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# Agricultural intensification affects birds' trait diversity across Europe

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## ABSTRACT

Agricultural intensification reduces the taxonomic diversity of bird communities, but its influence on functional diversity has been less studied. Here, we analyze the response of functional diversity of different cereal farmland bird communities across Europe to a gradient of agricultural intensification. We collected bibliographical information on life history traits (i.e. body mass, brain size, age of sexual maturity, clutch size, number of clutches, lifespan) of 30 species of birds recorded during field surveys in eight European countries. The index "brood value" was calculated to know each species' level of reproductive investment per clutch. Intensification gradients at two spatial scales were obtained from field data through PCA, related to management practices at the field scale and the variation in structure and composition of farmland at the landscape scale respectively. We calculated the functional diversity index (FD) and the community-weighted mean (CWM) for each trait and sampling area, and linear mixed models in relation to the two intensification gradients were performed. Results showed that stronger intensification at the field level favors the assembly of shorter-lived communities and bird species with smaller relative brain sizes, also decreasing overall trait diversity. It also restricts the range of strategies for parental investment, reducing the functional diversity of the brood value index. More intensive field management would favor bird communities dominated by generalist and even introduced and/or managed hunting species, while putting at risk those farmland- and grassland-adapted species, typically more associated with the provision of ecosystem services. This highlights the relevance of field management (agrochemicals use, ploughing frequency) for the functional composition of bird communities and the conservation of farmland biodiversity. These findings add to existing knowledge on how species' pace of life and cognitive capacity interact with drivers of global change, such as agricultural intensification.

## Introduction

Agricultural landscapes cover about 40 % of the total land area of the European Union (Eurostat, 2020). Over the last 20 years, agricultural intensification has continued, as evidenced by higher cereal production while the area used for crops has decreased (Eurostat, 2020). Farmland supports around 50 % of all bird species on the continent (Pain & Pienkowski, 1997), but farmland bird populations have declined sharply over the last decades, with the EU common bird index showing a dramatic 35.9 % fall in the abundance of common farmland birds between 1990 and 2021 and even stronger declines in shorter-term trends, by 20.2 % since 2006 and 7.8 % since 2016 (EUROSTAT, 2023).

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Agricultural intensification has been identified as the main pressure behind these negative trends, even over urbanization, changes in forest cover, and climate change (Rigal et al., 2023). Intensification reduces the amount of food available to birds and alters habitat structure at different spatial scales, resulting in an overall decline in habitat quality (Donald et al., 2006; Geiger et al., 2010a, Emmerson et al., 2016).

Agricultural intensification is a multifactorial process that occurs at different spatial scales (Benton et al., 2003; Firbank et al., 2008). At the field scale, intensive management practices include increased use of agrochemicals (synthetic fertilizers, herbicides and pesticides), sowing density and ploughing frequency - all of which can lead to a loss of biodiversity within fields (Emmerson et al., 2016). The removal of non-cultivated elements of the field and its surroundings (e.g. grass margins, hedgerows) leads to additional species extirpation (Firbank et al., 2008). At the landscape scale, these intensified practices lead to the simplification and homogenization of farmland habitats, further reducing the availability of habitats for wild species (Tscharntke et al., 2005). Finally, at the regional scale, specialization in specific crops also reduces habitat heterogeneity, further reducing the number of species found at the regional scale (Emmerson et al., 2016). This loss of ecological heterogeneity at multiple scales may therefore be a major driver of biodiversity loss in agricultural systems (Benton et al., 2003). For wide-ranging organisms such as birds, which may nest on fields or field boundaries, use different habitats complementarily (e.g. for mating, nesting and foraging), and move long distances in their dispersal processes, intensification can impose serious ecological constraints at different stages of their life cycle and at all relevant spatial scales.

Agricultural intensification has been shown to affect not only the taxonomic diversity, but also the functional diversity of biological communities (Tilman et al., 1997). Functional diversity is measured by the range, distribution and relative abundance of the functional traits of the organisms that make up ecosystems (Petchey & Gaston, 2006; Cadotte et al., 2011) and it is considered an appropriate approach for understanding the relationship between biodiversity, community structure and ecosystem functioning (Hooper et al., 2005; McGill et al., 2006). A plethora of different studies have examined the effects of agricultural management at different scales on functional diversity of different taxa, from plants to invertebrates and birds (e.g. Devictor et al., 2008; Flynn et al., 2009; Mendez et al., 2012; Guerrero et al., 2012; 2014; Hevia et al., 2016; Peco et al., 2017). Plant functional diversity studies typically measure morphological, physiological and phenological traits that correlate with life history traits as the main fitness determinants (Violle et al., 2007). In the case of birds, however, studies often use life history traits such as body mass, clutch size, age at sexual maturity or lifespan to assess the effects of human-induced changes on bird communities (e.g. Barbaro & van Halder, 2009; Jiguet et al., 2007; Amano & Yamamura, 2007; Ehlers-Smith et al., 2015). These traits, which are closely linked to the reproductive performance and survival of bird species, can provide information on their ecological and evolutionary dynamics.

