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LETTER

A cross-regional analysis of red-backed shrike responses to agri-environmental schemes in Europe

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Abstract

Agri-environmental schemes (AES) are the main policy tool to counteract farmland biodiversity declines in Europe, but their biodiversity benefit varies across sites and is likely moderated by landscape context. Systematic monitoring of AES outcomes is lacking, and AES assessments are often based on field experiments encompassing one or few study sites. Spatial analysis methods encompassing broader areas are therefore crucial to better understand the context dependency of species' responses to AES. Here, we quantified red-backed shrike (*Lanius collurio*) occurrences in relation to AES adoption in three agricultural regions: Catalonia in Spain, the Mulde River Basin in Germany, and South Moravia in the Czech Republic. We used pre-collected biodiversity datasets, comprising structured and unstructured monitoring data, to compare empirical evidence across regions. Specifically, in each region we tested whether occurrence probability was positively related with the proportion of grassland-based AES, and whether this effect was stronger in simple compared to complex landscapes. We built species distribution models using existing field observations of the red-backed shrike, which we related to topographic, climatic, and field-level land-use information complemented with remote sensing-derived land-cover data to map habitats outside agricultural fields. We found a positive relationship between AES area and occurrence probability of the red-backed shrike in all regions. In Catalonia, the relationship was stronger in structurally simpler landscapes, but we found little empirical support for similar landscape-moderated effects in South Moravia and the Mulde River Basin. Our results highlight the complexity of species' responses to management across different regional and landscape contexts, which needs to be considered in the design and spatial implementation of future conservation measures.

1. Introduction

Farmland covers almost half of Europe's land area, and is experiencing major biodiversity losses due to agricultural intensification, changes in land-use and landscape structure and farmland abandonment (Queiroz *et al* 2014, Kehoe *et al* 2017, Reif and Vermouzek 2019). Agri-environmental schemes (AES) are a major policy tool of the European common agricultural policy, designed to halt the deterioration of agroecosystems (Batáry *et al* 2015). Participation in AES is voluntary, and participating farmers are compensated for income losses associated with reducing farming intensity and maintaining or creating landscape elements such as tree lines, hedgerows and wetlands (Batáry *et al* 2015).

AES are among the biggest conservation expenditures in Europe (Batáry *et al* 2015). However, their effectiveness in enhancing biodiversity is repeatedly questioned, as different studies have found mixed support (Kleijn and Sutherland 2003, Concepción and Díaz 2019). While differences in study design may be one reason underpinning apparent variation in AES outcomes (Josefsson *et al* 2020), AES effectiveness is also likely moderated by the landscape context (Kleijn *et al* 2011). The intermediate landscape-complexity hypothesis (Tscharntke *et al* 2012) postulates that AES effectiveness is highest in structurally simple, rather than in extremely simplified or very complex landscapes. This is due to floor and ceiling effects, wherein AES measures cannot enhance biodiversity in highly modified, ecologically depleted landscapes, or effects are negligible in complex landscapes where biodiversity is already high (Tscharntke *et al* 2012). A meta-analysis by Batáry *et al* (2010) found cross-taxon evidence supporting this hypothesis in cropland but not in grassland areas, whereas in the synthesis by Scheper *et al* (2013) pollinators responded more positively to AES in simple compared to cleared or complex landscapes across agricultural land-use types, but with larger effect sizes in croplands than in grasslands. Farmland birds also responded more strongly to cropland-based AES in the synthesis by Staggenborg and Anthes (2022). This highlights the need for further research on how to improve the effectiveness of grassland-based AES.

Combining effect sizes from very different landscape contexts, study designs and taxa presents a challenge to meaningful interpretation and generalisation of such syntheses (Spake *et al* 2022). High variability in responses to AES may arise from overlooked effect modifiers, differences in spatial scales or in baseline biodiversity across studies (Spake *et al* 2022). Formal full-data analyses are therefore better suited for modelling context-dependent variations in ecological effects (Spake *et al* 2022, 2023). However, data availability limits large-scale, spatially-explicit empirical assessments due to a lack of systematic monitoring of AES impacts on biodiversity across Europe (Pe'er *et al* 2022). As a consequence, most AES studies rely on field observations collected in one or few regions (Hiron *et al* 2013, Concepción and Díaz 2019, Sharps *et al* 2023), typically within the same country (but see Concepción *et al* 2012, Kleijn *et al* 2006). An alternative approach is to use pre-collected biodiversity data from existing national monitoring schemes or from semi- or unstructured databases (i.e. opportunistic observations collected without following formal sampling protocols; Arazy and Malkinson 2021). In this case, additional effort is required to ensure the quality of the data and to correct for biases in monitoring effort and detection probability (Arazy and Malkinson 2021). Here, we used bird observations from three (sub)national biodiversity databases and field-level land-use data to study the responses of the red-backed shrike (*Lanius collurio*) to the area of grassland-based AES. These schemes involve the extensive management of permanent grassland, such as reduced mowing or grazing, or the protection of species-rich fields. We used species distribution models to model the effect of AES and other environmental covariates on the shrike's occurrence probability in three agricultural regions located in Spain, Germany and the Czech Republic. Moreover, we investigated the context dependency of AES effectiveness in these three regions using a recently developed analytical framework (Spake *et al* 2019). Specifically, we sought to: (i) quantify relationships between the area of grassland-based AES and red-backed shrike occurrence across three study regions, (ii) evaluate whether AES yield larger increases in occurrence probability in structurally or compositionally simple landscapes, relative to complex landscapes, and (iii) determine whether (landscape-moderated) AES relationships are similar across regions. Such understanding is crucial to inform future land-management decisions and to improve the spatial allocation of AES to maximise their effectiveness.

