Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: http://www.tandfonline.com/loi/tbis20

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To cite this article: Judith Zellweger-Fischer, Jael Hoffmann, Pius Korner-Nievergelt, Lukas Pfiffner, Sibylle Stoeckli & Simon Birrer (2018): Identifying factors that influence bird richness and abundance on farms, Bird Study, DOI: 10.1080/00063657.2018.1446903

To link to this article: https://doi.org/10.1080/00063657.2018.1446903

BIRD STUDY, 2018
https://doi.org/10.1080/00063657.2018.1446903

Identifying factors that influence bird richness and abundance on farms

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ABSTRACT

Capsule: Farmers can influence species richness and abundance of typical farmland birds positively, even on rather small farms (20–50 ha) within intensively farmed areas.

Aims: To assess the impact of farm settings, farm characteristics and heterogeneity of habitats on bird species richness and abundance, and to indicate which actions and measures farmers can take to promote farmland birds at a farm level.

Methods: Farmland bird species richness and abundance were modelled as a function of farm settings, farm characteristics and semi-natural habitats on 133 farms. The data were analysed at the farm scale, as this is the 'operating range' of a farmer, but also at the territory scale, which represents the range birds (mainly passerines) use during the breeding season. Additionally, effects of the farm variables on species abundance/occurrence were investigated for nine widespread species.

Results: Farmland bird species abundance (but not richness) was elevated on organic compared to non-organic farms. Farmland bird species richness and abundance increased with decreasing mean field size. Crop diversity had positive effects on five species at the territory scale. Several semi-natural habitats, especially hedgerows, were associated with higher bird species richness and abundance at both farm and territory scales. Settlement revealed rather negative effects at the farm scale, but several positive relations at the territory scale.

Conclusion: Birds, especially passerines, are restricted to a small area during the breeding season, and so even small farms can contribute to their protection by growing diverse crops, reducing field size and managing a diversity of semi-natural, uncropped habitats. These measures should ideally be accessible within the relatively small scale of a bird territory.

ARTICLE HISTORY
Received 13 March 2017
Accepted 27 November 2017

In large parts of Europe, farmland biodiversity has experienced strong declines over the past decades (Tucker & Heath 1994, Donald *et al.* 2006, EEA 2013). This has largely been attributed to the intensification of cultivation methods (Newton 2004). These processes are said to have strongly deteriorated the quantity and quality of breeding and foraging habitat of a range of farmland birds (Wilson *et al.* 1995, Browne *et al.* 2006). In arable landscapes, fast-growing and dense swards, large field sizes and simplified crop rotations have been identified as some of the main drivers of habitat loss for farmland species (Stoate *et al.* 2001). Increased pesticide use coincided with a marked decrease in invertebrate abundances, implying reduced food resources for birds (Benton *et al.* 2002). In grassland dominated areas, earlier and more frequent mowing have had similarly negative effects, particularly on ground-nesting species (Vickery *et al.* 2001, Guerrero *et al.* 2012). The rigorous removal of uncropped structures and semi-natural habitats has further contributed to the loss and the fragmentation of high-quality breeding habitat (Benton *et al.* 2003, Vickery & Arlettaz 2012). Intensification and habitat loss have thus reduced food resources and nesting places for a wide range of farmland bird species.

Semi-natural, uncropped habitats have been shown to be very valuable to farmland birds (Fuller *et al.* 2004). On the production area, in-field measures or low-input management of crops and grassland have revealed positive effects on bird abundances (Henderson *et al.* 2009, Meichtry-Stier *et al.* 2014). Such habitat typically creates a sparser, patchier and more open sward structure (McCracken & Tallowin 2004). Several studies on foraging behaviour found that birds especially benefitted from mosaics of varied vegetation structure, which facilitated the detectability and accessibility of food sources (Vickery *et al.* 2001, McCracken & Tallowin 2004, Atkinson *et al.* 2005, Schaub *et al.* 2010, Murray *et al.* 2016). Lengyel *et al.* (2016) also stressed the importance of a diverse

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Supplemental data for this article can be accessed at https://doi.org/10.1080/00063657.2018.1446903.

vegetation structure, particularly for birds, stating that vegetation height and cover determined species richness. Preserving and recreating diverse vegetation structure has thus been suggested as a key feature in enhancing farmland biodiversity (Benton *et al.* 2003, Kosicki & Chylarecki 2012, Hardman *et al.* 2016).

As one way of reinstalling and maintaining biodiversity-friendly habitat on farmland, specific options were designed and made eligible within agri-environment schemes (AESs). Benefits of such AES options have mostly been found at the plot/field scale and for lower trophic levels (plants and invertebrates; Knop *et al.* 2006, Woodcock *et al.* 2007, Humbert *et al.* 2012). Most of those AES benefits, however, have not propagated onto larger regional or national scales (Schneider *et al.* 2014). One reason for only partial success of AES options might be attributed to the fact that the farm – as the principle unit of decision making – has not received enough attention (but see Dallimer *et al.* 2009). Despite participating in AESs, farmers base their management decisions on farming optimization processes or subsidy payments rather than on what is most effective for biodiversity (Jahrl *et al.* 2012). While there is certainly a potential for enhancing farmland birds on large farms with several hundred hectares of land, much less is known regarding the possibilities smaller farms (of 20–50 ha) have to promote biodiversity. To our knowledge, studies on such a farm scale are rare, although a farm size of approximately 20–50 ha is common in many regions across Europe (Eurostat 2015). Thus, biodiversity-friendly habitats and management should be analysed not only at plot or landscape scale but also at the farm scale.

