

Maize fields as post-breeding habitat for songbirds: Influence of landscape composition, field margins, and weed infestation

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ABSTRACT

Agricultural landscapes cover nearly half of Europe's habitable land surface and play a central role in biodiversity restoration under the recently adopted EU Nature Restoration Law. Maize (*Zea mays*) cultivation has expanded rapidly worldwide and is generally considered of low value for birds during the breeding season. However, maize fields may provide critical resources for songbirds in late summer and autumn. Evidence for this remains limited because most existing studies are small in scale and short in duration. To identify factors shaping songbird presence in maize fields during late summer and autumn, we conducted a large-scale, long-term study (2016–2024) across 77 maize fields in Germany. We assessed bird abundance and species richness using mist-net captures and analysed their relationships with distance to field margins, surrounding habitat composition at multiple spatial scales, and levels of weed infestation. Bird abundance and species richness declined with increasing maize cover at the landscape scale. The influence of forest cover and woody structures varied substantially among species but had an overall positive effect on richness. At the field scale, higher weed infestation and proximity to field margins consistently enhanced bird numbers and richness. Our findings indicate that promoting heterogeneous landscapes, reducing distances to field edges, e.g., by farming small or narrow fields, and allowing moderate weed presence can increase bird abundance and richness in maize-dominated landscapes. These results provide farmers and policymakers with evidence-based guidance for aligning agricultural practices with the legally binding biodiversity restoration goals under the EU Nature Restoration Law.

1. Introduction

Agricultural landscapes cover almost half of the world's habitable land mass and have the potential to serve as important habitats for a wide range of wildlife species (Assandri et al., 2018; Blount et al., 2021; Ellis et al., 2010; Estrada-Carmona et al., 2022; Tschamtko et al., 2005). However, their suitability for biodiversity strongly depends on crop type, management intensity, and landscape composition (Benton et al., 2003; Estrada-Carmona et al., 2022; Fischer et al., 2011; Thiele-Bruhn et al., 2012; Westphal et al., 2003). The recently adopted EU Nature Restoration Law aims to halt and reverse biodiversity loss by restoring degraded ecosystems, including agricultural landscapes, through legally binding targets at Member State level (Union, 2024). Understanding how intensively cultivated crops such as maize *Zea mays* can support

wildlife is therefore of increasing importance to guide the implementation of effective, spatially explicit restoration measures.

In recent decades, maize cultivation has significantly increased, driven primarily by the demand for livestock feed and the production of renewable energy and bio fuels, covering over 200 million hectares globally (Food and Agriculture Organisation of the United Nations, 2025). In Germany, for example, maize cultivation increased by almost 70% between 2000 and 2024 with an expansion from 4.2% to 7.1% of the terrestrial area (Eurostat, 2025a, 2025b, 2025c).

During the breeding season, maize fields are generally considered to be of limited value for biodiversity, especially for birds (Best et al., 1990; Fischer et al., 2011). In Germany, only a few species, such as Northern Lapwing *Vanellus vanellus*, Eurasian Skylark *Alauda arvensis* (hereafter Skylark), Western Yellow Wagtail *Motacilla flava*, and Little Owl *Athene*

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noctua are known to occasionally use maize fields for nesting and/or foraging (Hötker et al., 2009; Neumann et al., 2009; Sauerbrei et al., 2014). For most bird species, the crop's reduced attractiveness during this period is mainly due to the late growth phase and intensive management.

However, outside of the breeding season, maize fields may represent valuable habitat as a stopover site, especially for migratory songbirds, e. g. as incidental substitute for destroyed or unavailable natural habitats (Blount et al., 2021; Fontanilles et al., 2024; La Sorte et al., 2014; Martínez-Abraín and Jiménez, 2016). Additionally, maize fields remain structurally intact until late autumn while other crops already have been harvested. Their dense and vertically structured vegetation resembles reed beds which is attractive for many songbird species (Bairlein, 1983; Fontanilles et al., 2020) and can support high densities of aphids and invertebrates in general, offering shelter and food (Blount et al., 2021; Otieno et al., 2019; Tremblay et al., 2001). Since pesticide applications typically cease by May or June (exact timing may vary regionally), arthropods and weeds can rapidly recolonize the fields from adjacent habitats, even under conventional farming practices and serve as foraging source (Barbercheck and Wallace, 2021; Marshall et al., 2003).

A few studies have documented songbird use of maize fields during summer and autumn, suggesting that such fields can serve as stopover sites or temporary foraging habitats for migrating and post-breeding birds (Degen and Jenni, 1990; Fischer and Gatter, 2011; Fontanilles et al., 2024; Gottschalk and Kövér, 2016). These studies report considerable variation in the species most frequently observed. For example, Eurasian Chaffinch *Fringilla coelebs* (hereafter Chaffinch), Common Chiffchaff *Phylloscopus collybita* (hereafter Chiffchaff), and European Robin *Erithacus rubecula* (hereafter Robin) dominated two maize fields near a wetland area in Switzerland (Degen and Jenni, 1990), while Eurasian Reed Warbler *Acrocephalus scirpaceus* (hereafter Reed Warbler), Eurasian Blue Tit *Cyanistes caeruleus* (hereafter Blue Tit), European Pied Flycatcher *Ficedula hypoleuca* being most abundant in two maize fields cultivated in a wetland in South-Western France (Fontanilles et al., 2024). Blue Tit, Great Tit *Parus major*, and Chaffinch (Fischer and Gatter, 2011) as well as Blue Tit, Eurasian Tree Sparrow *Passer montanus* (hereafter Tree Sparrow) and Reed Warbler (Gottschalk and Kövér, 2016) were the most abundant species in two maize fields in agricultural areas in South-Western and Central Germany. Aside from invertebrates and seeds of the accompanying vegetation, individuals of several species were also observed feeding on both the soft and hardened maize kernels directly from the cob, highlighting the potential forage source of maize fields during this period (Fischer and Gatter, 2011; Fontanilles et al., 2024). Additionally, Dellwisch et al. (2019) documented, that although some species avoided maize fields in late summer compared to other agricultural habitats, some species used these fields according to their share in the broader landscape composition.

Studies conducted during the breeding season further suggest that songbird use of maize fields is not uniform. Higher numbers of individuals were recorded along field edges compared to field centers (Fischer et al., 2011) and bird abundance and species composition were strongly influenced by surrounding habitats — particularly hedgerows and forests — both within maize fields (Best et al., 1990; Fischer et al., 2011) and in agricultural landscapes more generally (Pelosi et al., 2014; Šálek et al., 2025). Because many farmland bird species depend on complementary resources distributed across crop and non-crop habitats, local habitat effects are often mediated by the surrounding landscape composition (Klein et al., 2023; Tschamntke et al., 2024). Importantly, the spatial scale at which landscape composition best explains bird patterns appears to be species- and context-dependent (Morelli et al., 2013; Pelosi et al., 2014; Söderström and Pört, 2000).