2. Methods

2.1. Study regions

Our analysis encompassed three study regions in Europe: Catalonia (32 106 km^2) in Spain, the Mulde River Basin (5814 km^2) in Germany, and South Moravia (2089 km^2) in the Czech Republic (figure 1). The regions vary considerably in their climatic and topographical parameters and encompass different agricultural systems (Beckmann *et al* 2022). Cropland is the predominant land-cover type in the Mulde River Basin and in South Moravia. In contrast, Catalonia's farmland is more evenly split between cropland, fruit orchards (including olive, nut, citrus groves and vineyards), and grassland. In all regions, grasslands are abundant in the mountainous areas, i.e. in the Ore Mountains in the Mulde River Basin, in the White Carpathians in South Moravia, and in the Pyrenees in Catalonia. In 2019, 45% out of the 317 km^2 of grassland in South Moravia was under AES management; 18% out of the 1154 km^2 in the Mulde River Basin, and 2.5% out of 5215 km^2 in Catalonia.

2.2. Study species and datasets

We selected the red-backed shrike, a carnivorous passerine, as study species as its breeding range spans most of Europe and its observations are abundant across the three regions in the utilised datasets. High-quality habitats for this species consist of open grasslands and bare areas with scattered bushes, shrubs or low trees that provide perches and hunting posts (BirdLife International 2023), making it an ideal species to investigate the regulatory effects of landscape complexity on grassland-based AES. Its population declined dramatically between 1970 and 1990, likely due to loss of habitat and food resources resulting from agricultural intensification, though in Europe

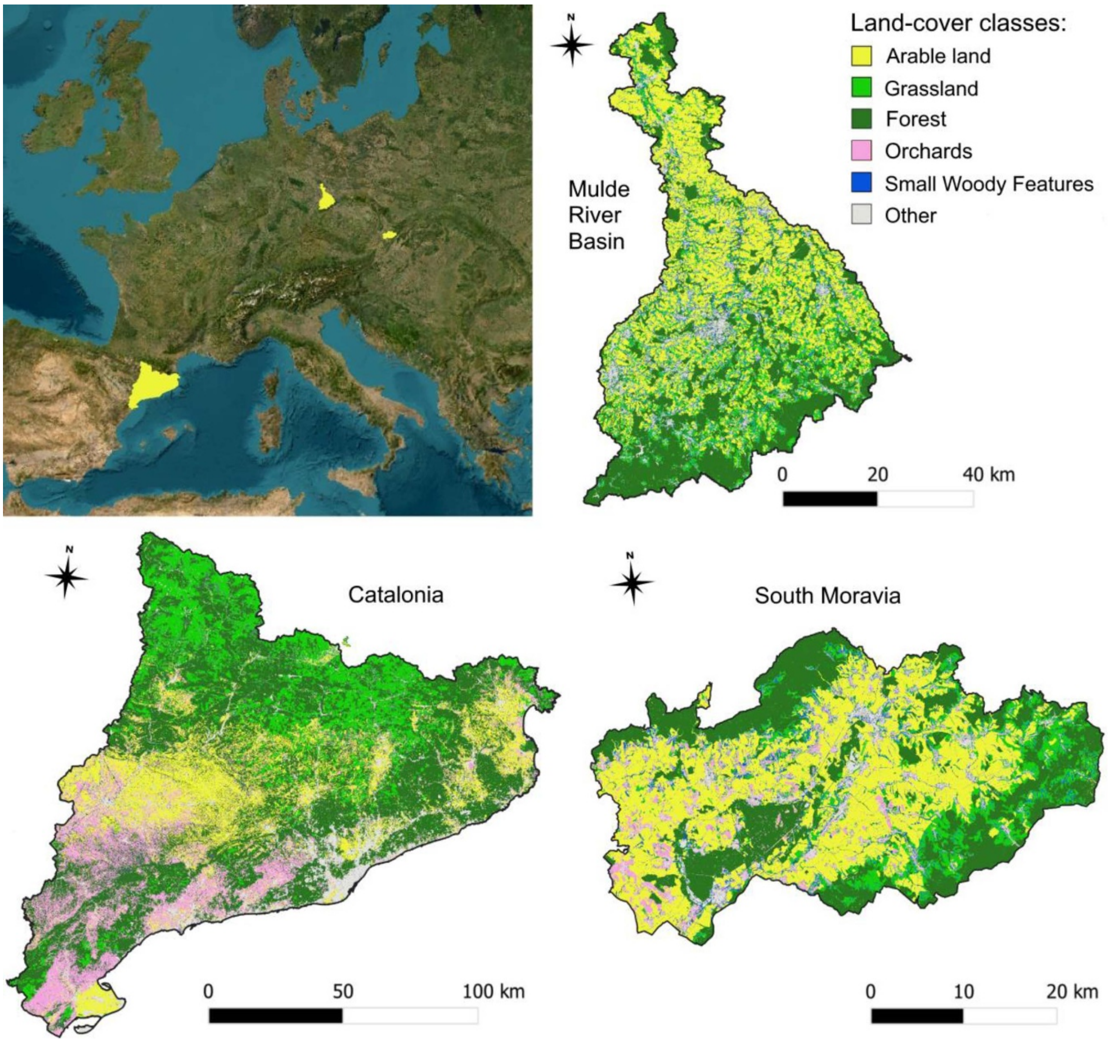

Figure 1. Location of the three study regions in Europe and their land-cover maps (see the methods subsection *Environmental data* for data sources and preparation). Satellite data source: © ESRI World Imagery.

numbers appear to have stabilised since (BirdLife International 2023).

We collated red-backed shrike records and those of other farmland species to generate pseudo-absence points, assuming that grid cells with records of other farmland birds were monitored and that the red-backed shrike was absent if not recorded. This assumption is reasonable for the red-backed shrike, a readily-identifiable species in both professional and citizen science projects (Dylewski *et al* 2017). This 'target-group approach' is a common and effective method to generate pseudo-absences and correct for spatial biases in biodiversity data, thus improving model performance, when monitoring effort is discontinuous (Phillips *et al* 2009, Ranc *et al* 2017). For the target group, we used species included in the European farmland bird index (Gamero *et al* 2017), which we complemented, separately for each region, with other common farmland species typical of Spain (Traba and Morales 2019), Germany (Busch *et al* 2020), or the Czech Republic (Hanzelka *et al* 2015). The complete list of species for each region is reported in table S1.

