Basic and Applied Ecology 86 (2025) 45–54

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

RESEARCH PAPER

Farmland bird decline is associated with a strong population limitation of open-habitat species

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ARTICLE INFO

Keywords:
Biodiversity
Demography
Farmland bird
Habitat loss
Population growth rate
Population trend
Recruitment
Survival

ABSTRACT

Farmland birds rank among organisms showing the steepest declines of their European populations. To combat these declines, it is essential to understand demographic mechanisms underlying the negative population trends. For this purpose, we employ a novel modelling approach on a long-term multispecies dataset collected by citizen scientists throughout Czechia. Using this approach, we calculated recruitment, adult survival and population growth rates for 13 farmland bird species on annual basis from 2004 to 2021, and related these demographic rates to species population trends estimated over the same period, as well as to their habitat preferences. We observed a negative relationship between recruitment and adult survival within most species. This relationship becomes increasingly more negative in species breeding in more open habitats. These species also showed steeper population declines and less positive correlation between adult survival and population growth rate than species breeding more woody habitats. These results indicate that the open-habitat farmland birds face strong population regulation. Under such regulation, higher adult survival in some years, that may occur due to, for instance, suitable weather conditions, does not leave much capacity for new recruits, and thus is immediately compensated by low recruitment. We suggest that these demographic processes are underpinned by decreasing carrying capacity of the open habitats which may occur due to shrub encroachment or afforestation of agricultural land that are widespread in Europe. At the same time, species preferring woody habitats enjoy increasing habitat availability in farmland which may lead to population increases over the long-term. Our results indicate that conservation actions are needed to improve the carrying capacity of the open habitats, especially during the breeding season. For example, some initiatives aiming for mitigation of climate change impacts by afforestation should be carefully reconsidered to avoid adverse impacts on open habitat species.

Introduction

Farmland covers the largest part of European land surface, hosting considerable number of animal and plant species (Stoate et al., 2009). Over the last decades of the Anthropocene, European farmland biodiversity faces a serious crisis and species associated with farmland are undergoing rapid declines (Steffen et al., 2011; Rigal et al., 2023). These declines are underpinned by a variety of drivers such as habitat loss, agricultural intensification and climate change (Raven & Wagner, 2021). Farmland biodiversity loss applies to nearly all taxa including plants, insects and vertebrates (Emmerson et al., 2016). Within these taxa, birds play a particularly important role as they are considered as reliable state-of-nature indicators (Fraixedas et al., 2020). Due to their high trophic positions and mobility, their population changes are shaped by factors acting at the landscape scale (Bowler et al., 2021). In addition, the existence of long time series of data on bird populations collected in many regions enables to study their trends at large temporal and spatial scales (Brlík et al., 2021).

Individual farmland bird species show considerable variability in their habitat preferences: some birds prefer continuous patches of woody plant vegetation such as hedgerows and woodlots, some others occupy scattered trees and bushes in open areas, and several species use treeless, fully open habitats covered solely by herbaceous vegetation (Kasprzykowski & Golawski, 2012; Reif et al., 2022). Previous studies

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https://doi.org/10.1016/j.baae.2025.03.010
Received 6 September 2024; Accepted 27 March 2025
Available online 2 May 2025
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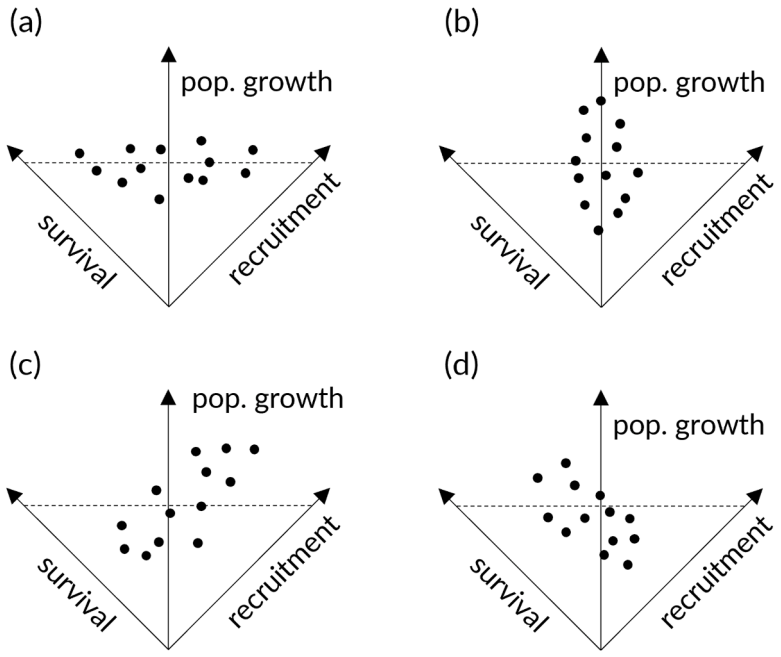

Fig. 1. Concept of the talon plot visualizing the relationships between adult survival, recruitment and population growth rate. Each point in the graph corresponds to a single temporal occasion (e.g., year). Survival and recruitment are the two major and independent orthogonal axes; population growth is their sum and thus corresponds to the vertical axis. Different horizontal levels thus correspond to the same level of population growth; the horizontal dashed line shows population growth = 1. The talon plot visualises the contributions of survival and recruitment at different levels of population growth, i.e., whether the temporal occasions with lower (or higher) population growth rates are related to lower (or higher) survival or recruitment. In this regard, four different scenarios can be distinguished: (a) survival and recruitment are negatively correlated, suggesting a strong and immediate regulation of population growth via high recruitment compensating for low survival and vice versa; (b) survival is positively correlated with recruitment, suggesting that common drivers simultaneously affect both parameters; (c) recruitment contributes more to population growth rate than survival; (d) survival contributes more to population growth rate than recruitment. See Telenský et al. (2024) for details.

Table 1
Population trends (2004–2021), together with 95% confidence interval (CI) and habitat preferences of 13 farmland bird species in Czechia. Population trend is the slope of regression line through relative abundances in respective years. Habitat preference is species' association with habitats ranging from forest interior (1.0) to open treeless landscape (7.0) according to Koleček et al. (2014). Significant trends are in bold.