The studies conducted in maize fields outside the breeding season likewise suggest that landscape composition and field characteristics—such as field size, shape, and weed abundance—may influence the maize field's suitability for different songbird species and species groups, potentially explaining the observed variation in dominant

species (Degen and Jenni, 1990; Fischer and Gatter, 2011; Fontanilles et al., 2024; Gottschalk and Kövér, 2016). Smaller and more irregularly shaped fields may increase edge density and habitat heterogeneity, thereby providing birds with a greater variety of resources such as shelter, weed-rich margins, and consequently, more prey in the form of arthropods (Benton et al., 2003; Redlich et al., 2018). In contrast, large homogeneous fields can reduce habitat diversity and increase the isolation of semi-natural habitats (Bosco et al., 2024; Tschamntke et al., 2005). Weed-rich vegetation may further improve habitat suitability by increasing the availability of seeds and insects within croplands (Smith et al., 2020), while proximity to field margins and semi-natural habitats can facilitate safer and more efficient foraging opportunities for farmland birds (Krüger et al., 2022; Pickett and Siriwardena, 2011). Consistent with these expectations, Gottschalk and Kövér (2016) found a negative association between abundance of Chiffchaffs— but not of other species—and the distance to field margins, suggesting a higher use of maize field perimeters compared to field centers. Additionally, Degen and Jenni (1990) recorded higher abundances of wood-associated bird species in parts of the maize field closer to hedges and forests, while species associated with more open landscapes had lower abundances in these areas.

Taken together, these studies suggest that songbird responses to maize fields are jointly shaped by local field characteristics and the surrounding landscape composition, and that these effects are likely to be scale-dependent and species-specific. However, these investigations (Degen and Jenni, 1990; Fischer and Gatter, 2011; Fontanilles et al., 2024; Gottschalk and Kövér, 2016) are largely limited by small sample sizes, often focusing on just one or two small fields (0.2 ha to 3.4 ha, one field in France with 10 ha) and single-year data, which restricts their generalizability and the breadth of ecological insights they can provide. Therefore, despite the existence of several studies addressing this topic, there remains a notable gap in our understanding of how broader spatial and temporal variability in field and landscape characteristics influence songbird use of maize fields and how maize cultivation needs to be adapted to support a higher bird richness and abundance in summer and autumn.

To address this gap, we conducted a large-scale, long-term study across 77 maize fields in Germany over nine years (2016–2024), encompassing diverse landscapes, field sizes, and cultivation practices. We recorded bird numbers and species richness by trapping them with mist-nets placed in the maize fields. Our study examines the influence of field- and landscape-scale characteristics on songbird abundance and richness in maize fields, including (i) weed infestation, (ii) distance to field margins (from the capture site), and (iii) the surrounding habitat composition at multiple spatial scales, (percent cover of maize, forests and woody structures in 500 m, 750 m, and 1000 m radii).

At the field-scale, we expect that 1) weed infestation positively affects songbird abundance and richness in maize fields, probably reflecting an increased availability of seeds, arthropod prey, and shelter. Additionally we anticipate 2) a higher abundance and richness at maize field margins compared to field centers, potentially reflecting a higher structural complexity and resource availability in edge habitats. Regarding the landscape-level, we expect that 3) high proportions of maize in the surrounding have a negative impact on songbird abundance and richness in maize fields, while 4) the impact of forests and woody structures in the surrounding should be species and trait-group dependent. We additionally anticipate that 5) the strength and nature of these landscape-level relationships may change depending on the spatial scale considered.

By assessing songbird abundance and richness across diverse agricultural settings, our study aims to provide evidence on how maize fields can function as habitats for songbirds during the post-breeding and migration periods. These findings offer valuable insights that are relevant for achieving biodiversity restoration goals outlined in the EU Nature Restoration Law.

2. Methods

2.1. Bird ringing

Between 2016 and 2024, standardized bird ringing (Anderson and Green, 2009) was conducted on a total of 77 maize fields (covering more than 1500 ha) across Germany to investigate avian use of maize crops (Fig. 1).

Fieldwork began in mid-July, coinciding with the period when maize fields provided suitable habitat and food resources for birds (i.e. when maize plants were shortly before or within their flowering period, reaching a height of around 150 cm). Ringing efforts continued until the harvest of the maize crops, which occurred between late August and early November, depending on crop type and regional and annual variations in agricultural schedules. For a detailed overview of trapping effort, see Supplement section 1.2. The study design was based on two complementary approaches:

- (i) German wide volunteer-based bird ringing (2016–2024): Throughout the study period, trained volunteer bird ringers conducted studies in maize fields in various regions of Germany on a total of 46 study sites. Many of these regions were monitored over several consecutive years, allowing for repeated sampling in consistent landscapes (Fig. 1, and Supplement section 1.1). Selected fields had organic as well as conventional farming practices, field sizes from 1.5 to 186 ha, and usually low or medium proportions of maize and forests and woody structures.
- (ii) Regionally focused professional bird ringing (2022–2024): Starting in 2022, bird ringing was conducted by a field team on a total of 31 study sites, each year focusing intensively on a specific region within Germany. These were Rottenburg in southwestern Germany in 2022, Seelow in eastern Brandenburg in 2023, and Cloppenburg in northwestern Germany in 2024 (Fig. 1, and Supplement section 1.1). Within each region, a broad range of maize fields was selected to represent diverse landscape compositions (low to high proportion of maize and proportion of forests and woody structures), field sizes from 0.4 to 147 ha, and organic

as well as conventional management practices. This ensured a high degree of variability and ecological representativeness.

Standardized mist-netting protocols were employed to ensure consistency across study sites and years, namely removing one line of maize plants to set up the mist-nets, a minimum total net length of 25 m (range: 27–192 m) with a mesh size of 16×16 mm, and at least ten ringing sessions lasting at minimum 4 h per site and year (range: 5–23 days). Due to early harvests, some sites failed to conduct ten ringing sessions and we excluded sites if the total time that mist-nets were open was below 30 h (range: 31–108 h). To avoid attracting birds, installation of playbacks or supplementary food were not permitted. Per trapped bird we recorded several parameters, of which species, ring number, date, time, and the number of the net were considered in this study.

All ringing activities were carried out under permits issued by the relevant national bird ringing centers and local authorities, in compliance with applicable legal and ethical guidelines (see Ethical Statement). Mist-nets were checked at least once per hour (and more frequently during extreme weather) to minimize stress and disturbance at the capture site. Captured birds were removed from nets, held briefly in opaque cloth bags, and handled outside the field to record species, sex (when possible), age, and morphological data. Per bird, handling time ranged between 1 and 5 min. All birds, including non-target species, were released immediately after handling.

2.2. Net-specific parameters

For each net at each study site, we measured several parameters that may influence the abundance and richness of birds in maize fields. Net locations were either recorded in the field using a handheld GPS device or digitized based on detailed aerial photographs provided by volunteers, on which they marked the net locations. The accuracy of the net locations is therefore approximately 5–10 m.

2.2.1. Weed infestation

To determine the weed infestation around each mist-net, the proportion of the ground covered by weeds was visually estimated in 5%

