

Habitat characteristics and the rate of decline in a threatened farmland bird, the Ortolan Bunting

Sirke Piirainen¹, Markus Piha², Tuomas Seimola², and Andreas Linden²

¹University of Helsinki

²Natural Resources Institute Finland

November 17, 2023

Abstract

Farmland habitats are witnessing steep declines in biodiversity. One rapidly declining farmland species is the Ortolan Bunting. 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 landscape structures, proportion of agricultural area in the landscape, diversity of crop types, proportion of bare ground, and temperature and precipitation of previous breeding season. The only region with a marginally positive growth rate was North Ostrobothnia, where the species often occupies newly established fields. High crop type diversity mitigated the declines by perhaps providing a wide array of feeding, hiding and nesting places. Bare ground benefited Ortolan Buntings by perhaps providing an easy access to food. The last Ortolan Buntings occurred in landscapes dominated by interconnected agricultural land which, we think, reflects the species' sociability and avoidance of forested areas. We suggest that agricultural intensification and the following potential reduction in food availability may be a cause of the decline of Ortolan Bunting. As general conservation measures, such as promoting set-aside land or field margins, have been inadequate, either in effect or in extent of application, it is evident that work remains. 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. Promoting more multi-functional and agro-ecologically managed agricultural landscapes would benefit a wider range of farmland species as well.

TITLE

Habitat characteristics and the rate of decline in a threatened farmland bird, the Ortolan Bunting

ABSTRACT

Farmland habitats are witnessing steep declines in biodiversity. One rapidly declining farmland species is the Ortolan Bunting. 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 landscape structures, proportion of agricultural area in the landscape, diversity of crop types, proportion of bare ground, and temperature and precipitation of previous breeding season.

The only region with a marginally positive growth rate was North Ostrobothnia, where the species often occupies newly established fields. High crop type diversity mitigated the declines by perhaps providing a wide array of feeding, hiding and nesting places. Bare ground benefited Ortolan Buntings by perhaps providing an easy access to food. The last Ortolan Buntings occurred in landscapes dominated by interconnected agricultural land which, we think, reflects the species' sociability and avoidance of forested areas.

We suggest that agricultural intensification and the following potential reduction in food availability may be a cause of the decline of Ortolan Bunting. As general conservation measures, such as promoting set-aside land or field margins, have been inadequate, either in effect or in extent of application, it is evident that work remains. 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. Promoting more multi-functional and agro-ecologically managed agricultural landscapes would benefit a wider range of farmland species as well.

KEY WORDS

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

1. INTRODUCTION

Several farmland bird species in Western Europe are declining rapidly primarily due to the intensification of agricultural practices (Burns et al., 2016; Jerrentrup et al., 2017; Tryjanowski et al., 2011). These practices include for example building sub-surface soil drainage systems, which cause habitat loss and change, increased fertilizer use leading to denser vegetation, fast crop growth and short turn-over rates, increased pesticide and herbicide usage resulting in lower abundance and diversity of food/insects/arthropods, and the specialization and standardization of agriculture, which tends to create homogenous landscapes with large fields of low crop diversity (Schifferli, 2001). The European Union has initiated several schemes with the aim to prevent the loss of biodiversity in agricultural habitats, but these schemes seem to have had limited success, preserving biodiversity only at the local scale and to moderate extent (Gamero et al., 2017; Kleijn et al., 2011).

The Ortolan Bunting, a small Palearctic migratory songbird, is an example of a species experiencing an extreme population decline. It breeds from Spain to Mongolia and from Iran to northern Finland and migrates to spend the winter in sub-Saharan Africa (Jiguet et al., 2019). Across Europe, the species has faced continuous population declines, with a general drop of 88% since 1980 (Jiguet et al., 2016). The status of the species is particularly alarming in Northern Europe, where it is critically endangered (Hyvärinen et al., 2019). In Finland, the decline has been approximately 99% within the past 30 years (Väisänen and Lehtikoinen, 2013), with only 2,600 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).

Understanding the reasons behind such dramatic declines as the one of the Ortolan Bunting can provide highly valuable information on how to manage farmlands in a more biodiversity-friendly way. Numerous threats such as habitat loss and degradation, climate change, and illegal hunting, are believed to explain the declines of Ortolan Buntings (Menz and Arlettaz, 2012). Especially the threats along the flyways have been studied intensively (Jiguet et al., 2016), and recently, the wintering habitats have been under investigation (Gremion et al., 2022).

Survival studies done in Norway and Finland show that Ortolan Buntings may not be suffering exceptionally great losses during their migration or wintering in Africa. In a study done by Nousiainen (2020) during 2013–2019, Finnish male Ortolan Buntings had an apparent annual survival rate of 43.3 % (41.9–58.0 %; in 15 other similarly sized passerine species). Similar, or somewhat higher, survival rates were found in the Norwegian Ortolan Bunting populations (Dale, 2016). Additionally, Nousiainen (2020) found that the survival was equally good throughout all the three main regions where the species occurs in Finland. Based

on this result, the survival of the male Ortolan Buntings is likely not particularly low, and thus does not appear to be the most important factor explaining the declines. In contrast, there were regional differences in population declines, with the steepest declines in southwestern parts of the population, where more than fourth of the population was lost annually (Nousiainen 2020, Piha & Seimola 2021). In summary, although the survival of females and juveniles were not examined in this study, this result already in itself hints that there might be some regionally varying factors regulating breeding success that might, at least partly, explain the dramatic declines in Ortolan Bunting populations. Hence, it seems that important reasons for the declines are to be found within the breeding areas.

The breeding habitat requirements of the Ortolan Bunting have been intensively studied, mainly in the agricultural habitats where the decline is steepest (Menz and Arlettaz, 2012). In general, the Ortolan Bunting has largely varying habitat requirements. In the most southern parts of its current distribution, in the Mediterranean and sub-Mediterranean Europe, Ortolan Bunting breeds in open shrubland and steppe-like habitats, and montane zones up to 2,500 m above sea level. In temperate Europe, it is primarily associated with cultivated land and shrublands in historically burnt habitats (see references in Menz and Arlettaz, 2012). In Nordic countries, the species is present in a range of different breeding environments; not only in farmland habitats, but also in clear cuts and peat production bogs (Dale and Christiansen, 2010; Dale and Olsen, 2002; Vepsäläinen et al., 2007). In Finland, the species is rarely observed in small, fragmented fields within forest dominated landscapes (Piha and Seimola, 2021). Within both natural and agricultural landscapes, 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). The fact that the species becomes often locally common after disturbance, for example after a fire or a clear cut, indicates that the species may behave like a pioneer species, typically colonizing the early stages of vegetation succession (Pons and Clavero, 2010).