Species	Population trend	Lower limit of 95% CI	Upper limit of 95% CI	Habitat preference
Sylvia borin	1.008	0.979	1.038	2.5
Turdus merula	**1.048**	**1.011**	**1.087**	2.7
Prunella modularis	1.014	0.977	1.051	3.0
Cyanistes caeruleus	**1.037**	**1.006**	**1.071**	3.0
Parus major	**1.036**	**1.005**	**1.070**	3.0
Sylvia atricapilla	**1.024**	**1.004**	**1.046**	3.3
Phylloscopus collybita	1.024	0.997	1.051	3.5
Phylloscopus trochilus	0.978	0.934	1.023	3.5
Curruca *curruca*	1.011	0.971	1.053	4.5
Emberiza citrinella	0.995	0.960	1.031	4.7
Acrocephalus palustris	**0.979**	**0.960**	**0.999**	5.5
Curruca communis	1.000	0.961	1.049	5.5
Emberiza schoeniclus	0.977	0.948	1.006	6.0

have shown that these habitat preferences predict population trends of respective species: these trends became increasingly negative when moving from species of continuous woody vegetation towards those occurring in open landscapes (Fartmann et al., 2018; Kämpfer et al., 2022; Reif et al., 2008, 2023). It is possible that the former species are less affected by intensive agricultural production and may even benefit from farmland abandonment, while the latter species suffer from both of these drivers (Storch et al., 2023).

To inform farmland management and policy, we need to shift our focus from linking population trends to various environmental factors to understanding demographic mechanisms that underpin the observed population changes (Morrison et al., 2021). Population growth rate of any bird species can be decomposed into two demographic rates: recruitment and adult survival (Julliard et al., 2004). Recruitment quantifies the rate of new individuals entering the adult population. It results from breeding productivity, i.e., the number of juvenile individuals produced per adult in a given year, and subsequent survival of these juveniles into the next year, when they recruit themselves into the adult population (Julliard, 2004). Adult survival quantifies the probability that an adult individual survives to the next breeding season (Johnston et al., 2016). Both recruitment and adult survival sum up to population growth, and their mutual relationship as well as their relative contributions to population growth rate can point to processes making population of a given species at risk (Morisson et al., 2022).

Unfortunately, obtaining data on birds' demographic rates is very difficult given their high mobility, large home ranges and skulking behaviour near their nests (Siriwardena et al., 2000a). Therefore, studies on demographic mechanisms behind farmland land population declines are scarce (Siriwardena et al., 2000b). Indeed, only a handful of studies examined farmland bird demographic rates and these studies were typically confined to small areas and a single species (but see Lauck et al., 2023). Such a narrow focus makes attempts to generalization, which are necessary for reaching robust management decisions, hardly possible (Morrison et al., 2022). One solution to the lack of data is to use data from citizen science projects that cover large areas and inform on demography of numerous species (Saracco et al., 2008). In this regard,

