IBIS
international journal of avian science
Ibis (2025) doi: 10.1111/ibi.70008

Spatial patterns of local dialects of the declining Corn Bunting (*Emberiza calandra*) in three regions with different population densities and small-scale landscape features

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Rapid dialect shift or disappearance due to anthropogenic disturbances such as habitat degradation and fragmentation is a common feature in farmland bird species. Here we explored the formation, maintenance and spatial structure of local dialect patterns in the Corn Bunting *Emberiza calandra*, a declining European farmland bird, in arable landscapes of northwestern and central Europe. This species displays a microgeographical song variation pattern, so-called local dialects. This consists of small groups of nearby males sharing the same song repertoire, which is usually composed of one dialect component and several specific song type components. The song units are discrete and the spatial boundaries between local dialects are clear. Territorial males were recorded in three local Corn Bunting populations in Poland, France and Belgium. Pairwise song dissimilarity was used to analyse quantitatively the spatial pattern of microgeographical song variation in the three regions in relation to farming intensity, landscape features and population trends in each region. We found different local dialect patterns in the three regions. As predicted, in Poland, where the Corn Bunting was abundant, we observed the classical pattern of a spatial mosaic of distinct local dialects occurring at a local scale. This classical pattern was less apparent in France and even less apparent in Belgium, where the Corn Bunting was in sharp decline. Our results also suggest that a higher local density of territorial males was correlated with a greater song sharing between neighbouring males, which supports the hypothesis that local dialects are a density-dependent phenomenon. Other results suggest that fragmentation of farmland habitats by patches of habitat unsuitable for Corn Buntings, such as woodlands and urban areas, contributed to the difference observed in the dialect-specific component of songs. Our findings point to anthropogenic causes, but long-term studies in the same areas and extension of the study to new areas would strengthen these conclusions and rule out other environmental factors or idiosyncrasies of individual populations.

Keywords: bird song, density, *Emberiza calandra*, farmland habitat, habitat fragmentation.

Geographical song variation is a widespread phenomenon among songbirds. In those species, song is a cultural trait that is passed down from one generation to the next through imitation of conspecifics (Mennill *et al.* 2018). Social learning may result in an imperfect copy of the song due to the production of small errors or improvisation by young birds during the learning phase (Lynch 1996, Lachlan *et al.* 2018). Some of these novel song variants can be transmitted to following

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generations and spread within a population. This process leads to a higher level of song sharing between nearby neighbours than with distant ones, depending on the specific learning mechanisms (Podos & Warren 2007). These song differences between places are called dialects. Some song components identify dialects, but song repertoires may vary between individuals (Marler & Tamura 1962, Mundinger 1982, Trainer 1983, Kroodsma 1996, Catchpole & Slater 2008). In some cases, dialects may act as a prezygotic barrier to reproduction, when females prefer mating with males that sing the local song (Crates *et al.* 2021, Wang *et al.* 2022), or when males react more strongly to other dialects, chasing away 'foreign' males (Slender *et al.* 2018). In some species, high song sharing between nearby males is linked to breeding success (Payne 1982, Espmark *et al.* 1989). Dialects can be detected at different spatial scales; large-scale dialects involve populations that cannot interbreed due to physical barriers or large distances (Irwin *et al.* 2001, Otter *et al.* 2020), as with the Puget Sound White-crowned Sparrow *Zonotrichia leucophrys pugetensis* (Nelson *et al.* 2004). Dialects can also be detected at very short distances, according to the dispersal capabilities of a species. Distances between these 'microdialects' range from hundreds of metres to a few kilometres. Examples of microdialects have been detected in several species including Dupont's Lark *Chersophilus duponti* (Pérez-Granados *et al.* 2016), Eurasian Wren *Troglodytes troglodytes* (Catchpole & Rowell 1993), Eurasian Skylark *Alauda arvensis* (Briefer *et al.* 2008, 2011), Black Redstart *Phoenicurus ochruros* (Draganoiu *et al.* 2014), Redwing *Turdus iliacus* (Bjerke & Bjerke 1981) and Common Rosefinch *Carpodacus erythrinus* (Martens & Kessler 2000).

The Corn Bunting *Emberiza calandra*, a farmland bird that has suffered a sharp decline in Europe (PECBMS 2025), is a good example of microgeographical song variation with clear boundaries, so-called local dialects (McGregor 1980). These characterize relatively small groups of males with a common song repertoire. Within each local dialect, several specific song types are also identified. These are song variants associated with a specific local dialect. These groups are spatially close to each other, but the song variation is discrete and distinctive, with clear spatial boundaries (McGregor 1980, McGregor *et al.* 1997).

The formation of small-scale dialects can result from different mechanisms. In some species, young birds learn and crystallize their repertoire in their native area, followed by short postnatal dispersal and subsequent high site fidelity, as in Song Sparrows *Melospiza melodia* (Nordby *et al.* 1999). Other species may crystallize their repertoire after postnatal dispersal, when settling in their first breeding territory. These young birds rapidly learn song types from one or several close neighbours during the first spring, resulting in a high song sharing pattern at a local scale (Beecher & Brenowitz 2005, Liu & Kroodsma 2006, Podos & Warren 2007, Catchpole & Slater 2008, Hensel *et al.* 2022). This latter learning process maintains dialect boundaries over time, independent of the origin of birds (Podos & Warren 2007).

Different habitats or environments also contribute to geographical song variations. These song variations could arise due to evolutionary processes such as ecological adaptation of parameters of the acoustic signal (e.g. song frequency, amplitude) to the local environment or habitat (Morton 1975). Alternatively, this could be the consequence of stochastic processes, as when random events lead to the isolation of a population that is then subject to cultural drift (Podos & Warren 2007, Irwin *et al.* 2008, Parker *et al.* 2012, Hill *et al.* 2013, Williams 2021). Anthropogenic disturbances such as loss, degradation and fragmentation of habitat are also increasingly recognized as creating barriers that impact vocal communication and cultural transmission between local populations (Laiolo & Tella 2005). Habitat fragmentation tends to reduce acoustic connectivity between local populations (Rogers 2003, Briefer *et al.* 2010, Rivera-Gutierrez *et al.* 2010, Pavlova *et al.* 2012, Pérez-Granados *et al.* 2016). There is evidence of dialect shift or even disappearance due to habitat disturbance, especially in farmland bird species. This is indirectly caused by modifications in the habitat matrix such as agricultural rotations, large-scale changes in land usage, transformation of natural habitat and alteration of the vegetation as the result of human activities (Rich 1981, Trainer 1983, Lijtmaer & Tubaro 2007, Laiolo 2010). Populations of the Yellowhammer *Emberiza citrinella* in Great Britain exhibit a lower dialect diversity than populations in New Zealand, where the species was introduced in the 19th century by British settlers. The decrease in song dialect diversity in Great Britain is caused by farming

intensification and loss of suitable habitats, and the decline of the species since the mid-20th century (Pipek *et al.* 2018). Dialects with clear spatial boundaries are rare, with most birds exhibiting clinal geographical song variations (Podos & Warren 2007). In the Corn Bunting, a local dialect pattern is limited to places with a high density of territorial birds (Osiejuk & Ratynska 2003). The density of the Corn Bunting is affected by farming intensity among other factors, with lower densities when farming intensity is high (Fox & Heldbjerg 2008). Spatial boundaries of local dialects are usually stable over time, even if individuals slightly modify minute details of their song from year to year (McGregor 1980, McGregor & Thompson 1988, McGregor *et al.* 1997). However, rapid and complete changes in the pattern and spatial distribution of local dialects were detected in north Cornwall, England, over a period of 14 years (Holland *et al.* 1996, Holland & McGregor 1997). These changes were probably linked to large-scale land use changes and the intensification of farming practices, which led to local extinction and recolonization processes in the same area. This makes the Corn Bunting a suitable model species to study spatial patterns of local dialects in fragmented and intensive farmland habitats.

When anthropogenic habitat disturbance impacts song features important for successful breeding, this could reduce individual fitness, reproductive success and population viability (Laiolo *et al.* 2008, Crates *et al.* 2021). Hence, bioacoustics can be an important tool in conservation and management of declining species with cultural traits (Laiolo 2010, Fracas *et al.* 2023).

In this study, we used spatial statistics and song dissimilarity measures to compare the songs of pairs of males and to define the local dialect patterns of the Corn Bunting among three different populations in temperate Europe. These populations are established in regions characterized by different levels of habitat fragmentation, farming intensity and population trends (Table 1). We predicted that the local dialect pattern would be less consistent in declining populations (lower song sharing level between nearby males), where local male density was low because of intensive farming and habitat degradation. We expected to find the classical local dialect pattern in regions where the Corn Bunting was abundant (higher song sharing level between nearby males) and where the farming practices were more extensive. We also predicted that the fragmentation of the farmland habitat would isolate local dialects, and song type distribution within local dialects. Hence, local dialects should cover larger areas in more open landscapes.

