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ORIGINAL RESEARCH

Differing abundance changes in birds and butterflies in boreal agricultural landscapes

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Abstract

Biodiversity is declining at an alarming rate, particularly in agricultural landscapes. Long-term monitoring data indicate that farmland birds and butterflies have declined, yet we lack an understanding of potential drivers of abundance change of these indicator taxa over space and time. Here, we studied abundance changes of birds and butterflies in Finnish farmlands from 2001 to 2023 at local and regional scales, sampled in the same study locations and regions. Additionally, we analysed if the abundance change is correlated between the two groups (taxa) at a site-level, and if changes in abundance over time can be attributed to comparable ecological, species-specific traits, reflecting variation in species temperature index, body size, and habitat breadth. We found that butterflies significantly declined in their abundance, which was not the case for birds. Additionally, abundance changes between geographical regions differed for both taxa, indicating that similar regional drivers are affecting species of both taxa. Species-specific traits did not explain varying abundance changes of both taxa. These results indicate that abundance changes are driven by taxon- and species-specific factors, rather than by more broadly comparable, ecological characteristics. Our results highlight the importance of utilising several different indicator species, representing different taxonomic groups, when assessing the implications of agricultural practices on biodiversity.

Keywords Biodiversity loss · Farmland birds · Climate change · Land-use change · Insect decline · Agroecosystems

Introduction

Biodiversity is declining globally at an alarming rate, and concerningly, these declines are significantly higher in and among farmlands than in other habitats (Fraixedas et al. 2020; Rigal et al. 2023). The demand for cheap, readily available food has shaped agriculture

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Extended author information available on the last page of the article into one of the leading causes of habitat loss globally, with up to 40% of land surface being dedicated to farming, and this has been predicted to grow in the coming years (Raven and Wagner 2021). Intensive agricultural practices have been linked with eroding farmland biodiversity (Donald et al. 2001; Balmford et al. 2025) and, with it, the ecosystem services that agriculture relies on (Watson et al. 2021). This biodiversity decline has been documented through various long-term monitoring programmes worldwide for several different taxa in several different ecosystems (IPBES 2016; Warren et al. 2021), yet rarely in the same areas over time and on a multi-taxon level (Aakkula and Leppänen 2014; Burgess et al. 2018).

Birds and butterflies serve as good indicator taxa of farmland biodiversity due to their diverse functional roles in ecosystems. These taxa are well known, relatively easy to survey, occupy most habitat types and have long-term monitoring programmes available (Devictor et al. 2012; Eglington et al. 2015; Warren et al. 2021). Both taxa have been listed as official indicators of farmland biodiversity in the new EU Restoration Law (EU Regulations 2024/1991). Furthermore, they have been previously used to predict changes in other taxonomic groups that lack such data sets (Thomas 2005; Anderle et al. 2024). The Finnish long-term monitoring data on these two taxa indicate that farmland birds and butterflies are showing declining trends (Kuussaari et al. 2007a; Heliölä et al. 2021, 2022; Lehikoinen et al. 2024), yet their abundance changes have not been studied within the same study system over a longer time series. Both birds and butterflies depend on small-scale (within field) habitat conditions as well as landscape-level conditions (across fields and farms), but as birds are highly mobile, they are more likely to respond to changes at larger spatial scales in a landscape (Ekroos et al. 2013; Franzén et al. 2013; Zhang et al. 2021). Additionally, differences in life history traits between the taxa can explain differences in abundance changes at varying scales (Kuussaari et al. 2007a; Pöyry et al. 2009, 2017). Those include, for example, differing generational times or sensitivities to climatic variables, shaping community structures (Heikkinen et al. 2010).

Past research has focused on the joint changes in community structures such as species richness or evenness among birds and butterflies with regards to varying farmland and other habitat conditions (Zingg et al. 2018; Eglington et al. 2015; Robbins and Opler 1997; Hällfors et al. 2024). However, we lack an understanding of the spatial and temporal abundance changes of these indicator taxa within areas under similar anthropogenic pressure, posed by agricultural land use. As population trends differ over space and time, greater local fluctuations have a stronger impact on the overall population stability (Sutcliffe et al. 1996). That is, larger fluctuations increase the extinction risk of local populations and if spatially and temporally synchronised, can lead to the regional extinction of the species itself (Hanski 1999). Understanding these population changes and how they relate to agricultural land use is crucial for the conservation of local populations, and farmland biodiversity as a whole.

Species-specific traits may influence species' sensitivity and resilience to land use and climate change (Franzén et al. 2013; Pöyry et al. 2009; 2017). For example, butterfly species with small body size and thus low mobility have been shown to be more sensitive to negative effects of urbanization than species with larger body size and higher mobility (Kuussaari et al. 2021). Furthermore, a narrow habitat breadth can limit a species' ability to respond and adjust to landscape changes (Seoane and Carrascal 2008; Ekroos et al. 2010; Swihart et al. 2003; Kuussaari et al. 2021). The species climatic niche in turn indicates the climatic limits a species can tolerate (Devictor et al. 2008; Bowler et al. 2015; Hällfors et al. 2024), with warm-dwelling species tending to fare better than cold-dwelling ones in the midst of climate change (Tayleur et al. 2016; Ramón-Martínez and Seoane 2024). It is not well-known whether the same traits consistently correlate with abundance changes across taxa. For example, the impact of species-specific traits on the speed of range shifts in the face of climate change do not seem consistent (MacLean and Beissinger 2017). For example, butterflies utilising forest edges as habitats have shown a stronger northward shift when compaired to butterflies with other habitat affinities (Pöyry et al. 2009). However, more recent studies have found that not all species traits are as reliable at predicting range shifts between species amidst climate change, but for example birds and moths that have a narrower thermal niche have been shown to exhibit stronger northward shift (Hällfors et al. 2024). Understanding the role of species traits and their links to the synchrony of species abundance changes between and among taxa, can reveal collective biodiversity responses to anthropogenic land use practices and highlight species groups in particular need for conservation actions.