Birds are well-established biodiversity indicators (Gregory *et al.* 2005, Tryjanowski & Morelli 2015) and are relatively easy to detect and monitor. On the one hand, they hold a high trophic position in agro-ecosystems, have wide-ranging habitat requirements and indicate ecological conditions of habitat at a large scale (O'Connell *et al.* 2000). On the other hand, most of the breeding birds occupy territories and remain within a relatively small area during the breeding season. Passerines often stay within an area of approximately 1 ha, where they look for most nesting and foraging resources (Glutz von Blotzheim & Bauer 1985–1997). We therefore conducted our analysis not only at the farm but also at the territory level. The farm scale represented a farmer's 'operating range', and the territory scale characterized habitat preferences during the breeding season.

The aim of this study was to quantify the effects of a range of variables on farmland bird species richness and abundance in intensively farmed areas. The following questions were addressed: Which factors are the most important in determining farmland bird species richness and abundance at the farm scale? Which of these factors are crucial at the territory scale? Are the variables and their effects identical at the farm and territory scale? Despite habitat requirements differing between species, what can a farmer do to optimize richness and abundance of farmland birds on his/her farm? We distinguished between factors which are 'given', such as the settings of a farm ('farm settings': e.g. climate, proportions of woodland edges and proximity to settlements) and factors which are directly modifiable by farming practices ('farm characteristics': e.g. livestock density and crop diversity), and 'habitats' (e.g. extensively used meadows, hedgerows).

Methods

Study area and farms

We collected data on 133 farms located in the Swiss Central Plateau (300–800 m above sea level; 46°55′N 7°21′E–47°35′N 8°43′E, online Appendix 1). The selected farms covered an average area of 24.6 ha (standard deviation, sd = 4.3; crops, grassland and buildings), which corresponds to the national average, and were as spatially consolidated as possible to minimize edge effects. The study farms were mixed farms (covering arable and grassland), as predominant in the Swiss lowland; the proportion of arable crops was 39.6% (sd 17.4). Of the study farms, 42 were certified organic, 80 were integrated farms (integrated production according to IP-Suisse) and 11 were conventional farms (meeting only cross-compliance regulations; Schweizerischer Bundesrat 1992). Conventional farms were under-represented in our sample. Thus, IP-Suisse farms and conventional farms were pooled, and a comparison was made between organic and non-organic farms. The farms differed mainly in their use of synthetic fertilizers and pesticides in arable crops. Hence, 'organic' can be understood here as a proxy for relatively low input arable farming.

Bird survey

For each farm, farmland bird data were collected in the breeding season of either the year 2009, 2010 or 2011. The entire farm area was surveyed three times between mid-April and the beginning of June. All surveys were carried out under favourable weather conditions (minimal wind, no rain) and between dawn and 11:00 hours. There was one observer per farm who surveyed the entire area by foot. For each encountered bird, status of breeding was noted according to the modified international atlas code and following the census method described in Schmid *et al.* (2004). For farmland species, precise observation points were mapped and collated to territories after the three visits according to the simplified territory mapping method (Schmid *et al.* 2001). Territories on the boundary of a farm (mostly territories in boundary woodland or hedges) were fully assigned to the farm if they were observed during at least two out of the three visits. If they were verified on one visit, they were counted as 0.5 territories.

Nine farmland species were common and widespread enough to build separate models for each species: Yellowhammer *Emberiza citrinella*, Sky Lark *Alauda arvensis*, Garden Warbler *Sylvia borin*, Short-toed Treecreeper *Certhia brachydactyla*, Red-backed Shrike *Lanius collurio*, European Goldfinch *Carduelis carduelis*, Tree Sparrow *Passer montanus*, Magpie *Pica pica* and European Starling *Sturnus vulgaris*. The first six species are listed in the Federal programme 'Environmental Objectives of the Agricultural Sector' (EOA species; BAFU and BLW 2008) and were thus of special relevance here. The EOA list contains a total of 47 bird species; 21 EOA species were found on the 133 study farms. For species occurring on less than 20 study farms, it was not possible to perform separate models. Among these were farmland species of special conservation concern, such as Common Redstart *Phoenicurus phoenicurus*, Common Quail *Coturnix coturnix* and Northern Lapwing *Vanellus vanellus*.