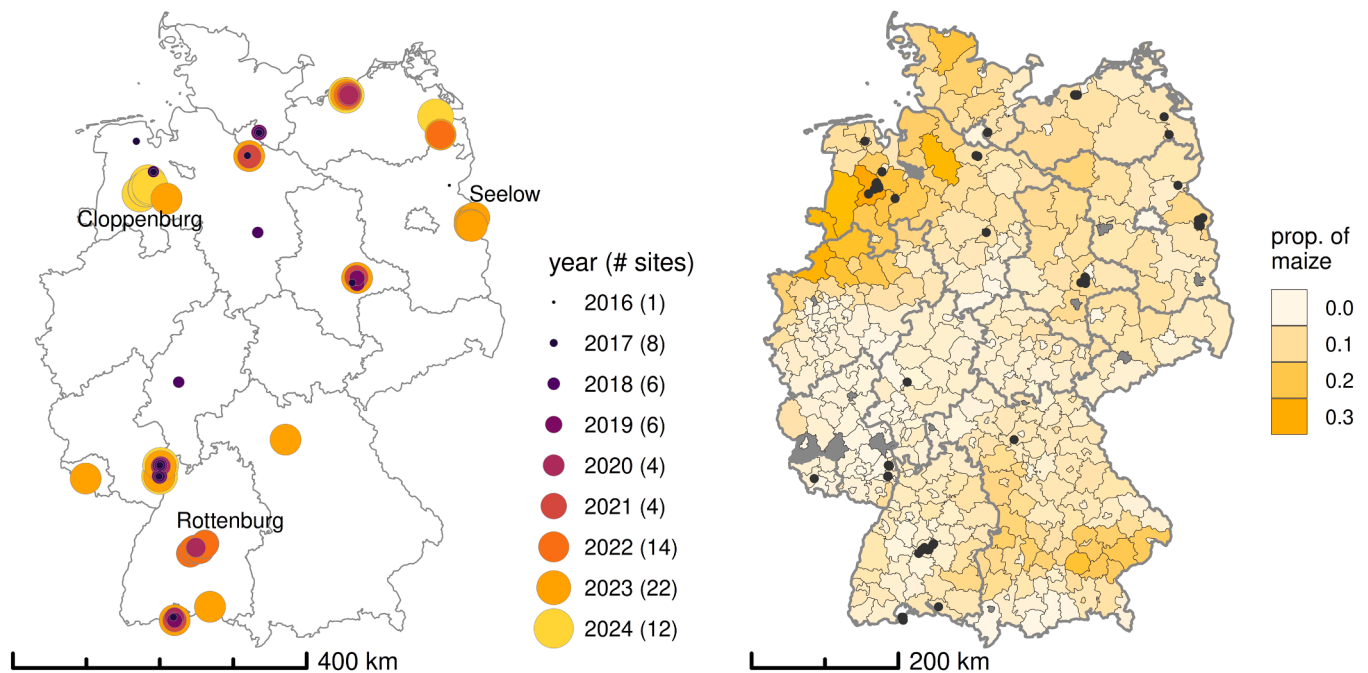


Fig. 1. Overview of study sites across Germany. Left: study sites per year. Regions with professional ringing are labelled with region names. Numbers in brackets give the total number of sites per year. Right: Overall proportion of land area covered by maize per district. Districts without available data are colored in grey. Study sites are given as black points. Data base for maize cultivation: [Statistische Ämter des Bundes und der Länder \(2020\)](#).

classes (Andújar et al., 2010). For this we considered the ground underneath the nets as well as adjacent maize rows. This approach was chosen to compensate for potential bias caused by the installation of the mist-nets, which can lead to increased weed growth due to higher solar radiation and precipitation, or by the manual removal of emerging plants beneath the nets. At least one estimate per net and month was recorded to account for spatial and temporal variation. All plant species except maize were included. Weed infestation was used as a primary indicator of habitat quality because it is a measurable and consistent feature across fields, and because we observed substantial variability in management practices—such as tillage intensity, weed control, and pesticide use—both within conventional and organic farming systems.

We acknowledge that visual estimation may introduce some subjectivity, but by having the same observer conduct all measurements within a site, we aimed to ensure comparability of relative differences over time and across sampling points.

2.2.2. Distance to field margin & field size

Mapping and processing of landscape data, distances and field sizes was done using QGIS version 3.40.4 (QGIS Development Team, 2025) and the package sf version 1.0–19 (Pebesma, 2018) in R version 4.5.1 (R Core Team, 2025).

We defined the distance to the field margin as the minimum distance between a net location (measured in the middle of the net) and the field boundary of the maize field. Additionally, field size was calculated based on field boundaries determined via satellite imagery or open geospatial data.

2.2.3. Landscape composition

We recorded the composition of the landscape within a 1 km radius around each net using a combination of field surveys (mainly for crop types and small woody structures) and internet sources on land cover data regarding i) settlements and infrastructure, ii) water bodies, and iii) woody structures and forests with a spatial resolution of down to two meters to include smaller structures such as hedges, tree lines and tracks. Therefore we extracted OpenStreetMap (OSM) data (OpenStreetMap Contributors, 2017) via the osmdata package version 0.2.5 (Mark Padgham, Rudis, 2023) in R version 4.5.1 (R Core Team, 2025). For a list of extracted OSM attributes, see Supplement section 1.3. To analyse possible influences of landscape scale on bird occurrence, the landscape composition per net was calculated within three radii (0.5, 0.75, and 1 km). Forests and any woody structures like hedges, orchards, and tree lines were summarized to the category ‘AST’ which stands for ‘areas covered with shrubs and trees’.

2.3. Analysis

We fitted a set of models to assess, which landscape- and field-level parameters influence bird abundance and species richness. Results on species-habitat relationships were used to infer criteria for a songbird-friendly maize cultivation.

2.3.1. Abundance per species

We modelled abundance per species for the most abundant 13 species, being trapped on more than 2.5% of all trapping occasions (see Fig. 3 for species list), since less abundant species comprised a high number of zero observations (> 97.5%), leading to convergence problems. Abundance was quantified as the number of individuals trapped per species, net, and decade (ten-day period within a year). Initial captures and recaptures of previously ringed individuals were not distinguished, as both repeated visits by the same individuals and the absence of such visits contribute to assessing the attractiveness of maize fields to songbirds. To account for variation in trapping effort – specifically differences in trapping duration and net area (h*m²) – we included *effort* as an offset term in the models (Korner-Nievergelt et al., 2015). The resulting density thus represents the number of individuals trapped

per 1000 hm², corresponding, for example, to four hours of trapping with a 250 m² net or 40 h of trapping with a 25 m² net.

Prior to modelling, we checked for collinearity between possible predictors. Due to collinearity among landscape composition variables, only the two variables of our main interest – *proportion of maize* and *proportion of AST* in the surrounding area (proportional, 0–1) – were retained as explanatory variables. To assess which parts of the maize fields are used more frequently, we added *distance to field margin* (numeric, in m) as further predictor, as well as *weed infestation* (proportional, 0–1). Temporal variation, i.e. migration phenology, was modelled using both linear and quadratic effects of *decade*, to allow for a maximum peak within the season. Spatial relationships among sites, e.g. regional differences in species composition, as well as dependencies due to spatial proximity, were taken into account by *spatial autocorrelation* (Korner-Nievergelt et al., 2015). For detailed figures displaying the explanatory variables, see Supplement section 1.4.

We used a zero-inflated negative binomial model to adequately depict a high amount of zero counts (between 75.0% and 97.1%) as well as overdispersed individual numbers (Korner-Nievergelt et al., 2015). Let $y_{d,n}$ denote the number of individuals per species s captured in decade d at net n . We assumed

$$y_{d,n} \sim \begin{cases} 0 & \text{with probability } \theta_s \\ \text{NegBinomial}(\lambda_{d,n}, \phi_s) & \text{with probability } (1 - \theta_s) \end{cases} \quad (1)$$

where θ_s is the species-specific zero-inflation probability and ϕ_s the overdispersion parameter. The expected abundance $\lambda_{d,n}$ was modelled on the log scale as:

$$\log(\lambda_{d,n}) = \alpha_s + \sum_p \beta_{s,p} \cdot \text{land}_{d,n,p} + \gamma_{s,1} \cdot \text{dec}_{d,n} + \gamma_{s,2} \cdot \text{dec}_{d,n}^2 + k_i + \log(\text{effort}_{d,n}) \quad (2)$$

where α_s is a species-specific intercept, $\beta_{s,p}$ are species-specific slopes for p net-specific covariates of *land* (distance to field margin, proportion of maize, proportion of AST, weed infestation), $\gamma_{s,1}$, $\gamma_{s,2}$ are species-specific linear and quadratic decade effects, k_i is a site-level spatial random effect, and $\log(\text{effort}_{d,n})$ the offset for sampling effort.