The datasets are sourced from (sub)national biodiversity databases curated by the Catalan Ornithological Institute (Catalonia), the Saxon State Agency for Environment, Agriculture and Geology (Mulde River Basin) and the Nature Conservation Agency of the Czech Republic (South Moravia). They include observations from standardised monitoring projects (breeding bird and Natura2000 monitoring) and opportunistic observations (e.g. from citizen science projects and special interest groups), which have been collated in the databases by the aforementioned institutions. The Catalan bird data was downloaded from the Global Biodiversity Information Facility in the form of a 1 × 1 km grid for the year 2019 (GBIF.org 2021). The bird data for the Mulde River Basin and for South Moravia were directly provided by the owning institutions as geolocalised point records. We filtered all datasets to remove observations with incomplete scientific names or missing year flags. To harmonise the spatial resolution of our models across regions, we aggregated the German and Czech point datasets to a 1 × 1 km grid (where grid cells containing a point observation were used as presences), matching the structure of the Catalan dataset. While the Catalan dataset for 2019 has a fairly good coverage of the whole region (figure S1), the spatial coverage in the German and Czech datasets varied considerably across years (figures S2 and S3). To increase sample size and spatial coverage in these two regions, we pooled data from 2016 to 2019, for which data on AES adoption was also available. If the same grid cell was monitored multiple times, we retained the most recent record. While species–environment relationships may vary across years, the red-backed shrike is a philopatric species, generally returning to the same breeding sites (Pasinelli *et al* 2007). Therefore, combining data from this limited time period is unlikely to bias our inferences on species–environment relationships.

2.3. Environmental data

We collated environmental variables known to influence the red-backed shrike distribution (Brambilla *et al* 2009, Roilo *et al* 2023). For each 1 km grid cell, we extracted the mean elevation (m; ELEVATION) from the Copernicus EU-DEM v1.1 and the maximum temperature (°C, TMAX) and the sum of mean monthly precipitation (mm, PRECIP) between May and July, corresponding to the red-backed shrike breeding period, from the CHELSA Climatologies 1981–2010 V2.1 (Karger *et al* 2017, 2020). Field-level information on land use (permanent grassland, crops or orchards) and adopted AES was available from the Integrated Administration and Control System (IACS) data provided by the Ministry of Climate Action, Food and Rural Agenda of Catalonia, the Saxon State Ministry for Energy, Climate Protection, Environment and Agriculture, and the Ministry of Agriculture of the Czech Republic. We focused on grassland-based AES and considered all those aimed at preserving extensively-managed and species-rich permanent grassland fields by preventing or reducing mowing pressure and the use of fertilisers and pesticides (table S2). The Catalan IACS data cover both agricultural and non-agricultural areas, and was hence used as base layer for the land-cover map and was complemented with the Copernicus Small Woody Features (SWF) 2015 layer. In the Mulde River Basin and in South Moravia, the IACS data only cover the agricultural parcels; we therefore rasterised and overlaid them onto the S2GLC Europe 2017 land-cover map (Malinowski *et al* 2020), again complemented by the SWF 2015 layer. From the resulting land-cover maps, we calculated the proportion of area covered by arable land (ARABLE), permanent grassland (GRASS), orchards (fruit and nut orchards, vineyards, olive and citrus groves; ORCHARD), SWF (SHRUBS), forest and other closed vegetation (broadleaf and coniferous forests, woodland, moor- and heathlands; FOREST). Moor- and heathlands are infrequent in the study regions but were classified as such as they provide closed ground cover for prey. Land-cover diversity (LANDDIV) in each grid cell was calculated using the Shannon diversity index as:

$$\mathrm{LANDDIV} = -\sum p_i \times \ln(p_i)$$

where p_i is the relative proportion of land-cover type i. The finest thematic resolution of the land-cover rasters was used, so that different e.g. forest (broadleaf, coniferous) and orchard types (fruits, nuts, vineyards, etc) counted as different land-cover types. We calculated the proportion of grassland-based AES from the IACS data for the year matching the bird monitoring data, which was 2019 in Catalonia and the year in which each grid cell was last monitored (between 2016 and 2019) in the Mulde River Basin and South Moravia.

Prior to modelling, we filtered the datasets to restrict our analysis to areas which could plausibly constitute red-backed shrike habitat. As we focused on grassland-based AES, we excluded grid cells with less than 1 ha of permanent grassland, which is the approximate territory size of the species (Brambilla *et al* 2009). The Catalan dataset (Roilo 2023) was additionally filtered to remove grid cells at elevations below 200 m a.s.l. and above 2000 m a.s.l., which are outside the altitudinal range limits of the red-backed shrike in Catalonia (Rodríguez-Franch *et al.*, 2021). Data preparation and statistical analyses were performed in R version 4.1.3 (R Core Team 2022; Roilo 2024).

2.4. Statistical analysis

We used generalised linear models (GLMs) to model the relationship between shrike occurrence and AES area in the three regions. We were primarily interested in the effect of AES and its potential interaction with landscape-structure moderators (SHRUBS and LANDDIV), which necessitated common support of AES across the ranges of SHRUBS and LANDDIV (Hainmueller *et al* 2019, Duncan and Kefford 2021). This means that, to compute the marginal effect of AES at a given value x_0 of a moderator, there needs to be sufficient observations of the moderator close to x_0 and variation in AES at x_0 (Hainmueller *et al* 2019, Duncan and Kefford 2021). To ensure this, and check whether the interaction effect between AES and its moderator(s) was reasonably linear on the scale of the linear predictor as assumed by the GLM, we produced linear interaction diagnostic plots using the R package interflex (Hainmueller *et al* 2019, 2021). We detected a lack of common support at the upper range of AES in all regions, as grid cells containing large areas of AES were rare (figures S4–S9). We therefore trimmed the datasets by setting upper limits to the range of AES at the 90th percentile of its value distribution, reducing the datasets to 2016 data points (1 km^2 grid cells) in Catalonia, 1113 in the Mulde River Basin, and 789 in South Moravia. To test the robustness of the results to different trimming approaches, we conducted a sensitivity analysis using two additional cutoff values, the 95th and 99th percentiles. The results were qualitatively similar across trimming approaches (tables 1, S3 and S4). Additionally, we checked that AES were not highly correlated with SHRUBS and LANDDIV, as this could lead to spurious interactions (Duncan and Kefford 2021). Absolute Spearman's correlation coefficients were always <0.2 between AES and LANDDIV and between AES and SHRUBS across all regions (figures S10–S12).