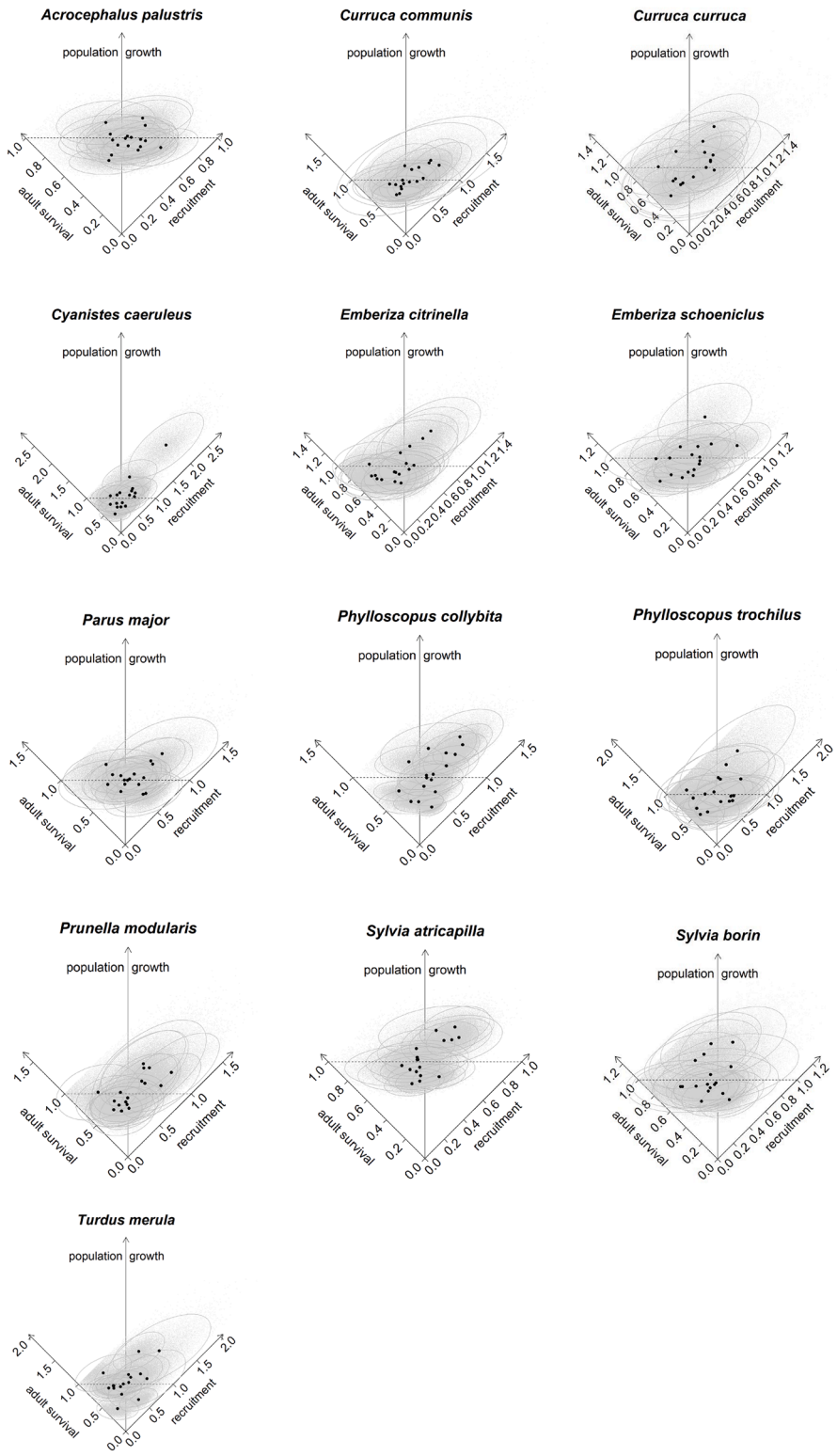

Fig. 2. Talon plots (see Fig. 1 for the concept) for 13 farmland bird species showing relationships between respective demographic rates over years 2004–2021 estimated using data from the Constant Effort Sites project in Czechia. Black points show mean estimates for each year, with 95% confidence ellipses, grey dots are the MCMC samples. Horizontal dashed lines correspond to population growth = 1.

the Constant Effort Sites (CES) project plays an important role. CES is based on a network of skilled volunteer ornithologists who ring the birds under a standardized protocol and produce capture-mark-recapture (CMR) data suitable for estimating demographic rates of individual species (Robinson et al., 2009).

Recently, Telenský et al. (2024) developed a modelling framework that enables quantification of recruitment, adult survival and population growth rate using CMR data collected within the CES. This framework is based on well-known Pradel (1996) demographic model and overcomes some crucial challenges present in CES data such as temporal turnover of sites (i.e., changes in the study area) and the occurrence of transient individuals, i.e., those that just pass through the study sites and do not

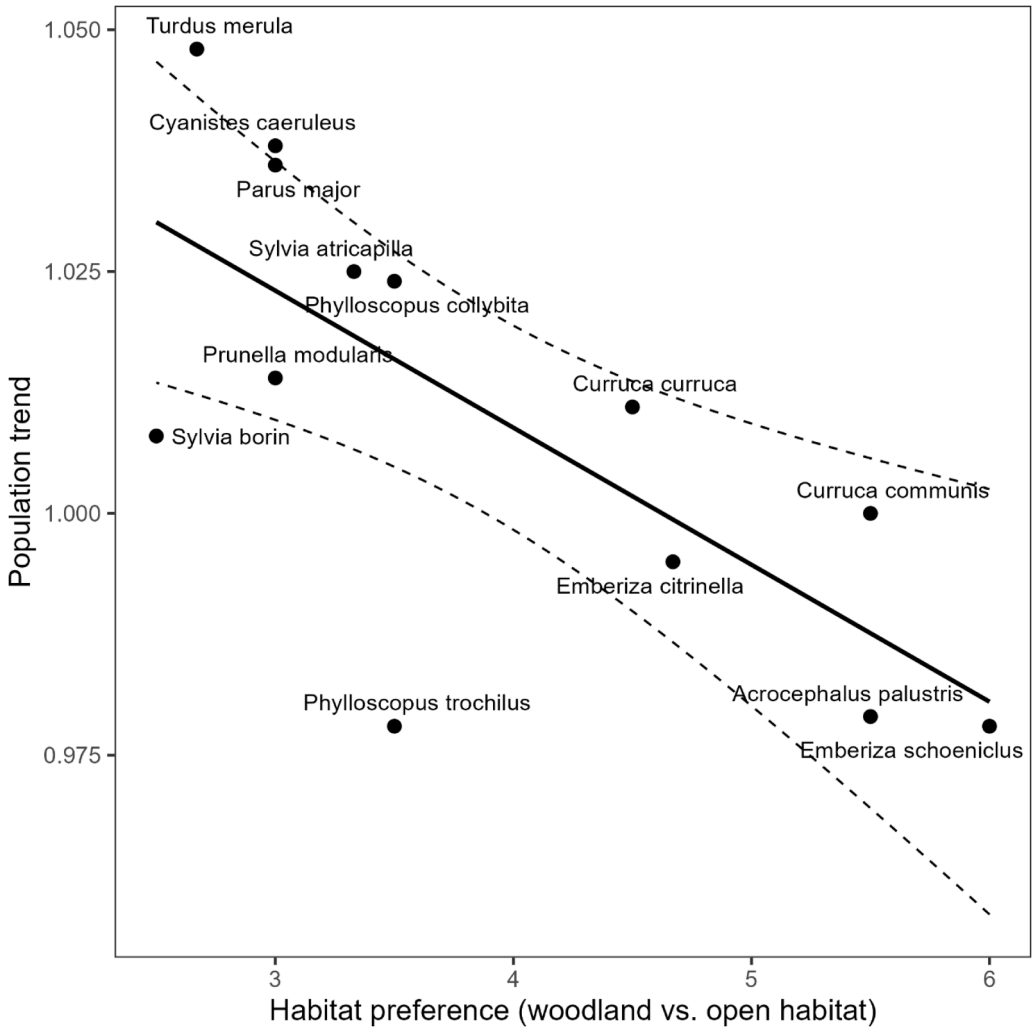

Fig. 3. Relationship between population trend (2004–2021) and habitat preference in 13 farmland bird species. Dashed lines depict 95% confidence interval. Habitat preference is species' association with habitats ranging from forest interior (1.0) to open treeless landscape (7.0) according to Koleček et al. (2014).

contribute to the demography of breeding population – these are very frequent in the populations in question (Telenský et al., 2024). Here we use this framework to exploit the CES data collected in Czechia, a country in Central and Eastern Europe where farmland birds have experienced particularly steep population declines in recent years (Reif et al., 2024).