In this study, we compare abundance changes between farmland birds and butterflies in Finnish farmlands during a 22-year period, 2001–2023. We combine long-term count data on farmland birds and butterflies with species-specific traits (species temperature index, body size and habitat breadth) to analyse whether the abundance changes differ between birds and butterflies. We pose the following questions:

i) Do farmland birds and butterflies show a similar trend in their abundance changes on a national or regional level over the last > twenty years?
ii) Are the site level long-term trends of birds and butterflies correlated?
iii) Do species traits affect the abundance change across two studied taxa?

We hypothesise that agricultural pressures induce parallel abundance changes in the studied taxa, which is observed as parallel trends at the national, regional and site level (Kuussaari et al. 2007a; Kotiaho et al. 2005; Heliölä et al. 2022; Kukkonen et al. 2022; Laaksonen and Lehikoinen 2013; Rigal et al. 2023; Lehikoinen et al. 2024). Furthermore, if species-specific traits explain taxon abundance changes in farmlands, we expect to identify species at higher risk from agricultural practices (Devictor et al. 2012; Hällfors et al. 2024; Kuussaari et al. 2007a; Zingg et al. 2018; MacLean and Beissinger 2017).

Methods

Study area

The data were collected as part of the Finnish national program to investigate the impact of varying agri-environmental schemes on biodiversity (Aakkula and Leppänen 2014). Thus it was necessary to collect data from different geographic areas with differing species communities and agricultural practices. All study sites ($N = 37$) were located on cultivated farmlands in southern Finland (Fig. 1).

Each study site was represented by a one-kilometer square, which was placed in farmland areas of three different regions of southern Finland (South-West, South-East and North-West; Fig. 1), comprising a total study area of 37 km^2 (Kuussaari et al. 2004). This allows the evaluation of regional effects on species abundances as land use practices vary between

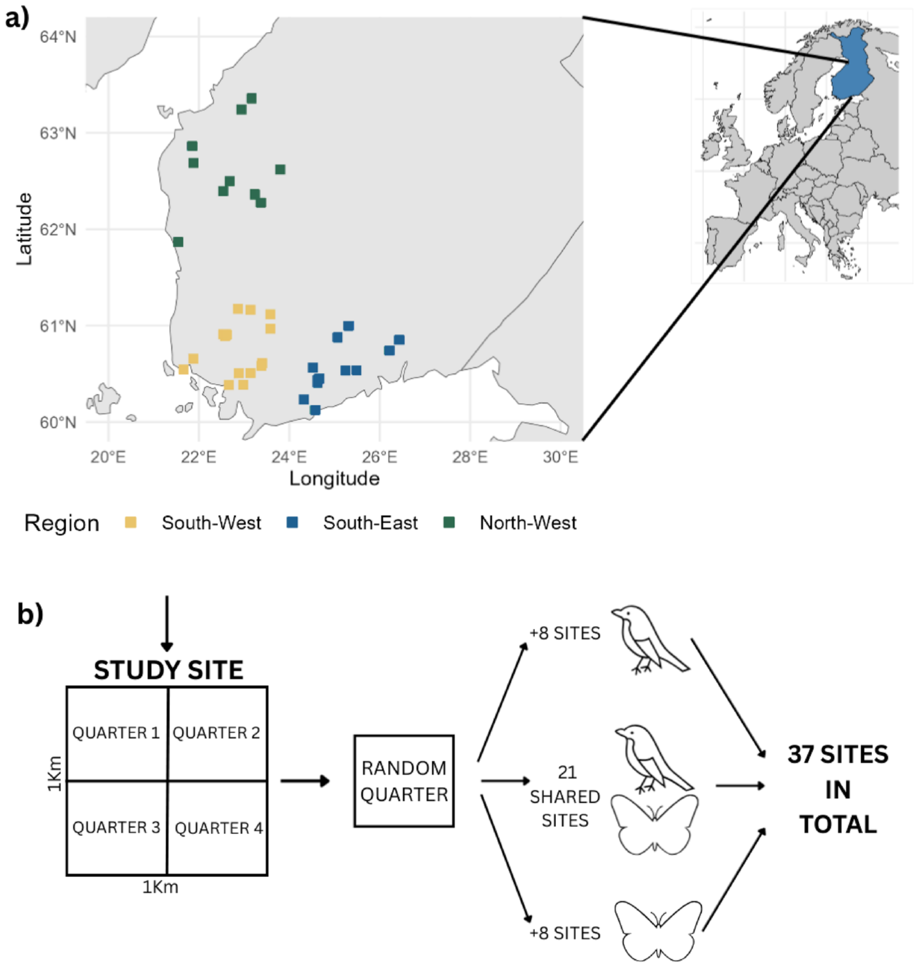

Fig. 1 (**a**) A map of the 37 study sites located in the three different study regions in Finland. South-West is in yellow, South-East is in blue and North-West is in green, followed by (**b**) the flow diagram of the study design