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). High crop type diversity seems to be important for the species since the species 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 and moving on the ground than uniformly dense growing crops (Schaub et al., 2010; Schifferli, 2001), 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 have been limited either 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 relationship between changes in the Ortolan Bunting's breeding habitat characteristics and the rate of decline of the species in a multiscale context where both territorial and landscape levels are considered simultaneously. We used an exceptionally large data set which covered approximately the whole Finnish breeding range area and nearly two decades of observations, collected with a comprehensive territorial mapping approach.

Specifically, we studied whether the rates of decline in Ortolan Bunting populations were associated with i) proportion of agricultural land cover within the landscape surrounding the subpopulation (landscape variable), ii) crop plant type diversity and the proportion of bare ground (crop variables), iii) density of roads, ditches, main drains, riverbanks and buildings (small-scale structure variables), or iv) temperature and rainfall from the previous year (weather variables), while also assessing v) potential regional variation in the declines.

We hypothesized that the reduction of small-scale structures, loss of diversity in crop types and reduction in the amount of bare ground have had negative effects on Ortolan Bunting population growth rate. We also expected that population growth rates are more negative in areas with smaller proportion of farmland in the landscape. In addition, we expected that cold and rainy breeding seasons reduced population growth to the

next year.

2. MATERIAL AND METHODS

2.1 Study area

Most of the studied Ortolan Bunting subpopulations, hereafter singing groups, were located along the coast of Finland and in the southern parts of the country, where agriculture in general is concentrated in Finland. Few study sites were in the eastern and Central Finland (Figure 1). The study area represents the northernmost distribution range limit of the species.

2.2. Bird data

The territories of the Ortolan buntings were mapped annually using a two-visit mapping method, which has been shown to be effective and reliable for mapping the species (Tiainen et al., 1985). The visits were made in May and the first half of June. Special attention was paid to simultaneous observations of singing males, to the territory locations, and to accurate estimation of territory numbers in territory concentrations. For each observed territory, its centre coordinates were recorded. In total 4,430 territories were recorded over the 19-year study period, from 2000 to 2018.

2.2.1 Forming singing group units

To form a study unit, we aggregated observations of territories from years 2000–2017 (observations from year 2018 were added in after the forming of singing groups) based on their proximity and surrounding landscape. Territories that were less than 500 metres away from each other, were considered to belong to the same singing group, i.e., subpopulation. Thus, we drew a 250-meter buffer around each territory observation within a singing group, merged the overlapping buffers and interpreted the outline as delineating the area occupied by that singing group (Figure 2). Ortolan Bunting territories have an average radius of about 100–300 meters (Vepsäläinen et al., 2007).

This kind of automatic forming of singing groups based on distance only produced sometimes very large singing groups which, in reality, might have consisted of several smaller groups separated by some natural boundary or other unfavourable matrix, such as a narrow stretch of forest or a busy road. Sometimes separate smaller singing groups were formed, when, in reality, they might have belonged to the same group despite the distance between the observations (or despite the failure to observe individuals between the observations). Therefore, in few cases a spatially very large singing group was divided into two or several smaller ones, or a few small and separate but adjacent singing groups were merged into one large group. When splitting a large group, the area along the split was proportionally divided to the newly formed singing groups. This ensured that a certain habitat area was not covered twice in separate singing groups. These exceptions (splits and merges) were always based on the observer’s perception on the field.

In total we formed 277 singing groups. Each singing group had an individual identification code (ID) and its centroid coordinates were recorded. Additionally, we recorded the region (REGION) and the municipality (MUN) within which a singing group was located (seven regions and 65 municipalities in total).

For each singing group we counted the annual number of territories (TERRI). For some years and some singing groups this information is missing, as not all sites have been visited annually, or because new locations (singing groups) have been added to the monitoring scheme during the study period. In total, the data consists of 1,474 annual territory mappings of singing groups.

2.3 Habitat and climate data

For each singing group area, we defined variables describing the habitat they occupied. From the Finnish topographic database (National Land Survey of Finland, 2023) we counted the length of roads, ditches, main drains and riverbanks (in metres) and the number of buildings within the singing group area. As there are little annual changes in these measures, 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 (AROAD, ASTREAM, ARIVER, ABUILD).

By combining data from the Finnish land and crop parcel registers (Finnish Food Authority, 2023) we counted the total area of crop species grown within a singing group area. For years 2000–2016, in cases where more than one crop species was grown per field parcel, the data were unspecific about the precise location of different crop plants within a field parcel. Therefore, in cases where a field parcel with multiple crop plants was only partly within the singing group area, the areas of crop species were estimated based on their relative proportions within the field parcel. In cases where crop data were untraceable or not available, we completed the data from field notes, when possible, otherwise the crop was classified as “unknown species”.

Based on plant type or growth form we classified crop species into ten crop types: 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). For each singing group area, we then counted the proportions of each of these crop types and based on those, a Shannon–Wiener diversity index of crop types (SHANG).

Crop types were further classified into two groups based on how much vegetative cover the plants form during the start of the Ortolan Bunting breeding season in early May. Crop types which provide only minor cover and leave substantial amounts of bare ground on the field, mainly as a result of the associated ploughing practice, were classified as ‘bare’ (spring cereals, open-ground vegetables, oil plants and legumes), and crop types that provide substantial 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 a singing group area (BARE).

To assess the interconnectedness of the agricultural landscape surrounding the singing group, we created a 5-km buffer around the singing group centroid and calculated the proportion of agricultural land cover (AGRI5) within the buffer using the Finnish Corine land cover data provided by the Finnish Environment Institute (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.

From the Finnish meteorological data (Aalto et al., 2016) we calculated the mean daily temperature (TEMP) and precipitation (PREC) of the previous summer (21. May–15. July).

2.4 Statistical analyses

To focus on the multiplicative population rate of change of Ortolan Buntings, we first delimited our data to only those cases that had data from two consecutive years, i.e., with no gap between annual observations. Then we created a variable describing the number of territories in a singing group during the previous year (TERPRE), and further removed from the data those observations, where TERPRE was zero (no territories observed the previous year).