Spatial autocorrelation among sites was modelled via a Gaussian Process prior on the site-level random effects $k \sim \mathcal{N}(0, \Sigma)$:

$$\Sigma_{ij} = \eta^2 \cdot \exp\left(-\rho^2 \cdot D_{ij}^2\right) + \epsilon \cdot \delta_{ij} \quad (3)$$

where D_{ij} is distance between sites i and j , η^2 the marginal variance parameter, ρ^2 a squared length-scale parameter, $\epsilon = 0.01$ a small nugget for numerical stability, and δ_{ij} the Kronecker delta (1 if $i = j$, 0 otherwise)

Following priors were specified: normal(0, 1) for α , β , γ , exponential (1) for ϕ_s , exponential(0.5) for ρ^2 , and exponential(2) for η^2 .

2.3.2. Abundance per trait group

For a more comprehensive picture of abundance, we grouped all trapped species in functional traits. Per trait, we summarized the number of individuals of all species belonging to respective trait levels. These traits (and levels) were i) habitat (farmland, forest, settlement, wetland, several habitats at once), ii) habitat structure (dense = 1, semi-open = 2, open = 3), iii) migration strategy (long-distance, short-distance, resident), iv) primary lifestyle (aerial, insectorial, terrestrial, generalist), v) trophic niche (granivore, invertivore, omnivore), and vi) Red List Classification of Germany (least concern = *, endangered = 2, vulnerable = 3, near threatened = 4) (see Supplement section 1.5 for a detailed list of species per trait and level). Migration strategy and habitat were derived from Kamp et al. (2020), habitat structure, primary lifestyle, and trophic niche from the dataset AVONET (Tobias et al., 2022). We selected these established datasets because they provide standardized trait information, which enhances the comparability and reproducibility of our

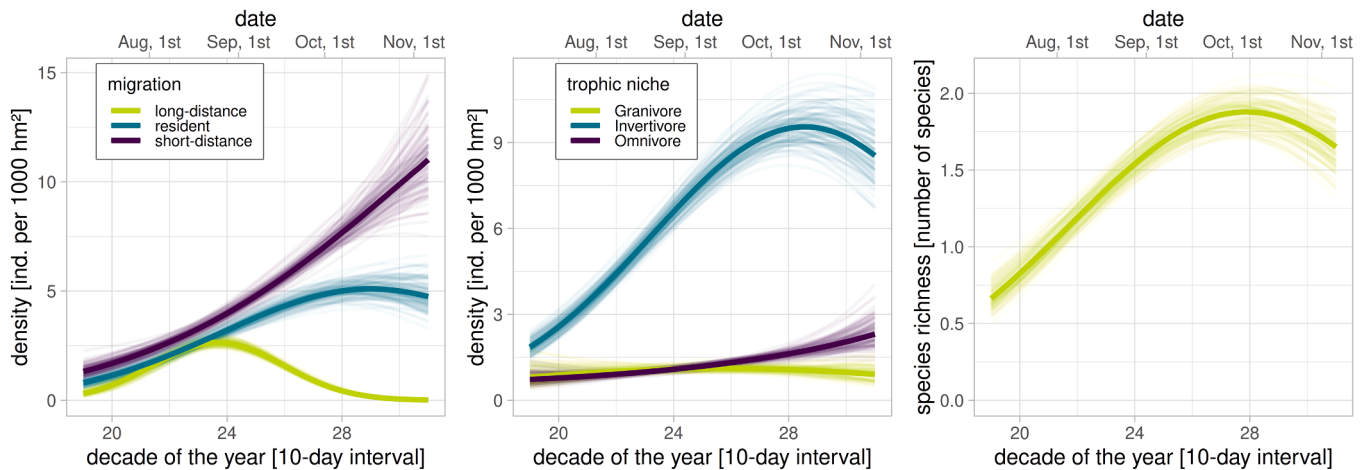


Fig. 2. Phenology of abundance per migration strategy (left), trophic niche (middle), and species richness (right) in maize fields (model with 0.5 km landscape scale). Displayed are median model predictions (bold lines) and a subset of 100 draws from the posterior distribution (thin lines). For predictions, other covariates were set to their mean values. See Supplement section 2 for further trait groups and species showing predicted abundance per decade.

analyses across different studies and regions. Note that for trophic niches we had to exclude aquatic predators (Jack Snipe *Lymnocyrtus minimus*, Common Kingfisher *Alcedo atthis*) and vertivores (Common Kestrel *Falco tinnunculus*, Sparrowhawk *Accipiter nisus*) from the analysis due to convergence issues arising from the low number of captures for these two niches. Additionally, Red List classifications were sourced from the most recent German Red List (Ryslavsky et al., 2020).

Each trait was modelled separately using the same model settings as for species-level abundance (see Eqs. (1) to (3)). The only difference is that $y_{d,n}$ denotes the number of individuals per trait level s (rather than species s) captured in decade d at net n (see Eq. (1)).

2.3.3. Species richness

Species richness, defined as the number of species trapped per net and decade, was modelled analogously, using the same covariates. However, because the relationship between species richness and trapping effort is less linear than that between abundance and effort, effort was incorporated as a linear and quadratic covariate rather than as an offset (Korner-Nievergelt et al., 2015). Additionally, we used a Poisson model, since the number of species was neither zero-inflated nor over-dispersed. Let $y_{d,n}$ denote the number of species captured in decade d at net n . We assumed

$$y_{d,n} \sim \text{Poisson}(\lambda_{d,n}) \quad (4)$$

where the expected abundance $\lambda_{d,n}$ was modelled on the log scale as:

$$\log(\lambda_{d,n}) = \alpha + \sum_p \beta_p \text{land}_{d,n,p} + \gamma_1 \text{dec}_{d,n} + \gamma_2 \text{dec}_{d,n}^2 + \delta_1 \text{effort}_{d,n} + \delta_2 \text{effort}_{d,n}^2 + k_i \quad (5)$$

where δ_1, δ_2 is the linear and quadratic sampling effort effect. For other parameters and priors, see section ‘Abundance per species’.

The models were fitted using the Hamiltonian Monte Carlo (HMC) sampler implemented in Stan (Stan Development Team, 2024), accessed via the CmdStanR interface version 0.9.0 (Gabry et al., 2025) in R version 4.5.1 (R Core Team, 2025). Numeric covariates were centered and scaled to one standard deviation prior to modeling. Each model had four chains each with 1000 warmup and 1000 sampling iterations and was validated through posterior predictive checks (see Supplement section 1.6). Trace plots showed good mixing and convergence, and posterior effective sample sizes were larger than 1000.

To assess whether the choice of reference radius for landscape proportions affected our results, each model was run three times using different radii (0.5 km, 0.75 km, and 1 km) for maize and AST.

3. Results

We trapped a total of 9374 birds of 71 species, including 909 recaptured birds of 27 species (recapture rate of 9.7%). The three most abundant species were Blue Tit with 1822 individuals (19.4% of all trapped birds), Chiffchaff with 1530 individuals (16.3%), and Great Tit with 1166 individuals (12.4%) (see also Supplement section 1.5 for further individual numbers).

3.1. Phenology

Overall, both bird abundance and species richness increased towards the end of the season (Fig. 2), with species richness peaking early in October (decade 28). Among the different migration strategies, only long-distance migrants reached their highest densities earlier in the season, in late August and early in September (decade 24). In contrast, resident species and short-distance migrants attained their highest densities in maize fields toward the end of the season (Fig. 2). Concerning the trophic niche, invertivores highly and omnivores slightly increased towards the end of the season, while abundance of granivores remained more or less constant throughout the season (Fig. 2).

