Research article

Habitat characteristics and the rate of decline in a threatened farmland bird, the ortolan bunting *Emberiza hortulana*

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Farmland habitats witness steep declines in biodiversity. One rapidly declining farmland species is the ortolan bunting *Emberiza hortulana*. In Finland, a staggering 99% of the population has been lost during the past 30 years. Changes in the breeding habitats have been proposed as a reason for the decline, although hazards during migration and wintering may also play a role.

We gathered a 19-year data set of Finnish ortolan buntings and studied which spatial characteristics, habitat features, and climate factors might explain the population growth rate at the singing-group level. As explanatory variables we used region, density of small-scale structures, proportion of agricultural area in the landscape, diversity of crop types, proportion of bare ground, and temperature and precipitation of previous breeding season.

Higher population growth rates were associated with higher crop type diversity and higher proportion of bare ground. The mosaic of various crop plants and bare ground may provide a wider array of feeding, hiding and nesting places, and an easier access to food. Higher growth rates were also associated with landscapes dominated by interconnected agricultural land, which may reflect the species' sociability and avoidance of forested areas. The North Ostrobothnia region had higher growth rates compared to other regions.

We suggest that northern populations of ortolan bunting should be targeted for further studies on feeding and breeding ecology as well as for urgent conservation actions, such as increasing crop type diversity and bare ground.

Keywords: agricultural intensification, farmland birds, habitat selection, population decline, species conservation, vegetation structure

Introduction

Several farmland bird species in western Europe are declining rapidly primarily due to the intensification of agricultural practices (Burns et al. 2016, Rigal et al. 2023). These practices include, for example, building sub-surface soil drainage systems, increased chemicalization, and agriculture specialization (Schifferli 2001). The loss of fallow land has also been shown to have a strong association with farmland bird declines (Traba and Morales 2019, Staggenborg and Anthes 2022, Hertzog et al. 2023).

The ortolan bunting *Emberiza hortulana*, a small Palearctic migratory songbird, is experiencing an extreme population decline across Europe, dropping 88% since 1980 (Jiguet et al. 2016). Its status is particularly alarming in northern Europe, where it is critically endangered (Lehikoinen et al. 2019). In Finland, the decline has been ca 99% within the past 30 years (Väisänen and Lehikoinen 2013), with only 2600 pairs remaining in 2020 (Piha and Seimola 2021). In Fennoscandia, ortolan buntings occur at their northernmost range limit and are genetically and demographically isolated from the rest of the European population, making them particularly sensitive to potential threats with no immigration to counteract the declines (Moussy et al. 2018). Numerous threats such as habitat loss and degradation, climate change, and illegal hunting are believed to explain the declines of the species (Menz and Arlettaz 2012). Threats along the flyways have been studied intensively (Jiguet et al. 2016), and wintering habitats have been under recent investigation (Gremion et al. 2022).

However, survival studies in Norway and Finland suggest that ortolan buntings may not be suffering exceptionally great losses during their migration or wintering in Africa, though a long-term decline of seed-food availability due to land-use changes has been documented in the Sahel (Zwarts et al. 2023a, b). Nousiainen (2020) showed that during 2013–2019 Finnish male ortolan buntings had an apparent annual survival rate of 43.3%, which was fairly similar to 15 other similarly sized long distance migrant passerine species (range: 42–58%). Somewhat higher survival rates (64–77%) were found in the Norwegian ortolan bunting populations (Dale 2016). Additionally, Nousiainen (2020) found that survival was equal throughout all three main regions where the species occurs in Finland. In contrast, there were regional differences in population declines, with the steepest declines occurring in southwestern parts of the population (Nousiainen 2020, Piha and Seimola 2021). Hence, there might be some regionally varying factors regulating breeding success that could, at least partly, explain the declines in ortolan bunting populations. Even though the most important reasons for the declines may lie elsewhere, the actions needed for recovery may not need to address the causes of the decline directly (Morrison et al. 2021). Rather, we need to identify actions that improve productivity and locations in which those improvements are achievable (Morrison et al. 2022).

The breeding habitat requirements of the ortolan bunting have been intensively studied, mainly in the agricultural habitats where the decline is steepest (Menz et al. 2009, Kosicki and Chylarecki 2012, Elts et al. 2015, Brambilla et al. 2016, Šálek et al. 2019). In the Mediterranean Europe, ortolan bunting breeds in open shrubland and steppe-like habitats, and montane zones up to 2500 m a.s.l. (Cramp and Perrins 1994). In temperate Europe, it is primarily associated with cultivated land, set-asides and shrublands in historically burnt habitats (Revaz et al. 2005, Kosicki and Chylarecki 2012, Šálek et al. 2019). In Nordic countries, the species is present not only in farmland habitats, but also in clear cuts and peat production bogs (Dale and Olsen 2002, Vepsäläinen et al. 2007, Dale and Christiansen 2010). In general, the ortolan bunting breeds primarily in relatively warm, dry areas, with well-drained soils and an annual rainfall below 600–700 mm (Cramp and Perrins 1994).