We standardised (z-scored) all explanatory variables and then fitted a global GLM with binomial distribution with the following model structure:

shrike_occurrence ∼ AES + ARABLE + GRASS + ORCHARD + FOREST + SHRUBS + LANDDIV + TMAX + PRECIP + ELEVATION + AES:SHRUBS + AES:LANDDIV.

To test for interactive effects of landscape complexity on AES effectiveness, we included two interaction terms: one for structural complexity (approximated by the SHRUBS cover) and one for compositional complexity (LANDDIV). In the Mulde River Basin, ORCHARD was excluded from the predictors since the area covered by permanent cultures is negligible. We fitted the global model and all its submodels, ranking them by their Akaike information criterion score corrected for sample size (AICc) using the MuMIn package (Barton 2022). Highly correlated pairs of variables (i.e. with an absolute Spearman's correlation coefficient > 0.7, figures S10–S12) were excluded from the same model. For the best model (with lowest AICc) in each region, diagnostic plots of model residuals were produced using the DHARMa package (figures S13–S15; Hartig 2022). We tested for spatial autocorrelation in the model residuals by means of spline correlograms using the ncf package (figures S16–S18; Bjornstad 2022). In the Mulde River Basin, spline correlograms showed evidence for spatial dependence, so we refitted the models as generalised additive models with a Gaussian process spline function of latitude and longitude using the mgcv package (Wood 2017, 2020). We set the smoothing basis dimension (k) to 150 and confirmed its adequacy using the gam.check( ) function of the same package.

To identify the most important predictors of red-backed shrike occurrence in each region and evaluate the evidence for a landscape-moderated effect of AES, we calculated the relative importance values for each predictor based on the sum of model weights across all models with substantial empirical support (with ΔAICc < 2; Burnham and Anderson 2002). To display the effect of each predictor, and of their interactions, on the occurrence probability of the red-backed shrike, we produced conditional plots graphed on an additive scale (probability), rather than the modelled scale (for ease of interpretation; Spake *et al* 2023), using the visreg package (Breheny and Burchett 2017). We produced maps of the probability of shrike occurrence by projecting the models to two land-use scenarios: the current AES adoption scenario, based on 2019 IACS data, and a hypothetical scenario in which all permanent grassland fields are converted to AES. Lastly, we produced an 'effect map' (Spake *et al* 2019), as the arithmetic difference between the two scenarios' projections, which visualises the change in occurrence probability of the shrike between the two scenarios, i.e. after the conversion of all grassland to AES.

3. Results

AES had a positive effect on shrike occurrence probability in all modelled regions (table 1). SHRUBS had positive coefficients across all regions and was included in all models with ΔAICc < 2 (relative importance score = 1 in all regions). In Catalonia and in South Moravia the interaction term AES:SHRUBS was selected among the predictors of top-ranking models with a negative coefficient, supporting the hypothesis of a higher AES effectiveness in structurally simpler landscapes. LANDDIV was positively related to shrike occurrence probability in all regions. The interaction term AES:LANDDIV was included in the 5th-ranked model for Catalonia with a low-valued but positive regression coefficient (0.03; table S5), indicating higher AES effectiveness in more compositionally diverse landscapes.

The adjusted R^2 was low in all Catalan (0.20) and South Moravian (0.05–0.07) models, but was higher in the models of the Mulde River Basin (0.58–0.60), in which the spatial Gaussian process spline explained much of the variation in the data (tables S5–S7).

The conditional plots of the best model in Catalonia showed that the positive effect of AES on the occurrence probability of the red-backed shrike was lower in landscapes with a high SHRUBS cover, even turning negative when SHRUBS was very high (figure 2). On the other hand, increasing LANDDIV had an opposite, though much less pronounced effect, with higher AES effectiveness in landscapes with higher land-cover diversity.

In the Mulde River Basin, none of the models with ΔAICc < 2 included an interaction term. The best model showed no evidence of a landscape-moderated effect of SHRUBS on AES (figure 3). Confidence intervals in the conditional plots were broad, likely because of the flexible Gaussian process spline added to the model to correct for spatial autocorrelation in the model residuals.

Table 1. Relative importance scores of model predictors, based on the sum of model weights across all models with ΔAICc < 2, calculated separately for each region and after trimming the dataset to the 90th percentile of AES. *Direction of effect* is + if the predictor's estimated coefficient is positive and − if it is negative. Estimated coefficients of all models are presented in tables S5–S7. Relative importance scores marked with bold indicate the predictors included in the best model (with lowest AICc) in each region. The term *s(X, Y, bs = 'gp', k = 150, m = 2)* is the Gaussian process spline used to correct for spatial autocorrelation in the model residuals. AES = grassland-based agri-environment schemes; LANDDIV = land cover diversity; SHRUBS = small woody features; ARABLE = arable land; ELEVATION = mean elevation; FOREST = forest and other closed vegetation; GRASS = permanent grassland; ORCHARD = fruit and nut orchards, vineyards, olive and citrus groves; PRECIP = precipitation; TMAX = maximum temperature.

	Catalonia		Mulde River Basin		South Moravia	
	Relative importance	Direction of effect	Relative importance	Direction of effect	Relative importance	Direction of effect
AES	**1.00**	+	**0.26**	+	**0.61**	+
AES:LANDDIV	0.10	+				
AES:SHRUBS	**1.00**	—			0.06	—
ARABLE	0.45	+			**1.00**	+
ELEVATION	**1.00**	+			0.14	—
FOREST	**1.00**	+	0.14	+	**1.00**	+
GRASS	**1.00**	+	0.38	+	**1.00**	+
LANDDIV	**0.72**	+	0.12	+	0.20	+
ORCHARD	**0.87**	—			**1.00**	+
PRECIP			**0.88**	+	0.14	—
SHRUBS	**1.00**	+	**1.00**	+	**1.00**	+
TMAX					**0.38**	+
s(*X*, *Y*, *bs* = 'gp', *k* = 150, *m* = 2)			**1.00**	/		

In South Moravia, the best model did not include any interaction term, and the conditional plots of AES at low, middle and high values of SHRUBS did not display any large interactive effect between the two variables (figure 4).