the regions, with more dairy farms in the north and crop farming being more dominant in the south (Tiainen et al. 2020), and as recognised by the Common Agricultural Policy with regards to varying agricultural support provided between different regions (Lehtonen and Niemi 2018). Each study square was divided into four equally sized quarters (Kuussaari et al. 2007b).

Birds and butterflies were surveyed in 2001, 2005, 2010 and 2022/2023 (see Appendix Table S1). Bird and butterfly counts were not conducted in all 37 study sites, but in a subset of those. Out of the 37 study sites, 21 included both taxa (hereafter called shared sites), 8 included only butterflies and 8 included only birds (Fig. 1 and Appendix Table S1). We therefore conducted the analyses on two different subsets of the data, i.e. on all surveyed bird and butterfly sites ($N=37$) and, only for the shared sites ($N=21$) to test differences in abundance trends at a site level (see Fig. 1 and Appendix Fig. S1).

Species count data

Butterfly data

Within the study square, butterfly counts were carried out in one randomly selected quarter per square. Transect counts were carried out following the method of Pollard and Yates (1993). Ten 50-m transects were placed in varying habitats within each study quarter, such as field margins, semi-natural grasslands, and forest edges, to ensure a full representation of the agricultural landscape. The transects were surveyed four times each season during June-July roughly in two-week intervals, and the observations from the four survey rounds were aggregated for each study year. For more detail on the butterfly surveys, see Kuussaari et al. 2007b), (2024). Only species observed in more than two years as well as in the first and last study year across all sites were included in the analysis of species abundances. This resulted in 31 butterfly species included in the analysis (See Appendix Table S2).

Bird data

Birds were surveyed in the whole area of a site (i.e. all four quarters) to include all farmland habitat and bordering forest edge, and additionally all neighbouring fields (Tiainen et al. 2007; Piha et al. 2007). The bird censuses were made using the territory mapping method with three early morning visits (from sunrise to mid-day) biweekly starting in the second week of May (see Tiainen et al. 1985). An essential practice of the territory mapping method was that careful attention was paid to simultaneous observations on same-sex individuals with territorial behaviour; this was recorded on a visit map. Afterwards, the observations were transferred to species maps where territory interpretation was made based on simultaneous recordings or considerable distance. Finally, centroids of observations interpreted to belong to a territory were entered to a digital database, from where the territories within the quarters were counted. In 2001, censuses were made with only two visits (in those cases by the most experienced field-workers; the test by Tiainen et al. 1985 showed that similar results could be obtained as with three visits).

For the bird data to be comparable to butterfly counts, counts from one quarter per site were chosen to match the survey effort within a site. This quarter was selected to be the same as that of the butterfly counts, or if no butterfly counts had been carried out in that site and year, a random quarter was selected. Like for the butterflies, data were filtered so that only species observed in more than two years as well as in the first and last study years across all sites were included in the analysis of species abundances. This resulted in 32 bird species included in the analysis (See Appendix Table S3).

Trait data

Three species traits were selected because they have been previously linked with occurrence or abundance changes in birds and butterflies: species climatic niche, body size, and habitat breadth (e.g. Kuussaari et al. 2007a, 2021; Pöyry et al. 2009, 2017; Keinath et al. 2017; Hällfors et al. 2024). They are also traits that have been measured and recorded for both birds and butterflies, allowing a comparison between the two taxa.

We used the species temperature index (STI), which is based on the mean temperature value across a species' range, and serves as a proxy for a species' climatic niche. We used the species-specific STI for birds (Lehikoinen et al. 2021), using the method described in Devictor et al. (2008). For butterflies, we used the species-specific STI values reported by Schweiger et al. (2014). In both cases, the range of the species was determined using monitoring data sets and the mean annual summer temperature weighted by the species distribution within their range was determined to calculate the STI, forming a continuous variable (Table 1).

The body size for butterflies was based on wing span from Marttila et al. (1990), and for birds we used body mass data from AVONET (Tobias et al. 2022). For *Corvus cornix*, we used weight data from the closely related *Corvus corone* (Tobias et al. 2022). Wing span has been used interchangeably before as a proxy for body mass and mobility, especially when comparing to other taxon as a life history trait (Hällfors et al. 2024), and is expressed on a continuous scale (Table 1).