3.2. Weed infestation

With the exception of seven bird species and two trait groups, weed infestation had an overall positive influence on bird abundance and species richness (Fig. 3, Fig. 4). At the species level, Common Reed Bunting *Emberiza schoeniclus* (hereafter Reed Bunting), Marsh Warbler *Acrocephalus palustris*, and Tree Sparrow exhibited the strongest positive relationships. Similar strong positive responses were observed at the trait groups among species inhabiting farmland and settlements, species with a terrestrial lifestyle, those classified as vulnerable or near threatened and granivores. The weakest or indifferent relationships were observed for Willow Warbler *Phylloscopus trochilus*, Dunnock *Prunella modularis*, Robin, and endangered species (Red List category 2).

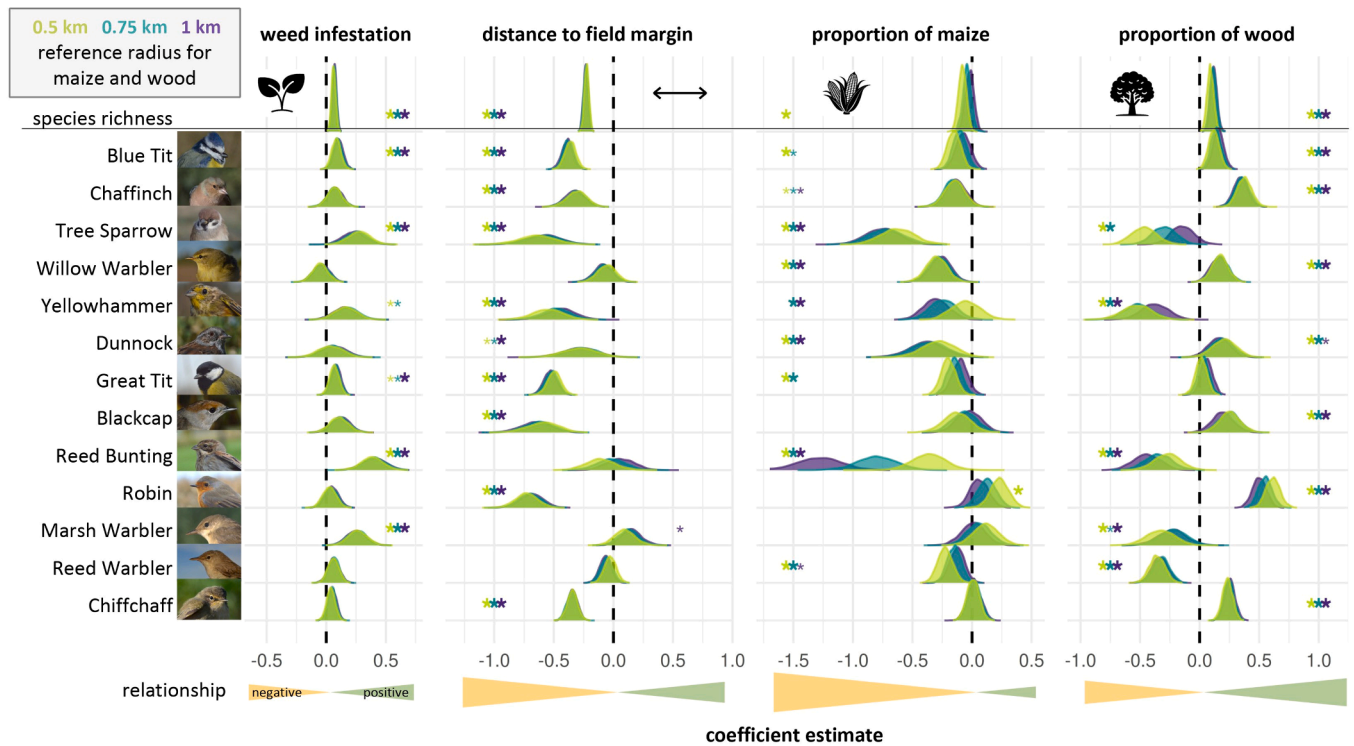


Fig. 3. Distribution of coefficient estimates of the relationship between abundance of different species as well as species richness with different net-specific parameters. Models were run on three different landscape scales to investigate the influence of land-use cover in the vicinity of 0.5 km, 0.75 km, 1 km of each mist-net. Negative coefficient estimates indicate a negative relationship and positive estimates a positive relationship between abundance or richness with the respective parameter. Each coefficient estimate is based on 4000 simulations. If the 95% (90%) credible interval is below or above zero, this is labelled with a respective bold (narrow) star. See Supplement section 2 for coefficient estimates and further figures showing predicted abundance and species richness per parameter. © Mirjam Rieger.

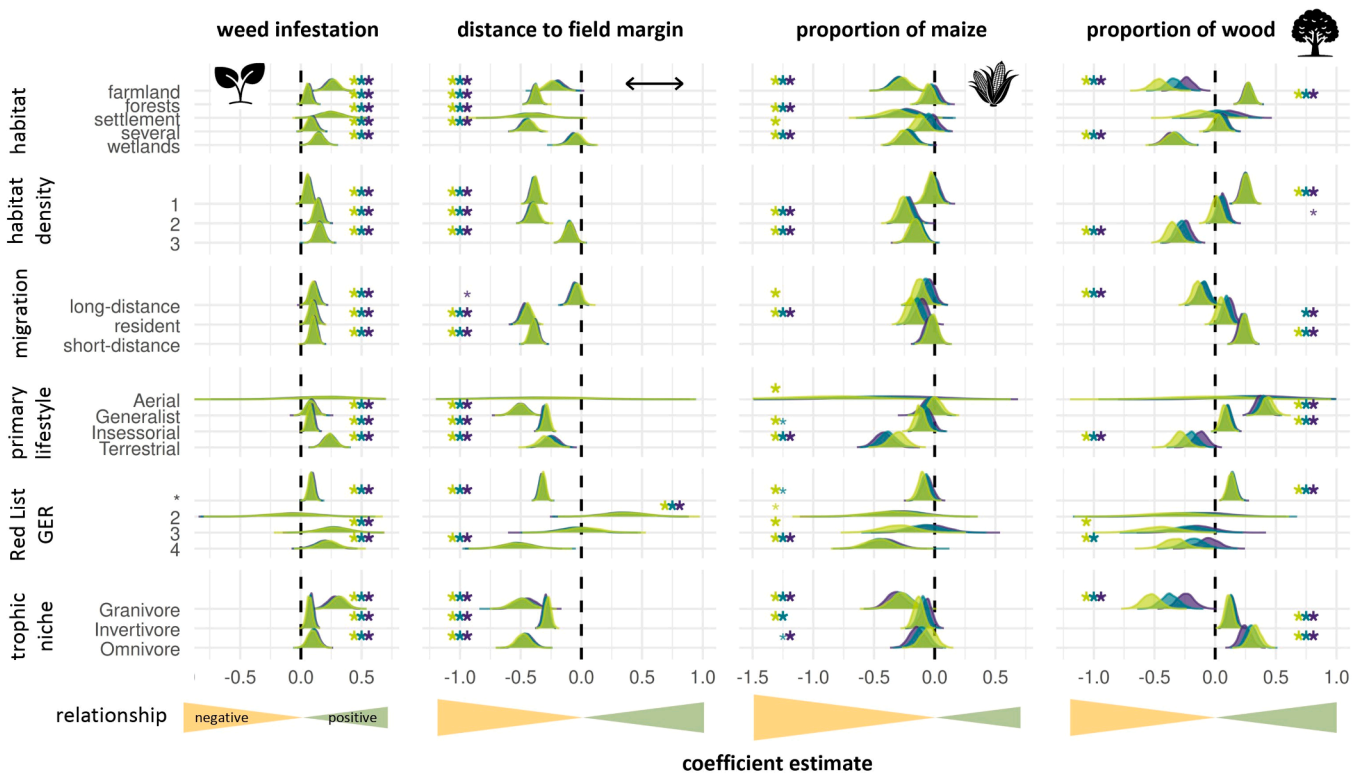


Fig. 4. Distribution of coefficient estimates of the relationship between abundance of different trait groups with different net-specific parameters. See Fig. 3 for legend and further explanations. Reference for habitat density levels: 1 = dense, 2 = semi-open, 3 = open. Reference for Red List categories: * = least concern, 2 = endangered, 3 = vulnerable, 4 = near threatened.

