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Landscape-scale effects of land use intensity on birds and butterflies

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ABSTRACT

Although today there is ample evidence that biodiversity is affected by agricultural land use intensification, little is known about how species respond to different land use intensity gradients at landscape scale. To properly describe the relationship between biodiversity and land use intensity, intensity indicators need to account for land cover, management intensity, and be assessed at landscape scale. The study was conducted in 91 landscapes of 1 km^2 in Switzerland. Three different land use intensity indicators were calculated: indicator 1 was defined as the ratio between agricultural and natural area; indicator 2 as the ratio between arable land and permanent grassland; and indicator 3 as the ratio between agricultural area and biodiversity promotion areas (BPA, i.e. wildlife-friendly managed areas under Swiss agri-environment schemes). Species richness and abundance of birds and butterflies were used as biodiversity indicators and trait-based community indices were used to describe bird community changes. Overall, we found that birds were affected by landscape composition and agricultural management, while butterflies were mainly affected by agricultural management. Specifically, from natural (e.g. forest dominated) to agriculture-dominated landscape, bird species richness showed a sharp decrease when 80% or more of the landscape was farmed. Butterfly species richness followed a hump-shaped curve. None of the species groups was significantly correlated with the proportion of arable land versus permanent grassland. Yet species richness of birds and butterflies significantly changed with the proportion of BPA: the lower the proportion of BPA, the lower the observed richness. Finally, when the proportion of agricultural land increased, populations of migratory birds and hedge/tree breeders decreased. We conclude that to further promote farmland biodiversity, natural areas, such as forests, hedges and waterbodies, should cover at least 20% of the agricultural landscapes and the proportion of BPA should be increased.

1. Introduction

The steadily growing human population and wealth lead to constantly increasing demand for land and agricultural products (Tilman et al., 2011). So far, this demand has been mostly met by developing and intensifying agricultural practices to reach higher yields and by converting natural habitats into agricultural lands, which has led to dramatic biodiversity declines (Donald et al., 2006; Sutcliffe et al., 2015). In Europe, agricultural landscapes have developed over centuries, being influenced by long-term historical management (Burgi et al., 2015) and species that typically depend upon open and semi-open landscapes (Fischer et al., 2008). The value of farmland has been recognized and nowadays biodiversity conservation efforts focus not only on natural (pristine), but also on agricultural landscapes. In this context, agri-environment schemes (AES) have been implemented since the early 1990s by the European and the Swiss government to counteract the loss of biodiversity and to restore the naturally diverse farmland habitats. In Switzerland, all farmers receiving direct payments are required to fulfill the proof of ecological performance (comparable to the EU's cross compliance) which requires among others, that at least 7% of the farmland is managed as biodiversity promotion areas BPA (former *ecological compensation areas*). Today there is ample evidence that biodiversity is affected by land use and agricultural intensification (e.g. Stoate et al., 2001; Kleijn et al., 2009). To describe land use intensity, a variety of indicators can be used including nitrogen input (Kleijn et al., 2009), pesticide use (Filippi-Codaccioni et al., 2010), yield (Mastrangelo and Gavin, 2012), crop cover (Filippi-Codaccioni et al., 2010) or input costs (Teillard et al., 2015). For a proper description of the relationship between biodiversity and land use intensity, land use intensity indicators need to account for changes in land cover, but also for changes in agricultural intensity. Simple indicators (e.g. crop vs. non-crop) ignore the differences in management intensity between crop types (e.g. 2–5 pesticide applications in cereals whereas 0–1 in grasslands), which are known to have direct negative effects on

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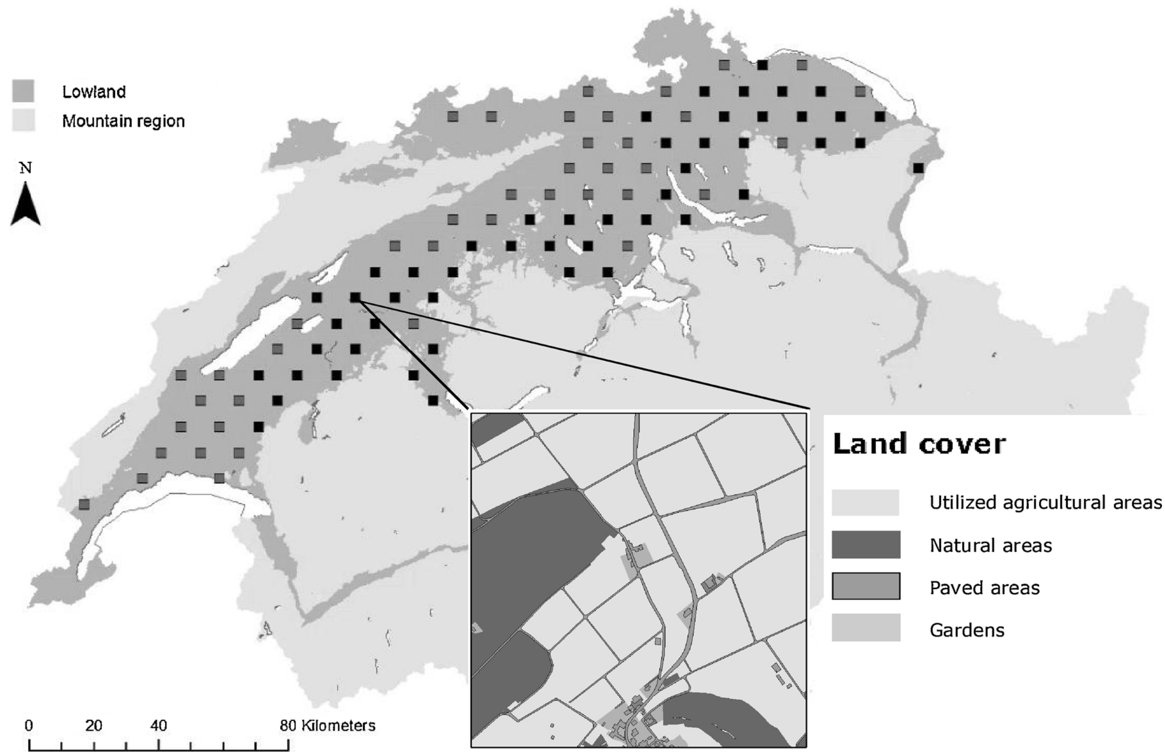

Fig. 1. Map of the study area with the selected landscape squares in the Swiss lowland (n = 91). The detail shows one landscape of one square kilometer, including the different land cover types. The locations of the landscapes (with at least 30 ha UAA) where additional information on agricultural management was available are indicated by the darker black squares (n = 50).

biodiversity (Filippi-Codaccioni et al., 2010). On the other hand, too complex aggregated intensity indices, which consider different management aspects in one index, may be of limited use because of constraints in interpretability (Herzog et al., 2006).

In this study we employed three land use indicators. Indicator 1 was the proportion of utilized agricultural area (UAA) in the landscape, defined as the ratio between agricultural and natural area. This indicator was meant to reflect the effects of land cover on biodiversity. Indicator 2 was the proportion of arable land within the UAA, defined as the ratio between arable land and permanent grassland. It was expected to reflect the different management intensities on arable land and permanent grassland. Indicator 3 was the proportion of non-BPA within the UAA, defined as the ratio between UAA and BPA. Hereby BPA are semi-natural farmland habitats such as extensively managed grasslands, high-stem orchards or wildflower strips with wildlife-friendly management prescriptions (Bundesrat, 2013). This indicator was meant to assess the effectiveness of agri-environment schemes (AES) at landscape scale. Species richness and abundance of birds and butterflies were used as biodiversity indicators. It is known that bird and butterfly communities respond to both land use type and management intensity, at local (field) and landscape scales (e.g. Rundlof et al., 2008; Jeliazkov et al., 2016).

