends.

Resumen

Los rasgos de las especies explican los cambios a largo plazo en la abundancia de aves nidificantes en medios agrícolas en Álava (Norte de España). Muchas especies de aves comunes en Europa han experimentado acusados descensos poblacionales en las últimas décadas, especialmente en medios agrícolas. Sin embargo, este declive no ha afectado a todas las especies, y para comprender los mecanismos que subyacen tras esta variabilidad interespecífica, se ha estudiado repetidamente su relación con diversos rasgos ecológicos propios de cada especie. En este estudio utilizamos este enfoque para analizar los cambios a largo plazo en la abundancia de los passeriformes nidificantes en áreas agrícolas del norte de España. Los cambios en la abundancia se cuantificaron repitiendo en 2015 y 2016 los mismos transectos realizados en 1988/89 en tres hábitats agrícolas situados a lo largo de un pronunciado gradiente Atlántico-Mediterráneo en la provincia de Álava. No se observó una reducción en el número total de aves, ya que la mayoría de las especies no asociadas estrechamente con medios agrícolas aumentaron su abundancia, mientras que el número de especialistas agrícolas que mostraron declives poblacionales fue similar al de aquellos que aumentaron. Los rasgos específicos explicaron una proporción sustancial de la variabilidad en los cambios de abundancia, ya que las especies propias de climas cálidos y las que ocupan medios con una estructura vegetal compleja mostraron cambios más positivos que las asociadas a temperaturas más frías y a hábitats más abiertos. Estos patrones se pueden explicar por los efectos del calentamiento global y del incremento en la cobertura de setos y bosques en el área de estudio. Aunque no se registró un declive a largo plazo en la abundancia total de las comunidades de aves estudiadas ni en la de especialistas agrícolas, las especies de espacios abiertos asociadas a climas fríos deberían ser objeto de especial atención.

Palabras clave: agricultura, cambio climático, cambio de usos de suelo, passeriformes, tendencia poblacional.

Laburpena

Azken hamarkadetan, zenbait hegazti-espezie arrunten populazioek beherakada handiak izan dituzte Europan, batez ere laborantza lurretan. Hala ere, beherakada horiek ez dira gertatu espezie guztietan. Espezieen arteko aldagarritasun prozesu horren azpiko prozesua ulertzeko behin eta berriz aztertu izan da hainbat ezaugarri espezifikoekin zein lotura dagoen. Guk ikuspegi hori erabili dugu laborantza-lurretan passeriforme habiagileen ugaritasunean epe luzera gertatzen diren aldaketak aztertzeko Araban, (Espania iparraldean). Ugaritasun-aldaketak kuantifikatzeko, 2015ean eta 2016an errepikatu egin genituen Arabako nekazaritza-habitatetan 1988/89an egindako linea-transektu berberak.

Transektu horiek Atlantiko-Mediterraneo gradiente nabarmenean kokatutako hiru habitat ezberdinetan burutu ziren: landazabal kantauriarra, zereal-soroak eta mahastiak. Hegaztien guztizko ugaritasuna ez zen gutxitu, batez ere laborantza-lurretako habitatekin estuki lotuta ez dauden espezie gehienek aldaketa positiboak erakutsi zituztelako. Laborantza-lurretako espezialisten artean, aldiz, hazi eta gutxitu egin ziren espezie-kopuruak antzekoak izan ziren. Ezaugarri espezifikoek ugaritasun-aldakortasunaren funtsezko proportzio bat azaldu zuten. Izan ere, klima hotzean bizi diren espezieek eta landaredi-egitura konplexuarekin habitatak okupatzen dituztenek aldaketa positiboagoak izan zituzten, baldintza beroagoak eta habitat irekiagoak nahiago dituztenek baino. Patroi horiek klima-beroketak eta azterketa-eremuan gertatutako hesi eta baso-estalduraren igoerak azal ditzakete. Aztertutako hegazti-komunitateen eta nekazaritzako espezialisten guztizko ugaritasunak gainbeherarik izan ez bazuen ere, klima hotzei lotutako espazio irekietako espezieek arreta berezia jaso beharko lukete.

Gako hitzak: klima-aldaketa, lurzorua erabilaren aldaketak, nekazaritza, passeriformeak, populazio mailako joera.



Introduction

Populations of many common bird species in Europe have been declining at an alarming rate in recent decades, leading to a net loss of avian abundance and biomass (Inger *et al.*, 2015; Burns *et al.*, 2021). But not every bird species has shown this decline, as environmental factors affect their population dynamics in different ways and cause divergent patterns of increasing or decreasing abundance over time. To understand the mechanisms behind this interspecific variability in bird population trends, its relationship with species-specific ecological and life-history traits has been repeatedly studied at different scales in Europe (Julliard *et al.*, 2003; Sirami *et al.*, 2008; Howard *et al.*, 2020; Gregory *et al.*, 2023; Storch *et al.*, 2023).