Habitat breadth for butterflies was determined by Komonen et al. (2004) as the number of habitat types occupied by a species, dividing habitat types into four classes. This created three categories of habitat breadth for butterflies: narrow breadth occupying only one habitat type, medium occupying two and broad occupying three or more (as only two butterfly species occupied all four habitat types, these were grouped with the broad category). For birds, the habitat breadth was calculated using densities of species in 5 different habitat types; clearcut-shrub, forests, peatlands, arable land and human settlements, using survey data from the Finnish Line Transect data (Fraixedas et al. 2017). Based on species densities in these five categories, we calculated the habitat evenness values for each species (using the method described in Fraixedas et al. 2017). We then divided the species into three equally large classes based on the habitat evenness values, whereby birds preferring the widest range of habitat types were grouped into class three (Broad) and those found in the most restricted range of habitat types were grouped in class one (Narrow). This formed a categorical variable of three habitat breadth classes for both taxa, with species classified as exhibiting narrow, medium or broad habitat breadths (Table 1).

Statistical analysis

Analysing abundance changes and regional impacts

All statistical analyses were carried out in R version 4.4.2 (Core Team 2024). To answer our first study question, i.e. to determine bird and butterfly abundance changes over the years at the national and regional level, we used a generalised linear mixed model with the library *glmmTMB* (Brooks et al. 2017), with a negative binomial error distribution to account for potential overdispersion of the count data across all counted bird and butterfly sites (No of sites = 37, with 29 sites per taxa, and a total number of observations in the data set, sample size = 6895). Species total counts per quarter were used as a continuous

Table 1 The mean and standard deviation (SD) of the continuous response (abundance) and explanatory variables species temperature index (STI) and body size

Variable	Bird mean	Bird SD	Butterfly mean	Butterfly SD
Abundance	0.901	2.106	3.790	10.511
STI	11.890	0.919	7.702	1.381
Body size	120.914	173.056	37.887	12.345

response variable to the explanatory variables of year with the interaction of the taxonomic group. We included a random intercept on site as well as a random slope per species over the years (year|species; model A). We scaled the continuous covariate year to zero mean and unit variance. Autocorrelation was checked with the library *performance* (Lüdecke et al. 2021), and spatial autocorrelation was checked with the library *DHARMa* and function *testSpatialAutocorrelation* (Hartig 2024), with no significant spatial autocorrelation found in the model residuals (Appendix Spatial autocorrelation results). Model performance was checked with simulated residuals testing for uniformity, dispersion and zero inflation with the library *DHARMa* (Hartig 2024). To account for regional differences, we ran a separate model, adding region as an interaction term to the other two explanatory variables, i.e. having a three-way interaction with year and taxonomic group and keeping the random factors site and (year|species) (model B).

For the second study question, i.e. are the site level long-term change rates of birds and butterflies correlated, a two-step approach was run for the 21 shared sites counted for birds and butterflies between 2001 and 2022/2023 to test site-level correlation in abundance change between birds and butterflies ($N=2646$). First, bird and butterfly abundance change was analysed separately per site, with the species total counts per quarter as the continuous response variable and year as a factor explanatory variable, as well as site as random intercept. From the model results, we extracted the slope (year coefficient) and standard error (SE) per site and taxonomic group and then averaged the SE per site across both taxa (mean_SE). Second, we ran another model correlating the bird slope coefficients to the butterfly slope coefficients, with an added model weight of 1/(mean_SE)^2, to ensure estimates with higher uncertainty were given less weight in the model output (model C).

Relation to species traits

For the third study question, to determine if taxonomic abundance changes are linked to species traits, we used generalised linear mixed models (negative binomial) with the library *glmmTMB* (Brooks et al. 2017). We ran three separate models for each of three traits (i.e. body mass, STI, and habitat breadth), using the same model structure (models D) where species total counts per quarter across all sampled sites were used as a continuous response, explained by a three-way interaction between species trait, year and taxonomic group. The random factors were kept the same as before with a random intercept on site and random slopes per species (year|species). If the three-way interaction between trait, year, and taxonomic group was found not significant and having a higher AIC value than the model without, it was dropped and a two-way interaction model between the year and taxa as well as the year and trait was carried out. In all models, we allowed for a random slope per species over the years, as well as random intercept per site, and we scaled all continuous covariates to zero mean and unit variance.

Sensitivity analysis

To ensure that the varying sampling effort for birds in 2001 did not affect the results (two visits in 2001 vs. three visits in other years), a sensitivity analysis was carried out by removing the 2001 year from the data set (see Appendix Table S4). Additionally, the effect on bird species abundance change of random quarter allocation for differing sites was tested in a sensitivity analysis with no impact found (see Appendix Table S5). Similarly, the impact of only utilising data for the 21 shared sites (see Appendix Table S6), as well as utilising only Farmland Indicator Species of both birds and butterflies, were analysed in further sensitivity analyses (see Appendix Table S10).

Finally, a sensitivity analysis was carried out on birds and butterflies separately to understand whether species of certain habitat types were driving the observed abundance change patterns (habitat grouping). This categorical variable for butterflies was determined by Kuussaari et al. (2007a) having semi-natural grassland, forest/edge and arable field as habitat groups and for birds by Bosco et al. (2024) having open field, edge, farmyard and forest habitat groups. Sample sizes per habitat grouping as well as model results can be found in Appendix Table S7-9. Model A was rerun for the abundance change, with the variable taxa being replaced with habitat grouping.

Results

Abundance trend comparison and regional differences

Overall, butterflies had significantly declined in their abundance over the last 22 years ($p=0.003$), while this was not the case for birds ($p=0.110$, Table 2, model A).