At the territory level in agricultural habitats, the ortolan bunting is associated with field margins featuring structural elements such as isolated trees and hedges which are used for perching and singing (Grützmann et al. 2002, Löffler and Fartmann 2023). Also, high crop type diversity seems important because it primarily nests and forages on the ground (Berg 2008), and a single crop type rarely provides a suitable vegetation structure throughout the breeding season. Low vegetation structure with patches of bare ground is more easily accessible to birds foraging on the ground than uniformly dense growing crops (Schifferli 2001, Schaub et al. 2010), while higher and denser vegetation is needed for hiding the nest.

Despite extensive studies on ortolan bunting breeding habitat requirements, few have directly linked habitat factors to the population growth rate of the species. Furthermore, many of the previous studies were limited to small geographical areas, conducted solely at the territory scale or focused on the occurrence probability (or density of territories) over a single year or a few years.

We investigated the association between changes in the ortolan bunting's breeding habitat characteristics and the rate of change of the species populations in a multiscale context where territorial, landscape and regional levels are considered simultaneously. We used an exceptionally large data set which covered approximately the whole Finnish breeding range area (ca 200 000 km²) and nearly two decades of observations.

Specifically, we studied whether the rates of change in ortolan bunting subpopulations were associated with 1) proportion of agricultural land cover within the landscape (landscape variable), 2) crop plant type diversity and proportion of bare ground (crop variables), 3) density of roads, ditches, main drains, riverbanks and buildings (small-scale structure variables), or 4) temperature and rainfall from the previous year (weather variables), while also assessing 5) potential regional variation in the declines.

We hypothesized positive associations between ortolan bunting population growth rate and increases in density of small-scale structures, diversity in crop types, proportion of bare ground, and proportion of farmland in the landscape. In addition, we expected that cold and rainy breeding seasons reduce population growth to the next year due to potentially lowered breeding success.

Material and methods

Study area

Most of the studied ortolan bunting subpopulations, here-after singing groups, were located in western and southern Finland, where most of country's agriculture is concentrated. Fewer study sites were in the eastern and central regions, which have less farmland (Fig. 1). The study area represents the species' northernmost distribution range limit.

Bird data

The territories of the ortolan buntings were mapped annu-ally using a two-visit mapping method, which was proven effective and reliable for mapping the species (Tiainen et al. 1985). Visits occurred in May and the first half of June. Special attention was paid to simultaneous observations of singing males, territory locations, and to accurate estimation of territory numbers. Centre coordinates were recorded for each territory. In total 4430 territories were recorded over the 19-year study period (2000–2018).

Forming singing group units

Ortolan buntings are social birds that form singing groups of several males (Cramp and Perrins 1994) holding territories typically of 100–300 m in radius (Vepsäläinen et al. 2007). We expect that territories farther than 500 m apart or sepa-rated by some natural boundary, like a narrow stretch of for-est or a busy road, belong to different singing groups. Due to high male site fidelity (Dale et al. 2005), annual observations of territories in the same area were assumed to belong to the same singing group. To create study units, the singing groups, observations from 2000–2017 (plus 2018 data after form-ing) within 500 m of each other were aggregated. Then, 250 m buffers around each territory within a singing group were merged to define the group's area (Fig. 2). Occasionally, this method produced very large singing groups which, in real-ity, might have consisted of several smaller groups separated by some landscape feature. Smaller singing groups were also formed that might have belonged to the same group despite the distance between the observations (or missed observa-tions). Therefore, subjective adjustments were made to reflect the observer's perception on which birds formed a singing group (17 large divided into two or several smaller ones; 13
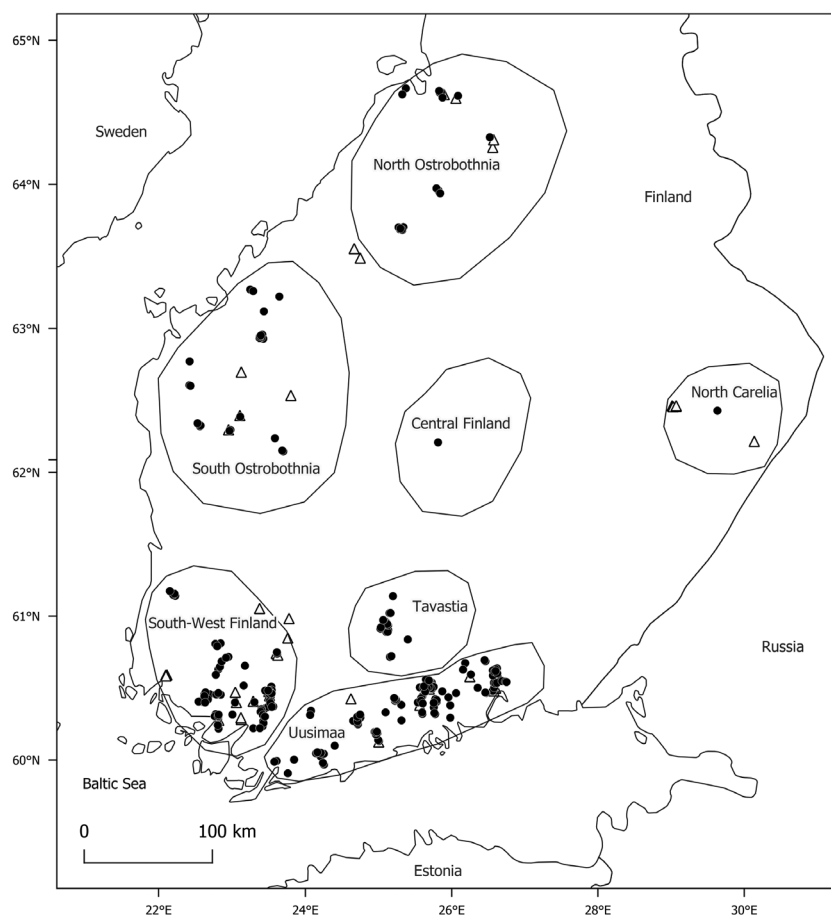