We aim to quantify demographic rates, namely recruitment, adult survival and population growth rate, together with long-term population trends, for a set of farmland bird species differing in their habitat preferences. We predict that the species preference for open habitat will be associated with the steepest declines. The exploration of demographic rates can uncover the mechanisms underlying these declines (Fig. 1). If recruitment and adult survival are negatively related to each other, the simplest explanation is that low survival is compensated by higher recruitment and vice versa, which could be a result of a strong and immediate population regulation (Julliard, 2004). Theoretically, this regulation could restrict potential for population recovery in declining species. We test whether this mechanism applies to Czech farmland birds and explore the habitat preferences of species undergoing the strongest regulation.

Materials and methods

Data

To estimate demographic rates, we used CES data collected from 2004 to 2021 in Czechia. CES is based on work of voluntary bird ringers who capture birds' during their breeding season by mist nets (Telenský et al., 2020). On each site, birds are being captured 9 times per breeding season each year using the same number of mist nets (at least 70 m per site), so the sampling effort is kept constant at each site over years. During each capture event, the newly captured birds are ringed with an aluminium ring of a unique alphanumeric combination, and the recaptured birds are recorded. Capture events take place regularly throughout the whole breeding season from May to July. For the purpose of our study, we used data from 50 CES sites scattered throughout the whole Czechia. See Telenský et al. (2020) for more details on the CES dataset.

Out of the 16 species that provided enough data to estimate demographic rates, we selected 13 species associated with farmland. We extracted habitat associations of these species along the gradient from woody to open habitats from Koleček et al. (2014). The information in Koleček et al. (2014) is based on national literature compendia and assigns each species to 1–3 habitat types from the forest interior (value = 1) to open treeless landscape (value = 7). Habitat preference of a given species is the mean of the values of habitat types assigned to that species (Table 1). For example, a species assigned to open treeless landscape

Table 2
Correlations of adult survival and recruitment, adult survival and population growth rate, recruitment and population growth rate, respectively, in 13 farmland bird species. Significant results are in bold.

Species	Corr. adult survival vs. recruitment	Lower limit of 95% CI	Upper limit of 95% CI	Corr. adult survival vs. population growth rate	Lower limit of 95% CI	Upper limit of 95% CI	Corr. recruitment vs. population growth rate	Lower limit of 95% CI	Upper limit of 95% CI
Prunella modularis	−0.226	−0.734	0.419	0.248	−0.395	0.755	**0.844**	**0.556**	**0.967**
Turdus merula	−0.115	−0.656	0.502	0.403	−0.182	0.813	**0.823**	**0.542**	**0.957**
Acrocephalus palustris	−0.473	−0.854	0.139	0.356	−0.286	0.800	**0.575**	**0.023**	**0.892**
Curruca *curruca*	−0.209	−0.731	0.430	0.334	−0.279	0.790	**0.804**	**0.469**	**0.957**
Curruca communis	−0.439	−0.854	0.235	0.104	−0.553	0.694	**0.800**	**0.446**	**0.965**
Sylvia borin	−0.156	−0.704	0.488	0.520	−0.043	0.867	**0.697**	**0.232**	**0.931**
Sylvia atricapilla	−0.216	−0.722	0.407	0.296	−0.303	0.770	**0.827**	**0.538**	**0.962**
Phylloscopus collybita	0.049	−0.528	0.601	0.465	−0.080	0.834	**0.877**	**0.658**	**0.972**
Phylloscopus trochilus	−0.188	−0.728	0.455	0.389	−0.223	0.804	**0.776**	**0.397**	**0.955**
Cyanistes caeruleus	0.080	−0.555	0.657	0.395	−0.239	0.836	**0.926**	**0.783**	**0.986**
Parus major	−0.396	−0.830	0.261	0.322	−0.318	0.794	**0.669**	**0.177**	**0.929**
Emberiza citrinella	−0.312	−0.785	0.330	0.233	−0.394	0.741	**0.805**	**0.468**	**0.956**
Emberiza schoeniclus	−0.335	−0.781	0.276	0.282	−0.338	0.755	**0.752**	**0.373**	**0.943**

(value = 7) and open landscape with solitary trees and bushes (value = 6) has its habitat preference value of 6.5.

Statistical analysis

To quantify the demographic rates, we use a simple decomposition of population growth rate λ_t (the relative change of resident population size from year t to year $t + 1$) into adult survival ϕ_t (the proportion of individuals surviving from year t to year $t + 1$) and recruitment f_t (the rate of new individuals entering the resident adult population in year $t + 1$, per adult individual present in year t):

$$\lambda_t = \phi_t + f_t$$

To carry out this demographic analysis, we use the extension of the Pradel (1996) model according to Telenský et al. (2024), which is able to estimate survival, recruitment and population growth rate in a single model (Fig. 1), while accounting for transient individuals – non-resident individuals that are just roaming through the study area (Oro & Doak 2020). Not accounting for the transients would otherwise cause bias in the estimates of demographic rates (Orgeret et al., 2014). Therefore, the Telenský et al. (2024) model includes a new parameter: residency probability – the probability that an individual captured in a given year is resident (not a transient). Transient individuals cannot be distinguished from residents upon capture; however, transients are assumed to have zero probability of recapture (Pradel et al., 1997).

At each site, we pooled the data from all nine CES visits in a given year into a single temporal occasion. To take into account the residency probability including its potential changes (see Figure 5 in Telenský et al., 2024), we model it as a linear (on the logit scale) function of year – thus estimating its intercept and temporal slope. In line with Telenský et al. (2024), we used an additional information on whether the bird was captured during multiple visits in the year of its first capture (hereinafter "inaugural year"). This information further helps to confirm residency status of a bird already in its inaugural year (see Telenský et al., 2024). We modelled both the capture probability and the probability of recapture within the inaugural year as constant over time with a random site effect. All models are implemented in the Bayesian environment using Nimble (de Valpine et al., 2017), using three parallel chains with 200,000 iterations, disposing the first 80,000 as burn-in and using only every 40th iteration. We used uniform priors for probabilities and standard deviations, and a flat normal for the slopes. Nimble models were run from scripts written in R 4.0.3 (R Core Team, 2020). Convergence was assessed visually and using the psrf (potential scale reduction factor) from the *gelman.diag()* function in R package 'coda' – all psrf values were lower than 1.014. Derived parameters (recruitment, population growth) were calculated post-hoc on the Markov Chain Monte Carlo (MCMC) samples of the primary model parameters (survival, seniority) to ensure the proper propagation of the uncertainty of estimates.