This species trait approach has revealed several common patterns, mostly related to climate and land-use changes. Among them, the stronger declines both of cold-dwelling species in relation to those preferring warmer conditions (Herrando *et al.*, 2019; Rigal *et al.*, 2023; Storch *et al.*, 2023), and of species occupying open habitats in relation to those inhabiting forests have been frequently reported (Seoane & Carrascal, 2008; Sirami *et al.*, 2008; Storch *et al.*, 2023). It has also been widely mentioned a generalised homogenization of bird communities, caused by an increase in generalist species to the detriment of specialists (Julliard *et al.*, 2003; Le Viol *et al.*, 2012; Morelli *et al.*, 2020), as specialist species appear to be more vulnerable to ecological disturbances (Futuyma & Moreno, 1988; Devictor *et al.*, 2008).

Understanding the relationships between species traits and bird population trends is particularly relevant in agricultural areas, as bird species associated with this habitat

have suffered the greatest population losses in Europe (Burns *et al.*, 2021). This process has taken place mainly as a consequence of farmland intensification (Kleijn *et al.*, 2008; Rigal *et al.*, 2023) and, in areas of low productivity, land abandonment (Suárez-Seoane *et al.*, 2002; Herrando *et al.*, 2016).

In this study, we analysed the relationships between interspecific variability in long-term bird abundance change and specific traits in farmlands in Álava. Original data were obtained by means of line transects carried out in 1988/89 (Nuevo, 1990), which were repeated using the same methodology in 2015 and 2016. Since it is located in the transition zone between the Eurosiberian and Mediterranean regions, the study area shows a high diversity of climate conditions, and hosts both northern and southern species near their range margins (Martí & del Moral, 2003). In this way, our data allowed us to compare their abundance changes in areas close to their tolerance limits, where populations are expected to be more vulnerable to the effects of environmental pressures (Sexton *et al.*, 2009; Jiguet *et al.*, 2010).

The surveyed farmlands were mostly located in high-productivity areas intensively farmed throughout the study period. This contrasts with the situation that characterises most local studies addressing long-term changes in farmland bird populations in southern Europe (but see Santos, 2021). These have mainly dealt with the effects of landscape simplification (Santana *et al.*, 2017; Gaüzère *et al.*, 2019), farmland intensification (Cabodevilla *et al.*, 2022), and, above all, land abandonment (Preiss *et al.*, 1997; Sirami *et al.*, 2008; Fonderflick *et al.*, 2010; Regos *et al.*, 2016; Galarza & Zabala, 2024). In the study area, the agricultural landscape has not suffered such profound modifications and, therefore, the analysis of changes in their bird populations can offer a different perspective to that of those studies.

Our objectives were to assess if long-term changes in bird species abundance in the study area were in line with the declines widely reported in Europe, particularly in the case of species closely linked to farmland habitats. We also tested whether interspecific variability in these changes could be explained by species-specific traits related to their degree of specialization and their thermal and habitat preferences. To provide the background to interpret our results, we used aerial photographs and vegetation maps to record land-use changes in the studied farmlands over the years between the two sampling periods.

Methods

Study area

Bird surveys were carried out in the province of Álava, and some adjacent localities in the provinces of Burgos and La Rioja (Figure 1). This area is located around the border between the Atlantic and the Mediterranean regions, showing a steep gradient of

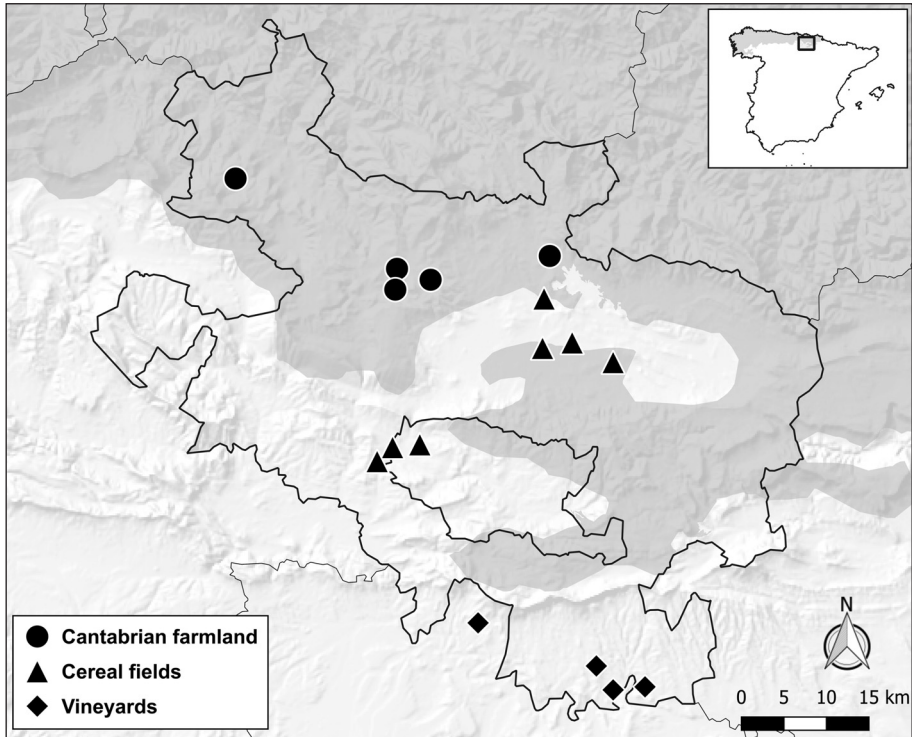


Fig. 1.- Map of the study area showing the limits of the province of Álava and the location of the bird transects. Light grey: Mediterranean region; dark grey: Atlantic region (source: Ministerio para la Transición Ecológica, 2018).