Figure 1. Map showing the centroid coordinates of each ortolan bunting singing group (black circles) that was visited in at least one pair of consecutive years between 2000 and 2018, and had at least one territory in the first of those surveys (n = 238). Singing groups were classified into seven major regions indicated with black line. Discarded singing groups (n = 41), not fulfilling these criteria, are indicated by triangles.
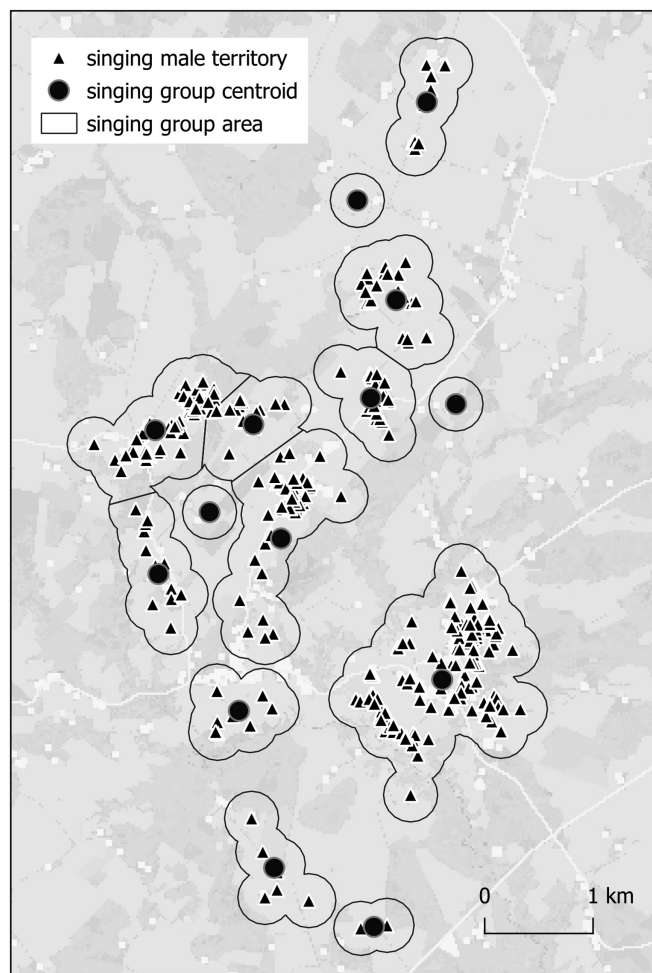
Figure 2. Map depicting separate ortolan bunting singing groups which are formed by aggregating close-by territories (observations of individual singing males, black triangles). Singing groups are delineated by a black line representing the range occupied by that singing group. Singing group range centroid is indicated by a black circle.

small and separate merged into larger groups), mainly based on the quality of the habitat between the observations.

In total we formed 277 singing groups, each with a unique identification code (ID), centroid coordinates, region (REGION, seven in total) and the municipality (MUNICIPALITY, 65 in total).

For each singing group we counted the annual number of territories (TERRI). This information is occasionally missing for certain years or groups due to irregular visits or addition of new groups. In total, the data consists of 1474 annual territory mappings of singing groups.

Habitat and climate data

Habitat variables were defined for each singing group area. From the Finnish topographic database (National Land Survey of Finland 2023) we measured the length of roads, ditches, main drains and riverbanks (in metres) and counted the number of buildings. We used data from years 2005, 2010 and 2016 to cover the years 2000–2007, 2008–2012

and 2013–2018, respectively. We then divided each of these measures by the area of the singing group to form a variable describing the density of each small-scale element (ROAD, STREAM, RIVER, BUILD).

We calculated the total area of crop species grown within each singing group by combining data from the Finnish land and crop parcel registers (Finnish Food Authority 2023). For years 2000–2016, the precise locations of multiple crop plants within a field parcel were unspecified. In such cases we estimated the areas based on their relative proportions within the field parcel. Missing crop data was completed from field notes or classified as 'unknown species'.