The maps of effect produced using the best model for each region showed large increases in occurrence probability in all regions (figure 5; figure S19). While in the Mulde River Basin and in South Moravia the changes in occurrence probability were only positive and varied in strength depending on the amount of converted grassland (figure S19), in Catalonia the map of effect showed negative changes following grassland conversion to AES in certain landscapes with very high SHRUBS cover (e.g. in the northern tip of Catalonia; figure 5).

4. Discussion

4.1. Implications of the utilised bird datasets

Our analysis used existing bird monitoring data derived from (sub)national datasets integrating multiple data sources. As such, we had no control over the spatial and temporal patterns in the monitoring effort, and our *post-hoc* study design (i.e. focal and target-group species selection, dataset filtering and trimming to reach substantial common support) aimed to correct for such biases and to illustrate approaches to using 'imperfect' biodiversity data. Such approaches are particularly relevant as unstructured biodiversity databases are increasingly used in research and hold great potential for ecological applications (Brown and Williams 2019, Heberling *et al* 2021). While several studies have investigated AES effects on bird abundance or species diversity, the majority of studies are conducted at relatively small extents, typically in cropland areas in the United Kingdom, Germany or the Netherlands (Staggenborg and Anthes 2022, but see Billeter *et al* 2008, Concepción *et al* 2012, Sasaki *et al* 2020 for cross-country examples). Here, we collected cross-regional evidence of AES effects on red-backed shrike occurrence. This was made possible by the availability of existing bird data, as extensive fieldwork spanning three large regions would not have been feasible. A main concern of using semi-structured datasets is whether causal relationships can be reliably inferred (Josefsson *et al* 2020). In this paper, we defined AES effectiveness as the estimated regression coefficient of AES in our models, rather than as an effect size measured in a field experiment. Nonetheless, our methodology is reliable in detecting and describing correlative relationships between AES cover and shrike occurrence across different regions, which we detail in the next section.

4.2. Cross-regional variability in landscape-moderated AES effectiveness

In all regions, we found positive relationships between the area of AES and the probability of red-backed shrike occurrence. These findings are important as they contribute to the relatively scarce literature on AES assessments in grasslands: the meta-analysis by Staggenborg and Anthes (2022) on effect size estimates of European AES on farmland birds reviewed 129 studies, of which only 27 were in grassland-dominated areas.