Fig. 1.- Mapa del área de estudio que muestra los límites de la provincia de Álava y la localización de los transectos. Gris claro: región mediterránea; gris oscuro: región atlántica (fuente: Ministerio para la Transición Ecológica, 2018).

decreasing precipitation towards the south. This sharp climatic contrast is reflected in the farmland landscape, which, from north to south, can be divided into three main types:

- *Cantabrian farmland*: With a mean annual rainfall of around 1,000 mm, and dominated by intensively managed grasslands devoted to livestock grazing and hay and silage production, with hedgerows and patches of *Quercus* spp.
- *Cereal fields*: The most widespread farmland type in the study area, located in the transition zone between the Eurosiberian and the Supramediterranean climatic belts (Rivas-Martínez, 1987), and with an annual rainfall of 600-900 mm. Winter wheat and barley are the dominant species grown, interspersed with irrigated crops such as sugarbeet, oilseed rape and field beans. Steeper terrain is covered by oak patches (mainly *Q. faginea*) and open shrublands with common juniper *Juniperus communis*.

- *Vineyards*: Located at the head of the Ebro Valley, an area with a mean annual rainfall of 400-600 mm included in the Mesomediterranean climatic belt (Rivas-Martínez, 1987). Vineyards dominate the landscape, alternating in some places with cereal fields, and almond and olive groves. Many agricultural plots are bordered with hilly terrain covered by xerophilous pastures and sclerophyllous scrub.

Bird surveys

The same transects of variable length conducted by Nuevo (1990) in 1988/89 were carried out again in May/June of 2015 and 2016, recording the birds seen or heard with no distance limits. While each transect was surveyed just once in 1988/1989, the new surveys were conducted twice, once in 2015 and once in 2016, to account for year-to-year population fluctuations (McCain *et al.*, 2016). Comparisons were done considering data collected in 2015 and in 2016 separately, thus the comparisons and analysis have been performed between periods with similar survey effort. A total length of 13.91 km was covered in the Cantabrian farmland (five transects of 2.78 ± 0.29 km), at a mean altitude of 559 m a.s.l., 28.24 km in the cereal fields (seven transects of 4.03 ± 2.56 km, at a mean altitude of 524 m), and 14.94 km in the vineyards (four transects of 3.74 ± 2.16 km, at a mean altitude of 498 m). Bird surveys in 2015/16 were conducted on similar dates as the original ones in 1988/89 (mean difference: 1.25 days, maximum four), during the first four hours after sunrise avoiding rainy days, fog or strong winds. While one observer conducted the 1988/89 fieldwork, two were involved in the new surveys, each one carrying out half of the transects in 2015 and the other half in 2016. In this way, each transect was covered twice, once in 2015 by one observer and once in 2016 by the other one.

Bird species traits

The interspecific differences in abundance change were related to four different species' traits: two traits related to the degree of specialization; one trait related to habitat preference, and the fourth trait related to climatic niche.

- Degree of specialisation related traits: Specialisation is a broad concept that can be defined and measured in many different ways (Morelli *et al.*, 2019). We specifically used two independent and unrelated ($r = 0.016$, $N = 31$, $P = 0.933$) indexes: (a) Specialization Index (SI), taken from Morelli *et al.* (2019), a multidimensional index derived from five different measures of ecological specialization related to diet, foraging behaviour, foraging substrate, habitat, and nesting site, and (b) Habitat Specialization Index (HSI), based on the Habitat Breadth Index defined by Carrascal & Lobo (2003), which focused on the species' distribution breadth along a structural

complexity gradient, taking into account the relative abundance of the corresponding species across six habitat categories ranging from those lacking or with very sparse vegetation to dense mature forests. HSI was calculated as the inverse of the Habitat Breadth Index obtained by these authors.

- Habitat preference related trait: To quantify the habitat preferences of bird species we focused on the vegetation volume of their preferred habitats. We used the Structural Complexity Index (SCI) given as well by Carrascal & Lobo (2003), who calculated it after giving a score to the six habitat categories already mentioned, ranging from 0 to 5 as the vegetation volume increases. From the weighted mean of the abundance of each species across these habitat categories, an average score for the vegetation volume and structural complexity of its occupied habitats was obtained.
- Climatic niche related trait: To quantify the thermal preferences of the different species the variable Mean Temperature (MT) in spring in the European breeding distribution area for each species was used. It was extracted from Gregory *et al.* (2009), and corresponded to the mean temperature in the period March-August of each species' European distribution area as shown by Hagemeyer & Blair (1997). The difference between the maximum and minimum temperature values for the European range of each species (Gregory *et al.*, 2009) was also initially explored, although it was finally discarded as it was highly correlated with MT ($r = -0.814$).