We classified crop species into ten crop types based on their plant type or growth form: spring cereals (proportion of all observed crop types 0.54), grasses (0.26), winter cereals (0.06), oil plants (0.06), open-ground vegetables (0.03), legumes (0.02), herbs (0.01), unknown species (0.01), fruits and berries (0.005) and bioenergy crops (mainly reed canary grass, 0.003). Based on the proportions of crop types, we calculated a Shannon–Wiener diversity index of crop types (CROPDIV).

Crop types were further classified into two categories based on the vegetative cover during the start of the ortolan bunting breeding season in early May, which is approximately the start of growing season in Finland. Crop types that provide minimal cover and substantial amounts of bare ground due to tillage practice, were classified as 'bare' (spring cereals, open-ground vegetables, oil plants and legumes), while crop types that provide vegetative cover were classified as 'cover' (grasses and winter cereals, autumn-sown oil-seed rape). We then counted the proportion of 'bare' crop types within each singing group area (BARE).

To assess the interconnectedness of the agricultural landscape surrounding the singing group, we calculated the proportion of agricultural land cover (AGRI) within a 5-km buffer around each singing group centroid, using the Finnish Corine land cover data (Finnish Environment Institute 2023). We used data from years 2000, 2006, 2012 and 2018 to cover the years 2000–2003, 2004–2009, 2010–2015 and 2016–2018, respectively.

To assess the effect of weather of the past breeding season to the observed population growth, we calculated for each singing group the mean daily temperature (TEMP) and precipitation (PREC) of the previous summer (21 May–15 July) from the Finnish meteorological data (Aalto et al. 2016).

Statistical analyses

To focus on the per capita rate of change of ortolan buntings, we limited our data to cases with data from two consecutive years. Then we calculated the number of territories in each singing group during the previous year (TERPRE), and removed those observations, where TERPRE was zero (no territories observed the previous year).

These limitations reduced the number of observations (pairs of two consecutive annual territory counts of singing groups) to 678 and the number of individual singing groups to 238. The number of consecutive visits per singing group varied from 1 to 13 (mean 2.8) and the number of territories per

singing group from 0 to 26 (mean 4.25). Singing group areas ranged from 0.19 to 2.98 km² (mean 1.00 km², SD = 0.73). The spatial and temporal extent of the data remained approximately the same after the data limitations. However, from central Finland and north Karelia only three and one observations, respectively, remained, both from single singing group.

To model the change in number of ortolan bunting territories per singing group, we applied generalized linear mixed models with logarithmic link-functions, in which the number of territories (TERRI) constituted the response variable, and the natural logarithm of the number of territories in previous year (ln.TERPRE) the offset. Thus, all results of the fixed and random effects concern the population per capita rate of change (here defined as N_{t+1}/N_t or TERRI/TERPRE), through an exponential function, rather than the response variable (population size; N_{t+1}) per se. For example, the habitat covariates could be described as having linear effects on the logarithmic population growth rate $\ln(N_{t+1}/N_t)$, which is a common way to model environmental effects (Ruokolainen et al. 2009).

We performed model selection based on the simplest set of fixed effects, with variable REGION as the only fixed effect, to determine the most parsimonious approach for describing randomness, i.e. the random effect structure and error distribution – to be further used for studying the drivers of the decline as fixed effects. We compared 24 different models (Supporting information for full list of models), each including REGION as a fixed effect and number of territories in previous year (TERPRE) as a log-transformed offset, and either 1) no random effect (i.e. resulting in a GLM rather than a GLMM), 2) ID as random effect, 3) MUNICIPALITY as random effect, 4) ID nested within MUNICIPALITY as random effect, or 5–7) the previous four options with the addition of observation YEAR (factor) as random effect. These eight model combinations were evaluated using three error distributions all of which showed different dispersion patterns or relationships between the mean and the variance: 1) Poisson (presumes equidispersion; mean = variance), 2) negative binomial (modelling overdispersion) and 3) Conway–Maxwell–Poisson (COM-Poisson; Shmueli et al. 2005, accommodates both over- and underdispersion). As singing groups were sampled multiple times, we tested mixed models with singing group as a random intercept to account for dependency among observations within the same singing group. Including municipality as random intercept controls for possible spatial correlation in the average rate of change between singing groups located near to each other. Including year as random intercept controls for possible temporal correlation in the average rate of change between years close to each other. We used restricted maximum likelihood estimation (REML) to acquire unbiased estimators for the variance terms.

We ranked the candidate models using the Akaike information criterion with a correction for small sample size (AIC$_c$) to evaluate their relative fit with data (Burnham and Anderson 2002) and chose the model structure with the lowest AIC$_c$ value for further analysis of fixed effects.

Using the selected random structure, we studied which habitat variables explain the rate of change in the number of territories with 16 nested models varying in their fixed effects only. Each model included REGION as a fixed effect and TERPRE as a log-transformed offset variable. Additionally, the models contained all the possible combinations of the following groups of variables: 1) weather (TEMP and PREC), 2) crop (CROPDIV and BARE), 3) small-scale structural element (ROAD, STREAM, RIVER and BUILD) and 4) landscape (AGRI) variables (Table 1 for full list of models). Model selection was performed using maximum likelihood estimation, and the candidate models were ranked using the AIC$_c$. If multiple models had ΔAIC$_c$ < 2, they were all selected for model averaging. All continuous variables were standardized before running the models.