METHODS

Study regions

This study was carried out between April and June in 2016, 2017 and 2018 in Belgium, France and Poland, respectively (Fig. 1). In each country, we selected populations in regions dominated by arable land. Regions were chosen based on the following characteristics: Corn Bunting population status and trend; farming intensity; fragmentation of the farmland habitat; and land use proportion of the main habitat types – farmland, forest and urban areas (Table 1). Intensive farming is characterized by the investment of large amounts of capital, labour, fertilizers and herbicides into larger fields in order to increase production, while extensive farming uses less labour and resources on smaller fields (Benton *et al.* 2003). Farming intensity was indirectly assessed by several indicators recorded from maps, based on the CORINE land cover map (CLC, EEA 2018) and visually in the field from the size and the shape of the arable fields, crop diversity and the presence of natural habitat. Narrow and small fields are reliable indicators of extensive farming, as well as the presence of arable weeds as an indicator of limited usage of fertilizers and pesticides (Bretagnolle & Gaba 2015). Fragmentation was also assessed visually, as was the presence of habitat unsuitable for Corn Buntings, such as urban areas, road networks and forests. We measured the surface area of farmland habitat, forest and urban areas, and calculated the percentage of their areas in the total study area in each of the three regions (Table 1).

The first sampled population was in the loamy region in the centre of Belgium, which was home to the last remaining population of the Corn Bunting in Benelux (Ory *et al.* 2015). In Wallonia, which constituted the main part of the study area in Belgium, the Corn Bunting is listed as endangered (Paquet *et al.* 2021). The farming practices were intensive, and the open fields were fragmented by the development of the road network and increasing urbanization (urban area accounting for 17.2% of the study area; Table 1).

Table 1. For each of the three studied regions, Corn Bunting regional status and population trends, farming practices (intensive or extensive), landscape characteristics (fragmented or unfragmented) and land use proportion (source: CLC 2018).

Country	Corn Bunting status and trend	Farming regimen	Landscape fragmentation	Land use proportion (CLC 2018)		
				Farmland	Forest	Urban areas
Belgium (BE)	Endangered (Wallonia red list)	Intensive	Fragmented by urban areas and road network	81%	1.8%	17.2%
France (FR)	Least concern but declining	Intensive	Unfragmented (open field)	86.6%	5.2%	6.2%
Poland (PL)	Least concern and abundant	Extensive	Fragmented by forest area	71.3%	19%	9.3%

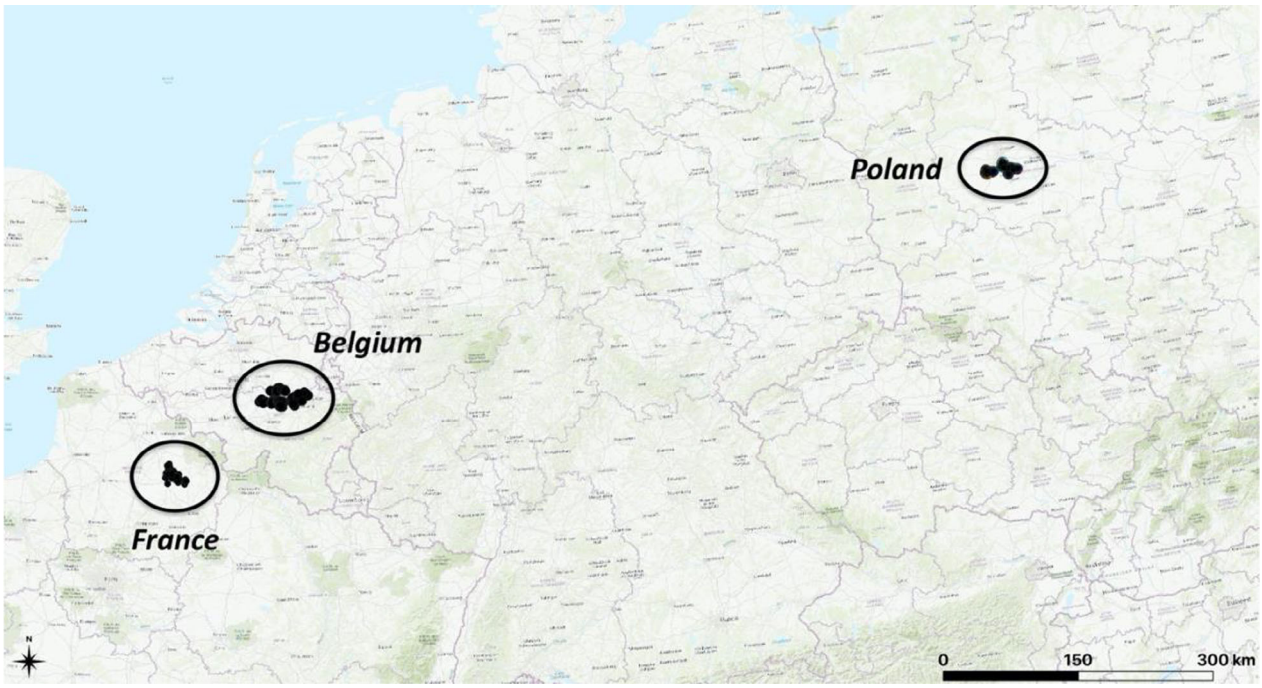


Figure 1. Study area map with the location of the males recorded in the three regions (Belgium, France and Poland).

The second population was located near Saint-Quentin, in Picardie (northeast France). It was in a typical rural area with villages, and open fields under intensive farming punctuated with dirt roads. The Corn Bunting was also declining in this region but remained relatively common in farmland habitats and was listed as Least Concern (Picardie Nature 2023). Three additional sites dominated by extensive hay meadows along the Moyenne Vallée de l'Oise were also included.

The third population was south of Poznań, in the Wielkopolska region (western Poland). The western part of Poland was one of the regions with the highest densities of Corn Buntings in Europe (EBCC/RSPB/BirdLife/CSO 2022). Around Poznań, despite agricultural intensification, large extensive farming areas remained with low inputs of mineral fertilizers and pesticides, and small, long, narrow and weedy fields. However, intensification is occurring (larger fields, more homogenized landscapes with less diversified flora and natural habitat patches). The arable landscape was also surrounded by artificial woodlots of Scots Pine *Pinus sylvestris* (forest area accounting for 19% of

the study area; Table 1). Overall, the landscape of the Polish study site had a similar configuration as in Belgium, with farmland habitat patches embedded in a matrix of unfavourable habitats. However, the cause of the fragmentation was quite different: urban areas in Belgium, and natural habitats in Poland. The Polish study area also included a Natura 2000 site, with hay meadows along the Warta river (Rogalińska Dolina Warty). Natura 2000 is a coordinated network of protected areas in the European Union (EEA 2018). To record enough singing males in each of the three regions, the size of the sampled areas was larger in Belgium than in France and in Poland.

Song recording

Songs were recorded in the morning (05:00–12:00 AM), during the breeding season (from the end of April to June) in 2016 (Belgium), 2017 (France) and 2018 (Poland). Windy and rainy days were avoided. In each location, suitable habitats were explored using all roads and paths to detect singing Corn Buntings. Locations where birds were recorded were visited on only one day to avoid repeated recordings of the same individual, given that no birds were marked. Only male Corn Buntings sing (Garamszegi *et al.* 2007). They often use a few song posts located within the breeding territory, which covers a radius of 100–150 m (Meyer *et al.* 2007). This distance was calculated to avoid recording the same individual.

All recorded and observed birds were geolocated with a GPS device with a 3- to 5-m accuracy. Maps were created with QGIS 3.10.4 (Quantum 2015) in Lambert 93 projection. A Tascam DR-680 recorder was used with an omnidirectional micro Sennheiser ME64/K6 and a Telinga universal parabola (Telinga Microphones, Uppsala, Sweden). The sound files were saved in a 24-bit WAV file format at a sampling rate of 44.1 kHz.

Spatial distribution pattern and identification of clusters

A nearest neighbour analysis (NNA) was used to establish the spatial distribution patterns (clustered, random or dispersed) of the Corn Bunting breeding territories in each of the three regions. For this analysis, we used the locations of all observed singing Corn Buntings. This analysis was performed with the SpatialEco package in R (Evans & Ram 2021). This is a distance-based method used in spatial point pattern analysis that calculates the distance between each point of the dataset and its nearest neighbour. It then estimates the expected distance of the closest neighbour given the assumption that the points are randomly distributed. It compares the average observed value to the expected one, which is calculated based on the hypothesis that these points follow a complete spatial randomness pattern. The nearest neighbour index (NNI) is the ratio between the average observed and expected values. The *Z*-score, which follows the normally distributed *Z* statistic, gives the level of confidence in the NNI. This method is sensitive to the area considered in the analysis. Therefore, we constructed a convex hull around the points where we recorded songs. The area of this convex hull represented the area effectively sampled. If the NNI is lower than 1 and the *Z*-score is negative, it means that the spatial pattern is clustered. NNI allowed us to compare the degree of spatial aggregation between the three regions.

Next, a density-based spatial clustering application with noise (DBSCAN; Ester *et al.* 1996) algorithm was performed with the DBSCAN package in R (Hahsler *et al.* 2019) to delineate spatial clusters of Corn Buntings. This is a non-parametric algorithm that detects spatial clusters of arbitrary shape (i.e. not necessarily circular). The delineation of the clusters is based on a radius (epsilon, or ε) around each point, which must be determined before running the algorithm. If the distance between two points is equal to or less than the value of ε, then they are considered neighbours. Points that are beyond the radius are considered as noise or outliers and are not included in a cluster. This was appropriate for defining the spatial distribution of Corn Buntings, which tended to form clusters of breeding territories of various shapes at the local scale. The optimal value of ε was calculated in metres for each region based on K-distance graphs. We set the minimum number of points to form a cluster at five.