Farm-scale and territory-scale analysis of bird species richness and abundance

To examine bird species richness and abundance on farms, we chose a two-scale approach, a farm scale and a territory scale. At the farm level, we analysed overall species richness (number of species per farm), EOA species richness (number of EOA species per farm) and EOA species abundance (number of territories per farm of EOA species, online Table S1). In addition, for the nine widespread species mentioned above, abundance (for Tree Sparrow, European Starling and Yellowhammer) and occurrence (for Sky Lark, Garden Warbler, Short-toed Treecreeper, Red-backed Shrike, European Goldfinch and Magpie) was modelled (see 'Statistical analysis' below). Further, a territory-scale analysis was conducted for these nine species, reflecting habitat preferences at a finer scale.

Farm-scale explanatory variables

For each farm, detailed information and official data on field size, grown crop types, livestock density etc. were collected during interviews with the farmers in the winter before field work (Table 1). A part of the variables described 'farm settings'. These factors potentially influence bird species richness and abundance but cannot be directly controlled by farmers, such as region, climate, proportions of settlement and woodland (Table 1). As a climatic variable we used long-term averages of rainfall from March to May (Table 1). A second group of variables described 'farm characteristics' which mostly indicated farming/management intensity, such as farm type (organic/non-organic), livestock density or crop diversity (Table 1).

Semi-natural habitats, the third group of variables, were surveyed in the field and mapped if they fulfilled a predefined minimal ecological quality (according to Graf *et al.* 2011). The habitat assessments were carried out by trained field workers during the vegetation period (May–August) in the same year when bird surveys took place. The mapped habitats were aggregated into four groups according to their structural properties: semi-natural elements (SNEs, elements covering small areas of, e.g. ruderal vegetation, herbaceous strips, ponds), semi-natural meadows, hedgerows and trees (Table 1).

Territory scale explanatory variables

The same explanatory variables as mentioned above were used for the territory-scale analysis, except for field size which was not meaningful at this scale (fields were usually larger than the territory area). Since most of the explanatory variables were highly skewed at the territory scale, they were categorized as factors with two to four levels (Table 1).

The area within 50 m of the territory centre was defined as the 'occupied territory'. Territory size varies by species, habitat quality, season etc., but often covers approximately 1 ha (Glutz von Blotzheim & Bauer 1985–1997). Thus, a radius of 50 m was assumed, resulting in an area close to that size. In a few cases, the occupied territories of the same species overlapped. This was the case for 30 out of 363 Tree Sparrow territories and for 10 out of 302 European Starling territories. We did not correct for this slight inaccuracy.

To find out about a species' selected habitats, the occupied territories were compared to randomly generated, non-occupied 'stochastic territories' with the same dimension (50 m radius). With the help of a geographical information system (GIS) device, random

Table 1. List of explanatory variables including a short description and indication of mean ± standard deviation (sd). The same variables were used for farm-scale analysis (column 'farm scale') as for the territory-scale analysis (except mean field size which was only available for the farm scale). For the territory-scale analysis, these variables were categorized due to high skewness at the territory scale (column 'territory scale'). The explanatory variables were grouped in farm settings, farm characteristics and semi-natural habitats.

Variable group	Variable name	Description	Farm-scale analysis			Territory-scale analysis
Farm settings			Unit	Mean ± sd	Transformation	Unit
	Region	Farms were grouped into four regions near the cities Zurich, Lucerne, Solothurn, Berne	4 categories		-	4 categories
	Rain	Average rainfall from March to May (long-term mean 1961–90)	mm	285 ± 29	Scale	Above / below mean*
	Settlement	Proportion of settlements along the boundaries of a farm	%	13.9 ± 11.8	Arcsin-square-root, scale	Presence/absence
	Woodland	Proportion of woodland/forest edge along the boundaries of a farm	%	18.4 ± 16.5	Arcsin-square-root, scale	Presence/absence
	Farm size	Area per farm (crops, grassland and buildings)	Hectares (ha)	24.6 ± 4.3	First three orthogonal polynomials	NA
	Year	Year of survey, either 2009, 2010 or 2011	-	-	-	Year not included, as stochastic territories were not assigned a specific year
Farm characteristics						
	Farm type	Farms were either organic or non-organic (i.e. integrated or conventional)	2 categories		-	2 categories
	Livestock density	Proxy for intensity of land use	Number of livestock units/ha	1.3 ± 0.8	Scale	Above / below mean*
	Arable	Proportion of arable land in farm area	%	39.6 ± 17.4	Scale	Presence/absence
	Field size	Mean field size	ha	1.2 ± 0.3	Scale	NA
	Crop diversity	Crop types	Shannon index	1.3 ± 0.3	Scale	Number of crop types
Semi-natural habitats						
	Semi-natural Meadows	Proportion of extensively used (unfertilized and late-cut) semi-natural meadows of a predefined ecological quality (see habitat mapping in the methods)	%	1.8 ± 3.0	Arcsin-square-root, scale	Presence/absence
	Hedgerows	Total length of hedgerows	m/ha	12.8 ± 14.5	Log, scale	Presence/absence
	Trees	Number of standard fruit trees (minimal stem height 1.2 m)	trees/ha	2.7 ± 2.0	Scale	5 or more / less than 5
	SNE	Proportion of remaining small semi-natural elements (without meadows, hedgerows and trees), i.e. ruderal vegetation, ponds, herbaceous strips	%	2.6 ± 3.6	Arcsin-square-root, scale	Presence/absence

*the mean calculated over 133 farms.

points were selected as territory centre points. All centre points of stochastic territories were at least 100 m apart from each other and from the centres of occupied territories. For each occupied territory of a species, we generated approximately 1000 stochastic territories in total. All farms were used here, including farms which held no occupied territory of the species. For each species, we analysed whether occupied territories differed from stochastic territories regarding the explanatory variables (Table 1).