Lastly, we tested the final averaged model for any remaining spatial autocorrelation. We computed the Dunn–Smyth residuals based on Poisson distribution for each observation. We aggregated the data by calculating the mean residuals from all observations belonging to the same singing group. These mean residuals were then 'back scaled' so that the variance was the same for all singing groups, even though the number of observations contributing to the mean varied. This was done by multiplying the mean residual by the squared number of observations used for calculating the mean. Using this singing group specific (scaled) residual, we then tested for spatial autocorrelation by computing the Moran's I statistics. We found no evidence of remaining spatial autocorrelation (Moran's I = 0.001; p = 0.78).

All statistical analyses were performed in the R program, ver. 4.3.1 (www.r-project.org). Models were fitted with 'glmTMB' package (Brooks et al. 2017), and model selection and model averaging were conducted with the 'MuMln' package (Bárton 2023).

Results

Among the 24 models of random effect structure, the model with YEAR as the only random effect and COM-Poisson error distribution was selected as the most parsimonious one (Supporting information).

From the 16 alternative fixed effects models (all including the permanent variable REGION), the three models with the lowest AIC$_c$ values included the landscape variable AGRI and the crop variables (CROPDIV and BARE), together or separately (Table 1). The full averaged coefficient estimates from these three models are presented in Fig. 3.

Crop type diversity (CROPDIV), proportion of bare ground (BARE) and the proportion of farmland within the landscape (AGRI) were, as expected, positively associated with higher per capita rates of change (Fig. 4). The full averaged coefficient estimates for CROPDIV, BARE and AGRI were 0.03, 95% CI [−0.03, 0.10], 0.01 [−0.03, 0.06] and 0.05 [−0.02, 0.11], respectively. However, in all of them, the estimates did not differ from zero (Fig. 3), meaning that the associations were weak. Compared with the north Ostrobothnia region, all the other regions had lower rates of change (Fig. 5). In north Ostrobothnia the rates of change

Table 1. Ranking of AIC_c values of 16 competing models, with different sets of explanatory variables for the per capita rate of change between two consecutive years. The models build on a null model with log link function and COM-Poisson error, where the number of territories is (technically) the response variable, explained with region and an offset variable, which is the natural logarithm of the number of territories previous year (i.e. R-syntax for the formula: TERRI ~ 0 + REGION + offset(log(TERPRE))). The column 'Additional explanatory variables' describes which other fixed effects variables are included. 'K' is the number of estimated parameters, 'logLik' the log-likelihood, 'AIC_c' the Akaike information criterion corrected for small sample size, 'ΔAIC_c' the difference in AIC_c compared with the most parsimonious model, 'w' is the Akaike weight, and pseudoR^2 is the conditional coefficient of determination.

Additional explanatory variables	K	logLik	AIC_c	ΔAIC_c	w	pseudoR^2
AGRI + CROPDIV + BARE	12	−1346.22	2716.92	0.00	0.31	0.025
AGRI	10	−1348.41	2717.15	0.23	0.28	0.022
CROPDIV + BARE	11	−1348.15	2718.70	1.78	0.13	0.022
none	9	−1350.42	2719.11	2.19	0.10	0.019
AGRI + CROPDIV + BARE + TEMP + PREC	14	−1345.86	2720.36	3.45	0.06	0.027
AGRI + TEMP + PREC	12	−1348.10	2720.68	3.76	0.05	0.024
CROPDIV + BARE + TEMP + PREC	13	−1347.89	2722.32	5.40	0.02	0.023
TEMP + PREC	11	−1350.19	2722.78	5.86	0.02	0.020
BUILD + ROAD + STREAM + RIVER + AGRI + CROPDIV + BARE	16	−1345.12	2723.07	6.15	0.01	0.026
BUILD + ROAD + STREAM + RIVER + CROPDIV + BARE	15	−1346.81	2724.34	7.42	0.01	0.023
BUILD + ROAD + STREAM + RIVER + CROPDIV + BARE	15	−1346.81	2724.34	7.42	0.01	0.023
BUILD + ROAD + STREAM + RIVER	13	−1349.20	2724.94	8.02	0.01	0.020
BUILD + ROAD + STREAM + RIVER + AGRI + CROPDIV + BARE + TEMP + PREC	18	−1344.77	2,726.57	9.66	0.00	0.028
BUILD + ROAD + STREAM + RIVER + AGRI + TEMP + PREC	16	−1347.12	2727.07	10.15	0.00	0.025
BUILD + ROAD + STREAM + RIVER + CROPDIV + BARE + TEMP + PREC	17	−1346.56	2728.05	11.13	0.00	0.025
BUILD + ROAD + STREAM + RIVER + TEMP + PREC	15	−1348.98	2728.69	11.77	0.00	0.021

were on average only slightly above one, indicating stability or a minor increase in the population, whereas for the rest of the regions the rates of change were on average below one, indicating a decline in the population.