Statistical analyses

Bird numbers for the original surveys were derived from the abundance data (individuals/km) given in Nuevo (1990). For subsequent analyses, only those passerine species with at least 15 individuals recorded in 1988/89, 2015 or 2016 were considered, with the exception of hirundines (highly mobile species not included in the 1988/89 data) and the Iberian Chiffchaff *Phylloscopus ibericus*, not treated separately from its congener *P. collybita* in the data sources for the species traits values.

The total number of individuals for each species in 2015 and 2016 were highly correlated ($r_s = 0.945$, $N = 31$, $P < 0.001$), but they were significantly higher in the former year (paired Mann-Whitney test, $U = 374.5$, $P = 0.004$). Therefore, they were treated separately in all analyses.

Population change index between the original and the new surveys were calculated using the formula:

$$PCI = \frac{n_{ia} - n_{ib}}{\max(n_{ia} - n_{ib})}$$

where n_{ia} and n_{ib} are the number of individuals of the species i recorded in 2015 (or 2016) and 1988/89, respectively. Due to the limited sample size, total numbers across the three farmland types were used for each species. PCI values obtained in this way

were highly correlated with those of individual habitats ($P < 0.001$ in all cases, including only those species with at least five individuals recorded in the corresponding habitat in any of the study years): Cantabrian farmland ($r = 0.84$ in 2015 and $r = 0.86$ in 2016, $N = 23$), cereal fields (0.84 and 0.81 , $N = 26$), and vineyards (0.80 and 0.92 , $N = 20$), so they adequately summarised population changes registered in the three surveyed farmland habitats.

Our results refer to two sets of surveys separated each other by 27 years. We assessed the ability of the PCI to reflect population trends over this period by correlating the PCI of the species included in the analyses with the mean interannual change from 1998 to 2013 for their breeding populations in Spain derived from the SACRE programme (SEO/BirdLife, 2013).

To assess if the population change for farmland specialists as a group differed from zero, we used the one-sample Wilcoxon test. We considered as farmland specialists those species included in the European Farmland Bird Index, a widely used indicator integrating the population trends of common farmland bird species in the European Union (pecbms.info/trends-and-indicators). The same test was also applied to the group of species not included in this index, common in the studied farmlands but not closely linked to agricultural habitats.

To relate the changes in species abundance with the species-specific traits, we fitted a general linear model (GLM), with the population change index as the dependent variable and the four specific traits as predictors. No collinearity issues were detected among predictors ($R < 0.5$ in all pair-wise correlation tests). We calculated the corrected Akaike Information Criterion for small samples (AICc) for each possible combination of predictor variables using the R package “MuMin” (Barton, 2020), and retained the model with the smallest AICc, searching also for alternative models with $AICc < 2$. The relative contribution of each selected variable to the model explanatory power was calculated through the “relaimpo” R package (Grömping, 2006), and the proper behaviour of residuals was checked with the “Dharma” R package (Hartig, 2022). The predicted effects of each variable were plotted using the “visreg” package (Breheny & Burchett, 2018).

Data from 2015 were used to build the model, and those of 2016 to test its robustness against year-to-year variations. In this way, the predictor variables selected in the 2015 model were used to build a new model with the 2016 PCI values, to verify that their contribution remained significant.

Since bird species are phylogenetically related, they should not be considered as independent units (Harvey & Purvis, 1991). To assess the potential influence of this effect in our results, and following Revell (2010), we tested for phylogenetic autocorrelation in the residuals of the final model by means of the Moran's I test (R package “ape”; Paradis & Schliep, 2018), whose lack of significance implies that phylogenetic auto-

correlation does not affect the results (Reif *et al.*, 2011). Phylogenetic information was obtained from the BirdTree.org website (Jetz *et al.*, 2012): for the subset of species included in our model, 100 phylogenetic trees were downloaded, and these were used to build a consensus tree from which a matrix of phylogenetic proximities was obtained through the R package “adephylo” (Jombart *et al.*, 2010). All analyses were conducted in R v4.3.1. (R Core Team, 2023).

Land-use changes

To compare land uses in the two survey periods, we defined a 300 m wide band along our transects and divided it into 100x100 m (1 ha) squared units. Only squares completely included within the 300 m-band were used in the analyses. Aerial photographs from 1984/85 (resolution of 0.5 m) and 2015 (resolution of 0.25 m) were visually inspected to verify the presence inside these squared units of the following land uses: grasslands, vineyards, cereals and other herbaceous crops, woodland, shrubland/rough pasture, hedgerows, almond/olive groves, and urban areas (residential areas, isolated buildings, and busy roads). Photographs from 1984/85 were used as they were the good-resolution available images closest in time to the 1988/89 surveys. For each land use, the number of squares where the particular land use type was present was counted, regardless of its extension. This count was compared between the two periods. As an additional supportive source of information, vegetation maps published in 1990 (scale 1:25,000) and 2007 (scale 1:10,000) were used. These maps were not available for the only transect (3.05 km) carried out in La Rioja, whose land uses were therefore recorded only from photographs. Aerial photographs and vegetation maps were obtained from the GeoEuskadi website (www.geo.euskadi.eus), and the software used was QGIS 3.8 (QGIS Development Team, 2019).