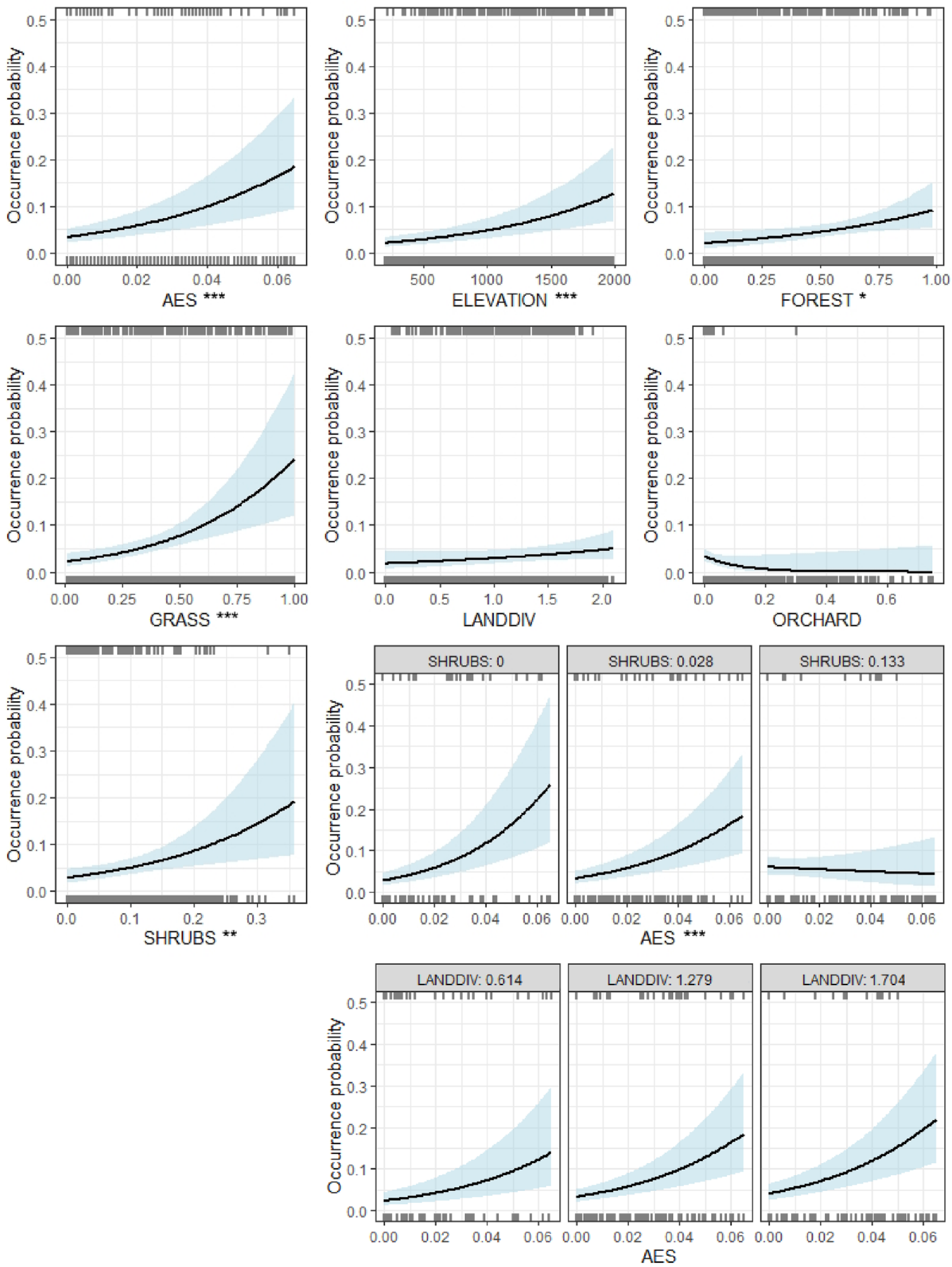

Figure 2. Conditional plots displaying the effect of the predictors included in the best model for Catalonia on the occurrence probability of the red-backed shrike. Relationships were graphed for each predictor with all other covariates held at their medians. To visualise interactive effects of SHRUBS and LANDDIV with AES, plots describing the effect of AES on occurrence probability were produced for the 10th, 50th and 90th percentiles of their value distributions. As logistic regressions are inherently interactive (Spake *et al* 2023), plots were produced also for the interaction term AES:LANDDIV, though it was not among the predictors of the best model. Shading shows average estimated standard errors. Ticks on the upper and lower border of the plots represent data points. Asterisks indicate whether predictors are significant at the 0.05 (*), 0.01 (**), or 0.001 (***) levels.

Our results showed that the positive effect of AES on shrike occurrence probability diminished at high levels of structural landscape complexity (SHRUBS), though at varying degrees across regions. Differences in the environmental subniches among shrike populations may be the cause (Chandler *et al* 2022). The red-backed shrike is considered a farmland species throughout Europe, but has been shown to inhabit

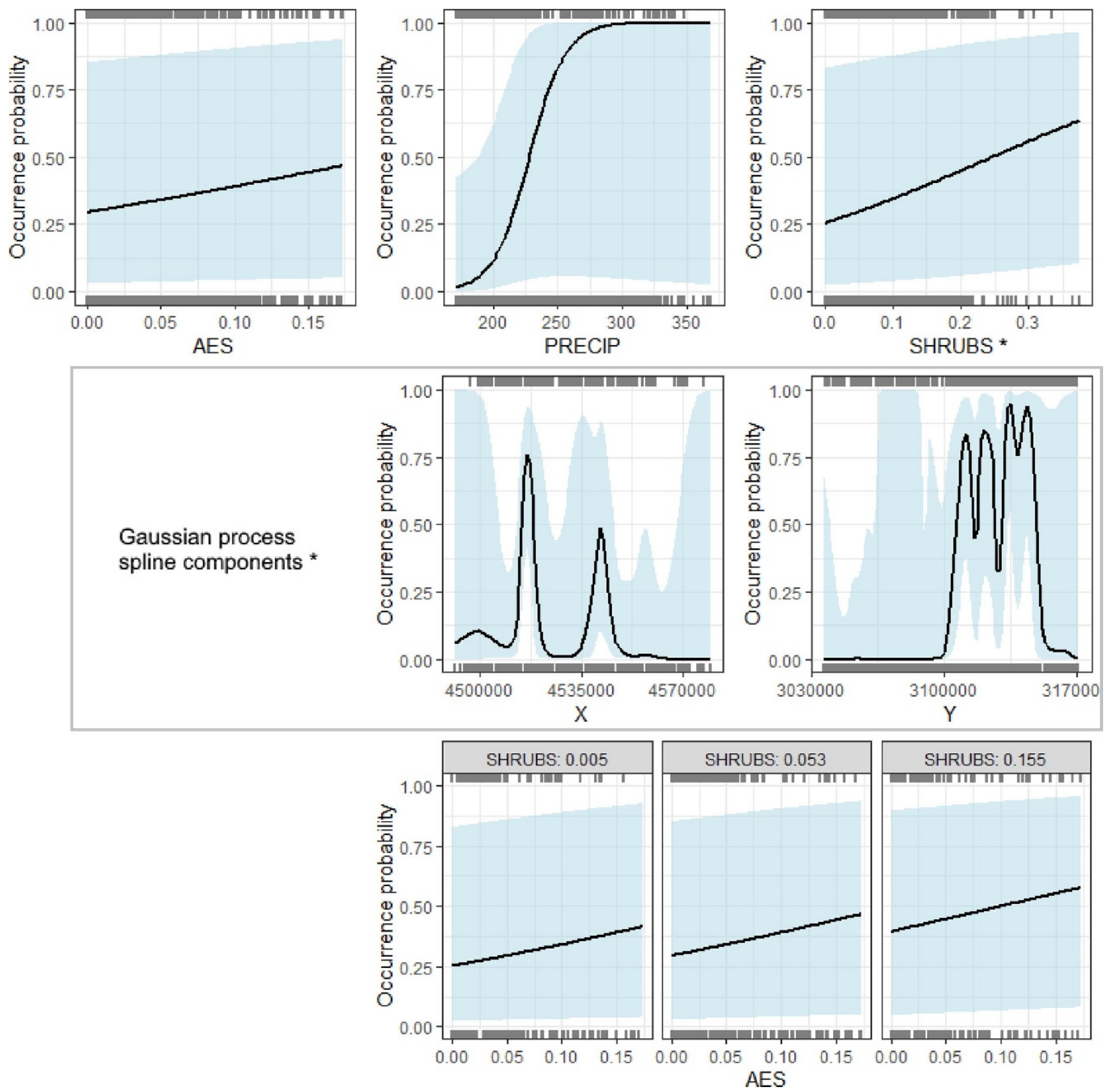

Figure 3. Conditional plots displaying the effect of the predictors included in the best model for the Mulde River Basin on the occurrence probability of the red-backed shrike. Relationships were graphed for each predictor with all other covariates held at their medians. Conditional plots for the spatial covariates (*X* and *Y*) included in the Gaussian process spline are also shown. The interaction term AES:SHRUBS was not among the predictors of the best model, however logistic regressions are inherently interactive (Spake *et al* 2023). Thus, to visualise potential interactive effects of SHRUBS with AES, plots describing the effect of AES on occurrence probability were produced for the 10th, 50th and 90th percentiles of the value distribution of SHRUBS. Shading shows average estimated standard errors. Ticks on the upper and lower border of the plots represent data points. Asterisks indicate whether predictors are significant at the 0.05 (*) level.

forest clear-cuts in Scandinavia, displaying high plasticity in its habitat preferences (Bakx *et al* 2020). Applying our analytical framework to boreal habitats could clarify how landscape context moderates habitat suitability of different clear-cuts for this species.