In Finland, the average logarithmic rate of population growth was –0.22 (SE = 0.05), excluding central Finland and north Karelia which had low sample sizes.

All analyses were performed to a data set excluding the two regions with only one singing group: north Karelia and central Finland, but the results remained the same (Supporting information).

Discussion

Importance of crop type diversity and bare ground

Our study revealed a modest positive association between the per capita rate of change of ortolan bunting population and the two crop variables: crop type diversity and proportion of bare ground. Ground-feeding birds, like the ortolan bunting, may struggle in finding food (insects, other arthropods etc.) within dense vegetation (Schifferli 2001), while they need taller or denser vegetation safe nest sites. Monoculture rarely provides suitable vegetation structure for both nesting and foraging throughout the breeding season. Therefore, a mosaic of diverse crop plants with varying sowing times, sward heights and densities, along with patches of bare ground, may better support the ortolan bunting, mitigating reproductive costs and enhancing breeding success and chick survival. This complementary way of the ortolan bunting to use its habitat has been described also in, for example shorebirds (Jackson et al. 2019) and wild bees (Mandelik et al. 2012). Our results demonstrate the importance of, and the need to manage heterogeneity in habitat structure, both in time and space (Benton et al. 2003, Hiron et al. 2015, Galpern et al. 2020). Furthermore, high crop diversity and bare ground,
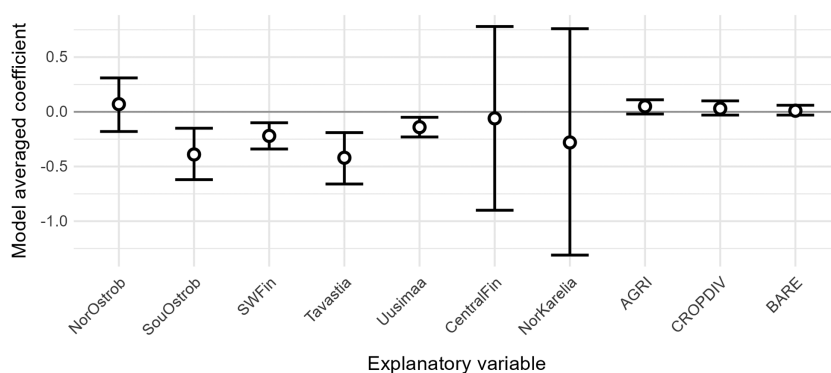