The addition of regions to the model impacted the results of taxon abundance over the years (Table 2, model B). There was no significant three-way interaction between the taxa, year and the study region, and hence this was dropped from the model. Across both taxa, the South-East region of Finland showed a stronger decline in abundance over the time period compared to the other two regions ($p=0.007$, Table 2; Fig. 2) (Table 3). The butterflies remained in significant decline over the years (interaction Year*Taxa; $p=0.002$; Table 2).

Site-level correlation

The two-step change rate coefficient model for the shared site data indicated that there was no correlation between abundance changes of birds and butterflies at the same sites ($N=2646$; model C: Intercept estimate ± SE: 0.469 ± 0.124, t = 3.775, $p=0.001$; Slope estimate ± SE: 0.104 ± 0.176, t = 0.592, $p=0.561$; Fig. 3).

Influence of species traits

The species-specific traits of species temperature index, body mass and habitat breadth did not explain differences in the abundance trends of birds or butterflies (Table 2, models D-F). There was no significant three-way interaction between taxa, year, and species-specific traits, and hence this term was dropped from the models. Therefore, only two two-way interactions were included in the models, between year and taxa as well as trait and year. Regardless of the trait model, butterflies consistently show significant decline over the time period, while birds showed no detectable change in abundance.

Table 2 The model output of the five GlmmTMB models (A, B, D, E and F) on the **abundance** of birds and butterflies in different regions observed on territory or transect counts, for a total of 37 sites and 63 species (*N* = 6895)

Term	Estimate	SE	z-value	*p*-value
*Model A: year*taxa*	Marginal R^2: 0.066		Conditional R^2: 0.704	
Intercept	**−0.482**	**0.187**	**−2.584**	**0.009**
Year	−0.004	0.005	−0.722	0.470
Taxa (butterfly)	**0.454**	**0.180**	**2.519**	**0.012**
Year*Taxa (butterfly)	**−0.017**	**0.005**	**−3.007**	**0.003**
*Model B: year*region + year*taxa*	Marginal R^2: 0.070		Conditional R^2: 0.705	
Intercept	**−0.476**	**0.186**	**−2.555**	**0.011**
Year	−0.004	0.005	−0.704	0.481
Region South-East	0.008	0.075	0.107	0.915
Region North-West	0.060	0.079	0.762	0.446
Taxa (butterfly)	**0.450**	**0.180**	**2.495**	**0.013**
Year*Region South-East	**−0.012**	**0.004**	**−3.235**	**0.001**
Year*Region North-West	0.007	0.004	1.821	0.068
Year*Taxa (butterfly)	**−0.017**	**0.006**	**−3.032**	**0.002**
*Model D: year*STI + year*taxa*	Marginal R^2: 0.072		Conditional R^2: 0.704	
Intercept	**−0.483**	**0.186**	**−2.595**	**0.009**
Year	−0.004	0.005	−0.688	0.491
STI	−0.101	0.153	−0.661	0.509
Taxa (butterfly)	**0.455**	**0.180**	**2.530**	**0.011**
Year*STI	0.008	0.005	1.782	0.075
Year*Taxa (butterfly)	**−0.017**	**0.005**	**−3.086**	**0.002**
*Model E: year*body mass + year*taxa*	Marginal R^2: 0.068		Conditional R^2: 0.704	
Intercept	**−0.482**	**0.186**	**−2.587**	**0.010**
Year	−0.004	0.006	−0.731	0.465
Body mass	−0.001	0.001	−0.382	0.702
Taxa (butterfly)	**0.454**	**0.180**	**2.523**	**0.012**
Year*Body mass	< 0.001	0.001	0.677	0.499
Year*Taxa (butterfly)	**−0.017**	**0.006**	**−3.014**	**0.003**
*Model F: year*Habitat breadth + year*taxa*	Marginal R^2: 0.092		Conditional R^2: 0.706	
Intercept	**−0.509**	**0.186**	**−2.738**	**0.006**
Year	−0.004	0.006	−0.672	0.502
Habitat breadth Medium	−0.029	0.255	−0.122	0.911
Habitat breadth Broad	0.384	0.250	1.539	0.124
Taxa (butterfly)	**0.407**	**0.181**	**2.246**	**0.025**
Year*Habitat breadth Medium	−0.007	0.008	−0.787	0.431
Year*Habitat breadth Broad	0.006	0.008	0.756	0.450
Year*Taxa (butterfly)	**−0.018**	**0.006**	**−3.091**	**0.002**

A random effect of site and (year|species) was applied to the model. The estimate, standard error, z-value and p-value are given for each model. Taxa is the taxonomic groups of birds and butterflies with birds as reference level. For the factor region the South-West of Finland was the reference level and for factor habitat breadth the narrow habitat breadth was the reference level. Three-way interactions were dropped when found non-significant and having lower AIC values than models with a two-way interaction. Significant results are highlighted in bold