These limitations reduced the number of observations (annual territory counts of singing groups) to 678. The number of individual singing groups also reduced to 238. The number of consecutive visits (annual territory counts) per singing group varied from 1 to 13 (mean 2.8) and the number of territories per singing group varied from 0 to 26 (mean 4.25). Singing group areas ranged from 0.19 to 2.98 km² (average 1 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 Carelia only three and one observations, respectively, remained and they were, in both cases, from only one 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 the statistical analysis we first did model selection based on the model with the simplest set of fixed effects, 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 12 different models, each with only the categorical variable region (REGION) as a fixed effect and number of territories in previous year (TERPRE)

as a log-transformed offset, and either i) no random effect (i.e., resulting in a GLM rather than a GLMM), ii) ID as random effect, iii) MUN as random effect, or iv) ID nested within MUN as random effect. These four model combinations were evaluated using three error distributions: i) Poisson, ii) COM-Poisson and iii) negative binomial; all of which show different dispersion patterns or relationships between the mean and the variance. Option ii) accommodates both over- and underdispersion, while option iii) can model overdispersion only. As singing groups were sampled multiple times, we wanted to test applying a mixed model in which singing group is used as random intercept, as this models a dependency structure among observations (variation in the average rates of change) from the same singing group. Including municipality as random intercept controls for possible spatial correlation in the average rate of change between singing groups which are located near to each other. In the fitting of the models, we used restricted maximum likelihood estimation (REML) in order to acquire estimators for the variance terms which are not biased.

We ranked the candidate models by the Akaike information criterion with a correction for small sample sizes (AICc) to evaluate their relative fit with data (Burnham and Anderson, 2002) and chose the model with the lowest AICc value as the best model structure for further analysis of fixed effects.

Based on the selected random structure (see Table S1 in Supplementary material), we studied which habitat variables explain the decrease in number of Ortolan Bunting territories within a singing group, by creating 16 nested models varying in their fixed effects only. All models included region (REGION) as fixed effect and number of previous year territories (TERPRE) as a log-transformed offset variable. In addition to these, the models contained all the possible combinations of the following groups of variables: i) weather (TEMP and PREC), ii) crop (SHANG and BARE), iii) small-scale structural element (AROAD, ASTREAM, ARIVER and ABUILD) and iv) landscape (AGRI5) variables (see Table 1 for full list of models). In the model selection for different fixed effects models, we used maximum likelihood estimation. Again, we ranked the candidate models by the Akaike information criterion with a correction for small sample sizes (AICc) to evaluate their relative fit with data (Burnham and Anderson, 2002) and chose the model with the lowest AICc value as the best model. Prior to running the model, all continuous variables AGRI5, PREC, TEMP, SHANG, BARE, ABUILD, ARIVER, ASTREAM and AROAD were scaled by subtracting the mean and dividing with the standard deviation.

All statistical analyses were done in the programming environment R program, version 4.3.1 (R Core Team, 2023). Models were fitted with glmmTMB-package (Brooks et al., 2017) and model selection was conducted with the MuMin-package (Barton, 2023).

3. RESULTS

Regarding the 12 models of random effect structure, the model with no random effects structure and COM-Poisson error distribution was selected as the most parsimonious one (Table S1 in Supplementary material).

Regarding the 16 alternatives fixed effects models (all including the permanent variable REGION), the model with the lowest AICc included also AGRI5 and crop variables, SHANG and BARE (Table 1).

Compared with the North Ostrobothnia region, which showed stable or slightly positive population growth, all other regions were associated with strongly negative rates of population change (Table 2, Figure 3). Crop type diversity (SHANG) was, as expected, associated with positive rates of change (Table 2, Figure 4). Considering the proportion of farmland within the landscape surrounding the singing group (AGRI5) and the proportion of bare ground within the singing group's range (BARE), the coefficient point estimates show a positive association with the rate of change but do not differ clearly from zero (Table 2, Figure 4).

In the whole of Finland, the average logarithmic rate of population growth was -0.21 ($SE = 0.04$; excluding Central Finland and North Carelia which had so low sample sizes).

4. DISCUSSION

Our results showed that the multiplicative population rate of change of Ortolan Buntings within the study period from 2000 to 2018 was positively associated with greater crop type diversity and with higher proportion

of bare ground within a singing group's range. Also, the proportion of farmland surrounding the singing group had a positive association with the rate of population change. Notably, the mean rate of population growth was positive only in the North Ostrobothnia region, while all other regions showed negative growth rates.

4.1 Importance of crop type diversity and bare ground

Our study revealed a positive association between Ortolan Bunting population growth rate and the two crop variables, crop type diversity and proportion of bare ground. Albeit the association was rather weak for bare ground. High crop type diversity at the territory scale may emerge as a critical factor, as single crop types rarely offer suitable vegetation structure for both nesting and foraging throughout the breeding season. Ground-feeding birds, like the Ortolan Bunting, may face challenges in finding food (insects, arthropods etc.) within impenetrable, tall and dense vegetation (Schifferli, 2001) usually associated with intensive farming. On the other hand, various taller or denser vegetation is needed for providing safe nest sites. Therefore, a mosaic of diverse crop plants of different sowing times, sward heights and densities as well as patches of bare ground may better support the Ortolan Bunting which may otherwise suffer from higher costs of reproduction, reduced breeding success and chick survival.

The importance of these crop variables has been found in earlier habitat preference studies as well. In central Sweden, Ortolan Buntings were found to prefer habitats which had heterogeneous ground vegetation characterized by patches with bare ground, or at least sparse ground vegetation, intermixed with patches with taller vegetation (Berg, 2008). In Finland, in the Tavastia region, Vepsäläinen et al. (2005) showed that the area of field growing spring cereal, root crops, etc. (i.e., field not covered in springtime) had a positive effect on the occurrence of the Ortolan Bunting, although they witnessed a population crash happening in spite of an increase in the area of non-covered field. Santana et al. (2017) however, found that in open Mediterranean farmland, when considering bird species richness, it was more important what crops were grown than their diversity or spatial configuration. Also Morelli (2012) showed that the occurrence of Central Italian Ortolan Buntings was not clearly related to structural heterogeneity, rather the species seemed to be associated with sunflower fields, oats and alfalfa. Yet, the authors concluded that these crop types may be preferred because of certain structural characteristics that may increase space with bare soil, which would be consistent with our findings.

Climate change might affect, now and in the future, the choice between grains that are sown in the spring or in the autumn. If farmers choose to grow more autumn sown grains, the proportion of bare ground in the spring, at the time of feeding the nestlings, will reduce in the future. This change will most likely affect Ortolan Buntings negatively, starting from the southwestern populations which occupy areas that are specialized in growing grains. Similarly, the increasing popularity of direct sowing techniques might be reducing the amount of ploughed field areas i.e., bare ground, affecting Ortolan Buntings negatively.

4.2 Importance of interconnected agricultural landscape

Our findings revealed a weak positive connection between the proportion of farmland surrounding the singing groups and the population growth rate. Indeed, in Finland, we see that Ortolan Buntings are still surviving in singing groups located in landscapes that are characterized by interconnected agricultural areas.