Statistical analysis

Farm scale

To assess which factors influence overall bird species richness, EOA species richness, EOA species abundance and abundance of single species at the farm scale we built generalized linear mixed models (GLMMs), using the above-mentioned variables as fixed factors (see Table 1, also for the transformations used). Additional fixed factors were year (3 levels 2009, 2010 and 2011; used as a fixed rather than a random factor due to the small number of years) and farm size (see below). Since overdispersion had been observed in several models, the farm was included as an observation level random factor (farm ID) in all models. Species richness, EOA species abundance and the abundance of the three most common species (Tree Sparrow, European Starling and Yellowhammer) were modelled with Poisson models and log-link function. For six less common species, we modelled occurrence (presence vs. absence) using a binomial model with logit-link function.

To account for the effect of farm size (Table 1) and a potential non-linear species–area relationship, the first three orthogonal polynomials of area were included in all models. Cubic and quadratic terms were excluded stepwise if they were not significant. In the case of the Poisson models, we used the logarithm of area as an offset instead of the linear term, when the quadratic term was not significant.

We included all other explanatory variables (Table 1) in the models and did not perform further model selection. Model assumptions were assessed visually (residuals vs. fitted values, residuals vs. explanatory variables, observed vs. fitted values). Spatial autocorrelation was small as revealed by bubble plots and semi-variograms (farm scale) and posterior predictive model checking (territory scale). Thus, we performed GLMMs rather than generalized least squares models.

We used Bayesian inference which is suitable also for mixed models (frequentist inference only produces approximate statistics for mixed models) and which allows for posterior predictive model checking. The function sim from the R-package arm (Gelman & Hill 2007) was used to draw random samples from the joint posterior distribution of the model parameters (20 000 simulations), assuming flat priors. Based on the quantiles of these samples, the 95% credible interval (CrI) was obtained for each model parameter. An effect was termed statistically significant if the 95% CrI did not contain 0. To quantify effects, in figures as well as in textual descriptions, we present back-transformed relationships between a predictor of interest and the outcome variable. For this, we set other covariates to their average value and factors to their baseline level.

Territory scale

In the territory-based analysis we compared occupied territories to GIS-generated non-occupied stochastic territories. For each species, we modelled an index of presence for a territory as a function of the farm variables and habitat variables in a binomial model with a logit-link function. As mentioned above, predictors were categorized for these analyses (Table 1). To account for the repeated measurements of occupied and/or stochastic territories per farm, we included the farm as a random factor. Residual checks and inference were as on the farm scale.

Note that at the territory scale, there is no simple interpretation of the magnitude of the coefficients of fitted values. We model the probability that a territory is an occupied territory (as opposed to a stochastic territory), but this probability also depends on the number of stochastic territories in the data set. Hence, we simply think of an index of presence in these territory-scale binomial models.

Results

Farm scale

Farm settings

Overall species richness as well as EOA species richness and EOA species abundance were significantly higher in the Solothurn region compared to Berne, Lucerne and Zurich, in both farm-scale and territory-scale analyses. The year of survey did not have significant effects in any model, except that the occurrence of Goldfinch was reduced in the year 2011. Similarly, rain showed no strong effects on overall species richness, on EOA species richness or EOA species abundance; it was negatively related only to the abundance of Tree Sparrow (Table 2, online Table S2). Settlement and woodland significantly and negatively affected EOA species richness and abundance (Figure 1, Table 2), although on the species level the effect was sometimes positive and sometimes negative: the number of Yellowhammer territories was slightly elevated by woodland; the number of territories increased from 2.6 to 3 territories when the proportion of woodland increased from 10% to 60%. In contrast, settlement and woodland were negatively related to Tree Sparrow abundance, where the number of Tree Sparrow territories decreased on average from 3.9 to 2.2 when the proportion of woodland increased from 10% to 60%. A woodland proportion of 10% was related to a probability of Sky Lark occurrence of 17%, while 60% of woodland lowered that probability to merely 2%. The occurrence of Magpie was reduced with higher proportions of woodland, the occurrence of Garden Warbler decreased with higher proportions of settlement.