Song analysis

All recordings were analysed by a single observer by visually inspecting the sonograms with RavenPro 1.6 software (Bioacoustics Research Program 2014) using a Fast Fourier Transform (FFT

1024, Hanning window, overlap 50%). The sonogram revealed two distinct parts of the song: the song type component which is the first half of the song, and the dialect component which is the second half. They can easily be identified visually (Fig. 2; McGregor 1980, Latruffe *et al.* 2000, Osiejuk & Ratynska 2003). The local dialect pattern is identified when nearby males share the same unique dialect component and the same two or three song type components, which are specific to the dialect.

We limited the analysis to birds, which allowed us to record at least 25 songs. In a study conducted in the same region in Poland, 25 songs was the mean number of songs before a male Corn Bunting switched to a second or third song type (Osiejuk & Ratynska 2003). A catalogue of sonograms for each dialect component and their associated song type components was created for each region to facilitate the identification of the individual song repertoire of all recorded males. Dialect components were coded with capital letters, and song type components were coded with numbers (A1, A2, etc.). The repertoire of a male with one dialect component and several song type components would be coded as 'A(1, 2, 3)' and the repertoire of another male with two dialects, dialect A with two song types (1 and 2) and dialect B with only one song type (1), would be coded as 'A(1, 2) and B(1)'. The same letters and numbers were re-used for different dialects and song types at each study site and so song A1 in Belgium is not the same as song A1 in France or song A1 in Poland.

Song dissimilarity

The individual song repertoires of all recorded males in each region were used to calculate song dissimilarity between males within each region.

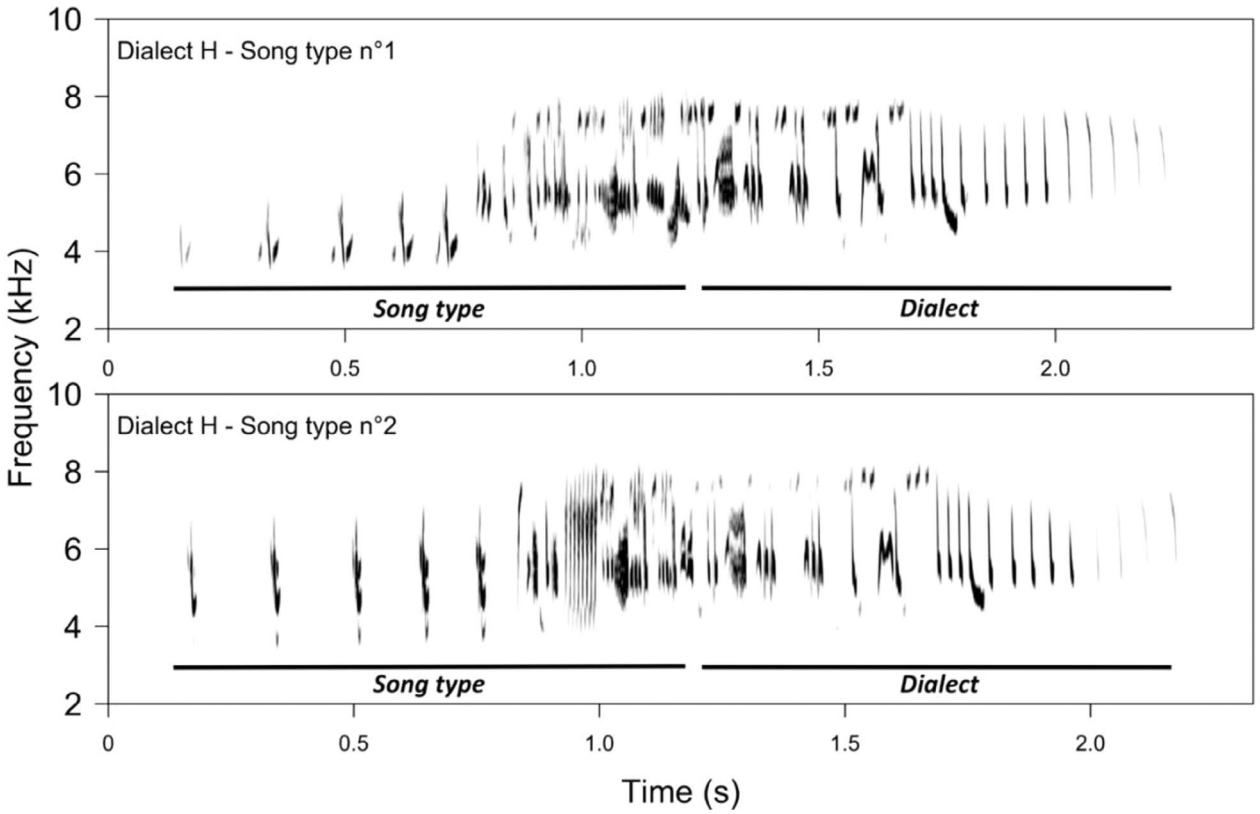


Figure 2. Example of sonograms from two Corn Bunting males recorded in France (Bernot). They both have the same dialect component (H) but two different song type components (1 and 2). The dialect component can be identified in the second part of the song, and the song type component is identified in the first part. If the second part of the song is identical, they belong to the same local dialect.

Table 2. Predictors used in the GLMM analysis.

Predictors (unity)	Type of variable	Measurement
Local density of territorial males (ind./km^2)	Continuous	We considered the area of the clusters, and not the entire area of the studied regions
The proportion of farmland habitat (%)	Continuous	Measured as a percentage of the area of each cluster (the same area used to calculate the local density)
The Shannon diversity index	Continuous	Calculated with QGIS 3.10.4, to account for habitat type heterogeneity
Fragmentation of the farmland habitat	Binary	Fragmented/Not fragmented
Farming intensity	Binary	Intensive/Extensive
Farmland habitat type	Binary	Arable lands/Hay meadows
Spatial distance to the nearest cluster (in metres)	Continuous	Calculated with QGIS 3.10.4, to account for proximity between clusters
Country, as a random factor	Categorical	Belgium/France/Poland

Binary matrices of presence/absence were built separately for the dialect component (Male × Dialect) and song type component (Male × Song type), for each region, resulting in two matrices per region. Based on these presence/absence matrices, song dissimilarities between males were calculated in each region with the Jaccard dissimilarity index, which is the most robust index for presence/absence data (Schroeder & Jenkins 2018). This index was calculated with the vegan package in R (Oksanen *et al.* 2007) as 2B/(1 + B), where B is the Bray–Curtis dissimilarity. Bray–Curtis dissimilarity was computed as follows (for binary data): $[(A + B) - (2*J)]/(A + B)$. A and B were the number of variations in the song repertoire of each male and J was the number of variations shared by the two males. This index value ranged from 0 to 1: if two males shared their whole song repertoire, $J = 0$; if nothing was shared, $J = 1$. When $0 < J < 1$, sharing was partial. This occurred, for example, when some males had two or three different dialect components in their repertoire and so shared only some part of their repertoire with other males, or, within the same local dialect, when some males did not share the same song type components.

The matrices obtained were used to quantify the dissimilarity in dialect and song type components separately. As dialect and song type each represented half of the song, their respective values were added and divided by two to obtain dissimilarity matrices for the whole song repertoire. The same procedure was applied at the scale of the spatial clusters identified with the NNA to obtain song dissimilarity values between clusters in each region.

Statistical analysis

Normal distribution of the data was checked using D'Agostino normality tests (D'Agostino 1970) before each statistical analysis. None of the variables followed a normal distribution. Hence, appropriate non-parametric tests were applied. We used the multiple pairwise Wilcoxon rank sum test with Bonferroni correction to compare the distribution of pairwise song repertoire dissimilarity between the three regions. Then, for each study area, an analysis of covariance (ANCOVA) with permutation test was applied (number of permutations 8000) to test the relationship between the song dissimilarities in the complete repertoires of males, two by two. The combination of an ANCOVA with a permutation test allowed us to deal with data that violated parametric assumptions. We also tested two independent variables: (1) whether both males were in the same cluster and (2) the distance separating them. As clusters covered areas of different sizes, we also tested the sharing distance between two males in the three regions. For this analysis, we used the geographical distance between males that shared their entire (with $J = 0$) or part of (with $0 < J < 1$) their song repertoire. A multiple pairwise Wilcoxon rank sum test with Bonferroni correction was applied.

We applied generalized linear mixed models (GLMMs) fitted to maximum likelihood to test the prediction that local dialects would be less distinct in an intensive farming landscape and with a lower local density of territorial males. We used the song dissimilarity within each cluster as the response variable, and several habitat, landscape and demographic variables as predictors (Table 2). We also performed the GLMM with the local

density of territorial males within clusters and the size of the clusters as response variables. A Gaussian error distribution was used as those three response variables were continuous and positive. The assumption of normal distribution and the homoscedasticity of the residuals were checked graphically for all models. Even if the response variables did not follow a normal distribution, the residuals of the models all followed a normal distribution. Those response variables were measured within each identified cluster in the three countries (n = 29 observations). For song dissimilarity, we performed the analysis separately for the whole repertoire (dialect component and song type component of the song) and for the dialect component alone. As song type components were specific to each dialect, we did not analyse them separately. The GLMM was performed with the lme4 package (Bates *et al.* 2009) in R.

Before performing the GLMM analyses, multicollinearity between predictors was tested using the Variance Inflation Factor (VIF) with the car package in R (Fox *et al.* 2007). This analysis allowed us to exclude predictors when they were highly correlated with other predictors. We only kept the predictors with a VIF score below 2 (Zuur *et al.* 2009).