We hypothesized that species richness and abundance of both species groups would peak at intermediate land use intensities, leading to a hump-shaped relationship between biodiversity and indicator 1. Indeed, landscapes situated at both extremes of the land use intensity gradient would be dominated by natural or agricultural areas, whereas landscapes with intermediate land use intensity would be composed of both, providing habitats for farmland and non-farmland species. Permanent grasslands are generally considered as a less intensive and more biodiversity–rich type of agricultural land use, we therefore expected biodiversity to be positively correlated with the share of permanent grasslands (Herzog et al., 2006) and negatively with indicator 2, respectively. Finally, as agri-environment schemes aim to promote biodiversity we expected that birds and butterflies would be positively correlated with the proportion of BPA and negatively with indicator 3 (Batáry et al., 2015).

Species responses to land use changes may vary according to specific ecological traits (e.g. habitat affinity, trophic level, or migratory status) or conservation status (Vandewalle et al., 2010; Newbold et al., 2013). To investigate this assumption, we divided and analyzed both taxa in three subgroups: total, farmland and Red List species. For birds, the community trophic index (CTI), the community migration index (CMI) and the community nest index (CNI) were used to further describe compositional changes along the land use intensity gradients. We expected that birds from higher trophic levels, such as insectivorous, would decrease with land use intensification (Teillard et al., 2015), as intensification negatively impacts abundance and availability of invertebrate prey (Vickery et al., 2001). Finally, as structural diversity (e.g. trees or hedges) decreases with land use intensification also cavity breeding birds and so the community nest index was expected to decrease.

2. Methods

2.1. Study sites

The study was conducted on the Swiss Plateau, the lowland region situated between the Jura Mountains and the Alps (mean altitude of 500 m, range 400–800 m). It is the most densely populated region of Switzerland, and its most important agricultural area. Farmland can be cultivated without major difficulties and agriculture in this region is highly intensive. The Biodiversity Monitoring Switzerland (BDM) conducts repeated biodiversity surveys in 520 systematically distributed landscape squares of 1 km × 1 km across Switzerland (BDM Coordination Office, 2014). For this study, 91 BDM landscapes located on the Swiss Plateau, with less than 25% cover of water bodies and paved areas were selected. The systematic sampling grid of the BDM ensured an even coverage of the whole study area (Fig. 1).

Table 1
Composition of study landscapes including land cover (a), crop cover (b) and BPA (c). BPA can be found in all crop types (on arable land, grassland and permanent crops).

a) Land cover		Mean area (± SD) per landscape (n = 91)
Utilized agricultural area (UAA)	Arable land, permanent grasslands and permanent crops	56 ha (± 23.6)
Natural area[a]	Forests (93%), hedges (1%), marshes (0.7%), waterbodies (4%), vegetated roadsides and gravel/rocks (1.3%)	30 ha (± 25.1)
Paved area	Buildings, streets, railroads, parking lots and other paved areas	8 ha (± 6.4)
Garden	Green spaces adjoining buildings	6 ha (± 8.1)
b) Crop cover		Mean area (± SD) per UAA (n = 50)
Arable land	Cereals, oilseed, root, and leguminous crops, vegetables and temporary grasslands	57% (± 24.1)
Permanent grassland	Intensively and extensively managed permanent grasslands	42% (± 24.3)
Permanent crop	Vineyards, fruit tree plantations, berries and perennial crops	1% (± 2.3)
c) Agri-environment schemes (AES)		Mean area (± SD) per UAA (n = 50)
Biodiversity promotion areas[a]	Extensively managed meadows (51%) and pastures (10%), less intensively managed meadows (6%), litter meadows (5%), orchards (22%), hedges (3%), wildflower strips (2%) and others (2%)	13% (± 5.8)

[a] The relative proportions of each type are given in brackets.

As the study focused on the effects of land use intensity at landscape scale, we used 1 km^2 sampling units (100 ha). Not only, is it a scale that has been used in studies looking at land use intensity (e.g. Temme and Verburg, 2011) and biodiversity (e.g. Baker et al., 2012; Feniuk, 2015), but it has also been suggested that for biodiversity conservation actions a landscape perspective needs to be adopted (e.g. Batáry et al., 2007; Jeliazkov et al., 2016).

2.2. Land cover data

Digitized information about land cover in the study landscapes was provided by the Swiss cadastral survey in 2014 for the cantons of St. Gallen, Thurgau, Luzern, Baselland, Bern, Aargau, Zürich, Fribourg and Vaud. The supplied GIS polygon layers were controlled and completed where necessary, using satellite images. Subsequently, the amounts of agricultural, natural, paved and garden areas were calculated for all 91 landscapes (see Table 1) using ArcGIS (Version 10.2.2). These land cover data were used to calculate indicator 1.

2.3. Agricultural survey data

Detailed information about crop type, field size and biodiversity promotion areas was provided by the cantonal agricultural offices (see Fig. B.1. in the Supporting material). These data were not available for 27 landscape squares in the cantons of Aargau, Vaud and Baselland. Based on the agricultural survey data from 2013/2014, we calculated the proportions of arable land, permanent grasslands and BPA in landscape squares with at least 30 ha of UAA (n = 50). These proportions were used to calculate indicators 2 and 3.

2.4. Land use indicators

To investigate how species, react to land cover and management intensity, three different land use indicators were defined:

$$Indicator\ 1 = \frac{UAA}{UAA + natural}$$

$$Indicator\ 2 = \frac{arable}{arable + permanent\ grassland}$$

$$Indicator\ 3 = \frac{UAA{-}BPA}{(UAA{-}BPA) + BPA} = \frac{UAA{-}BPA}{UAA}$$

All three indicators ranged from 0 (= least intense land use) to 1 (= most intense land use). Indicator 1, calculated for all 91 landscapes, was the ratio between utilized agricultural area (UAA) and UAA plus natural areas (both in ha km^{-2}). Natural areas included forests, hedges, gravel/rocks, marshes, waterbodies and vegetated roadsides (see Table 1 for detailed information). It can be interpreted as the proportion of agricultural land in the landscape when ignoring private gardens and paved areas.

Indicator 2 was the ratio between arable land and arable land plus permanent grassland within the UAA. Temporary grasslands (e.g. grass-clover stands) were included under arable land, as they are part of the crop rotations (sown with a species-poor mix, remaining for one to four years). It can be interpreted as the proportion of cropland versus grassland within the UAA, when ignoring the third crop category, permanent crops, which represented only 1% of the UAA in average.

Indicator 3 was defined as the ratio between UAA (without BPA) and areas managed as BPA. Biodiversity promotion areas (formerly *ecological compensation areas*) form part of the Swiss agri-environment scheme and are extensively managed areas, where neither pesticide nor mineral fertilizer application is allowed. A description of all BPA types can be found in the Supplementary material in Table B.2.