Farm characteristics

Farm type had no significant effect on overall species richness, but an effect on EOA species abundance. Organic farms held significantly higher EOA species abundance than non-organic farms. Tree Sparrow (not an EOA species) abundance was also significantly higher on organic farms. Livestock density and crop diversity had no discernible effects on overall species richness, EOA species richness and EOA species abundance. The proportion of arable land did not influence overall and EOA species richness and EOA species abundance, but showed a positive relation with occurrence of Sky Lark (raising the proportion of arable land from 10% to 80% increased occurrence of Sky Lark from 2% to 63%). On the other hand, the proportion of arable land was significantly negatively related with the occurrence of Red-backed Shrike (probability of occurrence of 49% at

Table 2. Summary overview of the effects of explanatory variables (farm settings, farm characteristics and semi-natural habitats) on species richness, EOA species richness and EOA species abundance at the farm scale as well as on selected bird species at the farm scale and at the territory scale. Significantly positive (+) and negative (−) relations are indicated (for statistical details see methods section). Response variables were either number of species (No.), abundance (Abu), occurrence (Occ) or index of presence (Pres).

	Resp. variable	Intercept	Region Lucerne	Solothurn	Berne	Year 2010	Year 2011	Rain	Settlement	Woodland	Type non-organic	Livestock density	Arable land	Field size	Crop diversity (farm scale)	No. of crops (territory scale)	Semi-natural Meadows	SNE	Trees	Hedgerows	Farm size linear	Farm size quadr.
Overall species richness																						
farm scale	No.	−		+										−		.						
EOA species richness																						
farm scale	No.	−		+					−	−				−		.	+					
EOA species abundance																						
farm scale	Abu	−		+			−		−	−	−			−		.	+			+		
Tree Sparrow																						
farm scale	Abu	−						−	−	−	−					.			+	+		
territory scale	Pres	−	+	+				−	+	−				.	.	+			+	+	.	.
European Starling																						
farm scale	Abu	−			+											.			+			
territory scale	Pres	−		+					+				−	.	.				+		.	.
Yellowhammer																						
farm scale	Abu	−		+	−				−	+				−		.	+			+		
territory scale	Pres			+						+				.	.	+		+		+	.	.
Sky Lark																						
farm scale	Occ	−		+	+				−	−			+			.	+					
territory scale	Pres	−		+	+				−	−°			+	.	.	−					.	.
Garden Warbler																						
farm scale	Occ								−							.	−			+	+	−
territory scale	Pres	−												.	.	+		+		+	.	.
Short-toed Treecreeper																						
farm scale	Occ	−											−			.			+			
territory scale	Pres	−							+	+				.	.	+				+	.	.
Red-backed Shrike																						
farm scale	Occ	−		+									−			.				+		
territory scale	Pres	−		+										.	.					+	.	.
Magpie																						
farm scale	Occ									−						.				+		
territory scale	Pres	−			+				+	−			−	.	.					+	.	.
Goldfinch																						
farm scale	Occ			+	+		−									.	+					
territory scale	Pres	−		+					+	−	−		−	.	.	+	+		+	+	.	.

° = woodland never found in occupied territories and thus excluded.