By that means, we estimated annual values of each vital rate, as well as their mean values over years (Fig. 2). In addition, we also post hoc calculated long-term population trend from 2004 to 2021 for every species (Table 1). The trend was estimated as a slope of regression line fitted through natural logarithms of the species' annual population indices. The annual population indices were set to 1 in the first year and in subsequent years they were calculated as a product of population growth rates from the first year up to the given year.

The linear correlation (expressed as Pearson product correlation coefficient, r) of annual values of recruitment and adult survival, respectively, with annual population growth rate, quantified their contribution to species' population growth in every species. We also calculated a correlation between annual values of recruitment and adult survival in every species. These correlations of the demographic rates were calculated on their MCMC posterior samples. For each MCMC sample of the parameters, we estimated the correlation with the cor.test () function and took one random sample from the distribution of the correlation coefficient given by cor.test(). This way, we constructed posterior distribution of the correlation coefficient which takes into account both the uncertainty of the correlation over years, as well as the uncertainty of the estimates of the demographic rates.

The species-specific correlation coefficients were used for further analysis performed across species. These analyses were based on linear correlations (quantified using Pearson product correlation coefficient, r) between pairs of respective variables. In this analysis, we first related species' long-term population trends to species' habitat preferences (i.e., position of a given species along the gradient from continuous woody vegetation to open treeless landscape) to learn what is the habitat preference that makes species are at the highest risk in farmland.

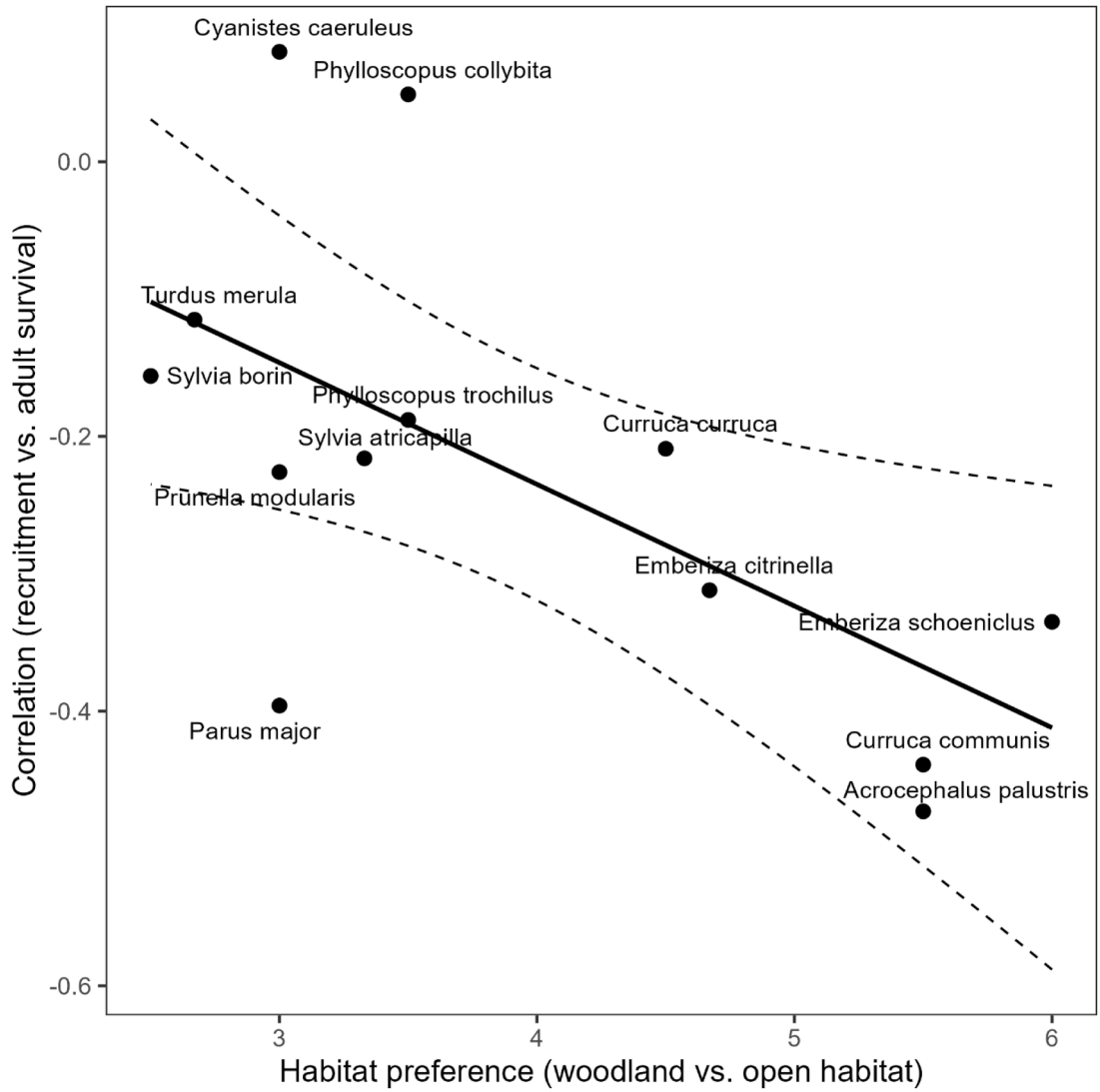

Fig. 4. Relationship of correlation coefficients from the correlation between adult survival and recruitment (across years 2004–2021) and habitat preference in 13 farmland bird species. Dashed lines depict 95% confidence interval. Habitat preference is species' association with habitats ranging from forest interior (1.0) to open treeless landscape (7.0) according to Koleček et al. (2014).