Results

Species abundance change

The total number of individuals recorded increased from 1,490 in 1988/89 to 2,073 in 2015 (+39%), and 1,641 in 2016 (+10%), while the total number of species decreased from 59 in 1988/89 to 52 both in 2015 and 2016. The 31 species included in subsequent analyses (those with at least 15 individuals recorded in any of the study years) represented 90% of total numbers in 1988/89, 94% in 2015 and 93% in 2016 (Table 1). The correlation between the PCI for these 31 bird species and their average interannual trend for the whole of Spain in 1998-2013 obtained through the SACRE programme was significant both in 2015 ($r = 0.52$; $P = 0.003$) and 2016 ($r = 0.50$; $P = 0.004$).

SPECIES	n 1988/89	n 2015	n 2016	PCI 2015	PCI 2016	SCI	SI	HSI	MT
<i>Pica pica</i>	72	24	29	-0.67	-0.60	2.84	0.06	2.84	14.42
<i>Corvus corone</i>	79	92	61	0.14	-0.23	3.56	0.01	3.56	14.36
<i>Parus major</i>	29	31	18	0.06	-0.38	3.98	0.10	3.98	14.50
<i>Cyanistes caeruleus</i>	14	24	19	0.42	0.26	4.38	0.08	4.38	14.67
<i>Calandrella brachydactyla</i> *	5	22	21	0.77	0.76	1.29	0.39	1.29	18.17
<i>Alauda arvensis</i> *	100	46	43	-0.54	-0.57	1.95	0.22	1.95	14.36
<i>Galerida cristata</i> *	85	50	45	-0.41	-0.47	1.50	0.32	1.50	16.36
<i>Cettia cetti</i>	3	17	15	0.82	0.80	2.75	0.16	2.75	17.53
<i>Hippolais polyglotta</i>	30	52	49	0.42	0.39	3.00	0.23	3.00	16.25
<i>Sylvia atricapilla</i>	39	116	73	0.66	0.47	4.00	0.23	4.00	14.61
<i>Curruca melanocephala</i>	0	17	15	1.00	1.00	3.20	0.34	3.20	18.74
<i>Regulus ignicapilla</i>	6	14	15	0.57	0.60	4.74	0.19	4.74	14.77
<i>Troglodytes troglodytes</i>	21	44	33	0.52	0.36	4.00	0.30	4.00	14.20
<i>Sturnus unicolor</i> *	55	189	111	0.71	0.50	3.10	0.13	3.10	17.88
<i>Turdus merula</i>	32	108	74	0.70	0.57	3.70	0.21	3.70	14.59
<i>Erithacus rubecula</i>	20	28	28	0.29	0.29	4.28	0.00	4.28	14.24
<i>Phoenicurus ochruros</i>	1	16	17	0.94	0.94	3.17	0.19	3.17	14.98
<i>Saxicola rubicola</i> *	36	72	51	0.50	0.29	1.90	0.41	1.90	15.69
<i>Passer domesticus</i>	55	113	102	0.51	0.46	2.52	0.16	2.52	14.34
<i>Petronia petronia</i> *	26	14	24	-0.46	-0.08	1.80	0.16	1.80	17.66
<i>Prunella modularis</i>	40	12	17	-0.70	-0.58	3.65	0.27	3.65	13.38
<i>Motacilla flava</i> *	23	55	87	0.58	0.74	2.36	0.19	2.36	14.52
<i>Motacilla alba</i>	22	6	8	-0.73	-0.64	2.88	0.14	2.88	14.26
<i>Fringilla coelebs</i>	18	63	58	0.71	0.69	4.11	0.05	4.11	14.47
<i>Chloris chloris</i>	31	88	77	0.65	0.60	3.09	0.40	3.09	14.61
<i>Carduelis carduelis</i>	13	145	83	0.91	0.84	3.50	0.25	3.50	15.07
<i>Linaria cannabina</i> *	122	118	107	-0.03	-0.12	2.51	0.47	2.51	14.86
<i>Serinus serinus</i> *	93	137	126	0.32	0.26	3.70	0.46	3.70	15.46
<i>Emberiza cirulus</i> *	33	35	39	0.06	0.15	3.14	0.57	3.14	16.85
<i>Emberiza citrinella</i> *	56	0	1	-1.00	-0.98	3.00	0.17	3.00	13.86
<i>Emberiza calandra</i> *	178	207	86	0.14	-0.52	1.89	0.70	1.89	15.67

Table 1.- Total number of individuals (n) recorded in the different study years, Population Change Index for 2015 (PCI₂₀₁₅) and 2016 (PCI₂₀₁₆), and values of the species traits: SCI: Structural Complexity Index; SI: Specialization Index; HSI: Habitat Specialization Index; MT: Mean Temperature in spring in their European breeding distribution area (see Methods). Species included in the European Farmland Bird Index are marked with an asterisk.