We propose two explanations for this result. Firstly, large and interconnected farmland areas tend to be more intensively managed than smaller, more scattered farmlands which usually include less intensively managed or even abandoned fields. In Germany, in the Wendland region, the Ortolan Bunting population was growing at the turn of the 21st century (approx. 1995–2007). This increase was connected with a major change in land use: a notable proportion of grassland was converted to arable land (Deutsch, 2007). Abandoned arable land will eventually have higher and denser vegetation cover, and possibly more predators, which will be unfavourable for Ortolan Buntings. In Italy, the dense afforestation and grassing after the abandonment of pastoral and agricultural activities are hypothesized to be the causes of Ortolan Bunting extinctions in the hills of Brescia (Leo et al., 2023). Also, in Sweden and England farmland birds are declining possibly due to both agricultural intensification and abandonment (Wretenberg et al., 2006). Also at its wintering grounds, the Ortolan Bunting seems to prefer extensively managed, structured and semi-open agricultural landscapes

(Gremion et al., 2022). It seems evident, that an intermediate level of management benefits the Ortolan Buntings by providing a suitable set of habitat characteristics.

Secondly, Ortolan Buntings are social birds that form singing groups of several males (Cramp and Perrins, 1994). Therefore the species shows an aggregated distribution pattern, one which is only partly determined by habitat structure and quality (Vepsäläinen et al., 2005). In large, interconnected farmland areas there is more space and suitable habitat for several singing males to establish territories. These males then, in turn, can attract more singing males, and eventually also females to the same area. A smaller, isolated farmland patch of otherwise ideal habitat might not be as attractive to the species, because it has a lower potential for formation of a new singing group. The disappearance of group structure in declining populations might hamper breeding even further. In Norway, the small Ortolan Bunting population has a strongly male-biased adult sex ratio due to female-biased natal dispersal away from the small and isolated distribution area. This skew logically affects the pairing success of males. In the Norwegian population, about half of all males are unpaired (Dale, 2011). In Finland, less than 70% of Ortolan males were paired in an inventory study (Piha and Seimola, 2021). If females disperse away from good but fragmented habitats, without finding better breeding sites or companions elsewhere, small local population might be heading to extinction slowly and irrespective of whatever conservation measures are made locally. The only measure that can help in this situation would be the rapid habitat restoration in the matrix between existing habitat fragments (Dale, 2001). Another, in this case potentially disadvantageous, aspect of sociability, is the strong site fidelity of adult Ortolan Bunting males. Adult males may maintain singing groups despite the habitat transforming to suboptimal for breeding. Site fidelity might hence further mask the results related to habitat characteristics.

In summary, at the landscape level, large and interconnected farmland areas represent open and sufficiently managed areas, possibly attracting conspecifics, and might therefore function as an ecological filter which can influence the preference for certain habitat characteristics. Otherwise good breeding sites might be neglected if they do not occur within interconnected farmland landscapes.

4.3 Positive growth rates only in North Ostrobothnia

Among all the regions, only North Ostrobothnia showed positive population growth rates, while South Ostrobothnia, Tavastia, South-West Finland, North Carelia, Uusimaa and Central Finland showed negative population growth rates.

Several factors might contribute to the observed variance in growth rates 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. Food seems to be plenty during the feeding period along the stretches of land between the peat extraction fields where willows and birches are growing (field observations).

Secondly, the specialization of farms has been intensive in Finland during the last decades, namely eastern and northern parts of the country are mainly specialized in cattle farming and southern parts in grains and vegetables (Hiironen and Ettanen, 2013). For example, in eastern Finland large farmland areas almost exclusively grow fodder grass hence leaving negligible amount of bare ground for the birds during spring.

Thirdly, concerning species distribution, it is important to consider that the presence of species in a particular location may not solely be due to the suitability of the habitat but also influenced by the fact that species had a means of getting there (spatial aspects of population dynamics, metapopulation dynamics) (Storch et al., 2003). The fact that the Finnish Ortolan Bunting population has declined less in the north and the resulting shift towards north could be a mere result of the deterioration of the southern habitats and the fact that the birds have no other direction to go to. However, field observations do not support this wholeheartedly. In Finland, there are two easily distinguishable singing type populations (dialects) in Finland, the northern and the southern, which are geographically isolated, and seem to be disconnected from each other without any significant immigration between populations (Piha & 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.

Research on the breeding- and population biology of Ortolan Buntings in different regions of Finland would elucidate whether the breeding of the species is failing and the causes for it, and which regions currently act as sources or sinks. Although, this research might already come too late as the Allee effect often occurring in extremely small populations, might impair deductions from such investigations. The fast decline of Ortolan Buntings has continued after the study period, in all regions of Finland (Piha and Seimola, 2021).

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

Surprisingly, small-scale landscape structures did not significantly influence population growth rate in this study. One explanation to this could be the way we formed these variables. By measuring the density of linear structures such as roads, main drainage ditches and riversides, we aimed at quantifying the potentially beneficial effect of edge habitats; for example, woody perennial vegetation, such as *Salix* sp. or *Betula* sp., providing an important source of larvae and insects to feed the nestlings. However, our variables lacked the information whether the roadside or drainage ditch had any such vegetation. Most likely they had at least some taller vegetation most of the time, but every few years the farmers tend to cut down the bushes along their driveways. It is possible that crop type diversity (SHANG) served as an indirect indicator of smaller average field plot size thus suggesting a greater availability of important edge habitat (ditches, field margins) for nesting.

Concerning the weather variables, likewise, Vepsäläinen (2005) did not find a link between weather conditions of previous year's breeding season and Ortolan Bunting densities. These results suggest that other variables are primarily driving the Ortolan Bunting declines.

4.5. Potential role of agricultural intensification in the decline of Ortolan Bunting

Our results show the importance of specific habitat characteristics such as high crop type diversity and availability of bare ground for the Ortolan Buntings. These preferred habitat characteristics are more typical for traditional, small-scale farming. The results also highlight regional variations. Notably, regions with higher agricultural intensification, like South-West Finland, showed lower population growth rates, suggesting a potential link between intensification and population decline. The fields occupied by Ortolan Buntings in North Ostrobothnia are usually rather new fields and have thus not been under intensive agricultural management as long as the fields occupied by Ortolan Buntings in South-West Finland have.