Second, we related the above-mentioned species-specific correlation coefficients (i.e., the coefficients from the correlation between recruitment and population growth rate, the correlation between adult survival and population growth rate, and the correlation between recruitment and adult survival, respectively) to species' habitat preferences to learn which demographic mechanisms act in different habitats. Third, we related the correlation coefficients to species' population trends to explore whether the demographic rates differ between increasing and decreasing species.

Results

From the 13 studied species, 8 showed population increase and 5 had decreasing population trend (Table 1), although these trends were not significant in some species. These population changes were significantly related to species' habitat preferences: the closer the association with open habitat, the greater the population decline; species that occupy continuous woody habitat were increasing ($r = -0.715$, $P = 0.006$; Fig. 3).

Recruitment and adult survival tended to be negatively related in individual species (Fig. 2), but these correlations were insignificant (Table 2). When these species-level correlation coefficients were related to species' habitat preferences, we found a negative relationship showing that the species occupying the most open habitats had the most negative correlation between recruitment and adult survival, while the correlation became less negative or even positive with increasing preference for continuous woody habitats ($r = -0.624$, $P = 0.022$; Fig. 4). These correlation coefficients were also marginally insignificantly related to population trends: the species with the most negative correlations between recruitment and adult survival tended to show the steepest population declines at the same time ($r = 0.531$, $P = 0.062$; Fig. 5).

Focusing on relationships of recruitment and adult survival to annual population growth rate within species, not surprisingly, we found solely positive relationships of either measure to growth rate in the studied species (Table 2). The relationships were stronger in the case of recruitment. Indeed, relationships between recruitment and population growth rate were significant in all species, whereas they were significant in the case of adult survival (Table 2). When examined across species, we found that the correlation between adult survival and population growth rate was more positive in species occupying woody habitats and became less positive, but still above zero, towards species preference for open habitats ($r = -0.575$, $P = 0.040$; Fig. 6). We did not find any such relationship for the correlation between recruitment and population

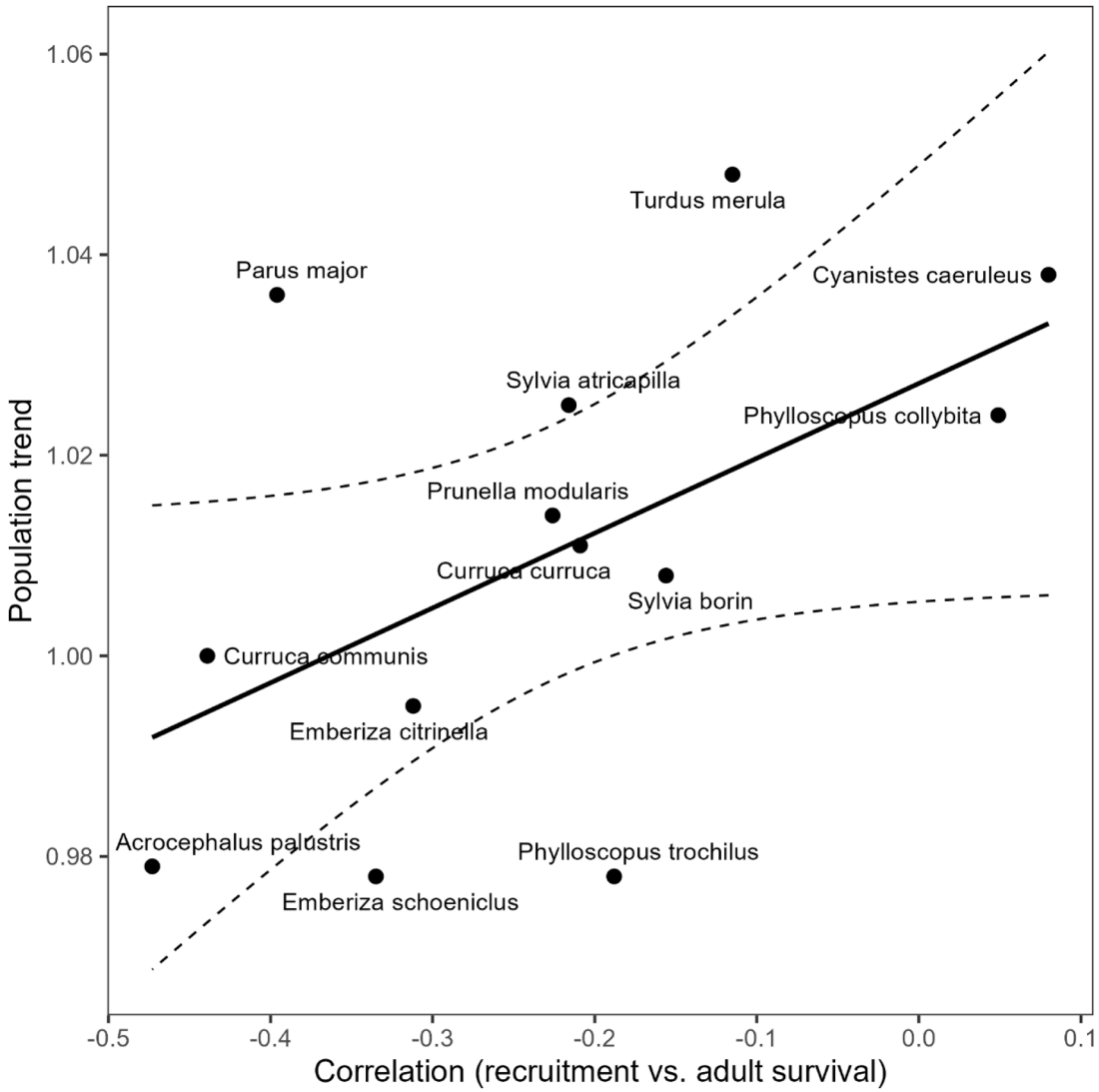

Fig. 5. Relationship between population trend (2004–2021) and correlation coefficients from the correlation between adult survival and recruitment (across years) in 13 farmland bird species. Dashed lines depict 95% confidence interval.

growth rate ($r = -0.310$, $P = 0.302$). Finally, neither the correlation coefficient between recruitment and population growth rate, nor the correlation coefficient between adult survival and population growth rate were related to population trend ($r = 0.456$, $P = 0.117$; $r = 0.250$, $P = 0.408$).