For the song dissimilarity analysis, the retained variables were the proportion of farmland habitat (%), fragmentation of the farmland habitat and local density of males (birds/km^2). For the local density analysis, the independent variables were the proportion of farmland habitat (%), fragmentation of the farmland habitat and type of farmland habitat (arable land/hay meadows). For the cluster size analysis, the independent variables were the proportion of farmland habitat (%), fragmentation of the farmland habitat, type of farmland habitat (arable land/hay meadows) and farming intensity (intensive/extensive).

All possible models that included a combination or subset of the predictors were tested. Model selection was performed with a model averaging procedure based on the corrected Akaike Information criterion (AICc; Burnham & Anderson 2002). This approach directly used the information of a set of models with an AICc value no more than 2 units higher than the model with the lowest AICc value. Model-averaged coefficients and unconditional standard error for each predictor were then estimated with the shrinkage version of the model averaging. Model-averaged coefficients were estimated as the mean of the coefficient value in all models weighed by the AICc weight of each model. All statistical analyses were carried out in R v4.2.2 (R Core Team 2021).

RESULTS

The song repertoires of 526 territorial males in the three regions (Belgium: n = 141, France: n = 93, Poland: n = 292; Fig. 3) were analysed. This represents 65.6% of the total observed territorial birds during our sampling in Belgium, 64.1% in France and 77.7% in Poland (Table 3). We identified 43 local dialects (Belgium: n = 18, France: n = 11, Poland: n = 14) and 126 song types (Belgium: n = 52, France: n = 31, Poland: n = 43; Table 3).

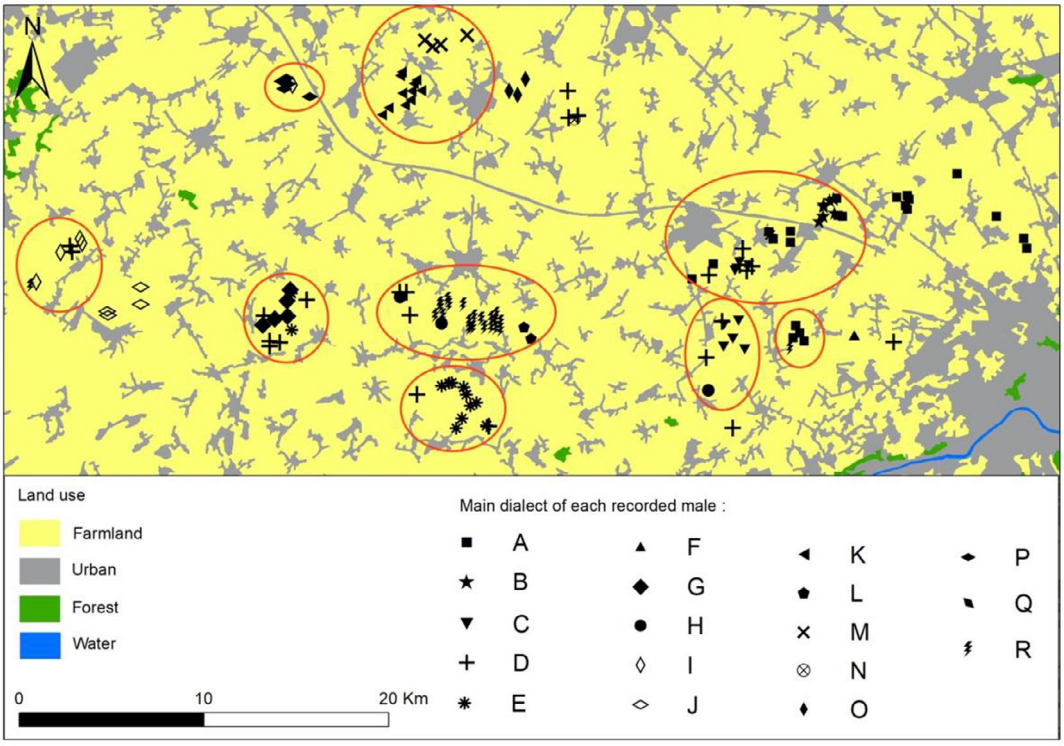
The distribution of repertoire dissimilarity between pairs of birds in the population was significantly different between the three countries (Wilcoxon rank sum test, $P < 0.001$; Fig. 4).

Corn Buntings in France were the most likely to have similar songs across the entire study area, while birds in Poland were the least likely to share repertoires over the entire study area.

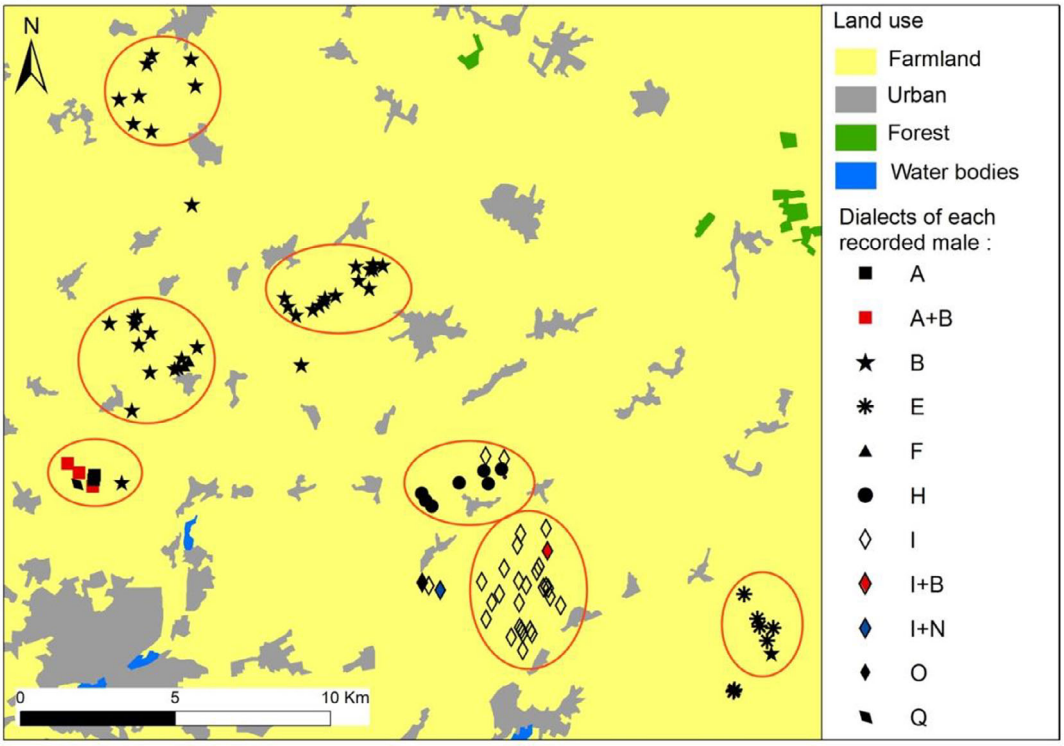
For the whole song repertoire and for the dialect component repertoire, the median values were slightly, but significantly, higher in Poland than in Belgium (Wilcoxon rank sum test, $P < 0.001$). Even if the median values were similar between the two populations (whole song repertoire and dialect component repertoire: 1, interquartile range (IQR) 1–1; Table 4), the half-density distribution showed a higher density of observations of pairs of males that did not share their repertoire in