Agricultural intensification may have detrimental effects on biodiversity through several means. Concerning the Ortolan Bunting, reductions in prey availability or accessibility due to habitat deterioration on the breeding grounds could be one of the main reasons behind the negative population growth rate of the species. Also, the role of nest predators might have changed due to habitat deterioration caused by agricultural intensification. Habitat change might have forced birds to nest in unsafe habitat types or reduced availability of alternative food sources may have caused generalist predators to change their diets (Evans, 2004). Krüger et al. (2018) showed that the Raccoon Dog (*Nyctereutes procyonoides*) is a potential new mammalian nest predator successfully invading agricultural habitats in Finland. The Raccoon Dog has colonized the country within the past 70 years, starting from the Southeast Finland and now has a distribution which covers most of Finland, except the northernmost parts (Kauhala and Kowalczyk, 2011). However, the densities of Raccoon Dogs are not yet high in the North Ostrobothnia region (Natural Resources Institute Finland, 2022), which could partly explain the higher growth rates of Ortolan Bunting there. Another, potentially also very damaging, predator is the feral cat which probably has an equal effect in all regions. The impact of increasing effectiveness of plant protectants (pesticides, herbicides, insecticides etc.) on the breeding and survival of Ortolan Buntings also remains unknown. Eng et al. (2019) studied the effect of neonicotinoids on migrating White-crowned Sparrows. They found that ingestion of imidacloprid by the birds during migratory stopover caused a rapid reduction in food consumption, mass and fat, and delayed their departure.

In summary, although our study did not directly investigate the relationship between the level of intensity

of agricultural practices and the population growth rate of Ortolan Bunting, our results, however, suggest a potential adverse impact of agricultural intensification on the decline of this species.

5. CONCLUSIONS AND CONSERVATION IMPLICATIONS

Current conservation efforts in farmland areas seem to be ineffective in mitigating the negative effects of agricultural intensification on bird populations. Measures taken so far might simply be too light to influence declining farmland birds. At present, it is often unclear whether current conservation measures have beneficial impacts at all or whether the measures are just inadequate, either at the local scale (too narrow field margins for example) or at the wider scale in which they are applied (too few farms applying the measures).

To conserve the Ortolan Bunting there clearly is a simultaneous need to avoid abandonment of agricultural areas, and to promote “de-intensification” of agricultural practices. This general recommendation would benefit also many other threatened farmland species. However, in the case of this very rapidly declining species, it is evident that more precise and finely targeted conservation actions need to be taken urgently at the remaining and still (somewhat) viable singing group locations.

Based on our results, we recommend applying conservation measures which increase the diversity of crop types. Often a field with a greater diversity of crop plant types also includes more bare ground as a result of various plant structures and related managing practices. Alternatively, if increasing diversity is not feasible, or additionally, we recommend establishing non-crop growing stripes of ploughed bare ground. We also recommend targeting these actions to populations living in interconnected farmland landscapes and in northern parts of the species’ distribution range as it is more likely that these populations act as sources, rather than sinks, of population growth.

In general, we agree with several researchers stating that we need more multi-functional, mixed, agro-ecologically managed agricultural landscapes that promote agricultural yield, biodiversity, and ecosystem services to conserve biodiversity in farmlands (Baudron et al., 2019; Tscharntke et al., 2012; Wilson et al., 1997).

REFERENCES

- Aalto, J., Pirinen, P., Jylhä, K., 2016. New gridded daily climatology of Finland: Permutation-based uncertainty estimates and temporal trends in climate. *J. Geophys. Res. Atmospheres* 121, 3807–3823. <https://doi.org/10.1002/2015JD024651>
- Bárton, K., 2023. MuMIn: Multi-model inference. R-package version 1.47.5 [WWW Document]. URL <https://cran.r-project.org/package=MuMIn> (accessed 11.3.23).
- Baudron, F., Schultner, J., Duriaux, J.-Y., Gergel, S.E., Sunderland, T., 2019. Agriculturally productive yet biodiverse: human benefits and conservation values along a forest-agriculture gradient in Southern Ethiopia. *Landsc. Ecol.* 34, 341–356. <https://doi.org/10.1007/s10980-019-00770-6>
- Berg, Å., 2008. Habitat selection and reproductive success of Ortolan Buntings *Emberiza hortulana* on farmland in central Sweden – the importance of habitat heterogeneity. *Ibis* 150, 565–573. <https://doi.org/10.1111/j.1474-919X.2008.00825.x>
- Brooks, M., E., Kristensen, K., van Benthem, K., J., Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* 9, 378. <https://doi.org/10.32614/RJ-2017-066>
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Burns, F., Eaton, M.A., Barlow, K.E., Beckmann, B.C., Brereton, T., Brooks, D.R., Brown, P.M.J., Fulaij, N.A., Gent, T., Henderson, I., Noble, D.G., Parsons, M., Powney, G.D., Roy, H.E., Stroh, P., Walker, K., Wilkinson, J.W., Wotton, S.R., Gregory, R.D., 2016. Agricultural Management and Climate

- tic Change Are the Major Drivers of Biodiversity Change in the UK. PLoS ONE 11, e0151595. <https://doi.org/10.1371/journal.pone.0151595>
- Cramp, S., Perrins, C.M., 1994. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Vol. 9, Buntings and new world warblers. Oxford University Press, Oxford.
- Dale, S., 2016. Cost of reproduction: a comparison of survival rates of breeding and non-breeding male ortolan buntings. J. Avian Biol. 47, 583–588. <https://doi.org/10.1111/jav.00898>
- Dale, S., 2011. Lifetime patterns of pairing success in male Ortolan Buntings *Emberiza hortulana*. Ibis 153, 573–580. <https://doi.org/10.1111/j.1474-919X.2011.01138.x>
- Dale, S., 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92, 344–356. <https://doi.org/10.1034/j.1600-0706.2001.920217.x>
- Dale, S., Christiansen, P., 2010. Individual flexibility in habitat selection in the ortolan bunting *Emberiza hortulana*. J. Avian Biol. 41, 266–272. <https://doi.org/10.1111/j.1600-048X.2009.04824.x>
- Dale, S., Olsen, B.F.G., 2002. Use of farmland by Ortolan Buntings (*Emberiza hortulana*) nesting on a burned forest area. J. Für Ornithol. 143, 133–144. <https://doi.org/10.1007/BF02465445>
- Deutsch, M., 2007. Der Ortolan *Emberiza hortulana* im Wendland (Niedersachsen) – Bestandszunahme durch Grünlandumbruch und Melioration? Vogelwelt 105–115.
- Eng, M.L., Stutchbury, B.J.M., Morrissey, C.A., 2019. A neonicotinoid insecticide reduces fueling and delays migration in songbirds. Science 365, 1177–1180. <https://doi.org/10.1126/science.aaw9419>
- Evans, K.L., 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146, 1–13. <https://doi.org/10.1111/j.1474-919X.2004.00231.x>
- Finnish Environment Institute, 2023. Corine land cover.
- Finnish Food Authority, 2023. Land parcel register.
- Gamero, A., Brotons, L., Brunner, A., Foppen, R., Fornasari, L., Gregory, R.D., Herrando, S., Hořák, D., Jiguet, F., Kmecl, P., Lehikoinen, A., Lindström, Å., Paquet, J.-Y., Reif, J., Sirkiä, P.M., Škorpilová, J., van Strien, A., Szép, T., Telenský, T., Teufelbauer, N., Trautmann, S., van Turnhout, C.A.M., Vermouzek, Z., Vikstrøm, T., Voříšek, P., 2017. Tracking Progress Toward EU Biodiversity Strategy Targets: EU Policy Effects in Preserving its Common Farmland Birds. Conserv. Lett. 10, 395–402. <https://doi.org/10.1111/conl.12292>
- Gremion, J., Marcacci, G., Mazenauer, J., Sori, T., Kebede, F., Ewnetu, M., Christe, P., Arlettaz, R., Jacot, A., 2022. Habitat preferences of the Ortolan Bunting (*Emberiza hortulana*) in its prime wintering grounds, the cereal-dominated Ethiopian Highlands. Ibis 164, 74–87. <https://doi.org/10.1111/ibi.12992>
- Grützmann, J., Moritz, V., Südbek, P., Wendt, D., 2002. Ortolan (*Emberiza hortulana*) und Grauammer (*Miliaria calandra*) in Niedersachsen: Brutvorkommen, Lebensräume, Rückgang und Schutz. Vogelkd. Berichte Aus Niedersachs. 34, 69–90.
- Hiironen, J., Ettanen, S., 2013. Peltoalueiden tilusrakenne ja sen parantamismahdollisuudet (No. 113), Maanmittauslaitoksen julkaisu. National land survey of Finland.
- Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U.-M., 2019. The 2019 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus.
- Jerrentrup, J.S., Dauber, J., Strohbach, M.W., Mecke, S., Mitschke, A., Ludwig, J., Klimek, S., 2017. Impact of recent changes in agricultural land use on farmland bird trends. Agric. Ecosyst. Environ. 239, 334–341. <https://doi.org/10.1016/j.agee.2017.01.041>