Discussion

Using CES data, we have decomposed farmland bird population dynamics in Czechia into recruitment (a product of breeding productivity and juvenile survival; these rates could not be separated given the data) and adult survival, and we estimated their contribution to annual population growth rate. CES data showed that population decline of Czech farmland birds was associated with species preference for open habitats as predicted. This preference was also linked to adult survival. Specifically, species that prefer open habitats had more negative correlation between survival and recruitment and less positive correlation of survival and population growth rate. Moreover, species with more negative correlation between recruitment and adult survival, indicating the expected strong immediate population regulation, tended to have more negative population trends. Within species, population growth rates correlated more with recruitment than with adult survival.

The more negative population trends in farmland bird species breeding in more open habitats have been widely reported by studies both in Europe and Czechia (Reif & Vermouzek, 2019; Kämpfer et al., 2022; Rigal et al., 2023). This congruence of our results with previous studies based on different datasets (typically on annual breeding bird counts) indicates that our CES data reflect a genuine pattern. However, our analysis of demographic rates goes beyond these findings and uncovers presumptive population processes underlying these declines. Specifically, we found that the farmland bird species preferring open habitat show a more negative relationship between recruitment and adult survival than species preferring woodland habitat. This negative relationship indicates that higher survival limits recruitment and/or that low survival is compensated by high recruitment (Muths et al., 2011). In any case, this implies strong, immediate population regulation limiting population decrease or increase suggesting that open habitat species could face some kind of a hard limit which restricts possibilities of population increases or decreases (Julliard, 2004). As the species with the most negative correlation between recruitment and adult survival tend to express the most negative population trends, it seems that such limitations act predominantly in decreasing populations and their pressure leads to continuing population declines.

The negative relationship between recruitment and adult survival implies that population regulation acts upon recruits that are entering the population and interact with adults (Fig. 1a). From the perspective of

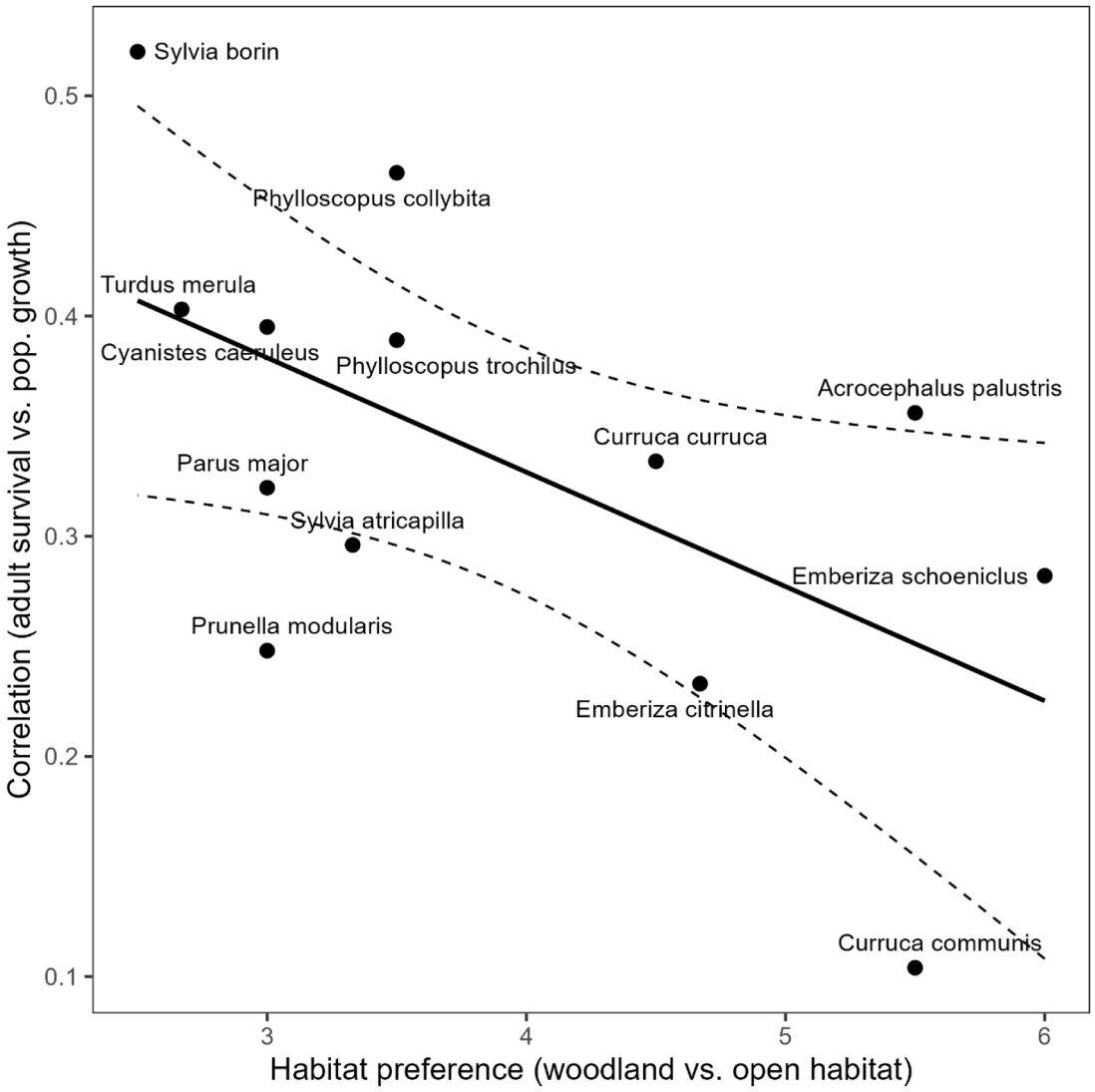

Fig. 6. Relationship of correlation coefficients from the correlation between adult survival and population growth rate (across years 2004–2021) to habitat preference in 13 farmland bird species. Dashed lines depict 95% confidence interval. Habitat preference is species' association with habitats ranging from forest interior (1.0) to open treeless landscape (7.0) according to Koleček et al. (2014).

bird ecology, these interactions most likely take place during the period of territory establishment or subsequent breeding (Petit & Petit, 1996). Potentially, such a relationship might result from resource limitation at the non-breeding grounds where a higher abundance of juveniles may restrict resources for adults and vice versa. However, such a situation is rather unlikely: at the non-breeding grounds, similar effects on adult and juvenile survival via non-selective pressures are expected. This would lead to an opposite result – a positive correlation between recruitment and adult survival (Fig. 1b), also shown in other studies (Boyd & Piersma, 2001; Julliard, 2004). Since this correlation tends to be negative, we suggest that the breeding season is more involved in open habitat farmland bird population limitation than the non-breeding season.