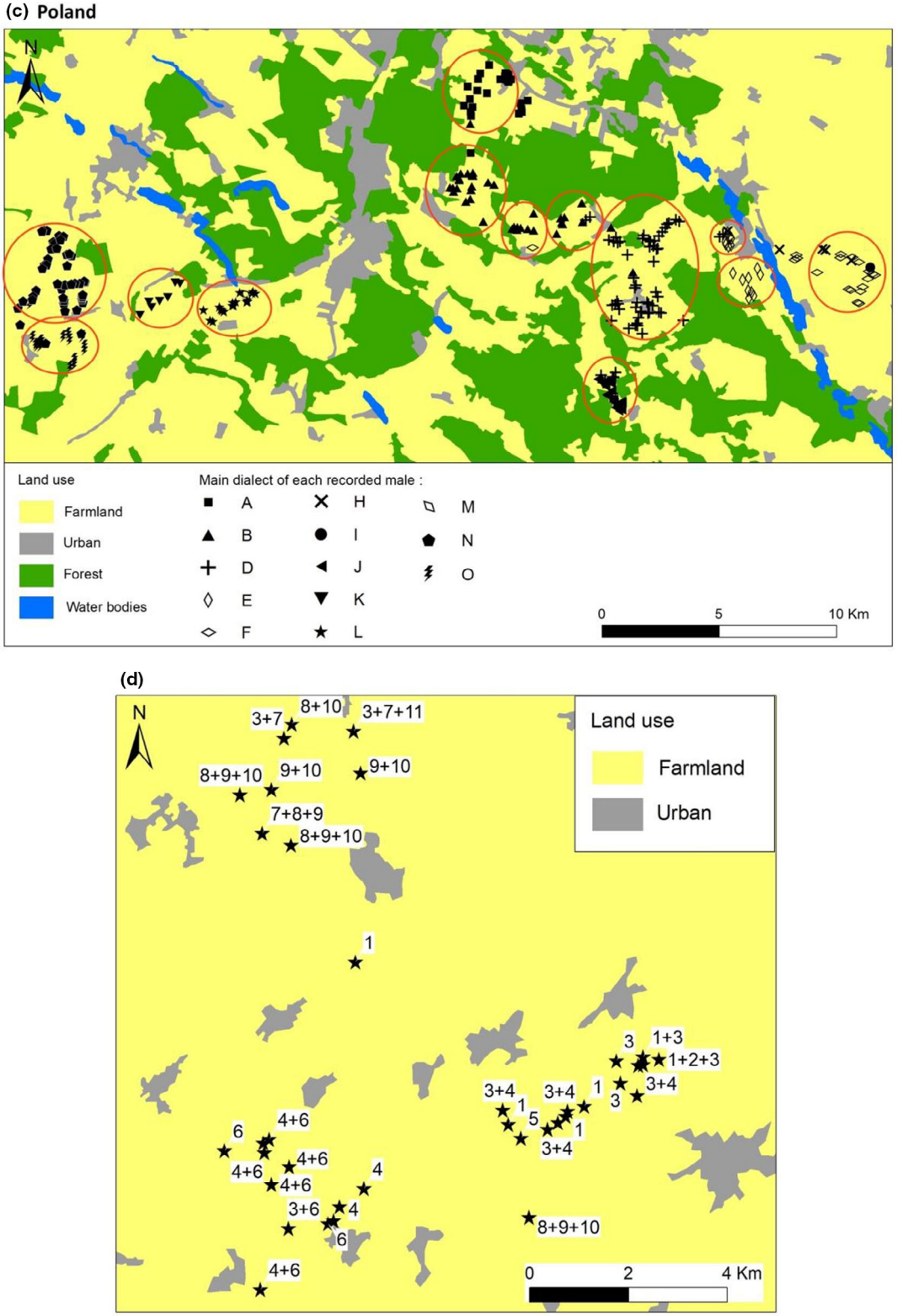
Figure 3. Maps representing the distribution of recorded males in the three regions: (a) Belgium, (b) France, (c) Poland. For each male, the symbol represents the dialect component of its repertoire. Red circles delimit the spatial clusters. (d) Example of three spatially distinct groups of territorial males with the same local dialect (represented by the star symbol) but with different song type repertoires (represented by the numbers; France). (e) Example of sub-groups of males within the same group sharing the same local dialect (represented by the triangle) but with different song type repertoires (represented by the numbers; Poland). Land coverage key: green, forest; grey, urban area; blue, water bodies; yellow, farmland habitat.

(a) Belgium



(b) France





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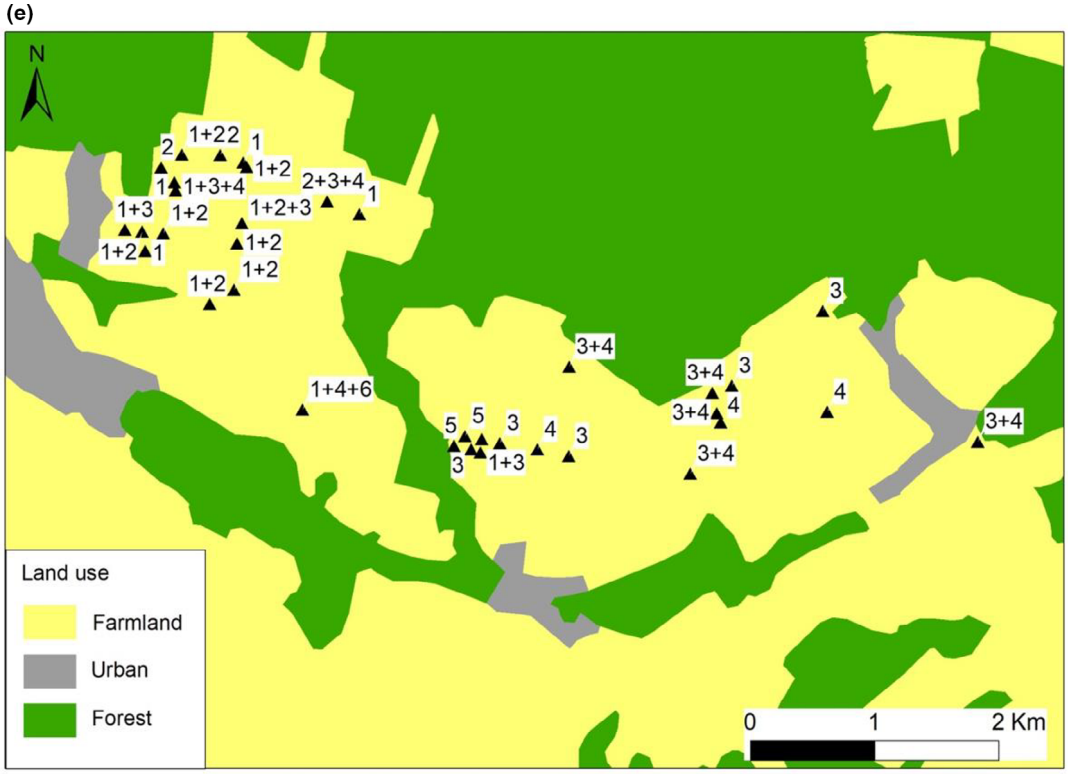

Figure 3. Continued

Poland, compared with Belgium (Fig. 4). The lowest song dissimilarity between two males was found in France, when considering only the dialect repertoire (component repertoire: 1, IQR 0–1; Table 4, Fig. 4b).

Identification of local dialect patterns and relationships with local densities, landscape and habitat variables

Males in all three populations were significantly clustered, but the degree of aggregation was higher in Belgium (NNI = 0.33) and in Poland (NNI = 0.34) compared with France (NNI = 0.54, Table 5). To delineate clusters of territories, the optimal values of ε were respectively: Belgium: ε = 2200 m; France: ε = 1500 m; Poland: ε = 1000 m with clusters covering a larger area in Belgium and a smaller area in Poland. Based on those values for each region, the DBSCAN algorithm identified a total of 29 clusters (Belgium: n = 9; France: n = 7; Poland: n = 13; Fig. 3 and Fig. S1), which ranged in size from 5 to 75 individuals.

The mean song dissimilarity between two birds was significantly lower between males in the same spatial cluster compared with males in different spatial clusters in the three regions (based on cluster membership, ANCOVA, $P < 0.001$; Table 6). There was no correlation with spatial distances between two males. Birds that were not part of the same cluster had very different songs (J close to 1) at all study sites. In contrast, birds within the same cluster were the most likely to have similar songs in Poland and were the least likely in Belgium. These results indicated that pairs of males in the same spatial cluster shared their song repertoire with each other more than with males in other clusters, independently of the spatial distance between them. This pattern suggested clear boundaries in song variation between spatial clusters.

The GLMM results (Table 7) showed that the song dissimilarities, both for the whole song repertoire and for dialects, were weakly but significantly and negatively correlated with the local density of males; higher male densities were associated with greater similarity of song types and dialects. The

local density of males within the clusters was higher in Poland than in France and Belgium (Fig. 5) and positively correlated with extensive farming practices and farmland habitats dominated by hay meadows (Table 8). Additionally, dissimilarity of the dialect component within clusters decreased as fragmentation of farmland increased.

Spatial patterns of song dissimilarity

As spatial clusters covered areas of different sizes (Table 5), we compared the spatial distances at which two males shared all ($J = 0$) or part ($0 < J < 1$) of their song repertoire between the three regions, using a multiple pairwise Wilcoxon test (Fig. 6). For the whole song repertoire, the median distance for total song sharing (dissimilarity = 0, for dialect and song types) was significantly lower in France than in the two other countries ($P < 0.001$). For the dialect repertoire, the median distance for total sharing was significantly lower in Poland than in the two other countries ($P < 0.001$). For partial sharing, both for the whole song and the dialect repertoire, the median distance was smallest for Poland, intermediate for France and largest for Belgium ($P < 0.001$; Table 9). GLMM did not detect significant relationships between the area covered by clusters or the mean distance between pairs of males in the same cluster and the tested predictors.

Table 3. For each of the three studied regions, total covered area, number of territorial males, number and proportion of males recorded, and number of dialect components and song type components.

	Belgium	France	Poland
Study area size, km^2	1264	602	743
Number of observed males	215	145	376
Number of males recorded (% of observed males)	141 (65.6%)	93 (64.1%)	292 (77.7%)
Number of dialect components	18	11	14
Number of song type components	52	31	43

These results highlighted that song sharing occurred over a small spatial range in Poland, with median values between 1.7 and 2.1 km. In France, median values for the dialect repertoire were higher but also over a small spatial range (between 3 and 3.9 km). If we consider the whole repertoire, the spatial range was wider (between 1 and 3.9 km). In Belgium, the spatial pattern of song sharing was less clear with median values ranging between 1.5 and 5.6 km. Those results accorded with the relationship between distance between males and their song dissimilarity (Fig. 7).

DISCUSSION

We found different local dialect spatial patterns in the three regions based on quantitative analysis of spatial distribution and song dissimilarity. As we predicted, local dialects were least well-defined in Belgium and not well-defined in France, the two regions where farming practices were intensive and the Corn Bunting was in sharp decline. In contrast, in Poland, where local dialects were well-defined, the species was still abundant, and the farming practices were more extensive.