Here we present the results of a large-scale study investigating the response of functional diversity of avian communities in cereal farmland ecosystems across Europe. More specifically, we examine the relationship between the diversity of traits (Functional Diversity) and average functional trait values (estimated as Community Weighted Mean) based on reproductive rates, life history and the ability to exploit altered environments, and agricultural intensification gradients measured at field and landscape scales. Our hypothesis is that agricultural intensification acts as an environmental filter on the functional diversity of ground-nesting farmland birds. Therefore, we expect (i) a decrease in trait diversity with intensification, due to the exclusion of species less adapted to intensive agricultural management. As birds are highly mobile organisms that typically exploit resources distributed across the landscape (Söderström & Pärt, 2000; Wretenberg et al., 2010; Geiger et al., 2010b; Concepción & Díaz 2010; 2011), we expect (ii) a greater influence of intensification at the landscape scale on their trait means and diversity. Given the higher level of disturbance associated with intensive management (e.g., increased agrochemical use and ploughing frequency, Emmerson et al., 2016), we also expect (iii) traits associated with fast-living species (i.e., species that favor present over future reproduction to cope with resource scarcity and habitat instability, Ricklefs, 2010; Sol et al., 2012; Sayol et al., 2020) to be favored. Finally, based on the low environmental heterogeneity of more intensive agricultural landscapes (Tscharntke et al., 2005; Emmerson et al., 2016), we expect (iv) smaller relative brain sizes with increasing intensification, as exploiting simplified environments may require smaller cognitive capacities (Sol, 2009). The association of relatively large brains with slow life rates (Saether & Bakke, 2000; Sol et al., 2012; Tieleman, 2018; Araya-Ajoy et al., 2018) also supports this expectation.

## Materials and methods

### *Study areas and farm selection*

The fieldwork was carried out in eight study areas in seven European countries (Fig. 1): Sweden (SE), Estonia (EE), Poland (PL), the Netherlands (NL), West Germany (WG), East Germany (EG), Spain (ES) and Ireland (IE). The study areas ranged from 30 x 30 km to 50 x 50 km to minimise within-region differences in species pools and to avoid excessive heterogeneity of landscapes and soil types within each area. In each study area, 30 to 32 arable farms were selected to represent a gradient of regional agricultural intensification. Farms were selected to maximise the range of cereal productivity in the sample, based on farmers' information on cereal yields in the three years prior to the fieldwork, and with an even distribution across the yield gradient of each area. As information on farm management was missing for about 5 % of the selected farms, 22 to 32 farms per study area were finally included in the analyses. Given the differences between countries in agricultural practices and the size of management units, individual farms were treated as the ecological units under study. For the purpose

**Fig. 1.** Location of the eight European study sites. All sites are named after the corresponding country, except for Germany, where two sites were located. 1: Sweden (SE), 2: Estonia (EE), 3: Ireland (IE), 4: Poland (PL), 5: The Netherlands (NL), 6: West Germany (WG), 7: East Germany (EG) and 8: Spain (ES).

of this study, farms were defined as groups of one or more fields, not more than 1 km apart, managed by the same farmer (owned or rented) and covering an area of not more than 1 $km^2$.

### *Bird surveys*

To ensure that bird counts were comparable, one 500 × 500 m survey plot was selected per farm. Although most of the survey plots consisted of fields belonging to one farm, in a few cases they included fields managed by another farmer. This was unavoidable in some countries, such as Spain and the Netherlands, due to farm structure, although its impact on data can be considered negligible due to management homogeneity within plots. Depending on the farm layout, each survey plot comprised one or more arable fields and permanent grasslands, but it always included at least one and up to five cereal fields managed by the same farmer. Most cereal fields were sown with winter wheat (79 %), the major crop in Europe (Eurostat, 2020). The remainder was winter barley (9 %), spring wheat (6 %), winter rye (5 %) or triticale (< 1 %). All survey plots were at least 1 km apart to minimize spatial auto-correlation in survey data. Surveys were carried out during spring and summer 2007, starting according to information on the phenology of local breeding birds, and repeated three times at three-week intervals. They were carried out between one hour after dawn and until noon, but never under windy, cloudy, or rainy weather. They were conducted by slowly walking the entire 500 × 500 m survey plot (our standard survey effort unit), so that each spot within the plot was no more than 100 m from the surveyor’s route. This procedure is a modification of the British Trust for Ornithology Common Bird Census protocol (Bibby et al., 2000). For each individual observed, its position and type of activity (e.g. singing, calling, foraging) was recorded on a detailed map.