The three indicators showed the following (Pearson) correlations: Indicator 1 & 2, R = 0.18, t = 1.25, df = 48, p-value = 0.219; indicator 1 & 3, R = 0.25, t = 1.82, df = 48, p-value = 0.075; and indicator 2 & 3, R = 0.4, t = 3.08, df = 48, p-value = 0.003. The positive correlation between indicator 2 and 3 indicates that landscapes with more arable areas (less permanent grasslands) have less BPA. As information on field size and crop diversity (e.g. number of arable crops) was available, we tested, if our land use indicators were correlated with these two variables. Indicator 1 (proportion of UAA) was not correlated with field size, nor crop diversity ($R < 0.2$, $p\text{-value} > 0.1$). Indicator 2 (proportion of arable land) was not correlated with field size (R = 0.09, t = 0.60, df = 48, p-value = 0.551), but with crop diversity (R = 0.69, t = 6.39, df = 48, $p\text{-value} < 0.001$), indicating that landscapes with more arable land also harbored more crop types. Indicator 3 (proportion of non-BPA) was not correlated with crop diversity (R = 0.10, t = 0.73, df = 48, p-value = 0.471), but with mean field size (R = 0.29, t = 2.09, df = 48, p-value = 0.042), indicating that landscapes with less BPA have larger fields.

2.5. Species richness and abundance

Data on species richness and abundance of birds and butterflies were provided by the Swiss Biodiversity Monitoring (BDM – Z7 indicator) and the Swiss Ornithological Institute (SOI – Monitoring common breeding birds). All selected landscapes were surveyed once in the years 2010, 2011, 2012, 2013 or 2014. Most bird counts were done in 2014 (63 out of 91), whereas butterfly counts were equally distributed over all five sampling years. Repeated transect counts (seven times per sampling year for butterflies and three times for birds) were used to assess species presence in the landscapes. Surveys were conducted along transects of 2.5 km (BDM Coordination Office, 2014).

For data analysis, birds and butterflies were classified into three groups, namely: 1) all; 2) farmland; and 3) Red List. Farmland birds included species that rely on farmland as primary habitat according to the Swiss Ornithological Institute. Farmland butterflies included species occurring in open land, including private gardens (Benz et al., 1987). Butterfly species complexes (e.g. complexes of *Pieris napi* or *Pieris hyale*) were not attributed to a certain habitat type. Consequently, individuals in species complexes were only considered in the group "all". For both taxa, species were categorized as Red List species if their status was rated as near threatened (NT), vulnerable (VU) or critically endangered (CR) in the Swiss Red List (Keller et al., 2010; Wermeille et al., 2014). Complete species lists with attributed habitats and Red List status can be found in the Supplementary material (Tables A.1. and A.2.).

2.6. Bird community indices

To describe how the bird community changed with the different land use intensity indicators, three trait-based community weighted means were calculated: the community trophic index (CTI); the community migration index (CMI); and the community nest index (CNI). The community indices comprised information on diet (CTI), nest (CNI) and migratory behavior (CMI) derived from the Swiss Ornithological Institute (species-specific categories can be found in the Supplementary material Table A.1.). We adapted the CTI index of Mouysset et al. (2012) and Teillard et al. (2015) by using four discrete species-specific trophic levels; 1 = granivorous; 2 = omnivorous; 3 = insectivorous and 4 = carnivorous. The CTI was calculated as follows:

$$CTI = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * STI_i$$

STI_i was the trophic index of each species i, weighted by its abundance, N_i, and divided by the summed abundances of all species, N_{tot}. A high CTI indicates that carnivorous and insectivorous species are dominant in the community. A low value indicates that granivorous species are dominant. Analogously, the CMI and CNI were calculated as followed:

$$CNI = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * SNI_i$$

$$CMI = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * SMI_i$$

The SNI_i is the nest index of each species i and the SMI_i is the migratory index of each species i. The CMI increases with the mean migratory distances of the community members (1 = resident; 2 = resident/short; 3 = short distance; 4 = long distance). For the community nest index (CNI) species were categorized into 1 = ground breeders; 2 = tree/hedge/reed breeders and 3 = cavity/building breeders. A high CNI indicates that the community is dominated by cavity/building breeders and a low value indicates that ground breeders are dominant. CNI and CMI were negatively correlated with each other (Pearson's correlation coefficient: CMI & CNI = -0.78, CTI & CMI = 0.53 and CTI & CNI = -0.23).

2.7. Statistical analysis

The aim of the statistical analysis was to describe the relationship between the biodiversity indicators and the land use indicators. Species richness and abundance of all, farmland and Red List birds and butterflies and the CTI, CNI and CMI, were used as response variables in the models. In a first step we tested for spatial autocorrelation in the response variables using Moran's I (R Package ape; Paradis et al., 2004). As significant spatial autocorrelation was detected in some response cases (p-value < 0.05), the XY coordinates were subsequently included as fixed effect in all models (Dormann et al., 2007). Probability distributions were defined using the R package *fitdistrplus* (Delignette-Muller et al., 2016). Accordingly, the link identity function for gaussian and the log link function for negative binomial distribution were included in the models. We fitted generalized additive models (GAMs) with the R package *mgcv*, using penalized regression splines with smoothing parameters selected by residual maximum likelihood (REML) (Wood, 2016). The land use indicators and the XY coordinates were included as covariates:

i) *GAM (y ~ s (Indicator 1) + s (X, Y))* n = 91
ii) *GAM (y ~ s (Indicator 1, k=5) + s (Indicator 2, k=5) + s (Indicator 3, k=5) + s (X, Y, k=10))*n = 50

The smoothing basis dimension (k) sets the upper limit on the degrees of freedom associated with a smooth (s). If k is not specified, the *mgcv* package applies cross-validation to automatically obtain the optimal degrees of freedom for the smoother. Because there can be problems (e.g. over-smoothing), when applying cross-validation on small (< 50) data sets, we manually selected the amount of smoothing for models with only n = 50 observations (see equation ii). We checked that k was not too low using basis dimension checking (p-value < 0.05 and k-index < 1 (Wood, 2016)). In addition, normality and homogeneity of the residuals were visually checked using QQ plots and the graph of residuals versus fitted values. GAMs can account for non-linear relationships between the response and the covariates. Partial residuals from the multivariate GAM models where extracted to fit different *a priori* defined curves (see Fig. 2). This approach allowed to assess the relationship between the response variable and the land use indicator of interest, given that the other indicators or XY coordinates were also in the model. The different curves (linear, quadratic, exponential and saturation) were fitted using non-linear least squares (function *nls* in R). In an applied context using *a priori* defined curves had the advantage of

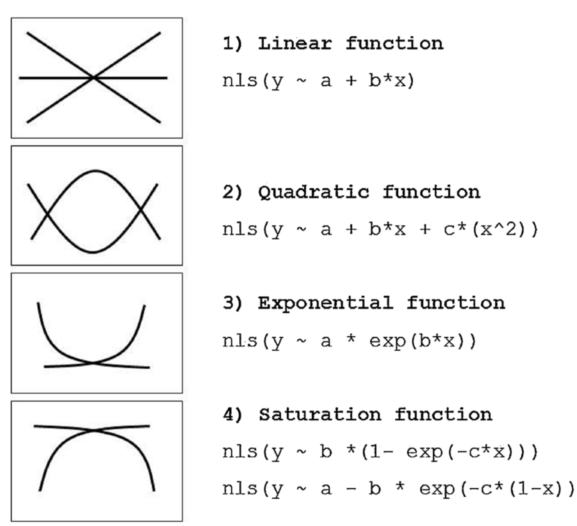

Fig. 2. The four curve functions, which were fitted to the partial residual plots of the GAM models. The parameters a, b and c were estimated by the *nls* function, while y is the partial residual and x the land use intensity indicator.