Tabla 1.- Número total de individuos (n) registrados en los diferentes años de estudio, Índice de Cambio Poblacional para 2015 (PCI₂₀₁₅) y 2016 (PCI₂₀₁₆), y valores de los rasgos específicos: SCI: Índice de Complejidad Estructural; SI: Índice de Especialización; HSI: Índice de Especialización del Hábitat; MT: Temperatura Media en primavera en el área de nidificación de la especie en Europa (véase Métodos). Se marcan con asterisco las especies incluidas en el Índice Europeo de Aves Agrícolas.

Twenty species were more abundant both in 2015 and 2016 than in the original surveys, and eight decreased. Data collected in 2015 and 2016 offered inconsistent results in three species: Carrion crow *Corvus corone*, Great tit *Parus major*, and Corn bunting *Emberiza calandra*. These species showed population increases when the PCI was calculated based on data collected in 2015, whereas they showed decreases if the PCI was based on data collected in 2016 (Table 1). In both study years, the greatest gains corresponded to Sardinian warbler *Sylvia melanocephala*, Black redstart *Phoenicurus ochruros*, European goldfinch *Carduelis carduelis*, and Cetti's warbler *Cettia cetti*. Yellowhammer *Emberiza citrinella*, White wagtail *Motacilla alba*, Dunnock *Prunella modularis*, and Eurasian magpie *Pica pica*, showed the greatest losses.

Among farmland specialists, the number of increasing and decreasing species was similar (seven and five respectively in 2015, six and six in 2016), while a positive population change was dominant for the rest of species (16 out of 19 increased in 2015, and 14 in 2016). Mean PCI for non-farmland specialists was significantly greater than zero both in 2015 and 2016, while the difference was not significant for farmland specialists in both years (Table 2).

		Mean PCI	V	P
Farmland specialists	2015	0.053	46	0.622
	2016	- 0.003	40	0.970
Other species	2015	0.380	151.5	0.024
	2016	0.307	148	0.035

Table.2- Mean values of the Percentage Change Index (PCI) for farmland specialists (species included in the European Farmland Bird Index) and the rest of species. Also shown are the V-values of the one-sample Wilcoxon tests used to assess whether the respective means were significantly different from zero.

Tabla 2.- Valores medios del Índice de Cambio Poblacional (PCI) para especialistas agrícolas (especies incluidas en el Índice Europeo de Aves Agrícolas) y el resto de especies. Se muestran también los valores del test de Wilcoxon para una muestra empleado para comprobar si las medias respectivas fueron significativamente distintas de cero.

For 2015, the model with the lowest AICc explained 30.1% of the deviance and included two predictors: Mean Temperature (MT) and Structural Complexity Index (SCI) (Table 3), both showing a positive relationship with PCI (Fig. 2). No phylogenetic autocorrelation was found in the residuals (Moran's I observed = -0.021, expected = -0.033, $P = 0.655$). The two selected variables were used to build a new model for 2016, in which both remained significant and together explained 32.14% of the total deviance. In both models, MT explained a higher proportion of the total deviance than SCI (17.55 vs 12.57% in 2015, 20.85 vs 11.29% in 2016).

		Estimate	se	t	P
2015	Intercept	-4.033	1.268	-3.18	0.004
	Mean Temperature	0.218	0.070	3.10	0.004
	Structural Complexity Index	0.306	0.111	2.76	0.010
2016	Intercept	-4.226	1.228	-3.44	0.002
	Mean Temperature	0.229	0.068	3.36	0.002
	Structural Complexity Index	0.292	0.107	2.72	0.011

Table.3- Results of the GLMs relating interspecific variability in abundance change from 1988/89 to 2015 and 2016 to those predictor variables leading to the model with the lowest AICc.

Tabla 3.- Resultados de los GLM que relacionan la variabilidad interespecifica en los cambios de abundancia de 1988/89 a 2015 y 2016 con aquellas variables predictoras que forman parte del modelo con el menor AICc.

Land use changes

Comparisons of aerial photographs revealed that, although cultivated plots continued to be by far the dominant land-use in the three studied farmland types, several changes took place from 1984/85 to 2015 (Table 4). The global picture showed a widespread increase in urban uses and in the extent of structurally complex habitat features: woodland cover in the Cantabrian farmland, hedgerows in the vineyards, and both elements in the cereal fields. Agricultural uses remained more or less the same, with the exception of a marked decrease in the presence of herbaceous crops (cereals) in favour of vineyards in the southernmost habitat.