Local dialect pattern was correlated with local density of territorial males

A higher song sharing within spatial clusters was correlated with a higher local density of territorial males. In Poland, where the Corn Bunting was abundant, we observed a classical spatial mosaic of distinct local dialects. All, or nearly all, of the males within a local dialect shared the same two or three song types. Among the three regions, local densities were the highest in Poland. Other studies have already suggested that higher local densities of males promote the formation of a clear local dialect pattern (McGregor *et al.* 1997, Latruffe *et al.* 2000, Osiejuk & Ratynska 2003).

The patterns observed in France and Belgium could correspond to a gradual erosion of the local dialect pattern linked to the decline of the species in these regions. In France, Corn Buntings were

Figure 4. Raw data points, interquartile range and the distribution of song dissimilarity scores for male Corn Buntings in each of the three study populations. Boxes show the range from the lower boundary of the second quartile to the upper boundary of the third quartile. Horizontal line indicates the median. (a) Whole song repertoire, (b) local dialect component repertoire.

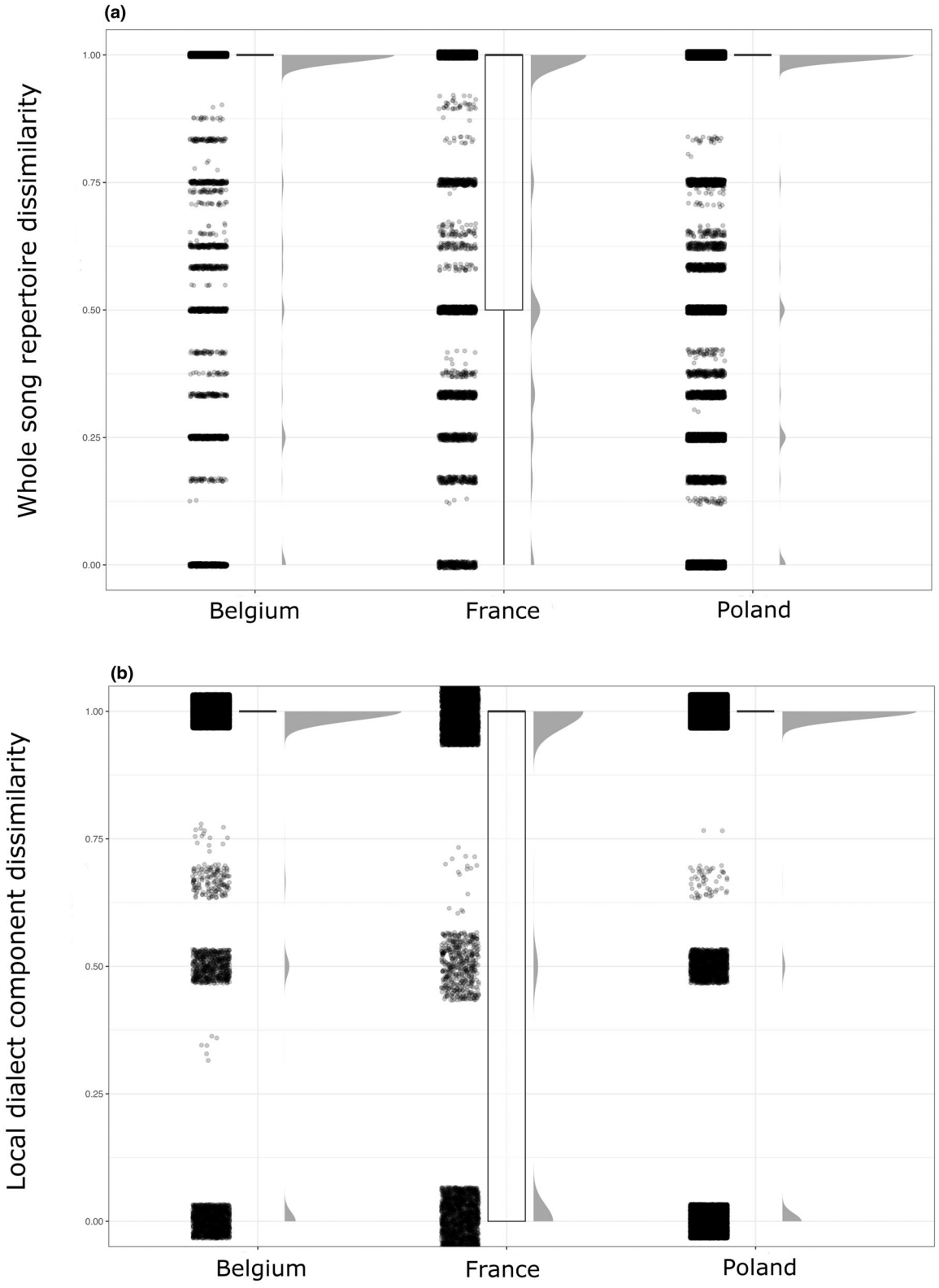

Table 4. Repertoire dissimilarity between two males in the three sampled regions, with, for each region, the number of observations, mean (±sd) and median dissimilarity and interquartile range (IQR).

Whole song repertoire dissimilarity (dialects and song types)					
Regions	Number of comparisons	Mean	sd	Median	IQR
Belgium	17 956	0.92	± 0.23	1	1–1
France	7921	0.8	± 0.31	1	0.5–1
Poland	82 944	0.89	± 0.26	1	1–1
Dialect repertoire dissimilarity					
Regions	Number of observations	Mean	sd	Median	IQR
Belgium	17 956	0.9	± 0.29	1	1–1
France	7921	0.7	± 0.44	1	0–1
Poland	82 944	0.87	± 0.33	1	1–1

Table 5. Results of the nearest neighbour analysis that described the spatial distribution of territorial male Corn Buntings in Belgium, France and Poland. The nearest neighbour index is an indicator of the degree of aggregation of spatial points. It is the ratio between the expected mean distance (if the spatial distribution is random) and the observed mean distance. The *z*-score is the standard deviation from the expected mean distance.

	Belgium	France	Poland
Observed mean distance (m)	405.20	414.31	184.30
Expected mean distance (m)	1233.40	771.50	547.50
Nearest neighbour index (NNI)	0.33	0.54	0.34
Z-score	−12.90***	−8***	−21***

Significance (*P* values): ***$P < 0.001$.

Table 6. Mean pairwise song dissimilarity ($J \pm$ sd) between pairs of males, whether they were located within the same cluster or in different clusters, for each of the three countries.

	Mean pairwise song dissimilarity (J)	
	Same cluster	Different clusters
Belgium	0.54 ± 0.2	0.97 ± 0.12
France	0.36 ± 0.08	0.96 ± 0.14
Poland	0.30 ± 0.2	0.96 ± 0.17

Table 7. Averaged coefficients and significance of the generalized linear mixed model results using the mean pairwise song dissimilarity within each spatial cluster in the three regions as the response variable (dialect component and the whole song repertoire were analysed separately).

	Predictors	Coefficients	se	*P* value
Song dissimilarity Whole song repertoire	Local density	−0.043*	0.026	0.027
Song dissimilarity Dialect component repertoire	Local density	−0.22*	0.21	0.035
	Fragmentation	−0.045*	0.044	0.045

se, standard error. Only predictors with associated *P* values ≤0.05 are shown. The other predictors were tested but were not considered significant.

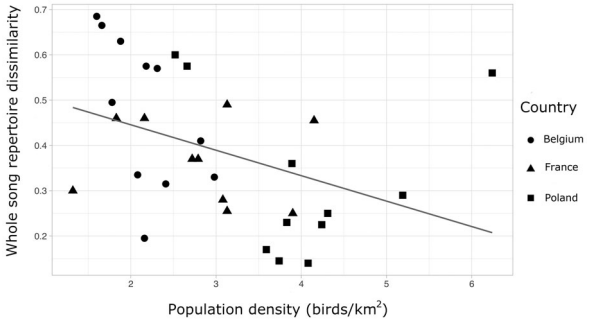

Figure 5. The relationship between population density and whole song dissimilarity scores. The correlation depicted by the line was significant (adjusted $R^2 = 0.51$, $P < 0.01$).

Table 8. Averaged coefficients and significance of the generalized linear mixed model results using local density as the response variable.

Predictors	Coefficients	se	*P* value
Favourable habitats	−0.02	0.02	0.32
Hay meadows	3.35***	0.73	0.00027
Non-fragmented habitat	1.12	0.48	0.07
Extensive farming practices	1.6***	0.88	0.00022

se, standard error. Significance ***$P \leq 0.0001$.

not found in all places with seemingly suitable habitats but were found aggregated in some distinct locations. Groups were not close to each other, as in Poland. Within these groups in France,