Cross-regional differences in landscape-moderated effects may also be due to differences in landscape configuration. While field size does not vary much within regions, it is on average much smaller in Catalonia (0.7 ha) than in the other two regions (∼6 ha; Beckmann *et al* 2022), resulting in a lower edge density in the latter. This or other factors, like baseline land-use intensity or ecological contrast (i.e. the difference in resource availability between AES and the surrounding conventionally-managed fields, Marja *et al* 2019), could be affecting the habitat selection of the red-backed shrike or masking landscape structure effects in the Mulde River Basin and in South Moravia.

Compositional landscape complexity (LANDDIV) was not often selected as a predictor in our models, and only in Catalonia we detected an interactive effect of LANDDIV and AES. Contrary to our expectations, this interaction was positive, although weak. This may be because unsuitable land-cover types (e.g. urban areas, water bodies) also contribute to land-cover diversity, but do not provide resources for the shrike. Grouping land-cover types

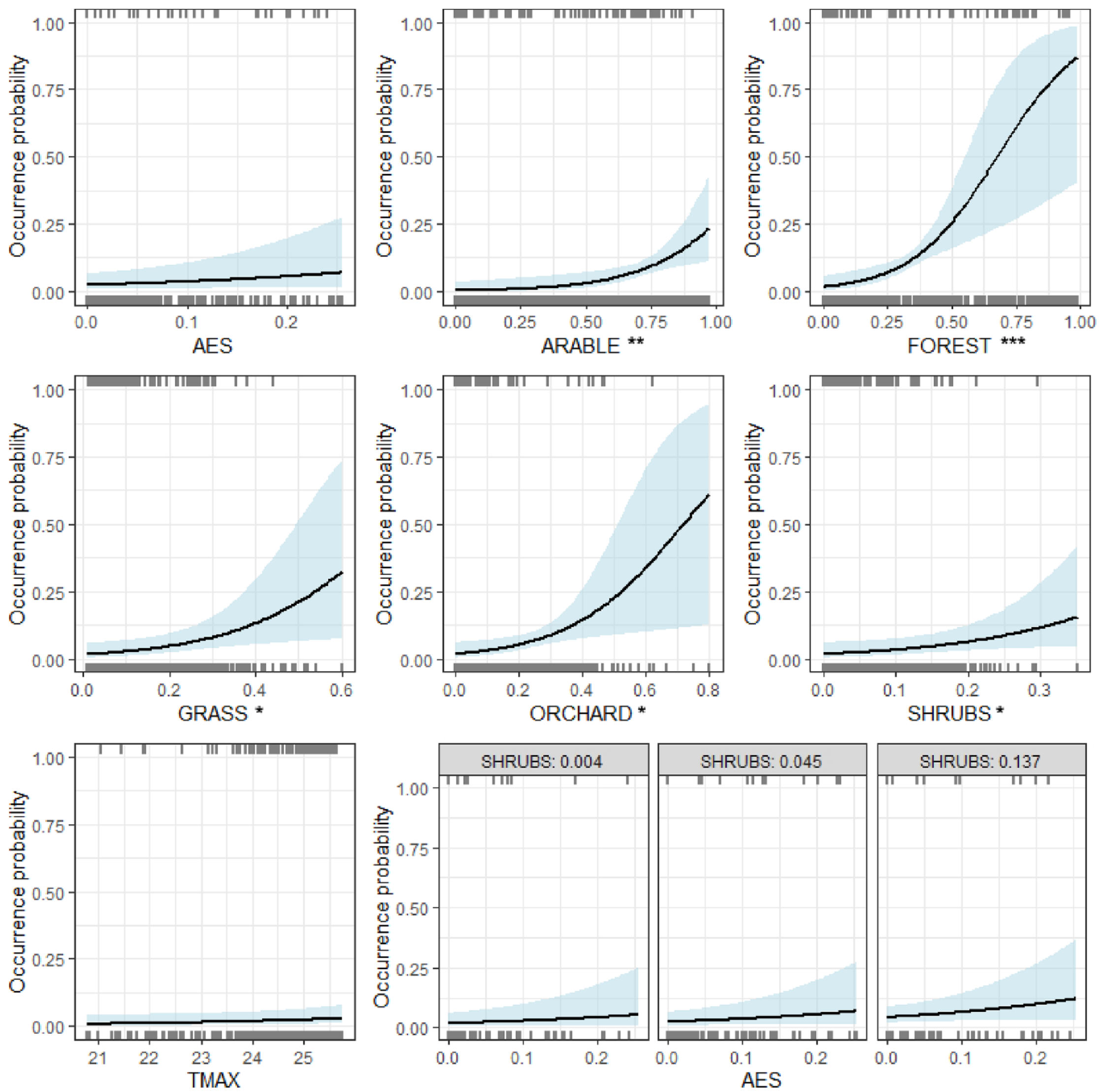

Figure 4. Conditional plots displaying the effect of the predictors included in the best model for South Moravia on the occurrence probability of the red-backed shrike. Relationships were graphed for each predictor with all other covariates held at their medians. The interaction term AES:SHRUBS was not among the predictors of the best model, however logistic regressions are inherently interactive (Spake *et al* 2023). Thus, to visualise potential interactive effects of SHRUBS with AES, plots describing the effect of AES on occurrence probability were produced for the 10th, 50th and 90th percentiles of the value distribution of SHRUBS. Shading shows average estimated standard errors. Ticks on the upper and lower border of the plots represent data points. Asterisks indicate whether predictors are significant at the 0.05 (*), 0.01 (**), or 0.001 (***) levels.

into (species-specific) functional groups to map functional landscape heterogeneity (Fahrig *et al* 2011) could be one way to test this.