Breeding territories of ground-nesting birds were determined using the three survey rounds. We recorded all bird species that made use of the sampled plots and would therefore be affected by their management. To establish the degree of use of cereal fields by the bird species recorded, these were assigned to three different categories considering different criteria to define breeding bird territories. Those criteria were based on the detection probability of a species in relation to its migratory and breeding behavior (see also Geiger et al., 2010a; Guerrero et al., 2012; Emmerson et al., 2016). To meet the criteria for being recorded as having a breeding territory, species of category A (see Table 1 for a list of the species considered) had to be observed at least twice displaying territorial behavior (carrying food to nest, calling, singing, conflicts indicating territory defense) at the same spot during different survey rounds. Category B comprised species unlikely to be present during all three survey visits due to their late phenology (e.g. long-distance migrants arriving relatively late), and species considered difficult to observe. This category required only one observation of territorial behavior. For category C species, direct evidence of breeding activities in any of the survey rounds was required. These categories were used consistently in all survey plots. Since breeding territories always occurred in cereal fields within the plots, all species analyzed can be considered dependent on cereal farmland and its management (Guerrero et al. 2012), even if other populations of the same species use other breeding habitat types elsewhere (e.g. ducks or waders).

### *Agricultural management data*

Information on farm management during the bird survey year was collected from a questionnaire sent to the managers of the one or more cereal fields on each farm containing each bird survey plot. Therefore, data on management practices were based either on a single large cereal field per plot (which could in fact occupy most of the survey plot), or on an average of up to five smaller fields managed by the same farmer within each survey plot. For this study, the following four field-level management variables were considered: yield, amount of nitrogen fertilizer used, number of herbicide applications and number of insecticide applications (Table 2). These variables are all related to the intensity of agricultural management at the field level (Geiger et al., 2010a; Guerrero et al., 2014; Morales et al., 2015). We considered five additional variables at the landscape scale: the size of the sampled field, the size of the farm, the number of different crops grown on the farm, and the average field size and land use diversity within circles of 1000 m radius centered on each survey plot (Table 2). These variables have been shown to explain the distribution and abundance of farmland birds (e.g. Brotons et al., 2005; Geiger et al., 2010a; Guerrero et al., 2012). Measurements were made using digitized maps from ortho-images of the study area and the Patch Analyst 3.12 extension to ArcView (see Rempel, 1999).

As agricultural intensification is a multidimensional process involving many correlated variables, it is often estimated by dimensionality reduction (Carmona et al., 2017; Flohre et al., 2011). Therefore, following Guerrero et al. (2014), we performed a principal component analysis based on eigenvalue decomposition without rotation on the measured indicators of agricultural management intensification (*princomp()* function in R). We retained two orthogonal axes that explained 60.5 % of the total variance, reducing the space to two dimensions (Appendix A: Table S1). The first axis (PC1) was related to management practices at the individual field level (contributed by yield, nitrogen fertilizer and number of herbicide and insecticide applications) and explained 35.3 % of the total variance. The second axis (PC2) was

**Table 1**
Ground-nesting farmland bird species detected in the surveys, considered breeding on focal fields. Categories assigned to define breeding depend on the species’ detectability and breeding behavior. Category A requires at least two observations of birds displaying territorial behavior at the same spot during different survey rounds. Category B requires one observation of territorial behavior (species unlikely to be present during all the three survey visits or species considered difficult to observe). Category C requires direct evidence of breeding activities.

| Scientific name | English name | Cat. | Scientific name | English name | Cat. |
|---|---|---|---|---|---|
| *Acrocephalus palustris* | Marsh Warbler | B | *Galerida cristata* | Crested Lark | A |
| *Alauda arvensis* | Skylark | A | *Gallinago gallinago* | Snipe | A |
| *Alectoris rufa* | Red-legged Partridge | B | *Haematopus ostralegus* | Oystercatcher | A |
| *Anas platyrhynchos* | Mallard | C | *Limosa limosa* | Black-tailed Godwit | A |
| *Anthus campestris* | Tawny Pipit | B | *Lullula arborea* | Woodlark | A |
| *Anthus pratensis* | Meadow Pipit | A | *Motacilla flava* | Yellow Wagtail | A |
| *Circus aeruginosus* | Marsh Harrier | C | *Numenius arquata* | Curlew | A |
| *Circus pygargus* | Montagu’s Harrier | C | *Oenanthe oenanthe* | Wheatear | A |
| *Cisticola juncidis* | Fan-tailed Warbler | A | *Otis tarda* | Great Bustard | B |
| *Coturnix coturnix* | Quail | B | *Perdix perdix* | Grey Partridge | B |
| *Crex crex* | Corncrake | B | *Phasianus colchicus* | Pheasant | A |
| *Emberiza calandra* | Corn Bunting | A | *Saxicola rubetra* | Whinchat | A |
| *Emberiza cirlus* | Cirl bunting | B | *Saxicola rubicola* | Stonechat | A |
| *Emberiza citrinella* | Yellowhammer | A | *Tetrax tetrax* | Little Bustard | B |
| *Emberiza hortulana* | Ortolan Bunting | B | *Vanellus vanellus* | Lapwing | A |