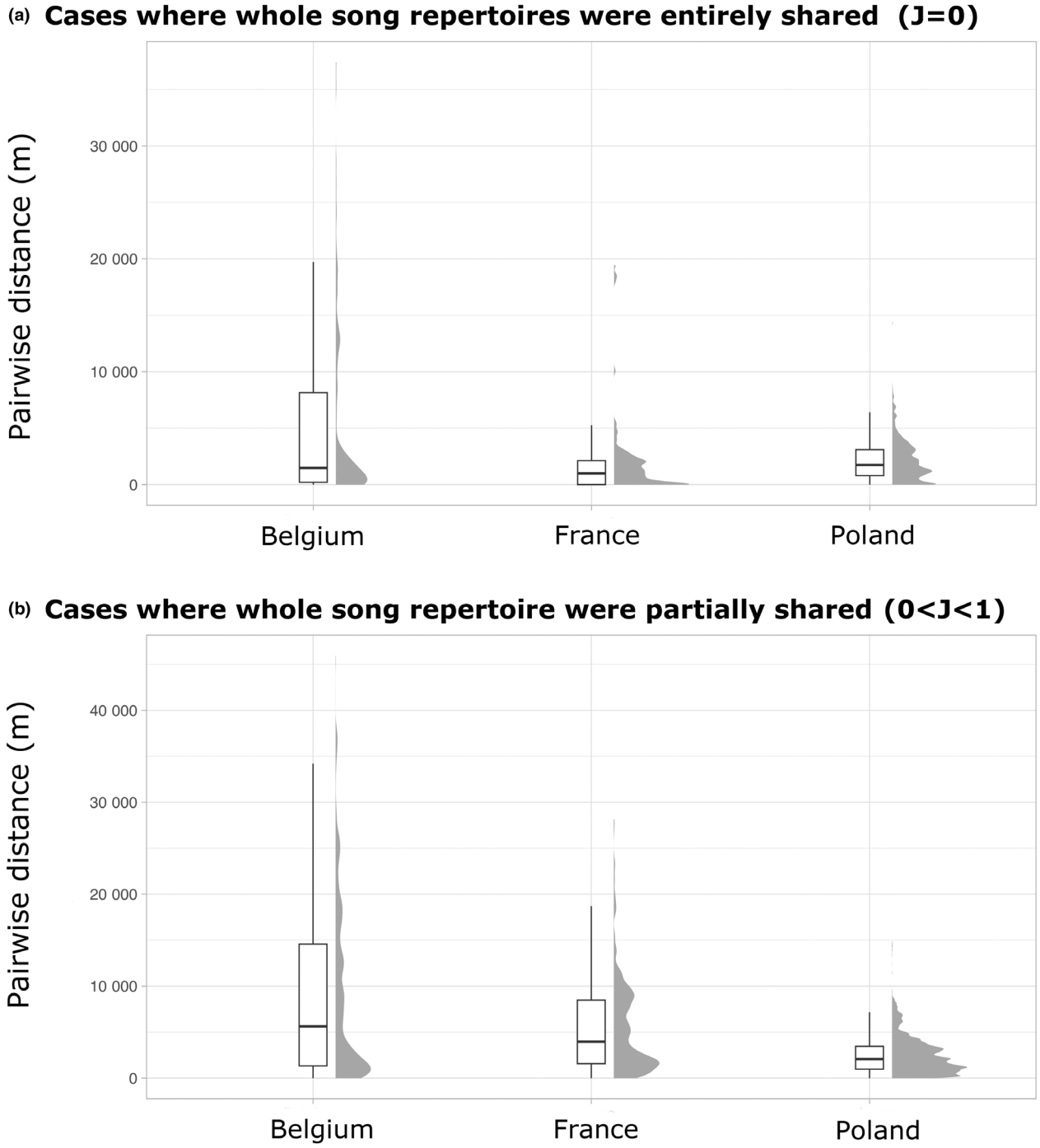

Figure 6. Raincloud plots representing, from left to right, raw data points, boxplot and distribution of spatial distances between pairs of males that shared their song repertoire (whole song repertoire) in the three studied populations. (a) Pairwise distances related to $J = 0$ (complete sharing); (b) pairwise distances related to $0 < J < 1$ (partial sharing).

all or almost all males shared the same dialect component but had dissimilar song type repertoires. In Belgium, where the population decline is more pronounced than in France, we also observed spatial clusters of territorial males only at some locations, with empty habitat between groups.

Table 9. Median distances (interquartile range in parentheses) calculated for each category of pairwise song dissimilarity (Jaccard Index, *J*) and for each sampled region. $J = 0$ corresponds to the complete sharing of the song repertoire, which is the definition of local dialect in the Corn Bunting (all birds sharing the same dialect component and the same two or three song type components). $0 < J < 1$ corresponds to the partial sharing of the song repertoire. The median distance was calculated both for the dissimilarity (*J*) based on the whole repertoire (dialect and song type components) and for the dialect component only, as some birds that shared the same dialect component did not necessarily share the same song type components.

	Whole song repertoire: Dialect & Song type components		
Range of pairwise song dissimilarities	Belgium	France	Poland
$J = 0$	1.5 km (0.2–8 km)	1 km (0–2.1 km)	1.7 km (0.8–3 km)
$0 < J < 1$	5.6 km (1.3–14.6 km)	3.9 km (1.6–6.8 km)	2 km (1–3.5 km)
	Song repertoire: Dialect component		
	Belgium	France	Poland
$J = 0$	2.6 km (0.85–12.3 km)	3 km (1.5–7.6 km)	2 km (1–3.3 km)
$0 < J < 1$	5.3 km (1.3–12.8 km)	3.9 km (1.6–8.5 km)	2.1 km (1–3.5 km)

Some of these groups included very few males. Within these groups, there was one dominant local dialect, but we also noticed the presence of several males with other local dialects. This eroding pattern may be explained by the lower local density of territorial males as the result of intensive farming and habitat degradation. Hence, if clusters of males do not form because there are fewer individuals, it may be more difficult for local dialects both to emerge and to survive.

Disturbance of the local dialect pattern was found in previous studies of Corn Buntings, when rapid land use changes had caused local extinctions followed by recolonization. The consequence was multiple founder effects with disturbance of local dialect patterns (Holland *et al.* 1996). This phenomenon was also reported for the Nuttall's White-crowned Sparrow *Zonotrichia leucophrys nuttalli*, which was impacted by large-scale and rapid habitat changes due to wildfire (Baker 1975, Baker & Thompson 1985). This founder effect was also observed when, following an overproduction of young birds during the last breeding period and/or high winter survival, some young males failed to settle in their native location, and may have tried to settle in other unoccupied locations of lower quality (Bednorz 1997, Osiejuk & Ratynska 2003). Founder effects or high winter survival were unlikely in our study, especially in Belgium where the population has been monitored since 2010 (Ory *et al.* 2015), and no significant land use change has been observed. Furthermore, the population has been in sharp decline since at least 1990, so a colonization of new locations following a year of an overproduction of young birds or a high winter survival would not explain the commingling of local dialects in Belgium.

The impact of the erosion of the local dialect pattern on territory defence and breeding success within local groups sharing the same local dialect in the Corn Bunting is not known. The local dialect seems to be important in territory defence as Corn Bunting territorial males respond more aggressively to foreign dialects (McGregor 1983, Garland & McGregor 2020). It is unclear whether females prefer males that sing the same local dialect as their father (McGregor *et al.* 1997). In other species, a link was established between high local song sharing and breeding success (Payne 1982) or territory tenure (Beecher *et al.* 2000, Wilson *et al.* 2000). In Redwings, song sharing was not correlated with the density of singing birds but with breeding success (Espmark *et al.* 1989). Erosion of the local dialect pattern could also impact the individual response to local songs. In Savannah Sparrows *Passerculus sandwichensis*, male discrimination of local versus foreign dialects breaks down when the individuals within a local population do not all sing the same dialect. Hence, in this species, the homogeneity of songs within a local population is necessary to modulate the response to the local dialect (Williams *et al.* 2024).