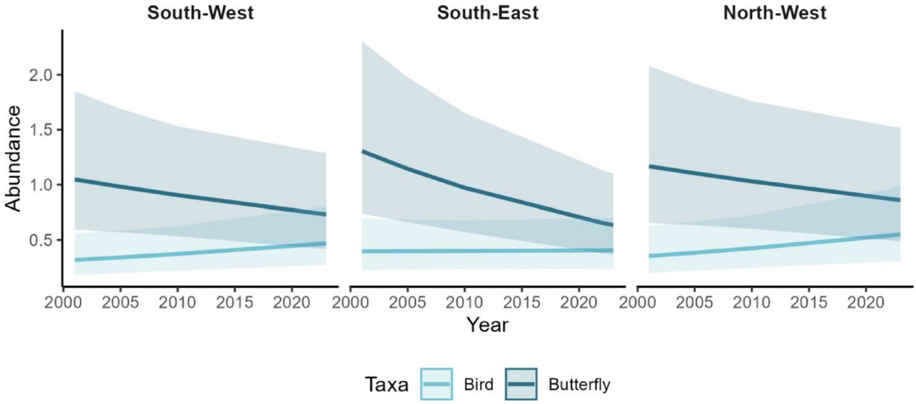

Fig. 2 The abundance trend of birds and butterflies in each study region (South-West, South-East, North-West) drawn from the model B estimates. The regression lines include the 95% confidence interval bands around. The South-East region shows a significant decline in overall abundance (Table 2)

Table 3 The results of the posthoctukey comparisons for effects of the three categories of region and habitat breadth from models B and F, computed using the library emmeans (Lenth 2025)

Contrast	Estimate	SE	z-ratio	*p*-value
Model B: pairwise ~ Region South-East ~ North-West	−0.019	0.007	−2.843	0.012
South-East ~ South-West	−0.017	0.006	−2.716	0.018
North-West ~ South-West	0.002	0.007	0.363	0.930
Model F: pairwise ~ Habitat breadth Medium ~ Broad	−0.012	0.014	−0.903	0.639
Medium ~ Narrow	−0.007	0.014	−0.472	0.885
Broad ~ Narrow	0.006	0.014	0.395	0.918

Discussion

As expected, we found that farmland butterfly abundances significantly declined over the last 20 years, as this has been the case documented in long-term monitoring data of farmland butterflies in several instances (Kuussaari et al. 2007a; Heliölä et al. 2021, 2022). However, contrary to our expectations, farmland bird abundances did not show a significant change over the years, which was found, with the same data already in half-way results of 2001–2011 (Tiainen et al. 2012). Furthermore, the site-specific abundance change of butterflies and birds from 2001 to 2022/2023 were not significantly correlated, contrary to expectations, as the same agricultural management and landscape structure could be expected to affect both species groups similarly (Zingg et al. 2018). These differences in indicator species abundance changes highlight the importance of considering several different indicator species, representing different taxonomic groups, when assessing the implications of anthropogenic activity on biodiversity (cf. Ekroos et al. 2013). Furthermore, no significant regional differences were detected between bird and butterfly abundance changes, which may indicate that similar drivers are affecting species across taxa, although the small sample size makes inference of regional patterns challenging. Finally, we did not find any significant impact of the three species-specific traits on abundance changes. Hence, significant declines in farmland