**Table 2**
Description of landscape and field scale measures of agricultural intensification used in the present study.

| | Variable | Description | Mean ± SD (max-min) |
|---|---|---|---|
| Landscape scale | Field size | Size of the sampled focal field (ha) | 11.27 ± 12.14 |
| | Farm size | Size of the farm to which the sample field belongs (ha) | 321.06 ± 558.01 (4120-12) |
| | Number of crops | Number of different crops grown on the farm to which the sampled field belongs | 5.00 ± 2.52 (18-1) |
| | Mean Field size | Average field size in in a 1000 m-radius circle centred on focal field (ha) | 12.69 ± 12.46 (51.38-0.54) |
| | Land use diversity | Shannon–Wiener index of land use diversity within a 1000 m radius circle centred on focal field. Considered classes: Arable land, Fallow land, Permanent crops, Forest, Semi-natural vegetation, Continuous and Discontinuous urban fabric. | 0.82 ± 0.43 (2.1-0) |
| Field scale | Yield | Cereal grain obtained in focal field (ton ha$^{-1}$) | 5247.02 ± 1878.03 (10700-820) |
| | N fertilizer | Total amount of nitrogen applied on the focal field (kg ha$^{-1}$) | 110.36 ± 96.75 (485-0) |
| | Herbicide application | Number of herbicide applications on the focal field during the agricultural year | 1.24 ± 1.06 (6-0) |
| | Insecticide application | Number of insecticide applications on the focal field during the agricultural year | 0.46 ± 0.75 (3-0) |

related to the structure of the surrounding landscape (defined by mean field size, land use diversity, farm size and focal field size) and explained 25.2 % of the variance. We used these axes as measures of the level of intensification at the local field and landscape scales, respectively, and interpreted them as gradients of agricultural intensification at their respective scales.

To get a better idea of the characteristics of agricultural intensification at the regions sampled, we plotted the mean values for each of the axes in each study area (Appendix A: Fig. S1). The result shows the gradients of intensification at the two spatial scales covered by the study. It is important to note that the possible effect of the study area was controlled for by including country as a random factor in all models (see details below).

### *Trait information and diversity calculation*

We surveyed the literature and public databases to compile data on traits for 30 ground-nesting species recorded in survey plots in the breeding season over the eight study areas (Table 1). Data on body mass (g), as well as on reproduction rates, and more precisely, clutch size and number of clutches per year, were obtained from Cramp (1992) and Del Hoyo et al. (2001). In cases for which trait values were provided as a range, the median of both extremes was used, while in those cases for which data from different populations were available, the average value was calculated.

We also compiled data on traits related with the species' life history: age of sexual maturity (years, also from Cramp, 1992; Del Hoyo et al., 2001) and maximum lifespan (years), which were based on records of oldest identified individuals from the European Union for Bird Ringing data base (EURING). These life-span records are biased towards the longest-living individuals, but since the bias occurs for all species, it is not expected to influence the estimation of diversity indices (see below). Life-span values compiled were also used to estimate reproductive life, by subtracting the age at sexual maturity.

In addition, we calculated a multi-trait index measuring the level of parental investment in each clutch: the brood value (Bókony et al., 2009), which is computed as shown.

$$\log_{10}\frac{1}{(n^{\circ}\,clutches * year^{-1}) * (reproductive\ life)}$$

Finally, as proxy for the species ability to exploit altered environments, we compiled data on the brain mass of each species from Mlíkovský (1989a; 1989b; 1989c; 1990). To remove the influence of specific body mass, relative brain size was calculated as the residual from the regression of log-transformed body mass on brain mass (e.g. Franklin et al., 2014).

With the aim of describing trait diversity at each bird survey plot, we used two sets of indices that capture different aspects of a given trait value distribution within a community or species assemblage (Petchey & Gaston, 2006). On one hand, we computed the weighted mean value for each trait or Community Weighted Mean (CWM; Guerrero et al., 2014; Carmona et al., 2017; Tarjuelo et al., 2021). The CWM of a trait is the average value of a trait in a community or assemblage weighted by the relative abundance of the species contributing to that average, as follows:

$$CWM_t = \sum_{i=1}^{n} (p_i * x_{ti})$$

Where $CWM_t$ is the community weighted mean of trait $t$, $p_i$ is the relative abundance of species $i$, and $x_{ti}$ is the particular value of trait $t$for species $i$.