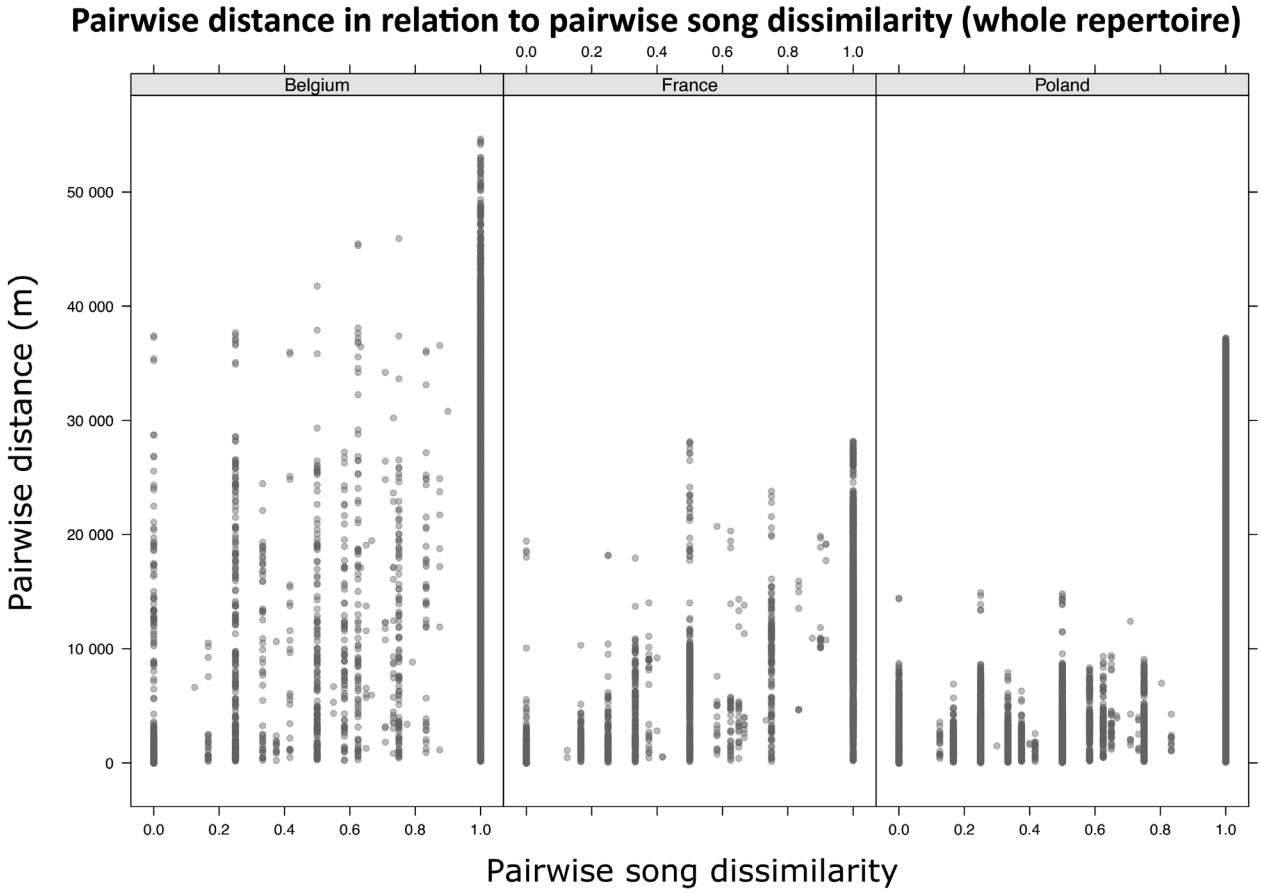

Figure 7. Scatterplots presenting the raw data of pairwise spatial distance in relation to pairwise song dissimilarity (whole song repertoire) for the three regions.

Our study also highlighted that higher densities of territorial males were found in farmland habitat dominated by hay meadows. In France, Corn Buntings are often found at high densities in extensive hay meadows along river valleys (Broyer *et al.* 2014, 2017, 2019). In Denmark, the highest densities were found in mixed landscapes of extensive grasslands and arable lands. The density declined where arable land dominated the landscape (Fox & Heldbjerg 2008). Corn Bunting densities were also lower where there were grazed pastures with high inputs of nutrients (Lilleør 2007). The presence of grassland and uncultivated strips in the farmland matrix seems favourable for Corn Buntings, as there are more weeds and consequently more invertebrates to feed upon (Brickle *et al.* 2000, Kosiński & Tryjanowski 2000, Mason & MacDonald 2000). In Scotland, where the Corn Bunting remains, nests are mainly found in dense swards of growing cereals and grass silage fields (Perkins *et al.* 2012, 2015).

Because the local dialect pattern was observed only in high local densities of territorial males, this could also be used as a complementary indicator of a healthy local population of Corn Bunting, as high territory density is often considered as reflecting a higher recruitment rate (Bock & Jones 2004). Variations in the density of territorial males would be likely to influence the level of male–male competition (Clutton-Brock & Vincent 1991, Kokko & Rankin 2006). In the Corn Bunting, a higher number of neighbours elicited a higher song output during the breeding season (Olinkiewicz & Osiejuk 2003). However, higher densities can also mean higher competition for food resources, or higher predation pressure, and hence could constitute an ecological trap (Lameris *et al.* 2016). This

is especially the case for some bird species in intensive farming habitats where food resources are scarce, as was shown for the Yellowhammer (Dunn *et al.* 2015). The Corn Bunting is sedentary and philopatric. Its song is crystallized during the first year of settlement and matches the dialect of its close neighbours (McGregor *et al.* 1997). Hence, dialect may help to identify the place where individuals originated. In Belgium, many individuals dispersed from the larger clusters where the local density was high. Those clusters were in Burdinne, Hannut and Lens-sur-Geer (Fig. 3). The distance ranged between 15 and 18 km, with one bird found 46 km from its local dialect. This may suggest that most of the favourable habitats were occupied locally, causing dispersal. In North Uist (UK), the postnatal dispersal distance of all ringed birds was no more than 5 km, with 80% of the individuals settling within 2 km of their birthplace (Shepherd *et al.* 1997). In Belgium, based on the very limited data available, the distances were higher, ranging between 0 and 26 km (IRSNCB; Walot 2017).

Fragmentation of the farmland habitat promoted the formation of a local dialect pattern

Although there were no replicates for the fragmentation type (each country has its own), the differences in the dialect component of the song might be related to fragmentation (involving both the loss and the breaking apart of habitats; Fahrig 2017), as there is no alternative explanation as plausible as this factor. For instance, the three populations are known to have similar dispersal regimens (they are all sedentary), which is another factor that could have contributed to differences in dialect patterns among populations (Yang *et al.* 2023).

Our results support the idea that fragmentation favoured the song sharing of the dialect repertoire within spatial clusters and could promote the formation of local dialects. Spatial aggregation was more pronounced in Belgium and Poland, two regions where the farmland habitat was fragmented either by the road network and urban areas (Belgium) or by woodlands (Poland). In these regions, local dialects appeared to be segregated and delimited by the presence of unsuitable habitats surrounding the farmland habitat. We also observed other spatially close local dialects that were separated by a river valley (Belgium) and by water bodies (Poland). Those landscape features are known to be barriers delimiting different dialect areas in other species, but at larger scales than those considered in this study (Capelli *et al.* 2020). Additionally, even if it was not statistically significant, the observations suggested that song type sharing between nearby males rather than local dialects could be more affected by isolation caused by small-scale landscape features. In Poland, we observed three close groups of males with the same dialect but with different song type repertoires (Fig. 3e). One of these groups was separated from the two others by a wooded strip, and its song type repertoire was quite different. In France, we observed the same phenomenon but with groups that were distant from each other (Fig. 3d). This pattern has also been reported in Corn Buntings in Portugal, with sub-groups of males that sang the same dialect but clustered according to their own song type pool (Latruffe *et al.* 2000). This could be due to cultural drift where seemingly isolated (geographically or acoustically) groups could diverge culturally. This might be caused by copying errors during song learning that persist within the same local population and contribute to geographical song variations (Slater 1989, Lachlan & Servedio 2004).

It is difficult to find a geographical relationship between habitat edges and song variation boundaries, especially at a local scale, because much of the studied song variation in songbirds is clinal. Several studies have suggested that small variations in habitat may shape dialect patterns, as in the Sage Sparrow *Amphispiza belli* (Rich 1981). In the Rufous-collared Sparrow *Zonotrichia capensis*, habitat structure and its stability through time were likely factors that maintained dialect boundaries (Nottebohm 1969, García *et al.* 2015). In the Hermit Warbler *Setophaga occidentalis*, habitat fragmentation at the local scale could partially explain the geographical song variation, but it was not a necessary landscape feature (Janes & Ryker 2013). However, the segregation and delimitation of local dialects by unsuitable habitat could also be due partially to choice of study sites in Poland. Trees and other kinds of landscape features are still commonly present in Polish farming landscapes (Goławski & Dombrowski 2002, Szymkowiak *et al.* 2014). Extensive farming landscapes are disappearing from

this part of Poland, replaced by artificial woodlots or, conversely, intensive farming has replaced woodlots and pastures with single-crop fields. Most of the recorded Corn Buntings in Poland were in a diversified landscape with extensive arable lands enclosed in a matrix of pine woodlots. In the present study, we lack recordings in more intensive farming and open landscapes in Poland to have a broader view of factors that promote spatial patterns of local dialect distribution.

In conclusion, our results allowed us to better understand the factors that contribute to the spatial pattern of Corn Bunting local dialects. The sharp decline of Corn Buntings in intensively farmed habitats has led to lower local densities of breeding territories accompanied by the erosion of the local dialect pattern. However, the consequences of this erosion for Corn Buntings remain unknown, as we lack information on the importance of local dialect patterns in territory acquisition and defence, and whether it can be a reliable indicator of healthy local populations. Additionally, we found that habitat fragmentation (urban areas, road networks and woodlands) appeared to favour the local aggregation of breeding territories, and to delimit the boundaries between local dialects. Our work provides a valuable baseline for long-term monitoring of dialect characteristics in the three study areas. Our findings point to anthropogenic causes, but long-term studies in the same areas and extension of the study to new areas would strengthen conclusions and rule out other environmental factors or idiosyncrasies of individual populations.

ACKNOWLEDGEMENTS

We would like to acknowledge Emmanuel Serusiaux, Pierre Devillers, Pascal Poncin and Jean-Yves Paquet for their support and helpful comments. We are grateful to Arnaud Beckers who kindly made the maps, to Maxime Metzmacher who provided valuable advice about bird recording and to Fanny Carion-Ellis who kindly corrected the text. We would like to thank the two anonymous reviewers for their very helpful comments and suggestions that improved the quality of the manuscript.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

FUNDING

This study was funded by the University of Liège and the Fund for Scientific Research (F.R.S-F.N.R.S.).

ETHICS STATEMENT

This observational study did not require any permit and complies with the laws of the countries in which it took place (Belgium, France and Poland). It is based on field observations without manipulation or disturbance to the studied birds.

AUTHOR CONTRIBUTIONS

Anne-Laure Geboes: Writing – original draft; conceptualization; methodology; formal analysis. **Tomasz S. Osiejuk:** Writing – review and editing. **Nicolas Magain:** Supervision; writing – review and editing.

Data Availability Statement

Recordings and raw data are available upon request to the first author.

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Received 10 August 2023;
Revision 22 October 2025;
revision accepted 31 October 2025.
Associate Editor: Esther Sebastián-González

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Spatial clustering of groups of close males performed with the DBSCAN algorithm (A: Belgium, B: France, C: Poland). The same colours were re-used for different populations in each of the three studied regions.