	Cantabrian farmland			cereal fields			vineyards		
	1980s	2015	variation	1980s	2015	variation	1980s	2015	variation
Grasslands	93.6%	97.0%	+2%	0%	0%		0%	0%	
Herbaceous croplands	0%	0%		99.8%	99.0%	1%	25.5%	7.0%	-73%
Vineyards	0%	0%		0%	0%		84.4%	96.7%	+15%
Woodland	17.0%	22.5%	+32%	1.7%	4.8%	+188%	2.5%	2.5%	0%
Shrubland/ rough pasture	14.9%	10.8%	-28%	10.3%	9.7%	-6%	63.0%	68.7%	+9%
Hedgerows	50.2%	46.8%	-7%	1.4%	13.0%	+800%	6.6%	13.2%	+100%
Almond/olive trees	0%	0%		0%	0%		9.9%	7.8%	-21%
Buildings + busy roads	5.4%	9.1%	+69%	1.2%	13.4%	+983%	2.9%	9.1%	+214%

Table.4- Presence percentage of the different land uses in the 1ha squares established to describe the habitat along the bird survey transects (Cantabrian farmland: 234 squares; cereal fields: 484 sq.; vineyards: 243 sq.).

Tabla 4.- Porcentaje de presencia de los diferentes usos del suelo en las cuadrículas de 1 ha definidas para describir el hábitat a lo largo de los itinerarios de censo de aves (campiña cantábrica: 234 cuadrículas; campos de cereal: 484 cuadr.; viñedos: 243 cuadr.).

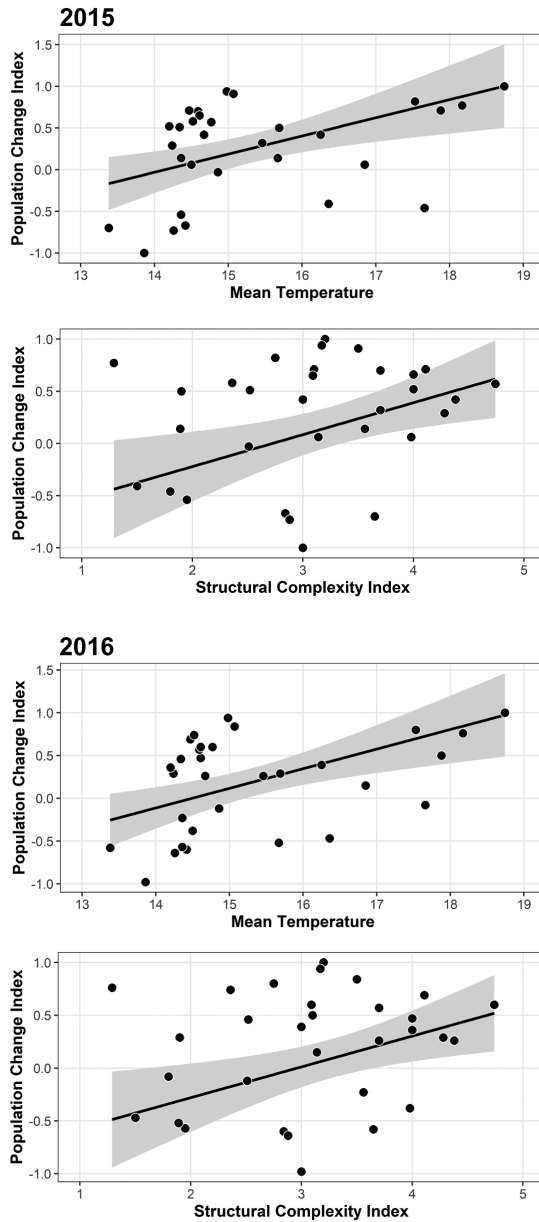


Fig. 2.- Graphical representation of the effects of the variables included in the models. Points represent raw data, lines are fitted to model predictions, and the shadow areas show 95% confidence intervals of the estimate.

Fig. 2.- Representación gráfica de los efectos de las variables incluidas en los modelos. Los puntos representan los datos brutos, las líneas corresponden a las predicciones del modelo, y el sombreado gris muestra los intervalos de confianza de la estima al 95%.

Discussion

Bird species abundance experienced substantial changes in northern Spanish farmlands from 1988/89 to 2015/16. Total abundance was higher at the end of the study period, largely due to the population increase of species not closely linked to farmland habitats, whereas among farmland specialists the number of increasing and decreasing species was similar. Most species with a negative population change were associated with farmland, among them some widely declining specialists reported to be negatively affected by agricultural intensification, such as the Eurasian skylark *Alauda arvensis*, the Crested lark *Galerida cristata* or the Yellowhammer (Keller *et al.*, 2020). But this pattern was not general, since other farmland specialists, e. g. the Short-toed lark *Calandrella brachydactyla* or the Yellow wagtail *Motacilla flava*, showed a clear increase.

These results agree with the findings of Díaz *et al.* (2022), who analyzed the dataset for farmland habitats of the monitoring programme of common breeding birds in Spain (SACRE) from 1998 to 2007. These authors reported a widespread increase in non-farmland birds in Spanish agroecosystems including annual, perennial and mosaic croplands, while farmland specialists showed a more stable trend. Interestingly, they showed that this pattern was found mainly in farmlands that were not part of the Natura 2000 network (as is the case of the study area), while the abundance of specialist birds of agricultural habitats showed a more negative trend in farmlands included in this protection figure.