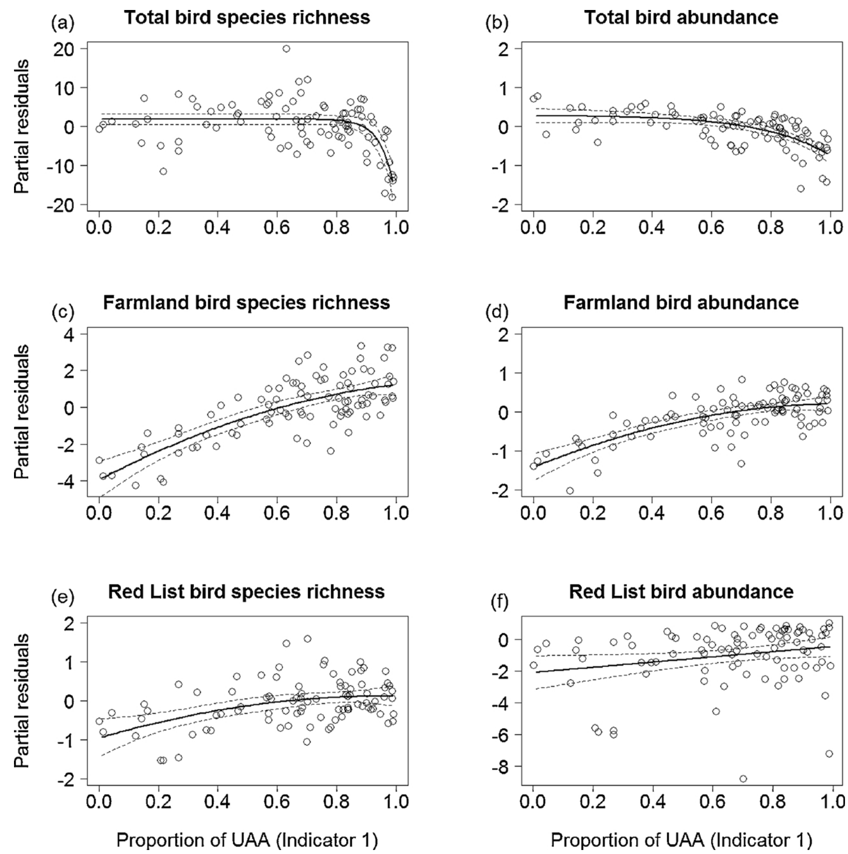

Fig. 3. Bird species richness and abundance along the land use intensity gradient of indicator 1 (n = 91) for: all- (a and b), farmland- (c and d) and Red List birds (e and f). Partial residuals and predictions with 95% confidence intervals from the best fitting curves are shown. Graphs b), d), e) and f) are on the log scale.

Table 2
Estimated degrees of freedom (edf), F (F) or Chi-square (Chi) statistic and approximate significance of smooth terms (Sign.) for Indicator 1 and XY coordinates in the GAM (n = 91). The adjusted R^2-value (adj. R^2) is as usual the proportion of variance explained by the model. The partial residual plots with the fitted curve functions are shown in Fig. 3 (for birds) and Fig. 4 (for butterflies).

			Indicator 1			XY coordinates			adj. R^2
			edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Bird	Species richness	Total	6.43	6.217	***	3.62	1.20		0.37
		Farmland	2.05	23.16	***	20.42	1.82	*	0.56
		Red List	1.79	10.07	*	7.70	22.76	*	0.29
	Abundance	Total	4.16	70.70	***	2.00	4.23		0.44
		Farmland	2.52	76.23	***	2.00	0.24		0.32
		Red List	1.00	8.83	**	3.20	2.13		0.05
Butterfly	Species richness	Total	2.92	16.68	**	10.04	40.23	***	0.36
		Farmland	2.51	8.65	*	9.93	45.22	***	0.40
		Red List	1.59	1.02		4.92	28.56	***	0.31
	Abundance	Total	1.00	0.66		2.00	16.15	***	0.16
		Farmland	1.87	2.99		2.00	17.24	***	0.18
		Red List	1.95	1.94		6.38	25.41	**	0.35

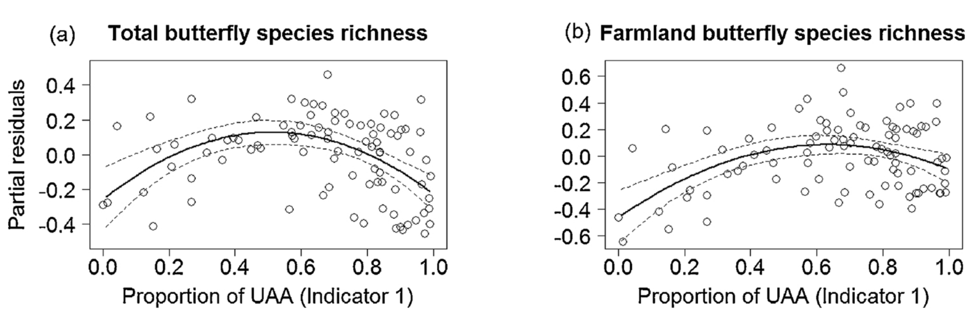

Fig. 4. Total (a) and farmland (b) butterfly species richness along the land use intensity gradient of indicator 1 (n = 91). Partial residuals on the log scale and predictions with 95% confidence intervals from the best fitting curves are shown.

facilitating the interpretation of the results. The best fitting curves were selected based on the AICc using the R package *AICcmodavg* (Mazerolle, 2016). Curve fitting was only conducted, when GAMs showed a significant result. All statistical analyses were conducted in R Version 3.2.5 (R Core Team, 2016).

3. Results

In the 91 landscapes, 106 bird species were observed. Per landscape, an average (± SD) 39.4 (± 6.6) bird species were detected, including 7.7 (± 2.0) farmland and 3.5 (± 2.4) Red List species. The bird abundance (i.e. number of breeding pairs per landscape) was on average 333 (± 126), range 93 to 714. Farmland bird abundance ranged from 5 to 108, with a mean of 39 (± 20). Only 11 (± 11) Red listed breeding pairs were observed on average. In all landscapes, 76 butterfly species were detected. Per landscape a mean of 23.0 (± 6.1) butterfly species were detected, including 14.9 (± 4.6) farmland species and 1.4 (± 1.6) Red List species. On average, 413 (± 223) individuals were observed per landscape (range 90–1123). Farmland butterflies had a mean abundance of 224 (± 171) and Red List butterflies 7 (± 13).

Detailed information about the land-/crop cover and the BPA in the 91 study landscapes can be found in Table 1. The agricultural survey data further showed that the mean field size was 1.25 ha (± 0.4) and the mean number of arable crops 7 (± 3). There were no linear correlations between mean field size or crop diversity per landscape, and total species richness of birds or butterflies (see Fig. B.3.). The proportion of arable crops ranged from 2.5% to 93.7% and the proportion of permanent grassland from 6.2% to 97.5% of the UAA. Overall 13% of the UAA were managed as BPA. The most common BPA types were extensively managed meadows (51%) and orchards (22%, see Table 1).