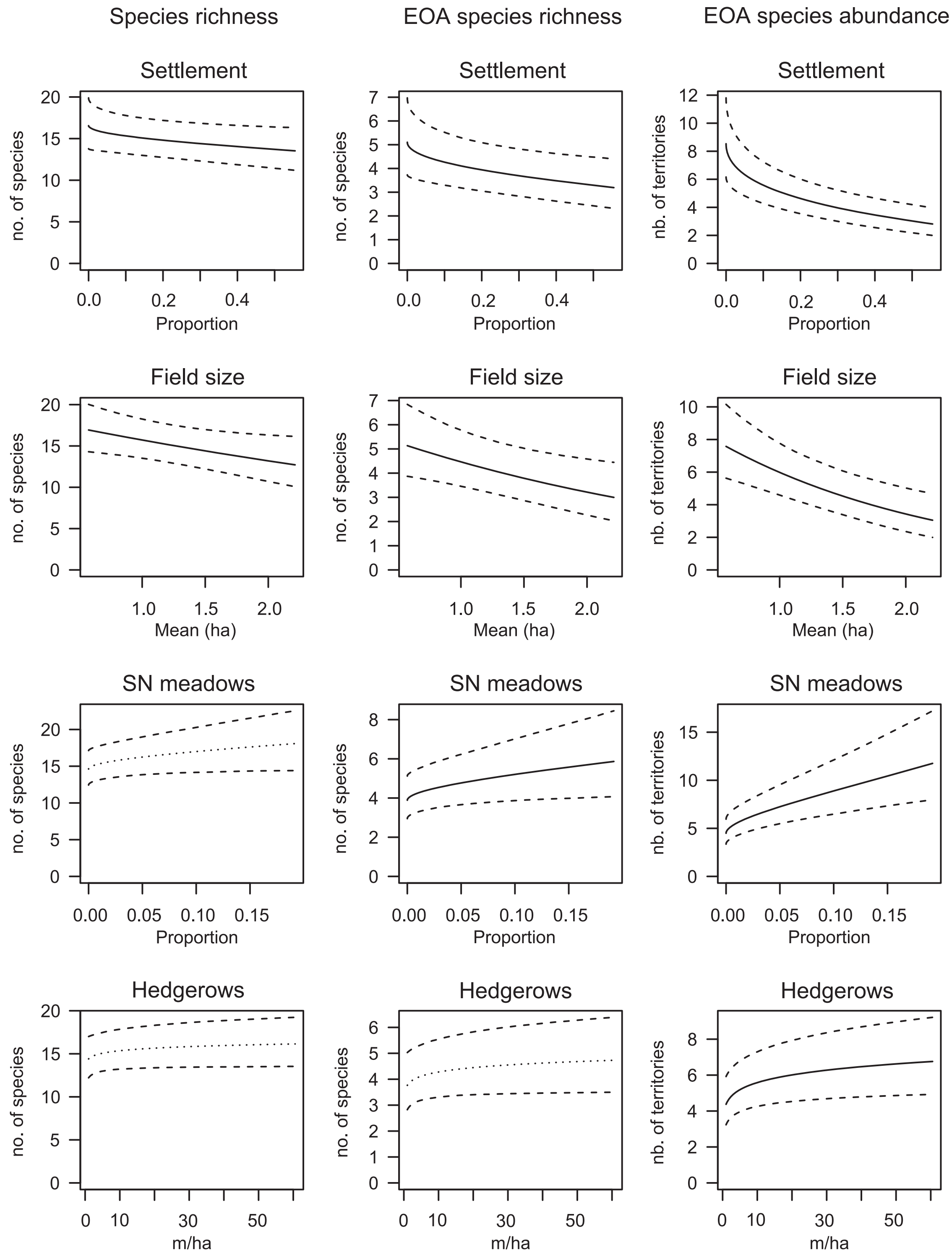

Figure 1. Relationships between selected explanatory variables (settlement, field size, SN meadows and hedgerows) and overall species richness, EOA species richness and EOA species abundance from the farm-scale analysis. EOA species abundance was calculated as the number of EOA territories per farm area. Shown are regression lines including 95% credibility intervals (dashed lines); all other variables were set to their mean. Significant trends (see methods) are shown in solid black lines.

10% arable land, but 0.2% at 80% arable land) and Short-toed Treecreeper (occurrence lowered from 47% to 2% when proportion of arable land increased from 10% to 80%). Mean field size was significantly negatively correlated with overall species richness, EOA species richness and EOA species abundance (Figure 1, Table 2). Yellowhammer abundance was significantly reduced with increasing field size (on average 3.6 territories when fields were 0.6 ha, but reduced to 1 territory when fields were 2 ha in size).

Semi-natural habitats

The proportion of semi-natural meadows positively influenced EOA species richness and EOA species abundance (and slightly but not significantly, overall species richness). Yellowhammer abundance, Goldfinch occurrence and Sky Lark occurrence were significantly positively correlated with the proportion of semi-natural meadows. Hedgerows did not affect overall species richness and EOA species richness, but had a strong positive influence on EOA species abundance (Figure 1), in particular on the abundance of Yellowhammer, as well as the occurrence of Garden Warbler, Red-backed Shrike and Magpie (Table 2). Abundances of Tree Sparrow and European Starling were markedly higher on farms with more fruit trees/orchards, and so was the occurrence of Short-toed Treecreeper. SNEs showed no significant relation to overall species richness, EOA species richness and EOA species abundance. The proportion of SNEs was generally very low (mean = 2.6% ± 3.6, range 0–21.6%, Table 1).

Territory scale

Farm settings

A comparison of occupied territories with stochastic territories revealed that farms in the Solothurn region had higher abundances of birds (as shown above), hence this region also had a higher probability for occupied territories (Table 2, online Table S3). Similarly, like at the farm scale, the only negative impact of rain was found for Tree Sparrow. The presence of settlements positively influenced the index of presence of five species at the territory level, contrasting with the negative effect of the proportion of settlement at the farm scale. The presence of woodland in the territory was positively related to the index of presence of Yellowhammer and Short-toed Treecreeper. On the other hand, woodland had a significantly negative effect on the index of presence of Tree Sparrow, Magpie and Goldfinch.

Farm characteristics

Farm type was not found to have a strong influence at the territory scale, except for the occurrence of Goldfinch which was lower on non-organic farms. Livestock density, too, revealed no obvious effects in the models. The presence of arable land in territories was negatively related to the index of presence of European Starling, Magpie and Goldfinch. Over both scales, arable land showed negative correlations with five species (Short-toed Treecreeper, Red-backed Shrike, European Starling, Magpie and Goldfinch). As expected for an open-ground breeder, the presence of arable land increased the index of presence of Sky Larks. While crop diversity did not reveal any significant relation at the farm scale, it positively influenced the index of presence of five species (Tree Sparrow, Yellowhammer, Garden Warbler, Treecreeper and Goldfinch, Table 2), but had a negative effect on Sky Lark.