Natura 2000 sites in agricultural areas host particularly diverse and abundant communities of specialist farmland birds, mainly as a consequence of their extensive management regimes (Palacín & Alonso, 2018). Hence, their populations are more vulnerable to the effects of farmland intensification than those occupying other agricultural areas already affected by this process, where they can have been depleted or even become extinct. Studies on long-term bird population trends could therefore fail to detect declines of some species if the studied habitats supported from the start of the surveys an impoverished bird community (Frenzel *et al.*, 2016; Santos, 2021). This is probably the case in the study area, where land consolidation projects were developed mostly in the 1960s and 70s (<https://web.araba.eus/es/agricultura/concentracion-parcelaria>). Mainly through increasing farmland plot size and decreasing landscape heterogeneity, these habitat modifications can have a profound negative effect on bird populations (Denac & Kmelc, 2021).

The scarcity of fallow lands in the study area also points to an intensive management regime all over the analyzed period. This habitat covered in 1988/89 less than 5% of field plots in cereal fields and vineyards (Nuevo, 1990), a situation that remained the same in the new surveys of 2015 and 2016 (pers. obs.). Fallows constitute a key habitat for birds in agricultural areas, and the decrease in their availability is strongly associated

with the negative trend of farmland bird populations in Spain (Traba & Morales, 2019). Therefore, their scarcity in the study area could have been a relevant factor leading to low population levels for many species since the time of the original surveys.

In agreement with many previous studies carried out in Europe (Eglington & Pearce-Higgins, 2015; Gaüzère *et al.*, 2020; Howard *et al.*, 2020; Gregory *et al.*, 2023), our models showed that interspecific variations in long-term bird population changes could be explained by the combination of specific habitat and thermal preferences. Mean spring temperature across the species' European breeding range was the variable with the highest explanatory power, with warm-dwelling species showing more positive changes than those preferring colder conditions. This pattern matches the results of several recent studies analysing global bird population trends in Europe and North America, which related it to the effects of climate change (Stephens *et al.*, 2016; Mason *et al.*, 2019).

In the Iberian Peninsula, the more negative trends of cold-dwelling birds have also been described for Catalonia by Herrando *et al.* (2019) for a 15-year period. On the contrary, Seoane & Carrascal (2008) found a weaker evidence for this pattern in the whole continental Spain over a 9-year timespan. In our study area the trend towards drier and hotter conditions, mainly in summer, is particularly pronounced (Sánchez Rodrigo, 2018), so the impact of climate change on bird populations could be more severe than in other Spanish regions, especially for species which find here their southern distribution limits (Pearce-Higgins *et al.*, 2015).

Seoane & Carrascal (2008) found that the larger increase of forest bird species in relation to those occupying more open habitats was the main factor explaining bird population trends in peninsular Spain. Although with a lower explanatory power than species' thermal preferences, our data also showed the relevance of this factor. Seoane & Carrascal (2008) attributed the positive trend of forest birds to an increase in plant growth and terrestrial primary net productivity caused by global warming. But for the study area, this pattern can more likely be explained by the increase in habitat availability derived from the expansion of hedgerow and forest cover detected over the study period, also described for nearby patches of Cantabrian farmland in coastal Bizkaia (Galarza & Franco, 2024).

This gain in woody cover may have been caused by several processes acting in all or part of the study area. Among them, the reduction in firewood collection and the recovery of riparian vegetation in many rivers and ditches after channelization works (Aseginolaza *et al.*, 1988) could have had a particular relevance. Likewise, the banning of stubble burning (a formerly common practice that frequently spread to field margins) and the almost complete disappearance of sheep grazing in marginal habitats (Gainzarain & Belamendia, 2015) have favoured as well the development of shrubs and trees.

It must be highlighted that population changes estimated from widely temporally separated surveys should be considered with caution, as they do not provide information on possible population fluctuations over time (McCain *et al.*, 2016). Furthermore, the fact that in this study old and recent surveys were conducted by different observers, inevitably gives rise to an observer bias of unknown magnitude (Sauer *et al.*, 1994). Nevertheless, we are confident that our results reflected real patterns, as the identified population changes were supported by overall long-term trends of bird populations recorded for the studied species in Spain (data from SACRE programme, SEO/BirdLife, 2013). Moreover, the observed patterns were shown to be robust against interannual variations, and agreed with what could be expected from recent trends in climate and woody cover in the study area.

Overall, we found that most common passerine species inhabiting farmlands in Álava increased their abundance over the 27-year period considered, although among farmland specialists the number of increasing and decreasing species was similar. Our results suggested that climate and land-use changes can explain a significant amount of the variation in species population change, with cool-dwelling species associated with open habitats decreasing the most. Some of them, such as the Skylark (Vulnerable) or the Yellowhammer (Endangered), are included in the Spanish Red List (SEO/BirdLife, 2021) and should therefore be the focus of special concern. For these species severely affected by farmland intensification, climate warming constitutes a double burden (Rigal *et al.*, 2023), which is likely to have particularly harmful effects on the southern boundary of their distribution areas (Pearce-Higgins *et al.*, 2015). The implementation of effective conservation measures related to farmland management that could offset the deleterious effects of climate change on their populations would be crucial for improving their conservation prospects (Eglington & Pearce-Higgins, 2012; Princé *et al.* 2015).

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