3.1. Proportion of UAA (indicator 1)

Bird species richness and abundance were strongly correlated with indicator 1. Both total bird species richness and abundance decreased with increasing proportions of UAA following a saturation curve. Farmland and Red List birds were both positively correlated with the proportion of UAA (Fig. 3). Regarding butterflies, only species richness, but not abundance, changed with the proportion of UAA (Table 2). Total and farmland butterfly species showed similar results, as 51 out of 76 butterflies were categorized as farmland species. The hump-shaped curves for butterfly species richness indicated that landscapes with intermediate proportions of UAA (roughly 50% UAA and 50% natural areas) had the highest butterfly species richness (Fig. 4). According to the GAM model outcomes, the CNI increased and the CMI decreased with the proportion of UAA (see Fig. 5 and Table C.1. in the Supplementary material).

3.2. Proportion of arable land (indicator 2)

Species richness and abundance of birds and butterflies did not respond to changes in the proportion of arable land or grassland (Table 3). Only the community composition of birds showed slight changes; the CTI decreased when the proportion of arable land increased (see Table C.1. and Fig. C.2. in the Supplementary material).

3.3. Proportion of non-BPA (indicator 3)

Total species richness of birds and butterflies significantly changed along the gradient of indicator 3: the lower the proportion of BPA within the UAA, the lower the observed species richness. Furthermore, the abundance of butterflies, but not birds, was correlated with indicator 3 (Table 3 and Fig. 6). However, regarding total bird species richness the trend was strongly influenced by one study landscape that

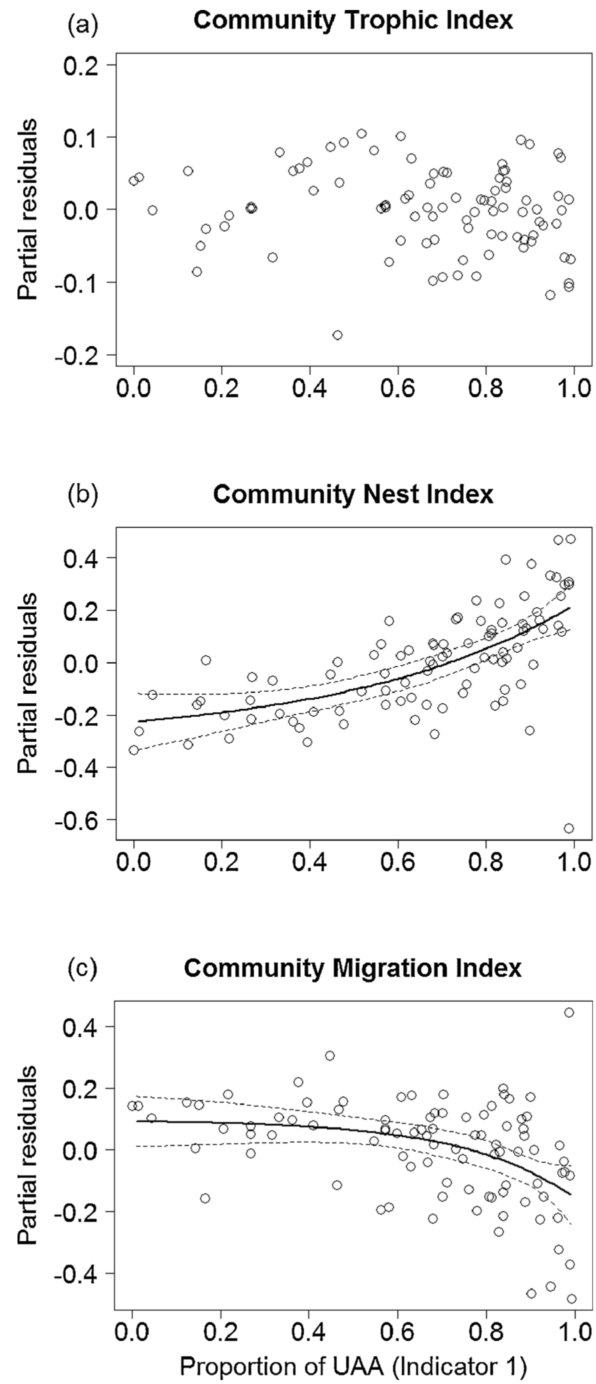

Fig. 5. Bird community composition changes along the land use intensity gradient of indicator 1 (n = 91). The CTI (a) did not show a significant change, the CNI (b) showed a non-linear increase and the CMI (c) a non-linear decrease. Partial residuals and predictions with 95% confidence intervals from the best fitting curve are shown.

harboured a particularly high number of bird species (point x = 0.75 and y = 20 in Fig. 6a). When this landscape was excluded from the analysis, the relationship with indicator 3 was not significant anymore (edf = 3.74, p-value = 0.09). In addition, as mean field size was correlated with indicator 3, we tested if the significant relationships changed, when this variable was included in the model. Results showed that the relationships remained qualitatively the same (see Table B.4. and Fig. B.5. in the Supplementary material).

Table 3
Estimated degrees of freedom (edf), F (F) or Chi-square statistic (Chi) and approximate significance of smooth terms (Sign.) for Indicator 1, 2, 3 and XY Coordinates in the GAM (n = 50). The adjusted R^2-value (adj. R^2) is as usual the proportion of variance explained by the model. The partial residual plots with the fitted curve functions are shown in Fig. 6.

			Indicator 1			Indicator 2			Indicator 3			XY coordinates			adj. R^2
			edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Bird	Species richness	Total	3.76	6.59	***	1.00	0.22		3.90	4.97	**	2.00	1.37		0.59
		Farmland	1.00	8.71	**	1.42	1.67		3.09	1.58		3.82	0.51		0.31
		Red List	1.00	1.19		1.00	1.16		1.24	8.27	*	2.40	0.63		0.21
	Abundance	Total	1.00	19.46	***	1.00	1.82		1.00	0.95		4.40	6.08		0.42
		Farmland	1.00	8.22	**	1.67	2.27		1.00	0.04		2.00	2.55		0.09
		Red List	1.00	1.67		1.00	0.74		1.00	1.64		2.00	0.16		0.00
Butterfly	Species richness	Total	1.21	1.16		1.00	0.58		1.00	4.63	*	6.97	2.76	*	0.38
		Farmland	1.00	0.25		1.00	0.98		1.00	3.70	.	6.72	2.73	*	0.32
		Red List	1.00	0.02		1.00	1.49		2.45	9.36	*	3.54	13.63	*	0.36
	Abundance	Total	1.00	0.31		1.72	0.95		1.00	8.18	**	2.00	16.30	***	0.21
		Farmland	1.00	0.39		1.27	2.03		1.00	8.27	**	2.00	20.88	***	0.04
		Red List	1.00	0.05		1.84	2.91		1.77	5.19	.	6.19	26.77	***	0.37

4. Discussion

In this study, we described how the diversity of birds and butterflies changed in relation to three different land use intensity indicators in 1 km^2 landscape units. The first indicator (indicator 1) was defined as the ratio between utilized agricultural area (UAA) and natural areas (mainly forest), the second (indicator 2) as the ratio between arable land and permanent grassland and the third (indicator 3) as the ratio between agricultural area and biodiversity promotion areas (BPA). Results showed that total bird species richness declined when over 80% of the landscape was farmed whereas butterfly species richness showed a hump-shaped curve (indicator 1). None of the species groups correlated with the proportion of permanent grasslands (indicator 2). Finally, both taxa positively correlated with the proportion of BPA (indicator 3), the higher the proportion of BPA, the higher the observed diversity.