3.3. Distance to field margin

Abundance and species richness were generally higher at field margins and declined markedly toward the field center (Fig. 3, Fig. 4). This pattern was most pronounced for Robin, Eurasian Blackcap *Sylvia atricapilla* (hereafter Blackcap), Great Tit and Tree Sparrow, as well as for species classified as near threatened, a generalistic lifestyle, as well as granivores and omnivores. Three species (Willow Warbler, Reed Bunting, Reed Warbler) and four trait groups (species associated with wetlands as well as an aerial lifestyle, long-distant migrants, vulnerable species) showed no clear response. In contrast, abundance of Marsh Warblers and endangered species – represented primarily by Whinchat *Saxicola rubetra* and Common Grasshopper Warbler *Locustella naevia* – increased with increasing distance to the field margin.

3.4. Landscape scale

The influence of maize and AST proportions on abundance and species richness varied between scales, although the directions of the relationship were generally consistent across radii (Fig. 3, Fig. 4). For some species and trait groups, as well as for species richness, larger radii yielded more ambiguous coefficients, whereas for others larger radii produced clearer distinctions (see next section for details). At the species level, differences between radii were more pronounced for maize than for AST. Among trait groups, variation across the three scales was greater for AST.

3.5. Proportion of maize and areas covered with shrubs and trees (AST)

Overall, the proportion of maize had a negative influence on species abundance and richness, with a few exceptions showing weak or indistinct responses (Blackcap, Marsh Warbler, Chiffchaff, species associated with dense habitats and forests in general, generalists, short-distance migrants, and endangered species) or even a positive influence for Robin at the 0.5 km landscape scale (Fig. 3, Fig. 4). Larger landscape scales generally weakened the negative relationship for species richness, as well as for Blue Tit, Great Tit, and Reed Warbler, and also for species that inhabit settlements or multiple habitats, long-distance migrants and residents, species with aerial or insessorial lifestyles, vulnerable species and invertivores. In contrast, the positive relationship between the proportion of maize and abundance of Robins decreased at larger landscape scales. For Yellowhammer *Emberiza citrinella* and Reed Bunting, as well as for terrestrial and omnivore species, the relationship between maize proportion and their abundance became more negative at larger landscape scales.

The proportion of AST in the surrounding had a positive relationship with species richness, but its influence on species and trait group abundance varied. For five species and eight trait groups there was a negative relationship between AST and abundance, whereas seven species and ten trait groups had a positive relationship. Tree Sparrow, Yellowhammer, Reed Bunting, farmland birds in general and granivores showed the strongest negative responses, and Robin, generalists and omnivores showed the most pronounced positive influence of AST proportion on abundance (Fig. 3, Fig. 4). With increasing landscape scales, the relationship between the proportion of AST and bird abundance generally became less negative for three species and six trait groups, most notably for Tree Sparrow, Yellowhammer, and Marsh Warbler, as well as for farmland and terrestrial birds, species classified as vulnerable or near threatened, and granivores. Conversely, the relationship became less positive for Robin, generalists, and omnivores, more negative for Reed Bunting, and more positive for residents and species inhabiting semi-open habitats. For species inhabiting settlements, the relationship even reversed from almost negative at a smaller landscape scale to nearly positive at a larger one.

When comparing the influence of maize and AST, many species and trait groups exhibited opposite (negative versus positive) or neutral

responses. However, four species and eight trait groups – such as Reed Warbler, Reed Bunting, Yellowhammer, Tree Sparrow, birds associated with farmland and wetlands, open habitats as well as long-distance migrants, bird with terrestrial lifestyle, vulnerable and near threatened species and granivores – showed consistently negative relationships with both, cover of maize and AST. In contrast, on smaller scales, the abundance of Robins was highest in landscapes showing high percent cover of both maize and AST (Fig. 3, Fig. 4).

4. Discussion

Our results directly address the challenges posed by the EU Nature Restoration Law by demonstrating that the importance of landscape composition for birds using maize fields varies markedly depending on spatial scale and across species and trait groups. The following points are particularly noteworthy. At the landscape scale, bird species richness and abundance decreased with increasing maize field cover, with the strongest effects observed at the 0.5 km scale. At the field level, weed infestation had consistently positive effects, while distance to field margins had negative effects on bird numbers and richness. Overall abundance and species richness increased towards the end of the season.

4.1. Phenology

The abundance phenologies of species with different migration strategies closely matched autumn migration patterns previously described for Germany (see Dierschke et al. 2011). The observed overall increase in both bird abundance and species richness in maize fields during autumn may be driven by two non-exclusive processes. First, despite the departure of many migratory species, autumn is characterized by the arrival of individuals from more northerly populations – particularly short-distance migrants – as well as by the dispersal of birds from nearby settlement areas and AST into farmland, where they often form mixed-species foraging flocks (e.g. finches, sparrows, and tits). Second, maize cultivated for silage or biogas is usually harvested between end of August and end of September, which leads to a reduction in the total area of maize fields left unharvested and a corresponding concentration of birds in the remaining grain maize fields.

Our study cannot disentangle the relative contributions of these processes, as we lack data on bird densities at the landscape scale surrounding the study fields. Nevertheless, our results highlight the greater attractiveness of long-lasting crops, particularly grain maize, for songbirds compared with early-harvested maize cultivated for silage or biogas.

4.2. Weed infestation

Bird abundance and species richness increased with higher levels of weed infestation in maize fields, confirming our a priori expectations. This positive relationship likely reflects the additional food resources provided by weeds, including seeds and associated invertebrates, improving foraging opportunities for birds, as well as increased structural richness that offers cover and shelter (Barbercheck and Wallace, 2021; Marshall et al., 2003; Smith et al., 2020). Farming practices that tolerate moderate weed presence while maintaining yield – such as reduced herbicide use, organic farming, no-till systems, or the use of nurse crops – may therefore contribute to an improved habitat quality of maize fields for birds, even though such practices were not directly assessed in this study.

4.3. Distance to field margin

Bird abundance and species richness generally increased towards maize field margins, confirming our anticipation of a strong positive edge effect. However, some species – including Marsh Warbler, Reed Warbler, Reed Bunting, and Willow Warbler – showed little or no

response to the distance to field margins, possibly reflecting species-specific habitat preferences or avoidance or ignorance of trees, hedges or human infrastructure typically associated with field edges (e.g., Dellwisch et al. 2019 who reported Reed Buntings avoiding hedges in late summers).