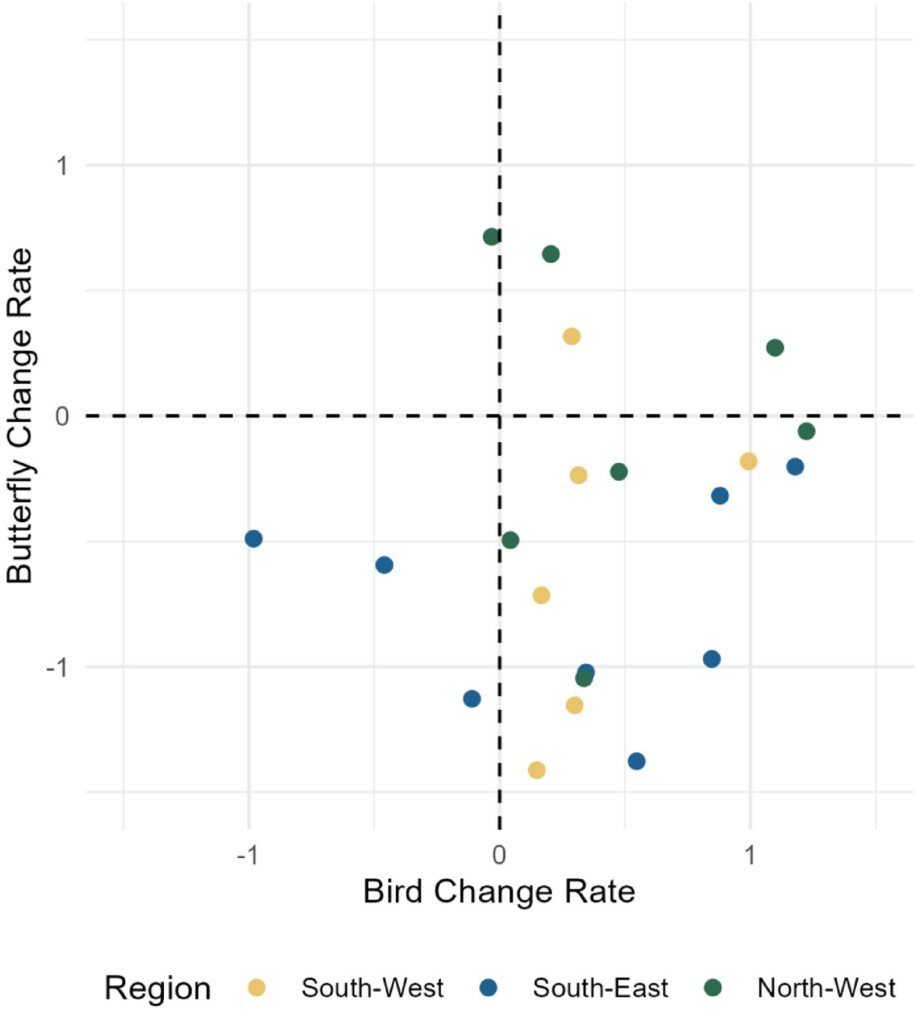

Fig. 3 The abundance change rate of birds and butterflies for the 21 shared study sites in the three different regions (South-West, South-East, North-West), where change rate between end points are positively correlated but not significantly so, since the majority of points lie in the quarter of positive bird but negative butterfly change rate (bottom right; Model C)

butterflies were not disproportionately affecting more habitat-specific species, smaller species, or species less adapted to cold temperatures, and variation in species-specific farmland bird abundance trends were not explained by these characteristics at all.

Bird and butterfly abundance trends

Our first and second hypotheses were not supported: birds and butterflies showed different trends at national, regional and site level. The decline in butterfly abundances was expected as such changes have been documented both in Finland (Kuussaari et al. 2007a; Kotiaho et al. 2005; Heliölä et al. 2022; Kukkonen et al. 2022) and worldwide (Wepprich et al.

2019; Warren et al. 2021; Edwards et al. 2025), particularly in agricultural areas (Warren et al. 2021). Butterfly species restricted to non-forest habitats, such as farmlands, have been found to be at a greater risk of extinction (Franzén and Johannesson 2007). Whereas our results suggest a general decline in butterfly numbers across species, in particular in the South-Eastern region, agricultural intensification has earlier been shown to reduce butterfly diversity (Kivinen et al. 2007; Ekroos et al. 2010). Similarly, intensive grazing on semi-natural grasslands has been linked with butterfly diversity decline (Nilsson et al. 2013). In contrast to butterflies, it is surprising that our results did not coincide with trends of farmland bird declines documented nationally and globally (Laaksonen and Lehikoinen 2013; Rigal et al. 2023; Carrascal et al. 2023). On the contrary, farmland bird populations in our study area seemed to be stable or partly even slightly increasing when regional differences were considered. This could be driven by certain species included in our analyses. In particular, many species breeding along farmland edges have increased recently in Finland, such as jackdaw *Corvus monedula* and Eurasian tree sparrow *Passer montanus* (Lehikoinen et al. 2024). It is also worth noting that our species list includes more than just the Farmland Bird Index species that have shown declines in their trends within Finland (Lehikoinen et al. 2024). However, our additional analyses on the species included in the Finnish Farmland Bird Index did not show declines, and therefore the discrepancy cannot be explained by how the species assemblage was delineated.

Furthermore, our results indicated that regional trends were not significantly different between birds and butterflies within this study context. The lack of regional differences between taxa indicate that similar drivers, such as agricultural management and landscape structure for example through intensification or land abandonment, are affecting bird and butterfly species similarly, across our study regions (Zingg et al. 2018). Between regions, both taxa have more negative abundance trends in South-East Finland compared to South- and North-West Finland. Previous research indicates that differences in regional conditions, such as precipitation and temperatures, as well as agricultural practices, can impact spatial variation in abundances of species (Crossley et al. 2021; Jerrentrup et al. 2017). For example, Southwestern Finland is a stronghold for cereal production while Northeastern Finland relies heavily on animal production (Tiainen et al. 2020) and these cause spatial variation in abundances of species (Lehikoinen et al. 2024). It is possible that the landscape characteristics, including differences in landscape structure and changes from mixed farming to specialised farming, particularly in South-East Finland, has disproportionately affected both birds and butterflies (Tiainen et al. 2020).

We also did not find similar abundance change rates between taxa based on the site-level comparison, although we had only 21 sites in this comparison. In fact, amongst the species included in this study, changes in bird abundances have been predominantly positive, in contrast to butterflies (Fig. 3). Results of our first and second study questions clearly indicate that different factors are driving the abundance trends of birds and butterflies. Insect populations including butterflies can have strong year to year variations (Heliölä et al. 2022), which may cause stochasticity in the trends compared to birds. It is well known that population sizes of insects can show substantial annual variation (Heliölä et al. 2022). The observed significant butterfly decline cannot be attributed to peak butterfly years for counts, as all the observation years fall into average years according to annual monitoring (Heliölä et al. 2022; Kuussaari et al. 2024). In addition, studies have shown that birds are not as strongly associated to specific habitats than butterflies, and therefore less likely to respond to them in the same way or to the same extent as butterflies (Debinski et al. 2006; Zingg et al. 2018; Anderle et al. 2024). Therefore, it could be that (some of) the butterfly species analysed within this study reflect those that are less sensitive to local field level farming practices, as most utilise field borders or semi natural grasslands, rather than the field itself, and that their decline could be linked to more specific habitat changes, such as larval host plant species abundances. On the other hand, the bird species taken into account could be those that favour landscape management changes on arable land, such as set-asides or fallow areas under agri-environmental schemes, supporting their abundance trends (cf. Peltonen-Sainio and Jauhiainen 2019; Tiainen et al. 2020; Ekroos et al. 2019; Bosco et al. 2024). Finally, birds respond to changes at larger spatial scales compared to butterflies, which have stronger habitat affinities and therefore being more sensitive to small-scale habitat changes that are not necessarily directly impacted by field-level factors (Ekroos et al. 2013; Zingg et al. 2018).