Figure 3. Model-averaged coefficients for variables used to explain factors contributing to the per capita rate of change of ortolan buntings. Coefficients are shown with open circles together with their 95% confidence interval error bars.
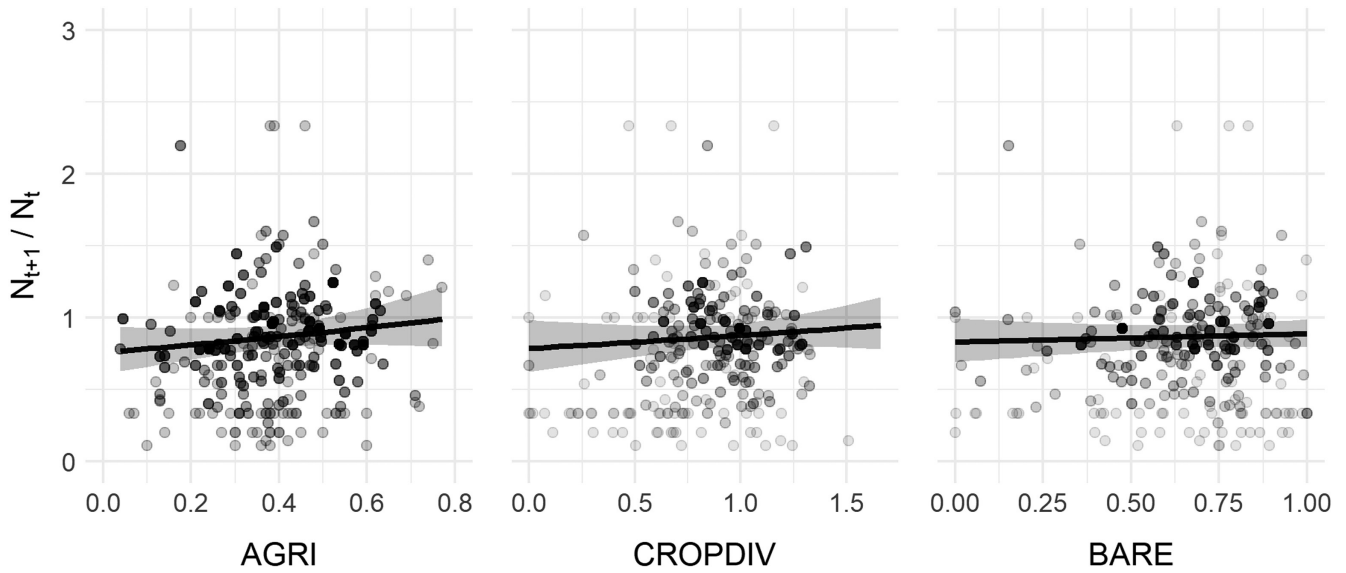
Figure 4. Plot illustrating the predicted effect of the crop plant type diversity (CROPDIV), the proportion of farmland surrounding the singing group (AGRI) and the proportion of bare ground within the singing group's range (BARE) on the population growth rate of ortolan bunting. The black thick line represents the conditional prediction for Uusimaa region, with a 95 % confidence interval around it (grey area), when TERPRE is kept constant at 1. Scattered circles illustrate the distribution of singing group growth rates averaged over time. This averaged data was generated by first adding 0.5 to the territory count, both the current and previous year (TERRI and TERPRE), and then aggregating the data by singing group and counting the average change in population growth rate and the average for each of the three environmental variables. The intensity of the colour of the circle indicates how many times that singing group was visited on consecutive years, i.e. how many observations were available for estimating the growth rate for that singing group (n = 1–13, mean = 2.8).
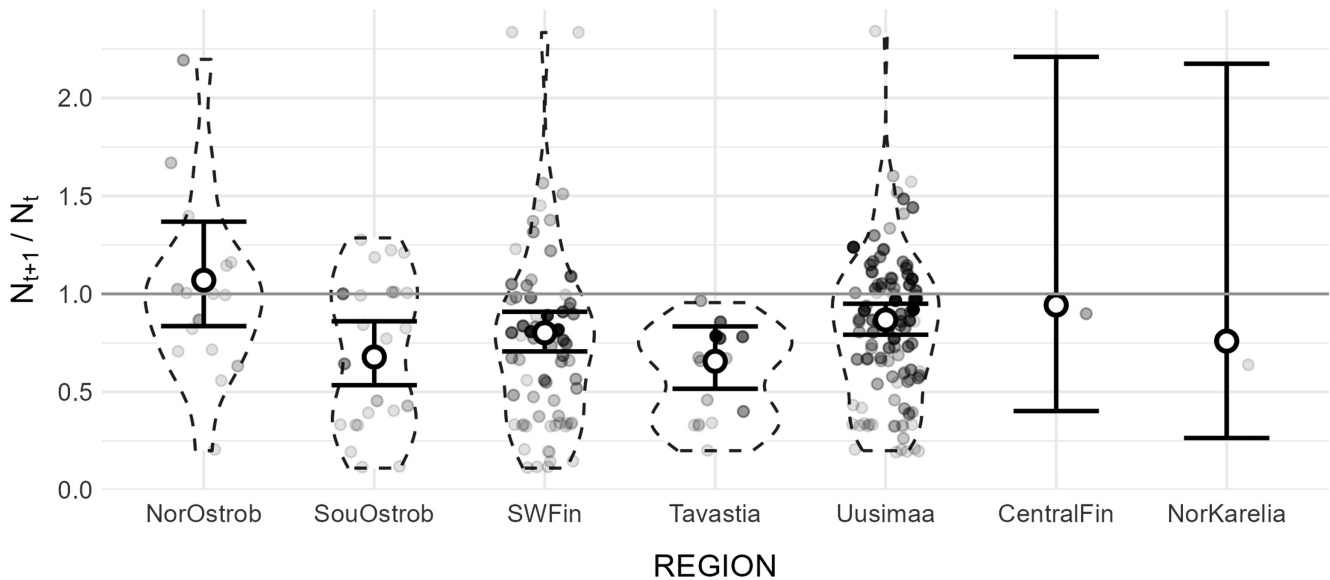

Figure 5. Model predictions of per capita rate of change of ortolan bunting in different regions of the species range in Finland. Model prediction point estimates are shown with black circles together with their 95% confidence intervals error bars. Violin plots and scattered circles illustrate the distribution of singing group growth rates averaged over time. These averaged data were generated by first adding 0.5 to the territory count, both the current and previous year (TERRI and TERPRE), and then aggregating the data by singing group and counting the average change in population growth rate per singing group. The intensity of the colour of the circle indicates how many times that singing group was visited on consecutive years, i.e. how many observations were available for estimating the growth rate for that singing group (n = 1–13, mean = 2.8). Notice that as central Finland and north Karelia only have one singing group each, no statistical inference can be made about the average range of change in these two regions.

are typical for traditional, small-scale farming, suggesting a potential link between agricultural intensification and population decline.

Our findings agree with past results at the territory scale. Berg (2008) found that ortolan buntings preferred habitats with heterogeneous vegetation characterized by patches of bare ground or sparse vegetation mixed with taller vegetation. Also, Vepsäläinen et al. (2005) showed that Finnish ortolan buntings occurred more often on fields not vegetated in spring (e.g. spring cereal or root crops). However, in Italy, Morelli (2012) showed that the occurrence of ortolan buntings was not related to structural heterogeneity, rather the species seemed to be associated with sunflower fields, oats and alfalfa. Nonetheless these crops may provide preferred habitat due to traits that increase areas with bare soil, consistent with our findings.