- Jiguet, F., Arlettaz, R., Bauer, H.-G., Belik, V., Copete, J.L., Couzi, L., Czajkowski, M.A., Dale, S., Dombrovski, V., Elts, J., Ferrand, Y., Hargues, R., Kirwan, G.M., Minkevicius, S., Piha, M., Selstam, G., Skierczynski, M., Siblet, J.-P., Sokolov, A., 2016. An update of the European breeding population sizes and trends of the Ortolan Bunting (*Emberiza hortulana*). *Ornis Fenn.* 93, 186–196.
- Jiguet, F., Robert, A., Lorrillière, R., Hobson, K.A., Kardynal, K.J., Arlettaz, R., Bairlein, F., Belik, V., Bernardy, P., Copete, J.L., Czajkowski, M.A., Dale, S., Dombrovski, V., Ducros, D., Efrat, R., Elts, J., Ferrand, Y., Marja, R., Minkevicius, S., Olsson, P., Pérez, M., Piha, M., Raković, M., Schmaljohann, H., Seimola, T., Selstam, G., Siblet, J.-P., Skierczynski, M., Sokolov, A., Sondell, J., Moussy, C., 2019. Unravelling migration connectivity reveals unsustainable hunting of the declining ortolan bunting. *Sci Adv* 5, eaau2642. <https://doi.org/10.1126/sciadv.aau2642>
- Kauhala, K., Kowalczyk, R., 2011. Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. *Curr. Zool.* 57, 584–598. <https://doi.org/10.1093/czoolo/57.5.584>
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tschardtke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends Ecol. Evol.* 26, 474–481. <https://doi.org/10.1016/j.tree.2011.05.009>
- Krüger, H., Väänänen, V.-M., Holopainen, S., Nummi, P., 2018. The new faces of nest predation in agricultural landscapes—a wildlife camera survey with artificial nests. *Eur. J. Wildl. Res.* 64, 76. <https://doi.org/10.1007/s10344-018-1233-7>
- Leo, R., Romanenghi, G., Franchini, D., Gobbini, M., 2023. Spontaneous renaturalization of open ecosystems in the hills of Brescia seen through the bird community. *Riv. Ital. Ornitol.* 93. <https://doi.org/10.4081/rio.2023.667>
- Menz, M.H.M., Arlettaz, R., 2012. The precipitous decline of the ortolan bunting *Emberiza hortulana*: time to build on scientific evidence to inform conservation management. *Oryx* 46, 122–129. <https://doi.org/10.1017/S0030605311000032>
- Morelli, F., 2012. Correlations between landscape features and crop type and the occurrence of the Ortolan Bunting *Emberiza hortulana* in farmlands of Central Italy. *Ornis Fenn.* 89, 264–272.
- Moussy, C., Arlettaz, R., Copete, J.L., Dale, S., Dombrovski, V., Elts, J., Lorrillière, R., Marja, R., Pasquet, E., Piha, M., Seimola, T., Selstam, G., Jiguet, F., 2018. The genetic structure of the European breeding populations of a declining farmland bird, the ortolan bunting (*Emberiza hortulana*), reveals conservation priorities. *Conserv. Genet.* 19, 909–922. <https://doi.org/10.1007/s10592-018-1064-9>
- National Land Survey of Finland, 2023. Topographic Database.
- Natural Resources Institute Finland, 2022. Game bag statistics.
- Nousiainen, I., 2020. Sinne ja takaisin — aikuisten peltosirkkukoiraiden (*Emberiza hortulana* Linnaeus, 1758) elossasäilyvyys Suomessa vuosina 2013–2019 (PhD Thesis). University of Helsinki.
- Piha, M., Seimola, T., 2021. Bird of the year 2020: the Ortolan Bunting - regional population estimates and trends. *Linnut-Vuosik.* 2020, 6–7.
- Pons, P., Clavero, M., 2010. Bird responses to fire severity and time since fire in managed mountain rangelands. *Anim. Conserv.* 13, 294–305. <https://doi.org/10.1111/j.1469-1795.2009.00337.x>
- R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P.F., Santos, J.L., Rotenberry, J.T., Beja, P., 2017. Combined effects of landscape composition and heterogeneity on farmland avian diversity. *Ecol. Evol.* 7, 1212–1223. <https://doi.org/10.1002/ece3.2693>

- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of Bare Ground as a Staple Commodity for Declining Ground-Foraging Insectivorous Farmland Birds. *PLOS ONE* 5, e13115. <https://doi.org/10.1371/journal.pone.0013115>
- Schifferli, L., 2001. Birds Breeding in a Changing Farmland. *Acta Ornithol.* 36, 35–51. <https://doi.org/10.3161/068.036.0112>
- Storch, D., Konvicka, M., Benes, J., Martinková, J., Gaston, K.J., 2003. Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position. *J. Biogeogr.* 30, 1195–1205. <https://doi.org/10.1046/j.1365-2699.2003.00917.x>
- Tiainen, J., Pakkala, T., Piironen, J., Vickholm, M., Virolainen, E., 1985. The changes in the farmland bird community of the municipality of Lammi, southern Finland, during the last five decades. *Lintumies* 20, 30–42.
- Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Tobolka, M., Herzon, I., Goławski, A., Konvička, M., Hromada, M., Jerzak, L., Kujawa, K., Lenda, M., Orłowski, G., Panek, M., Skórka, P., Sparks, T.H., Tworek, S., Wuczyński, A., Żmihorski, M., 2011. Conservation of Farmland Birds Faces Different Challenges in Western and Central-Eastern Europe. *Acta Ornithol.* 46, 1–12. <https://doi.org/10.3161/000164511X589857>
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59. <https://doi.org/10.1016/j.biocon.2012.01.068>
- Väisänen, R.A., Lehtikoinen, A., 2013. Suomen maalinuston pesimäkannan vaihtelut vuosina 1975–2012. *Linnut-Vuosik.* 2012, 62–81.
- Vepsäläinen, V., Pakkala, T., Piha, M., Tiainen, J., 2007. The importance of breeding groups for territory occupancy in a declining population of a farmland passerine bird. *Ann. Zool. Fenn.* 44, 8–19.
- Vepsäläinen, V., Pakkala, T., Piha, M., Tiainen, J., 2005. Population crash of the ortolan bunting *Emberiza hortulana* in agricultural landscapes of southern Finland. *Ann. Zool. Fenn.* 42, 91–107.
- Wilson, J.D., Evans, J., Browne, S.J., King, J.R., 1997. Territory Distribution and Breeding Success of Skylarks *Alauda arvensis* on Organic and Intensive Farmland in Southern England. *J. Appl. Ecol.* 34, 1462–1478. <https://doi.org/10.2307/2405262>
- Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T., Pärt, T., 2006. Population Trends of Farmland Birds in Sweden and England: Similar Trends but Different Patterns of Agricultural Intensification. *J. Appl. Ecol.* 43, 1110–1120. <https://doi.org/10.1111/j.1365-2664.2006.01216.x>

FIGURES AND TABLES

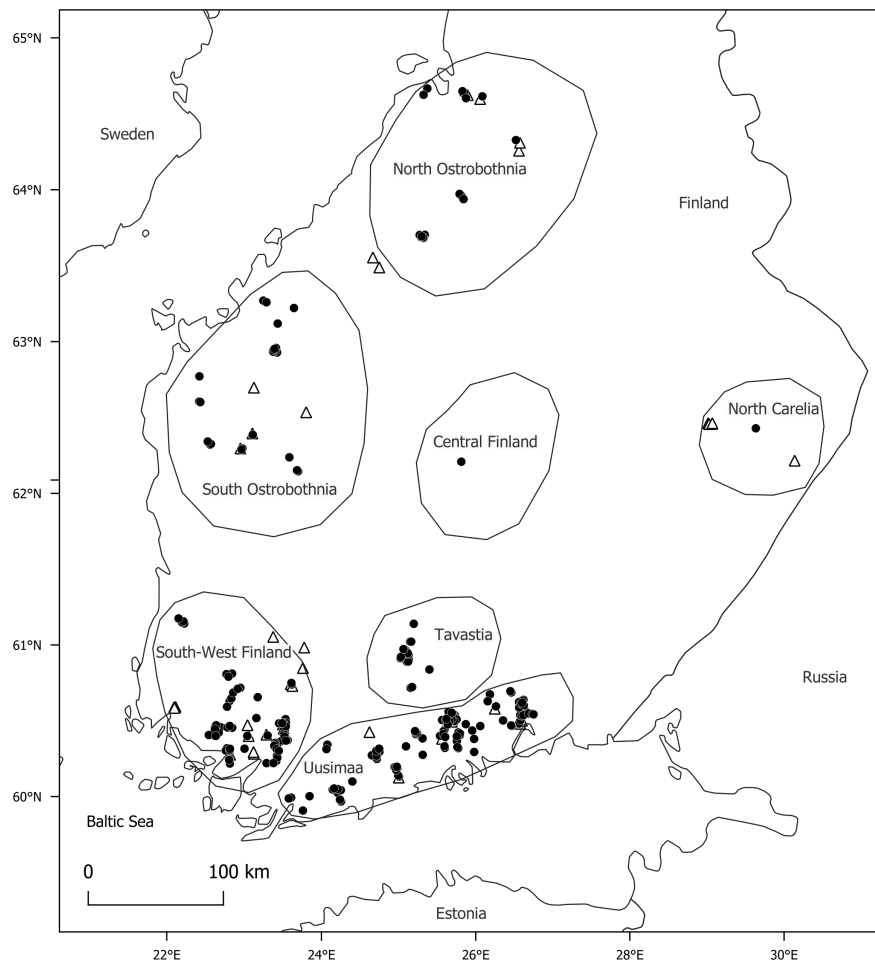


Figure 1. Map showing the centroid coordinates of each Ortolan Bunting singing group (black circles) which had been visited in at least one pair of consecutive years between 2000 and 2018, so that at least one male territory was observed ($n = 238$) in the first of those surveys. Singing groups were classified into seven major regions indicated with black line. Discarded singing groups ($n = 41$), not fulfilling these criteria, are indicated by triangles.

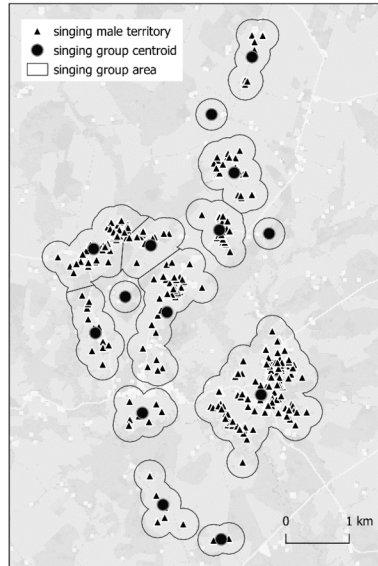


Figure 2. Map depicting separate Ortolan Bunting singing groups which are formed by aggregating close-by territories (observations of individual singing males, black triangles). Singing groups are delineated by a black line representing the range occupied by that singing group. Singing group range centroid is indicated by a black circle.