4.1. Proportion of UAA (indicator 1)

Although the proportion of agricultural area rather reflects land cover than land use intensity, we included this indicator as it is frequently used and because we wanted to compare the importance of land cover and agricultural management, which was reflected by the other two indicators. Bird species richness and abundance showed a decrease along indicator 1, reflecting the transition from natural (mainly forest dominated) to farmland dominated landscapes. The decrease started when more than 80% of the landscape was farmed, or in other words, when natural areas covered less than 20%. This is in line with the landscape moderation concept of Tscharntke et al. (2012) which considers landscapes with > 20% of non-crop area as structurally complex and supporting high species richness. We observed that landscapes dominated by forests were not particularly species rich. Forests in our study region were mostly managed beech-spruce stands. Biodiversity rich forest types such as unmanaged old-growth forest or alluvial forest were rare. The influence of indicator 1 on birds remained strong even when the proportion of permanent grasslands (indicator 2) and the proportion of BPA (indicator 3) were included in the model, which further emphasizes the importance of natural habitats such a forests, waterbodies and hedges for bird diversity (Vickery and Arlettaz, 2012). We also observed that farmland and Red List species positively correlated with indicator 1. Although Red listed bird species occur in all habitat types in Switzerland, percentages of threatened species are much higher in farmland than in others, such as forests, which explains this pattern (Keller et al., 2010).

Total butterfly species richness showed a hump-shaped relationship with indicator 1 meaning that landscapes with a mix of natural and agricultural areas harbored the highest butterfly species richness (Bergman et al., 2004; Ekroos and Kuussaari, 2012). However, the effect of indicator 1 diminished when indicators 2 and 3 were included in the model, leaving only indicator 3 (proportion of BPA) as significant variable. As butterflies are particularly influenced by local management (Ekroos and Kuussaari, 2012), in landscapes with more than 30 ha UAA, the proportion of BPA was the most important predictor for butterfly species richness (see also subsection 4.3 below and Jeanneret et al., 2003).

4.2. Proportion of arable land (indicator 2)

Contrary to our expectations, bird and butterfly species richness and abundance did not change with the value of indicator 2, the ratio between arable land and permanent grasslands within the UAA. In general permanent grasslands are associated with decreased agricultural intensity and arable land with increased agricultural intensity (but see Persson et al., 2010; Teillard et al., 2015). We therefore expected the proportion of arable land to be negatively correlated with bird and butterfly occurrences (e.g. Gil-Tena et al., 2015). The permanent grasslands in our study landscapes were mostly intensively managed (77% of the permanent grasslands,) with frequent fertilizer inputs and 4–6 cuts (or grazing events) per year. These species poor grasslands lost most of their diversity in the last decades (Bosshard, 2015). The intensive management leads to an impoverished plant community that offers fewer host and flowering plants for butterflies (Marini et al., 2009; Börschig et al., 2013). In addition, the frequent harvesting events have direct negative impacts on field invertebrates, including lepidopteran caterpillars (Humbert et al., 2010). Similarly, grassland intensification has important direct and indirect negative effects on birds, such as deterioration of nesting sites, wintering habitat, and loss of food sources (e.g. Vickery et al., 2001). The observation that none of the species groups correlated with the proportion of permanent grasslands, emphasizes that, strict management guidelines are needed to restore semi-natural conditions that favor biodiversity. In this context the CAP greening measures were criticized as they lack specific management guidelines to promote high-value permanent grasslands (Pe'er et al., 2014). Finally, the ratio between arable land and permanent grassland, without considering management intensity, may not be a good predictor for land use intensity (Teillard et al., 2015).

4.3. Proportion of non-BPA (indicator 3)

Our results provide evidence on the beneficial effects of biodiversity promotion areas (Swiss AES) on bird and butterfly populations at landscape scale: Total bird species richness, butterfly species richness

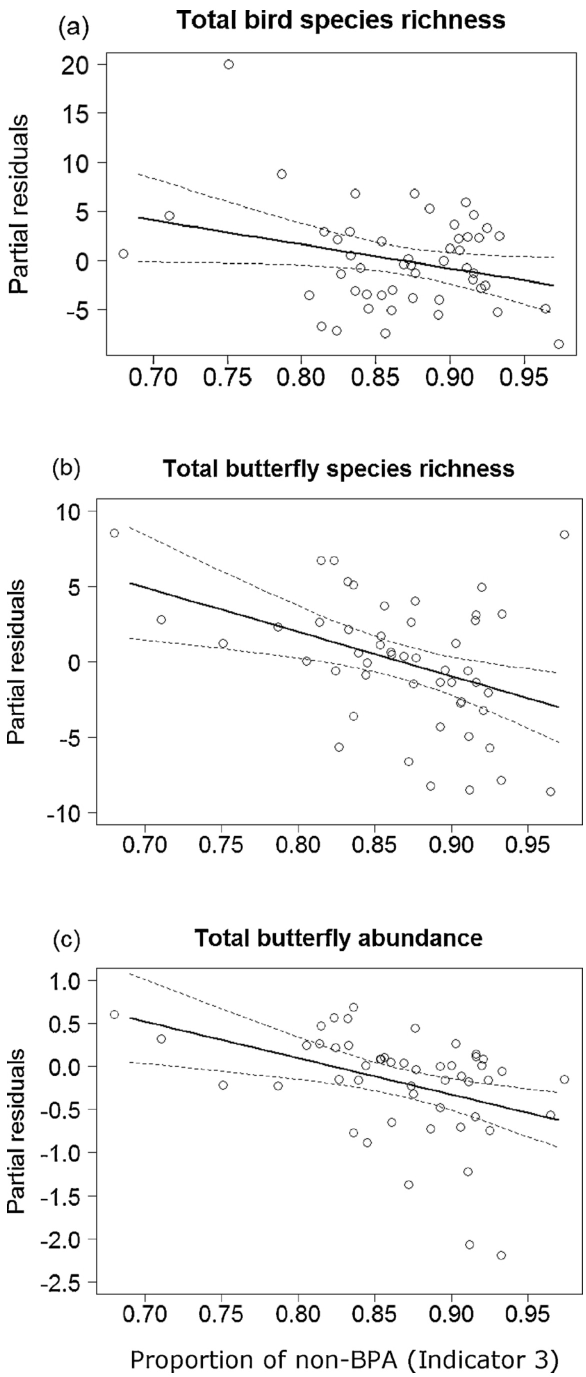

Fig. 6. Decreasing total bird (a) and butterfly (b) species richness and butterfly abundance (c) with decreasing proportion of BPA (indicator 3) in the landscape (n = 50). Partial residuals from the GAM and predictions with 95% confidence intervals from the best fitting curve are shown. Figure (c) is on the log scale.

and abundance increased with the proportion of biodiversity promotion areas in the landscape (i.e. they were negatively correlated with indicator 3). Although the effectiveness of AES has been questioned at the beginning (Kleijn and Sutherland, 2003), most evaluation studies have afterwards demonstrated increases in farmland biodiversity in response to AES (Batáry et al., 2015). Not only at field scale, but also at landscape scale can AES effectively foster birds (Baker et al., 2012; Prince and Jiguet, 2013) and butterflies (but see Roth et al., 2008; Aviron et al., 2011). The low intensity management of BPA increases resource availability and survival even in otherwise intensively managed landscapes (Pywell et al., 2011). However farmland birds did not show a positive response to the proportion of BPA, which suggests that other properties such as BPA type or quality play a more important role than quantity only (Birrer et al., 2007).