Semi-natural habitats

The presence of hedgerows had a significantly positive influence on the index of presence of seven bird species with the exception of European Starling and Sky Lark. The index of presence of Garden Warbler, for instance, increased from 1% to 18% if hedgerows were present, and that of Yellowhammer from 9% to 40%. Hedgerows were thus the most influential habitat variable at the farm and at the territory scale (Table 2). The presence of trees was positive for the two cavity breeders, European Starling and Tree Sparrow, as well as for Goldfinch. The presence of SNEs was positively related with the index of presence of Yellowhammer and Garden Warbler. The presence of semi-natural meadows was positively correlated with the index of presence of Goldfinch.

Discussion

Our study confirmed that the amount of semi-natural habitats and decreasing field size positively correlated with bird species richness and abundance. At the territory scale, within an area of approximately 1 ha, crop diversity is crucial when birds select their breeding territories. Landscape context and the setting of a farm are certainly important determinants of bird species richness and abundance (Tryjanowski *et al.* 2011, Tscharntke *et al.* 2012). Yet, our findings show that even farmers on relatively small farms (approximately 25 ha) can substantially contribute to providing valuable habitats for breeding farmland birds.

A recent analysis on a similar data set revealed significantly negative effects of the degree of consolidation, forest edge-length and settlement at the farm scale (Stoeckli *et al.* 2017). At the territory scale, however, the effect of settlement was mainly positive (except for Sky Lark which avoids all tall structures; Oelke 1968, Donald 2004). Apart from differing habitat requirements between species, the definition of ‘settlement’ varied between the two scales in this study: farm-scale settlement encompassed mainly larger built-up areas close to towns, while territory-scale settlement included mostly farm buildings, sheds and barns.

These might have provided more suitable breeding locations than farm-scale settlement. Other studies have also underpinned the importance of traditional rural buildings in providing breeding and foraging habitat for various farmland species (Hiron *et al.* 2013, Rosin *et al.* 2016). The uptake of such sites as remunerable options should be reconsidered within conservation policies and AESs.

The one region which was related to highest bird species richness and abundance was Solothurn, followed by adjacent area of Berne. The Solothurn area was the most rural one in our study with the largest contiguously farmed landscape. The presence of Sky Lark, a species of conservation concern, was elevated in the region Solothurn at farm and territory level, and in the region Berne at the territory level. The Sky Lark requires large farmed landscapes with an open aspect. This finding emphasizes the importance of landscapes which are still predominantly used for farming. In other regions of the Swiss lowland, urban development has sprawled into the landscape (Jaeger *et al.* 2007), leaving smaller and more fragmented entities of land to farming. The Sky Lark is one of the farmland species which has been negatively affected by this development, not only in Switzerland (Brambilla & Ronchi 2016, Sattler *et al.* 2016).

A second set of explanatory variables described farm characteristics (Table 1). These are variables which can be directly controlled or adopted by a farmer. The organic farm type revealed a significant positive impact on EOA species abundance, which is in accordance with previous findings (Bengtsson *et al.* 2005). EOA species richness, however, did not differ strongly between organic and non-organic farms in our data. Decades of intensive farming, including large-scale use of pesticides and fertilizers, might have masked the potential benefit of low-input farming, as it was found in a recent study from the Czech Republic where integrated farming was clearly positively related to bird and herbal plant species richness (Stefanová & Sálek 2014). Rather unexpectedly, livestock density did not show any significant effects, although it has regularly been used as an indicator of farming intensity and lower levels of biodiversity (Kleijn *et al.* 2009). In this study, livestock density has certainly not varied enough across the study farms to detect any differences (1.3 ± 0.8 livestock per ha, Table 1). At low intensity, grazing was shown to have positive effects on farmland bird species (Tryjanowski *et al.* 2005). Effects of arable land were positive for Sky Lark at the farm scale and at the territory scale, but rather negative for five other species, especially at the territory scale (Short-toed Treecreeper, Red-backed Shrike, European Starling, Magpie and Goldfinch). Species which use arable fields often prefer boundary areas, as these allow them to access neighbouring crops with varying vegetation structure (Schläpfer 1988, Perkins *et al.* 2002). However, arable fields are often several hectares in size and thus, boundary structures are 'out of reach'. Therefore, arable land might have been avoided at the territory scale, except by Sky Lark.

Large field sizes have been associated with low structural diversity, monotonous and species-poor landscapes (Weibull *et al.* 2000, Batáry *et al.* 2007, Ekroos *et al.* 2010, Batáry *et al.* 2011, Fischer *et al.* 2011). As expected, field size was correlated negatively with overall and EOA species richness as well as EOA species abundance in this study as well. Even in Switzerland, where average field size is small (approximately 2 ha), it apparently still makes a difference when farmers manage their crops in smaller units. Crop diversity, that is the number of different crop types, was positively related with five bird species at the territory scale: Tree Sparrow, Yellowhammer, Garden Warbler, Short-toed Treecreeper and Goldfinch. In general, birds seemed to choose nesting sites with access to a variety of crops to ensure nesting and feeding opportunities throughout the breeding season (Wilson *et al.* 1997). Small-parcelled fields, especially when combined with the cultivation of several crops (crop diversity was important at the territory scale), seem to be suitable for all studied bird species except Sky Lark, and so could make a valuable contribution towards enriching bird species richness and abundance.