On the other hand, we calculated the functional diversity index (FD) for each trait, which can be used as an indicator of the effects of a given environmental filter on the range of values of each trait in a given community or assemblage, as follows:

$$FD_t = \sqrt{\sum_{i=1}^{n} p_i (x_{ti} - CWM_t)^2}$$

where $FD_t$is the functional diversity of trait $t$, $p_i$is the relative abundance of species $i$, $CWM_t$is the community weighted mean for that trait and $x_{ti}$ is the particular value of trait $t$ for species $i$. This index has been used in different studies assessing functional diversity changes associated with land-use change (Mayfield et al., 2010; Peco et al., 2017; Guerrero et al., 2014; Carmona et al., 2020).

### *Statistical analyses*

We used both PC axes as explanatory variables to evaluate the relationships of our trait diversity indices (CWM and FD as response variables; five models for each response variable: body mass, clutch size, lifespan, relative brain size and brood value) with the level of agricultural intensification at field and landscape scales. This was done by means of Linear Mixed Models (*lmer()* function from the R package lme4, Bates et al., 2014), in which the country was introduced as random factor in order to control for geographical effects on trait diversity values. The assumptions of normally distributed and homogeneous residuals were checked by visually inspecting probability plots (Q-Q plots) and the residuals plotted against fitted values. When obvious deviations from these assumptions were found, response variables were transformed by either applying logarithmic or square root transformations, depending on which transformation was most suitable. Computations, graphs and statistical analysis were performed using R software (Team, 2021).

## Results

Of the five traits analyzed, only the models for lifespan and relative brain size were statistically significant (Table 3 and Table 4, Fig. 2). Both the community weighted mean and the functional diversity of both traits are negatively and significantly related to the axis that relates to agricultural intensification at the field level (PC1). In addition, the functional diversity of the brood value has a negative and marginally significant relationship with this same intensification axis (Table 4). The values of this axis increase with the intensity of agricultural management, expressed as inputs of synthetic fertilizers, pesticides, and crop production (Table S1). This indicates that intensification at the field level favors the assembly of less long-lived species with smaller relative brain sizes (Table 3, Fig. 2). Likewise, it favors the composition of communities with less variation in these traits, apparently penalizing species with longer lifespan and larger relative brain sizes (Table 4, Fig. 2). It also restricts the range of strategies for parental investment, reducing the functional diversity of the brood value index (Table 4).

However, none of the response variables analyzed showed statistically significant relationships with PC2 (Tables 3 and 4). This axis is related to landscape structure, showing higher values the more simplified the landscape is (i.e. the larger the fields and the farms are) and the lower the diversity of land cover is (Table S1).

On the other hand, an important difference is observed between the marginal R-squared and conditional R-squared values of the models, providing information on the contribution of fixed effects, representing agricultural intensification, and random effects, representing geographical variations (Tables 3 and 4). In this study, the low marginal R-squared values suggest that the fixed effects alone (i.e., agricultural intensification captured by the PC1 axis) explain a relatively small proportion of the total variation in the response variables. This indicates that other factors, beyond the considered fixed effects, are influencing the avian traits. On the other hand, the higher conditional R-squared values indicate that when both fixed and random effects (including the country-level variations) are considered together, a more substantial proportion of the total variation in the response variables is explained. This suggests that the country-level variations, represented by the random effects, contribute significantly to the observed patterns and provide additional explanatory power beyond the fixed effects.

## Discussion

Our results show a relationship between the diversity of some bird functional traits and agricultural intensification across European cereal farmland, and specifically with intensification of field management. Conversely, none of the traits analyzed seemed to be associated with landscape-scale intensification, either in terms of CWM or its variability measured as FD. Relative brain size varied with field-scale intensification, so that communities linked to less intensively managed fields had, on average, relatively larger brains. The variability around those averages, measured through FD, was also smaller as intensification increased, i.e. relative brain size was larger and more variable as fields were less intensively managed. The same trends were identified for lifespan: birds tended to be, on average, shorter-lived as field-level intensification increased, while lifespan was also less variable. In addition, brood value showed a marginal trend to be less variable as field management was more intensive. Therefore, prediction (i) that local intensification would be associated with a general decrease in bird trait diversity is only supported for relative brain size and lifespan, while a marginal trend of brood value diversity to decrease with field management intensification was found. However, prediction (ii) that traits would be more related to landscape heterogeneity and low intensity landscape management is not supported for either CWM or FD values. On the other hand, our prediction (iii), after which agricultural intensification would favor traits typical of fast-living species is supported based on our results on lifespan, which appeared negatively associated with field-scale intensification, both in terms of CWM and FD.