It is known that the effectiveness of AES depends on the structure of the wider landscape (Batáry et al., 2015) and that conservation measures, such as AES are most effective in landscapes with intermediate complexity (Concepción et al., 2012; Tscharntke et al., 2012). In addition, the configuration of the agricultural land, for example field size, can influence biodiversity (Batáry et al., 2017; Hass et al., 2018). In our study, landscapes with higher proportions of BPA, had the tendency to have smaller fields and lower proportions of arable land. This setting may have interacted with the shown effectiveness of AES. However, even if field size was included in the model, the beneficial effects of the proportion of biodiversity promotion areas remained.

We emphasize that BPA need to be managed according to strict biodiversity-friendly prescriptions (e.g. no fertilizer and pesticide use). This is an important condition for effective conservation measures, and one of the reasons why the new CAP greening measures (e.g. the ecological focus areas) were criticized (Pe’er et al., 2016).

4.4. Community indices

In our study, the mean trophic level (CTI) decreased when the proportion of arable land within UAA increased at the cost of grassland (Indicator 2). A similar trend was found in France where the ratio between grassland and arable land had a negative influence on the relative abundance of different farmland bird guilds (Teillard et al., 2014) and particularly on higher trophic levels species (Teillard et al., 2015). The community nest index (CNI) was positively correlated with indicator 1. This increase suggests that cavity and building breeders became relatively more abundant and hedge/tree breeders became relatively less abundant in landscapes with high proportions of UAA. Ground-breeding birds were rare in our study landscapes, they are particularly sensitive to agricultural intensification (Bas et al., 2009) and vanished from the Swiss lowlands in the last decades. On the other hand landscapes with high proportions of UAA harbor rural infrastructures such as farmsteads that provide nesting sites for cavity and building breeders (Hiron et al., 2013). Corollary, a high proportion of UAA means less natural areas such as forests and hedges, which negatively affects birds breeding in these natural structures. The increase of the CNI can therefore also point to the loss of birds breeding in hedges and trees. So far, few studies have assessed the relationship between land use intensity and migratory status of birds (Newbold et al., 2013). In our study the mean migratory distance of the community decreased with the proportion of UAA. Most migratory birds are insectivorous, shown to be more prone to intensification than other trophic levels (Jeliazkov et al., 2016).

4.5. Conclusions

In our intensified temperate agricultural landscapes, biodiversity was highest in landscapes with a mix of farmed and natural areas (e.g. forests). Whilst natural areas should cover at least 20% of the landscapes, increasing the proportion of biodiversity promotion areas (Swiss AES) further promotes biodiversity. The occurrence of permanent grasslands did not affect the biodiversity unless they were extensively managed as biodiversity promotion areas (BPA), showing the poor condition of intensively managed permanent grasslands (see also Bosshard, 2015). There are ongoing efforts to revise the current agricultural policies, notably the European Agricultural Policy (CAP). This study suggests that biodiversity promotion areas can effectively increase biodiversity in agricultural landscapes. Particularly the form and management requirements of the Swiss BPA may be used to improve the criticized ecological focus areas, which are a part of the new greening measures of the CAP (Pe’er et al., 2016).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.08.014.

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Appendix A

Table A.1. Bird species list

Bird species list, including minimal and maximal abundance per landscape and the number of landscapes out of 91 (N_{lan}) a given species was observed. Information on species traits (habitat, nesting, diet and migration) were obtained from the Swiss Ornithological Institute and Red List status from Keller *et al.* 2010. Abbreviations are: A = Agriculture, F = Forest, W = Wetland, S = Settlement, X = Ubiquitous, LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, NA = not available.

Name	Habit	Red List	Nest	Diet	Migration	Min. abund.	Max. abund.	N_{lan}
Accipiter gentilis	F	LC	hedge/tree	carnivorous	short	1	1	7
Accipiter nisus	F	LC	hedge/tree	carnivorous	short	1	2	14
Acrocephalus palustris	W	LC	reed	insectivorous	long	1	11	7
Acrocephalus scirpaceus	W	LC	reed	insectivorous	long	1	25	9
Aegithalos caudatus	F	LC	hedge/tree	insectivorous	resident	1	4	31
Alauda arvensis	A	NT	ground	omnivorous	short	1	35	32
Alcedo atthis	W	VU	cavity	carnivorous	res/short	1	2	5
Anas platyrhynchos	W	LC	ground	omnivorous	res/short	1	14	48
Anser anser	W	NA	ground	omnivorous	res/short	1	1	1
Anthus trivialis	A	LC	ground	insectivorous	long	1	1	1
Apus apus	S	NT	cavity	insectivorous	long	1	16	26
Apus melba	X	NT	building	insectivorous	long	30	30	1
Ardea cinerea	W	LC	hedge/tree	carnivorous	short	1	4	3
Asio otus	A	NT	hedge/tree	carnivorous	res/short	1	1	1
Buteo buteo	A	LC	hedge/tree	carnivorous	res/short	1	5	83
Carduelis cannabina	A	NT	hedge/tree	granivorous	res/short	1	8	11
Carduelis carduelis	S	LC	hedge/tree	granivorous	res/short	1	13	56
Carduelis chloris	S	LC	hedge/tree	granivorous	res/short	1	44	81
Certhia brachydactyla	F	LC	cavity	insectivorous	res/short	1	14	64
Certhia familiaris	F	LC	hedge/tree	insectivorous	res/short	1	12	41
Ciconia ciconia	A	VU	building	carnivorous	long	1	1	2
Cinclus cinclus	W	LC	cavity	insectivorous	res/short	1	3	12
Coccothraustes coccothraustes	F	LC	hedge/tree	omnivorous	res/short	1	16	21
Columba livia domestica	S	NA	building	omnivorous	resident	1	9	15
Columba oenas	F	LC	cavity	granivorous	res/short	1	3	17
Columba palumbus	F	LC	hedge/tree	granivorous	res/short	1	31	90
Corvus corax	X	LC	cavity	omnivorous	resident	1	1	25