Importance of interconnected agricultural landscape

We found a slight positive connection between the proportion of farmland surrounding the singing group and the per capita rate of change, suggesting two possible explanations. Firstly, larger and more connected farmland areas tend to be more intensively managed than smaller, more scattered farmlands, which usually include less intensively managed or even abandoned fields. Abandoned fields will eventually have higher and denser vegetation cover, and possibly more predators. The negative effect of dense grassing and afforestation following abandonment of fields has been demonstrated also in other breeding ortolan bunting populations (Deutsch 2007, Leo et al. 2023). Similarly, during their wintering period in Africa, birds prefer semi-open agricultural landscapes (Gremion et al. 2022). Overall, farmland birds seem to be declining due to both agricultural intensification and abandonment (Wretenberg et al. 2006), highlighting the importance of intermediate level of management to benefit not only the ortolan bunting, but also other species (Benton et al. 2003).

Secondly, ortolan buntings are social birds forming singing groups of several males (Cramp and Perrins 1994). In large, connected farmland areas there is more space and suitable habitat for several males to establish territories, attracting additional males and females (Campomizzi et al. 2008). Conversely, small, isolated farmland patches lack this attraction due to fewer or no other birds present. Also, Vepsäläinen (2005) noted the species' aggregated distribution pattern, influenced only partly by habitat quality. The disappearance of group structure might hamper breeding even further. In Norway, male-biased sex ratio due to female-biased natal dispersal away from the small and isolated areas affects mating success. In the Norwegian population, about 50% of all males are unpaired (Dale 2011), whereas in Finland, the same figure was 63% in 2020 (Piha and Seimola 2021). Additionally, adult males show high site fidelity, potentially masking habitat effects as they may maintain singing groups despite habitat deterioration.

Higher rates of change in north Ostrobothnia

Compared with all other regions, north Ostrobothnia showed on average higher per capita rates of change. Several factors might contribute to variance in rates of change between regions. Firstly, north Ostrobothnia boasts a substantial amount of newly established agricultural fields, mainly converted from peatlands. These areas have not yet been under heavy agricultural management practices, such as pesticides or turning of the soil. They often feature exposed mineral soil and natural vegetation with extensive growth of bushes (*Salix* sp.) and young trees (*Betula* sp., *Sorbus* sp., etc.), which offer abundant food resources (field observations). Also, in Norway the ortolan buntings are linked to peatlands; with most populations breeding on raised peat bogs (Dale 2000). On the contrary, regions with higher agricultural intensification, like south-west Finland, showed lower population growth rates, pointing to a potential link between intensification and population decline.

Secondly, farm specialization has been intensive in Finland. Cattle is raised in the east and north, while south has specialized in grains and vegetables (Hiironen and Ettanen 2013). This suggests that in northern and eastern Finland, where large cattle farms almost exclusively grow fodder grass, there is little bare ground available during spring. However, our results did not support this conclusion, perhaps because our study sites located mostly on the grain growing areas in the north Ostrobothnia.

Thirdly, a species' presence in a location may not solely depend on habitat suitability but also on the fact that species had a means of getting there (Storch et al. 2003). The shift of the Finnish ortolan bunting population towards north could result from habitat deterioration in the south, leaving the birds with no other option. However, field observations give little support to this idea. In Finland, there are two distinct singing type populations (dialects): northern and southern. These populations appear to have limited immigration between them (Piha and Seimola 2021). As birds generally learn their songs from one another, the persistence of these song types may indicate limited dispersal (via recruitment), which is likely in the context of a declining population (Laiolo and Tella 2005).

Small-scale landscape characteristics and weather: lack of impact on population growth

Unexpectedly, we found no association between small-scale landscape structures and the per capita rate of change. One explanation to this could be the way we defined these variables. By measuring the density of linear structures such as roads or ditches, we aimed at describing the effect of edge habitats; for example, woody perennial vegetation, such as *Salix* sp. or *Betula* sp., providing an important source of food. However, we could not identify whether the roadside or ditch contained such vegetation. They likely had taller vegetation at times, but every few years the farmers cut down the bushes.

Since we found no association between the rate of change and weather conditions of previous year's breeding season, it seems that other factors are primarily driving the decline. Likewise, Vepsäläinen (2005) did not find a link between weather and ortolan bunting densities.

Conclusions and conservation implications

Based on our results, which are weak but consistent with those of other studies, we suggest implementing conservation measures to enhance crop type diversity. Fields with greater diversity of crop plants often include more bare ground due to diverse plant structures and managing practices. Additionally, we recommend establishing non-crop growing stripes of ploughed bare ground, especially if increasing crop diversity is not feasible. We also recommend targeting these actions to populations of connected farmland landscapes and in northern parts of the species' range, which likely serve as population sources rather than sinks. Further research on the breeding- and population biology of ortolan buntings would be important to determine the causes of decline.

Author contributions

Sirke Piirainen: Conceptualization (supporting); Data curation (lead); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (lead). **Tuomas Seimola:** Conceptualization (equal); Data curation (equal); Writing – review and editing (equal). **Andreas Lindén:** Formal analysis (equal); Writing – review and editing (equal). **Juha Tiainen:** Data curation (equal); Writing – review and editing (supporting). **Markus Piha:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pc866t1wc (Piirainen et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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