Although the association of brain size diversity with agricultural landscape features (e.g. availability of field boundaries) has been shown in recent studies (Tarjuelo et al., 2021), this is the first time a relationship between field management intensity and relative brain size in farmland bird communities is found. Intensive field management reduces available resources for ground-nesting and other farmland birds (Guerrero et al., 2012; Emmerson et al., 2016), which is expected to benefit specialists thereby reducing behavioral innovation ability within communities (Shultz et al., 2005; Overington et al., 2011), which may explain this relationship.

As regards the negative relationship of lifespan and its diversity with field-level intensification, it might result from resource limitations associated with field-level intensification: resource-impoverished fields would be just unable to maintain larger species (Gaston & Blackburn, 1995), which also tend to live longer (Mourocq et al., 2016). Longer

**Table 3**

Results of models for Community Weighted Means (CWM) of bird life history and morphological traits considered. Parameter estimates (betas) and their standard error, t and p-values are provided, as well as model adjusted marginal $R^2$ as measure of variance explained by fixed factors and adjusted conditional $R^2$ as measure of variance explained by both fixed and random factors.

| | | Beta | Std. Error | df | t | p | Adjusted marg. $R^2$ | Adjusted cond. $R^2$ |
|---|---|---|---|---|---|---|---|---|
| CWM Body mass | | | | | | | | |
| | (Intercept) | 1.775 | 0.088 | 6.605 | 20.179 | 0.000 | 0.018 | 0.396 |
| | PC1 | -0.025 | 0.016 | 207.531 | -1.493 | 0.137 | | |
| | PC2 | 0.023 | 0.024 | 181.254 | 0.944 | 0.346 | | |
| CWM Clutch size | | | | | | | | |
| | (Intercept) | 0.629 | 0.019 | 6.676 | 32.703 | 0.000 | 0.005 | 0.461 |
| | PC1 | 0.000 | 0.003 | 209.700 | -0.151 | 0.880 | | |
| | PC2 | -0.004 | 0.005 | 196.600 | -0.823 | 0.411 | | |
| CWM Lifespan | | | | | | | | |
| | (Intercept) | 0.982 | 0.027 | 6.642 | 36.512 | 0.000 | 0.023 | 0.486 |
| | PC1 | -0.010 | 0.004 | 209.859 | -2.313 | 0.022 | | |
| | PC2 | -0.001 | 0.006 | 198.707 | -0.178 | 0.859 | | |
| CWM Brain size | | | | | | | | |
| | (Intercept) | -0.002 | 0.001 | 6.955 | -3.278 | 0.014 | 0.026 | 0.417 |
| | PC1 | -0.0001 | 0.000 | 208.400 | -2.076 | 0.039 | | |
| | PC2 | -0.0001 | 0.000 | 186.500 | -0.827 | 0.409 | | |
| CWM Brood value | | | | | | | | |
| | (Intercept) | -0.079 | 0.031 | 6.636 | -2.555 | 0.040 | 0.010 | 0.477 |
| | PC1 | -0.003 | 0.005 | 209.843 | -0.658 | 0.511 | | |
| | PC2 | -0.008 | 0.007 | 198.451 | -1.069 | 0.287 | | |

**Table 4**

Results of models for Functional Diversity (FD) of bird life history and morphological traits considered. Parameter estimates (betas) and their standard error, t and p-values are provided, as well as model adjusted marginal $R^2$ as measure of variance explained by fixed factors and adjusted conditional $R^2$ as measure of variance explained by both fixed and random factors.

| | | Beta | Std. Error | df | t | p | Adjusted marg. $R^2$ | Adjusted cond. $R^2$ |
|---|---|---|---|---|---|---|---|---|
| FD Body mass | | | | | | | | |
| | (Intercept) | 8.029 | 1.916 | 6.564 | 4.191 | 0.005 | 0.011 | 0.364 |
| | PC1 | -0.557 | 0.379 | 205.805 | -1.470 | 0.143 | | |
| | PC2 | 0.059 | 0.553 | 172.981 | 0.107 | 0.915 | | |
| FD Clutch size | | | | | | | | |
| | (Intercept) | 0.738 | 0.115 | 6.774 | 6.444 | 0.000 | 0.003 | 0.315 |
| | PC1 | -0.019 | 0.025 | 201.879 | -0.762 | 0.447 | | |
| | PC2 | 0.006 | 0.036 | 158.823 | 0.163 | 0.871 | | |
| FD Lifespan | | | | | | | | |
| | (Intercept) | 1.451 | 0.155 | 6.541 | 9.359 | 0.000 | 0.039 | 0.278 |
| | PC1 | -0.081 | 0.038 | 190.363 | -2.130 | 0.035 | | |
| | PC2 | -0.067 | 0.055 | 128.957 | -1.221 | 0.224 | | |
| FD Brain size | | | | | | | | |
| | (Intercept) | 0.273 | 0.022 | 7.142 | 12.323 | 0.000 | 0.028 | 0.176 |
| | PC1 | -0.014 | 0.007 | 157.322 | -2.105 | 0.037 | | |
| | PC2 | -0.001 | 0.010 | 83.129 | -0.117 | 0.907 | | |
| FD Brood value | | | | | | | | |
| | (Intercept) | 0.495 | 0.048 | 6.467 | 10.269 | 0.000 | 0.024 | 0.259 |
| | PC1 | -0.022 | 0.012 | 188.244 | -1.838 | 0.068 | | |
| | PC2 | -0.012 | 0.017 | 124.587 | -0.708 | 0.481 | | |