A similar concentration of birds near maize field edges was reported by Best et al. (1990) during the breeding season, with five times more birds recorded at field margins compared to field centres. In contrast, Gottschalk and Kövér (2016) found no overall spatial differences in abundance within maize fields, except for higher abundances of Chiffchaffs closer to the field edge. Several, non-mutually exclusive mechanisms may explain higher bird activity at field edges. First, edge effects may be explained by the function of field margins as an ecotone, e.g. reflecting spillover from adjacent habitats such as hedges and tree lines, with individuals using maize fields incidentally while moving between habitat patches, roosting, or foraging across multiple habitat types (Broughton et al., 2021; Dellwisch et al., 2019; Šálek et al., 2025). Second, field edges may provide reduced perceived predation risk and more favourable foraging conditions. Dense maize stands may restrict visibility, potentially increasing vigilance requirements in field interiors. Conversely, edge zones may allow better predator detection and reduced vigilance costs, thereby increasing foraging efficiency. Supporting this, Adams et al. (2023) showed that birds exposed to predatory acoustic stimuli in denser habitats resumed foraging more slowly than in more open conditions, suggesting increased vigilance requirements in structurally complex environments. Predation risk may also vary spatially depending on predator type, with mammalian predators being more strongly associated with edges and linear structures, while avian predators are more frequent in open areas (Krüger et al., 2018; Laux et al., 2024). Third, high edge-to-area ratios associated with smaller fields can increase habitat heterogeneity and connectivity to surrounding non-crop habitats, thereby promoting higher bird abundance and richness. This is supported by evidence that reduction in field size increase species richness across taxa, whereas agricultural consolidation leads to biodiversity losses. For example, farm enlargement following land consolidation at the former inner German border resulted in an approximately 15% decline in bird richness, primarily driven by landscape simplification rather than intensification (Noack et al., 2021). Similarly, higher perimeter-to-area ratios and smaller field sizes have repeatedly been associated with increased biodiversity across multiple taxa in agricultural landscapes (Clough et al., 2020; Morelli et al., 2013; Tscharrntke et al., 2024, 2021).

Overall, our findings highlight the importance of field margins and edge density for birds using maize fields during late summer and autumn. Collectively, these results indicate that edge proximity and field configuration are key determinants of habitat suitability in maize fields, with structurally heterogeneous fields and areas close to field margins likely enhancing resource accessibility and connectivity to adjacent habitats for songbirds. Field margins promoted by small-scale farming are likely particularly important for species that exploit multiple habitats simultaneously, as reduced distances between hedges, woody elements, and crops may lower energetic costs during foraging and movement. The ecological importance of field margins is further supported by Tremblay et al. (2001), who demonstrated that insectivorous birds contribute to pest control in maize fields, with their influence being particularly pronounced near field margins. Together, these findings suggest that policies promoting small-scale field structures — for example through financial incentives for maintaining smaller field sizes or establishing field strips — could substantially benefit songbird communities in agricultural landscapes.

4.4. Landscape scale

Our results show that the importance of landscape composition for birds using maize fields varies with spatial scale and among species and trait groups, confirming our prior assumptions.

For several species, increasing the spatial scale resulted in stronger, generally more negative relationships with maize cover, indicating that a higher proportion of maize fields in the broader surrounding landscape limits their use by songbirds. This effect was particularly pronounced for Tree Sparrow, Yellowhammer, Reed Bunting, and terrestrial birds in general. For many passerines, data on spatial range during stopovers and post-breeding periods remain scarce. However, Calladine et al. (2004) reported mean movement distances of approximately 1250 m for Tree Sparrow, and 600 m for Yellowhammer in winter, highlighting the importance of considering the larger landscape composition.

In contrast, other species as well as species richness showed more indifferent responses for the proportion of maize fields at larger radii, implying a greater reliance on the immediate field surroundings. This was especially evident for residents and long-distance migrants, invertivores, as well as Blue Tit, Great Tit, Marsh Warbler, Reed Warbler, and Robin. The latter two are also known to use only small areas of less than 300 m radius at their stopover sites during migration (Chernetsov and Mukhin, 2006; Chernetsov and Titov, 2001). Comparable results were also found by Morelli et al. (2013) for overall bird richness during the breeding season, where land cover diversity best explained bird richness in cultivated areas when considered at smaller scales (50–375 m).

Forests and woody structures (AST) had the strongest influence—both positive and negative—at smaller spatial scales (here: 500 m) with Reed Bunting as an exception which showed a more pronounced negative effect at a 1 km scale. This underscores how the absence or presence of nearby structural features can significantly impact bird abundance, depending on the specific species in question. This finding is consistent with previous studies showing that bird abundance in agricultural landscapes is often highly influenced by forest or woody cover at relatively small radii (110–310 m) within the landscape, although exact scales are species-dependent (Pelosi et al., 2014).

Overall, our results underline the scale-dependent and species-specific nature of landscape composition and emphasize the need to consider multiple spatial scales when assessing the ecological value of maize fields during late summer and autumn.

4.5. Proportion of maize and areas covered with shrubs and trees (AST)

Overall, we confirmed our expectations of increased bird abundance and species richness where the proportion of maize in the surrounding landscape was low. Exceptions to this pattern included Robin with high abundances at high proportions of maize at the 500 m scale, and Blackcap, Marsh Warbler, Chiffchaff, birds living in forests or densely vegetated habitats in general, endangered species, generalists, and short-distance migrants, with indifferent responses across all spatial scales. Note that all these exceptions with positive or no relationships with maize cover – apart from Marsh Warbler and endangered species – were also associated with high proportions of AST in our study. Associations with dense (stopover) habitats were also shown by previous studies (e.g., reed beds for Marsh Warbler, shrubs for Blackcap, and reed beds and shrubs for Robin and Chiffchaff (Bairlein, 1983)), since dense and tall habitats can provide concealment and shelter from predators and weather (Blount et al., 2021). If birds use maize fields primarily as temporary refuges during stopover (resting rather than refuelling), the immediate need may be primarily for protective cover rather than abundant food. Especially if other suitable habitats like dense shrubs, reed beds or hedges are missing, maize fields can be seen as suitable stopover habitats irrespective of the surrounding landscape and food supply.

We emphasize, however, that our data provide stronger support for a negative influence of high proportions of maize on overall abundance, which is consistent with landscape-scale studies showing negative influences of extensive maize cover on farmland bird populations during the breeding season. Sauerbrei et al. (2014), for example, reported declines in breeding populations of Skylark, Red-backed Shrike *Lanius collurio* and Corn Bunting *Emberiza calandra* where maize dominated

within a 1000 m radius. In late summer, Dellwisch et al. (2019) also found that the likelihood of songbirds visiting maize fields was lower (Skylark, Greenfinch *Chloris chloris*, Reed Bunting) or as expected (Whinchat, Goldfinch *Carduelis carduelis*, Yellowhammer) compared to the actual proportion of maize fields in the landscape but did not find a preferred use of maize fields. Additionally, landscapes with high maize cover may offer reduced structural heterogeneity (fewer hedges, margins, and weeds), lowering habitat suitability for many species that rely on alternative foraging habitats and a heterogeneous landscape (Fischer et al., 2011; Redlich et al., 2018). Our findings further support this pattern, as we observed a negative association between the proportion of maize in the surrounding landscape and the abundance of all three foraging groups examined—invertivores, omnivores, and granivores. Although some songbird species are known to utilize maize kernels as a food resource (Fischer and Gatter, 2011; Fontanilles et al., 2024; Perkins et al., 2007) and may exploit the high densities of arthropods found within maize fields (Fontanilles et al., 2024; Otieno et al., 2019), these habitats alone appear insufficient to meet all their ecological needs, such as suitable breeding and resting sites. Consequently, the simplification of agricultural landscapes towards maize monocultures may contribute to the decline of bird diversity and abundance by limiting both food resources and habitat heterogeneity.