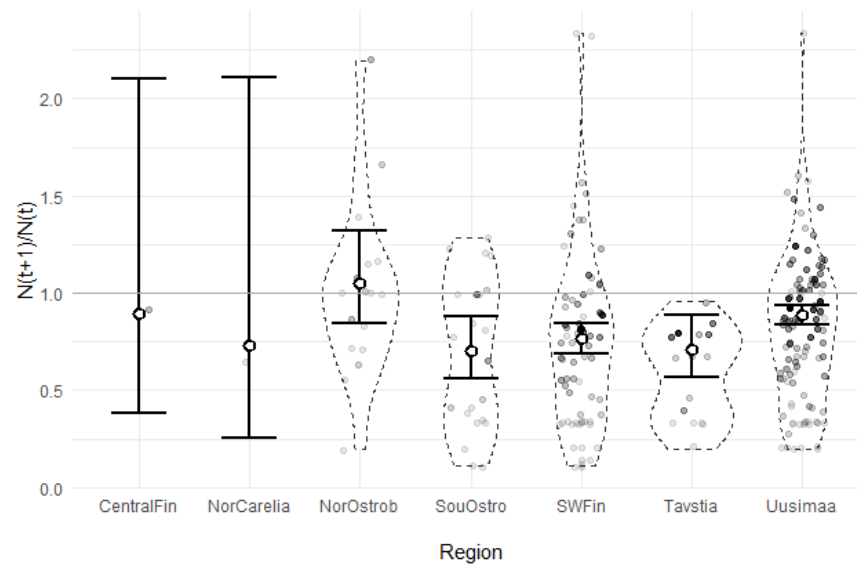


Figure 3 . Model predictions of multiplicative population growth rate of Ortolan Bunting in different regions of the species range in Finland. Model prediction point estimates are shown with black circles together with their 95 % confidence intervals error bars. Violin plots and scattered circles illustrate 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).

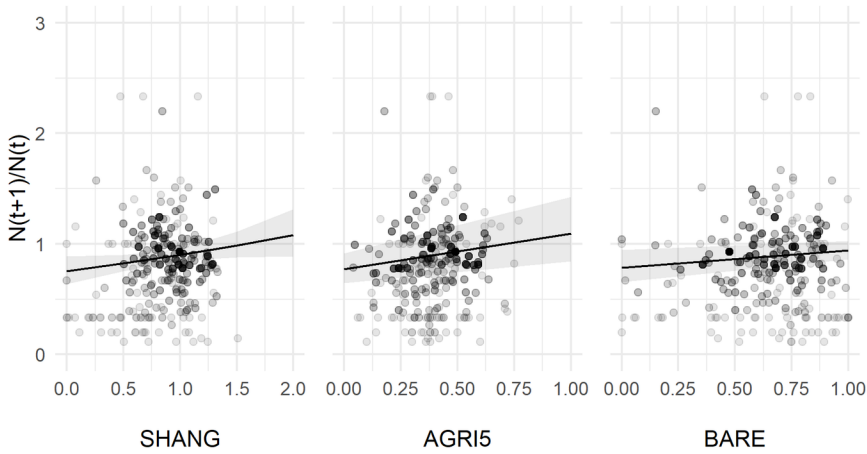


Figure 4. Plot illustrating the predicted effect of the crop plant type diversity (SHANG), the proportion of farmland surrounding the singing group (AGRI5) and the proportion of bare ground within the singing group’s range (BARE) on the population growth rate of Ortolan Bunting. The black thick line 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).

Table 1. Ranking of AIC_c values of 16 competing models, with different sets of explanatory variables for the multiplicative population growth 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: $TERRI \sim 0 + \text{region} + \text{offset}(\log(\text{TERPRE}))$). 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, and “w” is the Akaike weight.

| Additional explanatory variables | K | logLik | AIC_c |
|------------------------------------|----|-----------|---------|
| AGRI5 + SHANG + BARE | 11 | -1,354.50 | 2,73 |
| SHANG + BARE | 10 | -1,355.88 | 2,73 |
| AGRI5 | 9 | -1,357.03 | 2,73 |
| none | 8 | -1,358.39 | 2,73 |
| AGRI5 + SHANG + BARE + TEMP + PREC | 13 | -1,353.99 | 2,73 |
| SHANG + BARE + TEMP + PREC | 12 | -1,355.38 | 2,73 |
| AGRI5 + TEMP + PREC | 11 | -1,356.47 | 2,73 |
| TEMP + PREC | 10 | -1,357.84 | 2,73 |

| Additional explanatory variables | K | logLik | AIC |
|--|----|-----------|------|
| ABUILD + AROAD + ASTREAM + ARIVER + AGRI5 + SHANG + BARE | 15 | -1,352.93 | 2,73 |
| ABUILD + AROAD + ASTREAM + ARIVER + SHANG + BARE | 14 | -1,354.09 | 2,73 |
| ABUILD + AROAD + ASTREAM + ARIVER + SHANG + BARE | 14 | -1,354.09 | 2,73 |
| ABUILD + AROAD + ASTREAM + ARIVER | 12 | -1,356.75 | 2,73 |
| ABUILD + AROAD + ASTREAM + ARIVER + AGRI5 + SHANG + BARE + TEMP + PREC | 17 | -1,352.46 | 2,73 |
| ABUILD + AROAD + ASTREAM + ARIVER + SHANG + BARE + TEMP + PREC | 16 | -1,353.64 | 2,74 |
| ABUILD + AROAD + ASTREAM + ARIVER + AGRI5 + TEMP + PREC | 15 | -1,355.08 | 2,74 |
| ABUILD + AROAD + ASTREAM + ARIVER + TEMP + PREC | 14 | -1,356.23 | 2,74 |

Table 2. A summary table including parameter estimates for the best fitting model used to explain factors contributing to the multiplicative population growth rate of Ortolan Buntings.

| Explanatory variable | Estimate | SE | 95 % CI |
|---------------------------|----------|------|----------------|
| region North Ostrobothnia | 0.05 | 0.11 | [-0.17, 0.27] |
| region Central Finland | -0.11 | 0.43 | [-0.96, 0.74] |
| region North Carelia | -0.32 | 0.54 | [-1.37, 0.74] |
| region South Ostrobothnia | -0.35 | 0.11 | [-0.57, -0.13] |
| region South-West Finland | -0.27 | 0.05 | [-0.37, -0.17] |
| region Tavastia | -0.34 | 0.11 | [-0.56, -0.12] |
| region Uusimaa | -0.12 | 0.03 | [-0.18, -0.07] |
| AGRI5 | 0.05 | 0.03 | [-0.01, 0.10] |
| SHANG | 0.05 | 0.03 | [0.00, 0.11] |
| BARE | 0.04 | 0.03 | [-0.01, 0.09] |
| Dispersion parameter | 1.50 | | |