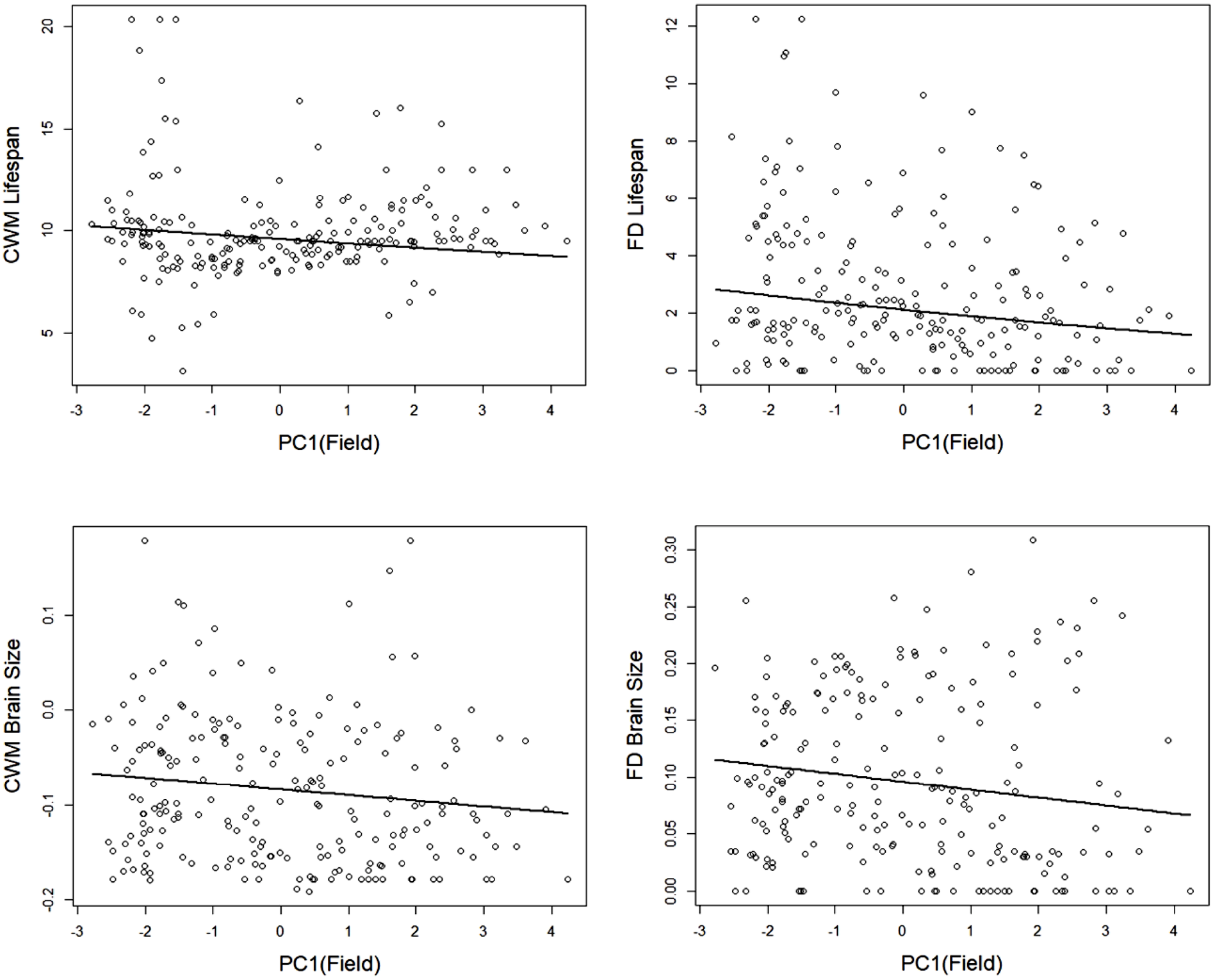

**Fig. 2.** Scatterplots of the response variables CWM and FD of lifespan and CWM and FD of relative brain size as a function of the agricultural intensification axis at field scale (PC1). The line represents the adjusted relationship based on the fitted mixed-effects models. No transformation was applied to the response variables for display.

lifespans are usually associated with species that prioritize survival and future reproduction over fecundity, a strategy selected in more stable or predictable environments (Ricklefs, 2010; Sol et al., 2012; Sayol et al., 2020). Consistently, our results suggest that intensive agricultural field management filters for communities dominated by fast-living species (lifespan is correlated with other traits indicative of species' pace of life, like age of sexual maturity, for example; Ricklefs, 2010). This would also be consistent with the marginal decrease of brood value diversity (Sol et al. 2020): in more intensive landscapes, species would tend to make a more similar investment in present clutches and broods.