Limiting factors acting during the breeding season may be linked to decreasing habitat availability. The open habitats preferred by these species become increasingly less available due to widespread forest and shrub encroachment (Kupková et al., 2021). Woody vegetation becomes denser and the open habitat unsuitable for such species (Wretenberg et al., 2007). This may lead to a full saturation of the remaining suitable patches of these habitats by territories of those species, leading to a strong immediate population limitation. Moreover, species breeding in open habitats may be more specialized than the species breeding in woody habitats, reinforcing the limitation by habitat availability (Devictor et al., 2010). By contrast, species occurring in farmland woody vegetation are typically generalists, often occupying also other habitats such as forest clearings or urban areas (Ram et al., 2020; Grünwald et al., 2024).

Besides the bush encroachment on open habitats, some of the species showing the strong negative correlation between recruitment and adult survival and preferring open habitats are associated with wetter sites – this is the case of Reed Bunting and Marsh Warbler. In these species, drying of open landscape may also play a role since climate warming and drainage lead to loss of numerous wet patches in farmland (Van Turnhout et al., 2007; Chytrý et al., 2020) which might be occupied by these open habitat species. In addition, even if the habitats are available on sufficient area, the limitation may act via habitat quality deterioration. In the case of open farmland, this factor is often connected to low food availability, especially for insectivores (Bowler et al., 2019). Several lines of evidence indicate that open farmland habitats provide impoverished food supply for birds due to unsuitable management practices and pesticide treatment (Stanton et al., 2018; Hološková et al., 2024). Moreover, unsuitable vegetation structure can deteriorate habitat quality for open habitat farmland birds during the breeding season (Tarjuelo et al., 2020; Sanz-Pérez et al., 2022; Hološková et al.,

2024).

Both recruitment and adult survival showed positive relationships to annual population growth rate in the focal farmland bird species, but only the former relationships were significant. One explanation may be that recruitment shows a stronger relationship due to its relatively higher variability compared adult survival. In birds, adult individuals have generally low mortality after surviving the first year of life, i.e., they are so called K-selected species (Bennett & Owens, 2002), so adult survival does not vary too much across years resulting in weaker relationships to population growth rate compared to recruitment, which involves both breeding productivity and juvenile survival, varies considerably and thus shows stronger relationships.

Species breeding in more open habitats showed a less positive correlation between adult survival and population growth rate than species breeding in more woody habitats. We contend that this pattern further supports our reasoning based on changes in breeding habitat availability playing the role in farmland bird population limitation. As the area of open habitats decreases (Klinkovská et al., 2024), higher adult survival in some "good years", that may happen due to, for instance, suitable weather conditions, cannot translate into higher population growth due to lower recruitment in those years, as the higher survival does not leave enough capacity for new recruits in the open habitat species. In contrast, species breeding in woody habitats experience increasing habitat availability (Grešlová et al., 2023). Under such conditions, temporarily improved adult survival does not limit recruitment (they are weakly or even positively correlated in woody habitat species), so it can translate into positive population growth rate. As a result, populations of woody habitat farmland bird species increase over the long term, while those of open habitats species decline.

From the conservation perspective, our results showed that farmland bird species occupying the open habitats are "caught" in a trap of strong immediate population regulation where higher adult survival is linked to a lower recruitment, and vice versa. Populations of species of the more open habitats thus seem to be at the carrying capacity of their environment which decreases over time as reflected by their decreasing long-term trends. Under these circumstances, it is hard to expect that populations of these species can naturally recover without our active manipulation of the carrying capacity. On the other hand, this finding is promising as the capacity can be increased by undertaking effective conservation actions. These should be focused on the breeding season as our results indicate that the populations are likely regulated at that phase of birds' annual cycle. Practically, conservationists should increase breeding habitat availability by reducing shrub and forest encroachment on open farmland and/or avoiding targeted afforestation, which is particularly important given the current initiatives of climate change mitigation by planting billions of trees (Anonymous, 2022). To conserve open habitat farmland birds, these plantings should not take place in farmland (Abeli & Di Giulio, 2023). Besides the breeding habitat availability, we can increase carrying capacity for open habitat farmland birds by improvement of habitat quality, e.g. by restoring wet sites or by introducing fallow fields with suitable vegetation structure (Sanz-Pérez et al., 2019). For this purpose, instruments of the EU's Common Agricultural Policy (agri-environment schemes, greening measures and eco-schemes) are available (Pe'er et al., 2022; Hološková et al., 2025).

CRediT authorship contribution statement

Jiří Reif: Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Tomáš Telenský:** Writing – review & editing, Formal analysis, Conceptualization. **Petr Klvaňa:** Writing – review & editing, Data curation. **Jaroslav Cepák:** Funding acquisition, Data curation. **David Storch:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Acknowledgements

We wish to thank to hundreds of volunteers who participate on the CES citizen science project in Czechia, and to Miroslav Jelínek who coordinated the project for many years. The study was supported by the Czech Science Foundation (23–07103S and 20–29554X), the Charles University, Prague (UNCE 204069), and the Ministry of Culture of the Czech Republic (DKRVO 2024–2028/6.I.a, National Museum of the Czech Republic, 00023272).

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