4.3. Policy and management implications

Our modelling framework may be particularly useful for designing and optimising the spatial implementation of measures targeting selected species, like priority and specialist bird species (Zmihorski *et al* 2016, Sharps *et al* 2023). We have shown that even single species' responses to management are complex and variable across different regions, and that this context-dependency needs to be accounted for to maximise conservation outcomes. AES design should allow for an optimised spatial targeting that can be adapted according to regional and landscape characteristics (Díaz and Concepción 2016). Advisory services and farmers' training can help ensure that the right measures are applied in the right places (Hölting *et al* 2022, Pe'er *et al* 2022). Co-designed measures (between practitioners and researchers; Hölting *et al* 2022) can also be an effective way of incorporating regional- and landscape-context knowledge, such as that presented in our study, into the design and allocation of future AES.

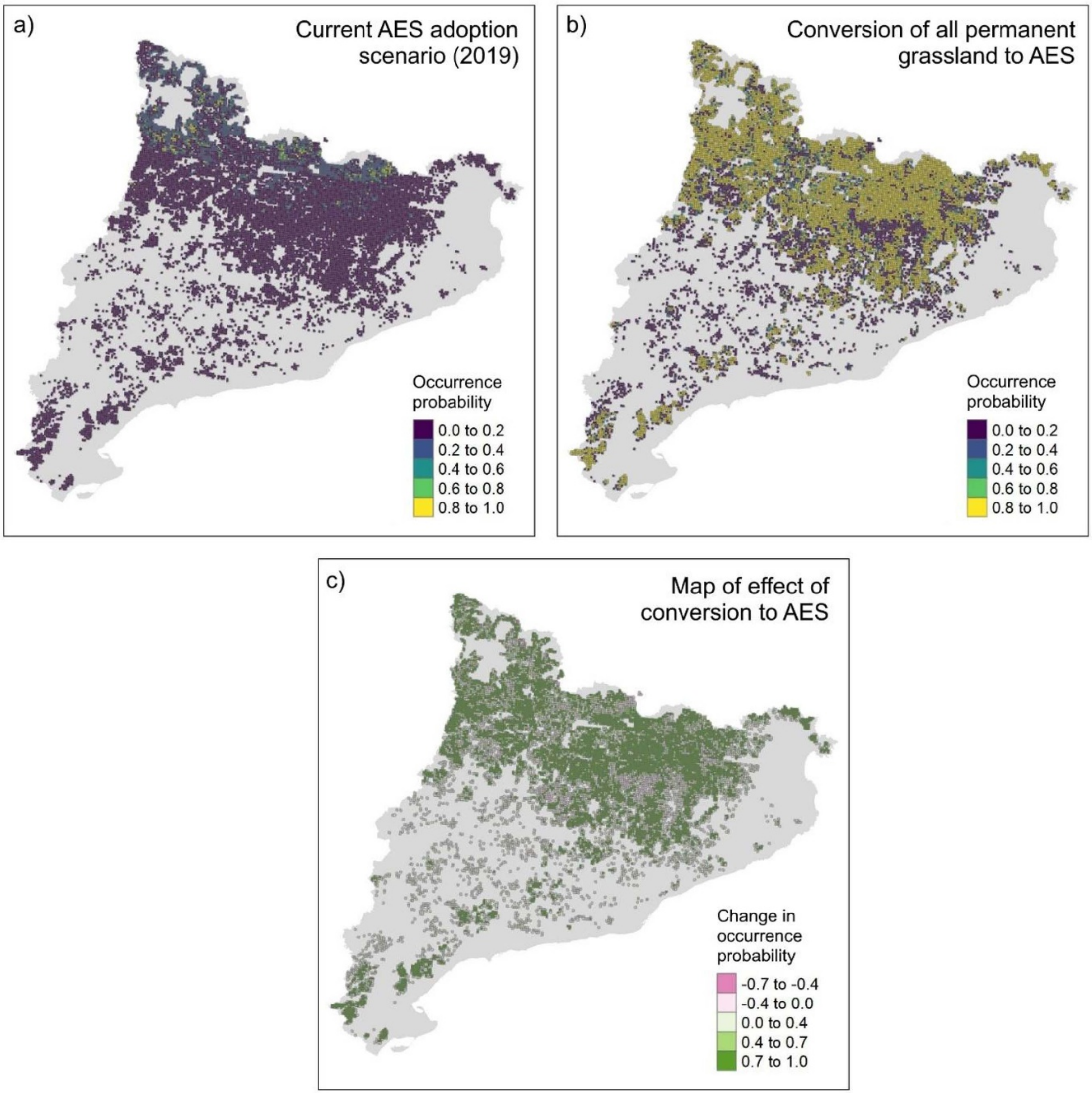

Figure 5. Predictions of occurrence probability of the red-backed shrike in Catalonia under the current, as of 2019, AES adoption (a), if all permanent grassland was converted to AES (b), and the change in occurrence probability after conversion to AES (c). Only grid cells with at least 1 ha of grassland and with an elevation between 200 and 2000 m a.s.l. are displayed.

5. Conclusions

This study illustrates how rigorous methodological workflows in spatial biodiversity analyses can correct for biases in imperfect datasets to answer complex ecological questions and inform management actions. We found consistently positive relationships between grassland-based AES and red-backed shrike occurrence probability, and that structural landscape complexity moderates AES effectiveness to varying degrees across different regions. Cross-regional variations may depend on varying species–environment relationships or cross-regional differences in edge density or land-use intensity. Accounting for such context-dependencies is crucial for improving the cost-effectiveness of conservation actions. The design of future AES should be flexible enough to allow for regional and local adaptation and improved spatial targeting.

Data availability statement

The data cannot be made publicly available upon publication because they are owned by a third party and the terms of use prevent public distribution. The data that support the findings of this study are available upon reasonable request from the authors.

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Author contributions (CRediT)

Stephanie Roilo: conceptualisation, methodology, formal analysis, data curation, writing—original draft, visualisation. **Rebecca Spake:** conceptualisation, methodology, writing—review & editing, supervision. **James M Bullock:** conceptualisation, writing—review & editing. **Anna F Cord:** conceptualisation, resources, writing—review & editing, supervision.

Conflict of interest

The authors declare no competing interest.

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