The lack of significant association of trait CWN and FD values with the landscape-scale intensification gradient is remarkable, given the importance of landscape structure for farmland birds shown in different studies (Brotons et al., 2005; Söderström & Pärt, 2000; Wretenberg et al., 2010; Concepción & Díaz, 2010; 2011). Indeed, landscape structure and composition have also been shown to influence the taxonomic functional composition of European farmland bird communities (Geiger et al., 2010b; Guerrero et al., 2011). However, here we have specifically analyzed trait diversity and thus our results do not necessarily contradict those studies. Moreover, the lack of a significant association of most FD values with intensification gradients at both scales (unlike what has been shown for weeds, Guerrero et al., 2014; Carmona et al., 2020) may be reflecting that the environmental filter imposed by agricultural intensification has not been working long enough as to reduce the trait variability. Birds have longer generation times than most arable plants (e.g. Begon and Twonsend, 2021) and thus population changes in trait diversity and their reflection at the community level may take much longer to be detected. In this context, it would be interesting to analyze time series of data to check whether these changes can be identified. Nevertheless, it is important to keep in mind that other factors beyond the agricultural intensification gradient are influencing trait diversity. Such factors, as pointed out by the higher conditional R-squared values of models, are likely related to country-level differences (treated as random effects) due to climate, land-use history, or biogeography. Furthermore, given the unavailability of site-specific data for trait values for all eight study areas, we have had to use average trait values across populations occurring throughout Europe, which might be an oversimplification, at least for some traits. This limitation may have made it difficult to detect stronger relationships with the site-specific intensification data.

By and large, and according to these results, in intensively managed fields bird assemblages would tend to be dominated by shorter-lived species, which also tend to be smaller and reach maturity earlier (Ricklefs, 2010). However, their brains are relatively smaller: the significant decrease of this trait's CWM values with field intensification supports our prediction (iv). This result suggests that exploiting simplified and resource-impoverished environments, like those resulting from agricultural intensification, may require smaller cognitive capacities, favoring species with smaller relative brain sizes (Sol, 2009). Gallinaceous (partridges, quail and pheasant) and waterfowl (ducks and geese) species fit this pattern, even if some of them, like the gray partridge, have declined in several European countries (e.g. Germany, France) due to strong and multi-scale agricultural intensification (e.g Kuijper et al., 2009). These are generalist species that can occupy many habitats other than cereal farmland, like wetlands, shrubland or even forest. Due to their larger size, they also have slower metabolic rates, and this might make them more efficient in resource-scarce environments (Auer et al., 2020) as those resulting from intensive field management (Emmerson et al., 2016). These species present relatively small brains in relation to their large body mass (Mlíkovský, 1989a).

In conclusion, agricultural intensification seems to promote a shift from specialist- (i.e. grassland birds with relatively larger brains and slower life paces) to generalist- (i.e. fowl and waterfowl species also found in very different habitats) dominated bird communities in European cereal farmland. Previous works have already documented similar shifts. For example, Devictor et al. (2008) showed a decrease in the degree of habitat specialization of bird communities with increasing landscape disturbance across France. Here we have shown that agricultural intensification affects the diversity of certain traits of farmland bird communities across Europe through changes occurring mainly at the field scale (i.e. intensive field management). Such changes would favor bird communities dominated by generalist species occupying also other types of habitats (e.g. ducks and geese) and even introduced and/or managed by man for purposes such as hunting (e.g. partridges, pheasant), while more genuinely farmland- and grassland-adapted species (larks, corncrake, bustards), associated with the provision of ecosystem services (e.g. weed control, nature recreation, Eraud et al., 2015; Faria & Morales, 2021) are being lost. This highlights the relevance of field management (i.e. agrochemical use, ploughing frequency) for bird community composition and further supports its role for the conservation of farmland biodiversity, already pointed out for taxa like arable plants and insects (Emmerson et al., 2016; Carmona et al., 2020). Further, our findings about the influence of agricultural intensification on farmland bird trait diversity add to those on how species life history and trait composition of biological communities interact with other processes driving global change, such as climate warming and urban sprawl (Jiguet et al., 2007; Sayol et al., 2020).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.11.007.

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