In summary, different trends of birds and butterflies could be caused by (but not mutually exclusive to) differing habitat preferences between taxa (Ekroos et al. 2013; Zingg et al. 2018), bias through abundant stable/increasing species (Lehikoinen et al. 2024), the different spatial scale used by the taxa (Debinski et al. 2006; Zingg et al. 2018; Anderle et al. 2024), changes of land use and management in fields that primarily would benefit birds (Peltonen-Sainio and Jauhiainen 2019; Tiainen et al. 2020), or for reasons that the larger climatic and habitat factors analysed in this study were not specific enough to explain the abundance trends. We also note that the marginal R^2 ranged between 5 and 10% in our models, and therefore that effects of time, region and taxonomic group had rather low explanatory power. Conditional R^2 in turn was high, around 70%, demonstrating that random effects of species and sites explained a large proportion of the overall variation.

Species-specific traits

None of the species-specific traits tested showed a significant link to abundance changes, contrary to what was hypothesized. As such, our results suggest that determinants of changes in abundances over time are very species-specific. First, the species temperature index did not affect either taxon abundance change, which is contrary to the findings of other studies (Bowler et al. 2015; Hällfors et al. 2024). Previous research has found a faster northward shift in butterflies when compared to birds with the warming climate (Devictor et al. 2012). However, our results revealed no effect with species temperature index on the abundance trends seen, indicating that species abundance trends of birds and butterflies were not connected with the characteristics of their climatic niche (e.g. Jiguet et al. 2010). Our expectation that warm-dwelling species would have more positive population trends than cold-dwelling species was thus not supported. Whilst it is likely that in some species climate change is an important driver of abundance changes (sensitivity analysis Appendix Table S6), our results suggest that other ecological mechanisms, e.g. related to resource use, are more important drivers of abundance change. It is also possible that climate change has had indirect effects via land-use change, but these effects may be masked by strong differences between individual species.

Secondly, the body mass of the taxon did not influence the abundance changes. As body size is hypothesised to be correlated with mobility (Sekar 2012; Thornton and Fletcher 2014), it could have been expected that body size could explain the difference in abundance changes within the two taxa (Kuussaari et al. 2021). Additionally, larger body size in species has been shown to have wider spatial responses to landscape scale changes (Thornton and Fletcher 2014). However, this was not the case in our study, with other drivers affecting the change, potentially related to more specific resource use.

Finally, habitat breadth of species was not found to significantly affect the abundance change of the taxa. Although habitat breadth has been linked to population trends through a decline in species with narrow niche breadths (Julliard et al. 2004; Kuussaari et al. 2007a; Siriwardena et al. 1998), the availability of habitats is a key requirement for this to be applicable. Land management shapes the available habitat and this may have been a larger driver of abundance trends rather than a species habitat breadth (Zingg et al. 2018). However, our study focuses on the most common species and we are thus unable to determine the impact of habitat breadth on rare species (Seoane and Carrascal 2008). Although we have good ecological reasons to expect habitat breadth to be important in general terms, the availability of complementary habitats e.g. for feeding and reproduction (nest sites or larval resources) may be important in mosaic farmland (Tiainen et al. 2020; Bosco et al. 2024). Such effects can be highly species-specific, which in turn can explain why broader characterisations of our study species cannot explain observed changes.

Therefore, our results suggest that other factors than used species specific traits of our study should be taken into consideration when explaining the trend differences between the taxa. It is possible that traits more directly related to resource use, or reproductive success, could shed more light on underlying ecological mechanisms. We also note that our analyses did not account for phylogenetic relatedness, which could mask more subtle effects of species-specific traits (Pöyry et al. 2009).

Conclusion

Our study revealed that farmland birds and butterflies, common indicators of farmland biodiversity listed also in the EU restoration law (EU Regulations 2024/1991), do not show similar trends in abundance changes over the last 22 years in Finland, highlighting that interventions in agriculture intended to strengthen biodiversity need to consider different requirements between taxa. Additionally, species-specific traits tested in this study seem secondary in explaining abundance changes in birds and butterflies. Farmland birds utilising larger landscape scales may be able to respond more swiftly to favourable changes in local land use and management, and hence in particular interventions that are short-aged in nature may benefit birds but not butterflies. On the other hand, butterflies are more dependent on semi-natural landscape elements with specific larval host plants, and hence biodiversity indicators based on farmland birds and butterflies are likely to reflect changes in different aspects of farmland ecosystems. Thus, our results highlight the importance of considering multiple indicator taxa to determine the impact of agriculture on biodiversity, and general farmland biodiversity declines should not be inferred solely based on one taxonomic group.

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Declarations

Competing interests The authors declare no competing interests.

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