The set of semi-natural habitat variables were especially important at the territory scale with 13 significantly positive relations. This underlines the importance of habitat establishment and maintenance for bird species richness and abundance on farms. However, we expected more positive effects of semi-natural meadows at the territory level, as this habitat type covered more area than the other habitat categories. The remaining SNEs (e.g. ruderal vegetation, ponds, herbaceous strips) did not show any effects at the farm scale, but were a bit more influential at the territory scale. Semi-natural habitats have repeatedly been shown to be major determinants of biodiversity, for example, by adding heterogeneity and structural diversity (Benton *et al.* 2003, Hendrickx *et al.* 2007). Their relatively poor performance here might be explained by the small size of SNEs (on average 928 m^2), and by the fact that there were too few SNEs available to yield further significant effects for breeding birds at the farm scale. Moreover, SNEs consisted of a diverse group of small habitat elements, and this might have masked further positive effects.

Trees had significant positive effects on Tree Sparrow and European Starling at both scales. These two species are cavity breeders, and can also be attracted with nest boxes which farmers install on their orchard trees. Generally, this is a simple and straight-forward conservation measure, and it is often implemented by farmers. However, nest boxes usually support only a few species which are often already abundant. For some species of conservation concern, installing specific nesting aids might be a valuable measure (De Jong 2009, Arlettaz *et al.* 2010) but often extensive habitat improvements are necessary to reinforce populations of endangered species (Mermod *et al.* 2009).

Hedgerows showed the largest effects in our models among the semi-natural habitats. The index of presence of several species was significantly positively correlated with the presence of hedgerows at the territory level, even when the species were not restricted to hedges, for example, Tree Sparrow and Short-toed Treecreeper. This might be attributed to the variable architecture of the hedges, covering a range from low and sparse shrubs to tall and mature tree hedgerows. Moreover, they were typically accompanied by herbaceous, no-input grass strips or other SNEs such as embankments and ditches. This combination of habitats and structural variety seemed to be attractive for a number of farmland bird species, and are a promising tool to improve structural richness, especially in simplified agricultural landscapes (Batáry *et al.* 2010).

We analysed effects on abundance/occurrence (farm scale) and index of presence (territory scale) of several bird species separately. However, due to their differing habitat requirements, it is not meaningful to promote only one type of option, as this would lead to only one type of habitat. Habitat diversity has been clearly linked to species richness (Lengyel *et al.* 2016), and habitat heterogeneity (structural richness) has been mentioned as a key prerequisite for a diverse set of farmland species (Benton *et al.* 2003). Farmers can substantially influence habitat diversity by implementing and managing a diverse set of habitats, especially those that are semi-natural. Moreover, farmers should create habitat mosaics at a suitable scale where they deliver accessible foraging and nesting spots for breeding birds. Some of these habitat types have become remunerable options within AESs, for example, meadows and pastures, hedges, grass margins and wildflower areas (Schweizerischer Bundesrat 1992, Defra 2003). Indeed, the list of options is long, but often a few are favoured by farmers because of feasibility or low maintenance, while the remaining options are simply not adopted. Therefore, recent studies have recommended that a combination of several options should be delivered by each farm within AESs (Hardman *et al.* 2016). Our results also indicate that bird species richness and abundance will be higher in landscapes offering a variety of different semi-natural habitats. Such habitats might be complemented with land under AES as well as land used for production but at low intensity and/or including in-field options (Henderson *et al.* 2009, Stoeckli *et al.* 2017).

As outlined above, farmers have the potential to positively influence bird species richness and abundance on their holdings, especially abundances, even on relatively small farms in intensively farmed areas. Rather than making general statements on what measures should be implemented to improve bird richness and abundance, AESs should allow for regional variation (Tworek *et al.* 2017), and farmers should have access to an advisory service to learn about their specific potential within their specific setting. Positive effects on bird species richness and abundance in the wider countryside can only be expected when farmers are made aware of their influence and when such efforts can be linked between farms, for example, through regional projects with local context and a local lead. Such projects have already proved fruitful (Flade *et al.* 2006, Meichtry-Stier *et al.* 2014, Dunford 2015) and are a promising concept for long-term conservation efforts which are also supported by the key players – the farmers.

Acknowledgements

We would like to thank all participating farmers, field assistants and the entire project team for their support. We are grateful to Kim Meichtry-Stier and Lukas Jenni for valuable comments on an earlier draft.

Funding

This project was sponsored by the Swiss Federal Office for the Environment and the Federal Office for Agriculture, the MAVA Foundation, the AVINA Foundation, the Ernst Göhner Foundation, the Sophie and Karl Binding Foundation, the Vontobel Foundation, the Dreiklang Foundation and the Strafin Foundation. It was also supported by BIO SUISSE and IP-SUISSE.

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