The relationship between AST and bird abundance in maize fields varied strongly among species and trait groups. This divergence largely reflected species-specific habitat associations. Species and trait groups that typically breed in or are closely associated with forests and trees (e.g., forest and insessorial species, Blue Tit, Chaffinch, Willow Warbler, Chiffchaff, Robin) were more likely to occur in maize fields with higher proportions of AST in the surrounding. This suggests that such fields are mainly used as supplementary habitats within a forest-dominated range of these species. Additionally, higher abundances of species with an invertivore or omnivore diet in maize fields with higher proportions of AST, indicate that such a landscape composition supports a greater number of prey arthropods. This is supported by several studies, reporting positive relationships between arthropod diversity or abundance and non-crop habitats like hedges or shrubs or landscape heterogeneity in general (Ponisio et al., 2015; Priyadarshana et al., 2024; Tschamtkke et al., 2024). In contrast, species that avoid trees or forests — such as reed-associated warblers, buntings, and sparrows — showed weaker or negative responses to nearby woody structures, likely reflecting their preferences for open or wetland habitats and reduced tolerance of forest edges. Some of these species are also associated with a granivorous diet (e.g. Tree Sparrow, Yellowhammer) reflecting their need of non-wooden habitats for foraging like stubbles, where they can search for leftover seeds (Anderson, 2014; Perkins et al., 2007; Robinson et al., 2001). Comparable contrasting patterns were reported by Degen and Jenni (1990), who found higher abundances of woodland-associated species such as Robin, Chiffchaff, Blue Tit, Great Tit, and Chaffinch in maize field sections located close to a forest edge, whereas species associated with open or farmland habitats, including Tree Sparrow, Greenfinch, Yellowhammer, and Reed Bunting, were more abundant in field sections situated farther from the adjacent forest. This complementary pattern is additionally supported by several studies in agricultural areas in general (Dellwisch et al., 2019; e.g., Fischer et al., 2011; Imai et al., 2017; Söderström and Pört, 2000).

Despite these differing responses among species and trait groups, AST had an overall positive influence on species richness in maize fields. This pattern is consistent with various studies, showing that the higher structural heterogeneity of landscapes containing woody elements, such as hedges, enhances (bird) species richness (Broughton et al., 2021; Fischer et al., 2011; Redlich et al., 2018; Šálek et al., 2025). In particular, hedgerows at field edges provide additional perching sites, shelter, and diverse food sources, which collectively support a broader range of bird species.

Taken together, these results indicate that many species and trait groups respond in opposite directions to an increase in maize and AST cover, typically showing negative associations with maize-dominated

landscapes but positive responses to woody structures. However, a subset of species showed negative responses between abundance and both landscape components, particularly groups associated with population declines in Germany (Kamp et al., 2020), such as farmland specialists, species inhabiting open habitats, long-distance migrants, granivores, as well as vulnerable and near-threatened species. For these species, neither dense crop cover nor woody elements appear suitable, suggesting a preference for open, extensive landscapes with low vertical structural complexity.

A notable exception were Robins, showing a preference for landscapes combining high proportions of both maize and AST. This suggests that Robins, a typical ground-dwelling bird species of wooded and bushy habitats (Cramp et al., 1993), could benefit from an overall dense cover provided by maize fields and nearby woody structures, potentially using both for shelter and foraging during post-breeding and migration.

In terms of agricultural practices, our findings suggest that extensive maize monocultures particularly in large, homogeneous blocks, may negatively affect bird communities. Our results indicate that a higher spatial concentration of maize fields, for example in areas near biogas plants, is associated with reduced bird abundance and richness across most species. This supports the general recommendations to maintain heterogeneous crop mosaics (Priyadarshana et al., 2024; Tschamtkke et al., 2024, 2005) and underscores the importance of cultivating only a moderate proportion of a single crop species in agricultural landscapes.

Woody structures and forest on the contrary increased overall species richness, highlighting their importance for maintaining structurally complex landscapes. Among these, previous studies emphasize that hedges stand out as key features that provide essential habitat elements needed for perching, foraging and seeking shelter (Broughton et al., 2021; Dellwisch et al., 2019; Šálek et al., 2025). However, some open-habitat species showed higher abundances in maize fields of more open landscapes. This indicates that conservation measures should be tailored to target species or species groups which regionally can take profit from maize field during the breeding season, e.g. Northern Lapwing and Little Owl (Sauerbrei et al., 2014) or Little Ringed Plover *Thinornis dubius* (Vozabulová et al., 2019). A balanced landscape that combines open spaces and areas with a high vertical structure, e.g. hedges, or other linear woody elements, is likely to attract a particularly high number of bird species.

4.6. Limitations

With regard to species richness and overall species composition, it should be noted that although mist netting currently represents one of the most effective methods for recording bird use of dense habitats outside the breeding season, the use of nets with a mesh size of 16 × 16 mm is likely to result in a bias towards smaller species. Larger birds (e.g. Wood pigeon *Columba palumbus* and even thrushes frequently escaping), more wary or experienced individuals (e.g., corvids), and species with high flight agility – such as swallows – which are often able to detect and avoid the nets are underrepresented. Consequently, our study provides a comprehensive but not entirely complete picture of the use of maize fields by birds. Our conclusions therefore apply primarily to small birds, especially songbirds.

Although we included a temporal variable (decade of the year) in our models to account for seasonal variation, our analysis is still limited by the absence of site-specific phenological data on maize growth stages. This prevented us from explicitly distinguishing between biologically distinct phases (e.g., flowering versus maturity) within the sampling period, potentially masking finer-scale temporal patterns in bird assemblages in relation to plant-stage related food availability.

5. Conclusion

In general, our prior expectations concerning bird abundance and species richness in maize fields in relation to different landscape and

field characteristics were confirmed. At the landscape scale, bird species richness and abundance decreased with increasing maize field cover. The presence of woody features on the contrary had an overall positive effect on species richness and the majority of species and trait groups, despite some open-habitat species responding negatively to increased wood cover. At the field level, increased weed infestation had consistently positive effects, while an increasing distance to field margins had negative effects on bird numbers and richness. Bird abundance and species richness additionally increased as the season progressed. Taken together, our findings suggest that maize cultivation can be managed in such a way that its ecological value as stopover and post-breeding habitat for songbirds can be increased without compromising agricultural production. High bird densities in maize fields may even provide benefits to farmers through pest control, as birds can reduce populations of herbivorous insects (e.g., Tremblay et al. 2001, Garfinkel et al. 2020). Our management recommendations are:

- 1) Avoid large maize monocultures and maintain spatially dispersed maize within crop mosaics to increase habitat heterogeneity and thus provide habitat for a wider range of species.
- 2) Preserve and incorporate forest elements and linear woody structures like hedges to support overall species richness, while considering that some open-habitat species in certain regions prefer more open landscapes.
- 3) Promote smaller fields to increase the length of field margins and thus increase songbird abundance and richness. Higher financial incentives (e.g., area-based payments for fields below a certain area) could support this.
- 4) Allow moderate weed presence to provide food and cover for songbirds, using practices such as reduced herbicide application, organic farming, no-till, or nurse crops.
- 5) Cultivate late-harvested crops like grain maize, still providing shelter and food for songbirds in late autumn.

CRedit authorship contribution statement

Wieland Heim: Writing – review & editing, Investigation. **László Kövér:** Writing – review & editing, Investigation, Conceptualization. **Mirjam R. Rieger:** Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis. **Thomas K. Gottschalk:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Ethical statement

For the trapping and handling of birds, permits were issued by the respective bird ringing centers and State agencies. Bird ringing is not considered an animal experiment under current laws of Germany, and therefore, no additional permit was required.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2026.110619](https://doi.org/10.1016/j.agee.2026.110619).

Data availability

Data and code to reproduce this study are available from the Zenodo repository [Rieger et al., 2026](https://doi.org/10.1016/j.agee.2026.110619).

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