Corvus corone	A	LC	hedge/tree	omnivorous	resident	1	18	90
Corvus monedula	A	VU	cavity	omnivorous	res/short	6	6	1
Coturnix coturnix	A	LC	ground	omnivorous	long	1	3	6
Cuculus canorus	X	NT	hedge/tree	insectivorous	long	1	7	22
Cygnus olor	W	NA	ground	omnivorous	resident	1	3	4
Delichon urbicum	S	NT	cavity	insectivorous	long	1	48	28
Dendrocopos major	F	LC	cavity	omnivorous	resident	1	16	80
Dendrocopos medius	F	NT	cavity	insectivorous	resident	1	5	6
Dendrocopos minor	F	LC	cavity	insectivorous	resident	1	2	9
Dryocopus martius	F	LC	cavity	insectivorous	resident	1	3	41
Emberiza calandra	A	VU	ground	omnivorous	res/short	2	5	2
Emberiza cirlus	A	NT	hedge/tree	omnivorous	res/short	1	1	1
Emberiza citrinella	A	LC	hedge/tree	omnivorous	res/short	1	18	71
Emberiza schoeniclus	W	VU	reed	omnivorous	short	1	1	5
Erithacus rubecula	F	LC	ground	omnivorous	short	1	56	83
Falco subbuteo	X	NT	hedge/tree	insectivorous	long	1	1	9
Falco tinnunculus	A	NT	hedge/tree	carnivorous	res/short	1	3	44
Ficedula hypoleuca	F	LC	cavity	insectivorous	long	1	13	26
Fringilla coelebs	F	LC	hedge/tree	omnivorous	res/short	5	101	91
Fulica atra	W	LC	reed	omnivorous	res/short	1	13	9
Gallinula chloropus	W	LC	reed	omnivorous	res/short	1	2	4
Garrulus glandarius	F	LC	hedge/tree	omnivorous	res/short	1	12	73
Hippolais icterina	X	VU	hedge/tree	insectivorous	long	4	4	1
Hirundo rustica	A	LC	building	insectivorous	long	1	26	62
Jynx torquilla	A	NT	cavity	insectivorous	long	1	1	1
Lanius collurio	A	LC	hedge/tree	carnivorous	long	1	7	12
Larus michahellis	W	LC	ground	omnivorous	res/short	1	1	1
Locustella luscinioides	W	NT	reed	insectivorous	long	2	2	1
Loxia curvirostra	F	LC	hedge/tree	granivorous	short	1	4	15
Luscinia megarhynchos	F	NT	hedge/tree	insectivorous	long	1	4	5
Milvus migrans	X	LC	hedge/tree	carnivorous	long	1	2	67
Milvus milvus	A	LC	hedge/tree	carnivorous	res/short	1	3	69
Motacilla alba	X	LC	building	insectivorous	short	1	12	82
Motacilla cinerea	W	LC	cavity	insectivorous	short	1	3	10
Motacilla flava	A	NT	ground	insectivorous	long	1	1	1
Muscica pastriata	S	LC	hedge/tree	insectivorous	long	1	15	53
Oriolus oriolus	F	LC	hedge/tree	omnivorous	long	1	11	13
Parus ater	F	LC	cavity	omnivorous	res/short	1	44	68
Parus caeruleus	F	LC	cavity	omnivorous	res/short	1	34	91
Parus cristatus	F	LC	hedge/tree	omnivorous	short	1	9	43
Parus major	F	LC	cavity	omnivorous	res/short	1	45	91
Parus montanus	F	LC	cavity	omnivorous	resident	1	2	4
Parus palustris	F	LC	cavity	omnivorous	resident	1	11	78
Passer domesticus	S	LC	cavity	omnivorous	resident	1	100	81
Passer montanus	A	LC	cavity	omnivorous	res/short	1	37	73
Pernis apivorus	F	NT	hedge/tree	insectivorous	long	1	1	2

Phasianus colchicus	A	NA	ground	omnivorous	resident	2	2	1
Phoenicurus ochruros	X	LC	cavity	insectivorous	short	1	29	85
Phoenicurus phoenicurus	A	NT	cavity	insectivorous	long	1	1	5
Phylloscopus collybita	F	LC	ground	insectivorous	short	1	66	84
Phylloscopus sibilatrix	F	VU	ground	insectivorous	long	1	2	7
Phylloscopus trochilus	F	VU	hedge/tree	insectivorous	long	1	4	6
Pica pica	X	LC	hedge/tree	omnivorous	resident	1	9	63
Picus canus	F	VU	cavity	insectivorous	resident	1	1	3
Picus viridis	X	LC	cavity	insectivorous	short	1	4	55
Podiceps cristatus	W	LC	reed	carnivorous	res/short	1	5	4
Prunella modularis	F	LC	hedge/tree	omnivorous	short	1	12	41
Pyrrhula pyrrhula	F	LC	hedge/tree	granivorous	res/short	1	3	15
Rallus aquaticus	W	LC	reed	carnivorous	res/short	1	1	1
Regulus ignicapilla	F	LC	hedge/tree	insectivorous	short	1	41	77
Regulus regulus	F	LC	hedge/tree	insectivorous	res/short	1	38	61
Saxicola rubicola	A	NT	ground	insectivorous	res/short	1	2	6
Serinus serinus	S	LC	hedge/tree	granivorous	short	1	11	44
Sitta europaea	F	LC	cavity	omnivorous	res/short	1	18	82
Streptopelia decaocto	S	LC	building	omnivorous	resident	1	7	27
Streptopelia turtur	A	NT	hedge/tree	granivorous	long	1	2	3
Strix aluco	F	LC	cavity	carnivorous	resident	1	2	9
Sturnus vulgaris	A	LC	cavity	omnivorous	short	1	41	85
Sylvia atricapilla	F	LC	hedge/tree	omnivorous	short	1	71	90
Sylvia borin	F	NT	hedge/tree	insectivorous	long	1	13	42
Sylvia communis	A	NT	hedge/tree	insectivorous	long	1	2	3
Sylvia curruca	F	LC	hedge/tree	insectivorous	long	1	1	1
Tachybaptus ruficollis	W	VU	reed	carnivorous	short	1	4	3
Troglodytes troglodytes	F	LC	ground	insectivorous	short	1	67	83
Turdus merula	F	LC	hedge/tree	omnivorous	res/short	2	88	90
Turdus philomelos	F	LC	hedge/tree	omnivorous	short	1	45	79
Turdus pilaris	A	VU	hedge/tree	omnivorous	short	1	12	35
Turdus viscivorus	F	LC	hedge/tree	omnivorous	short	1	24	59
Vanellus vanellus	A	CR	ground	omnivorous	short	2	3	2

Swiss Ornithological Institute: www.vogelwarte.ch/en/birds/birds-of-switzerland/

Keller et al. 2010: Rote Liste Brutvögel. Gefährdete Arten der Schweiz, Stand 2010. Bundesamt für Umwelt, Bern, und Schweizerische Vogelwarte, Sempach. *Umwelt-Vollzug*, 53.

Table A.2. Butterfly species list

Butterfly species list, including minimal and maximal abundance per landscape and the number of landscapes, a given species was observed (N_{lan}), within the total of 91 landscapes. Red List status based on Wermeille, Chittaro & Gonseth 2014 and habitat affiliation according to Benz *et al.* 1987. Abbreviations are: A = Agriculture, O = Other, LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, NA = not available.

Name	Habitat	Red List	Min. abund.	Max. abund.	N_{lan}
Aglais urticae	A	LC	1	74	77
Anthocharis cardamines	A	LC	1	15	48
Apatura ilia	O	VU	1	1	1
Apatura iris	O	NT	1	4	9
Aphantopus hyperantus	A	LC	2	170	80
Aporia crataegi	A	NT	1	3	2
Araschnia levana	O	LC	1	25	51
Argynnis adippe	A	LC	1	3	4
Argynnis paphia	O	LC	1	71	58
Aricia agestis-Komplex	NA	LC	1	6	20
Boloria dia	A	NT	1	7	9
Boloria euphrosyne	A	LC	1	1	2
Brenthis daphne	O	LC	1	12	16
Brenthis ino	O	NT	1	11	2
Brintesia circe	A	NT	1	19	2
Callophrys rubi	A	LC	6	6	1
Carcharodus alceae	A	NT	1	20	25
Carterocephalus palaemon	A	LC	1	1	5
Celastrina argiolus	O	LC	1	12	37
Coenonympha pamphilus	A	LC	1	98	78
Colias croceus	A	LC	1	47	37
Colias hyale-Komplex	NA	LC	1	130	64
Cupido alcetas	A	NT	1	22	20
Cupido argiades	A	NT	1	37	36
Cupido minimus	A	LC	1	2	2
Erebia aethiops	A	LC	74	74	1
Erebia ligea	O	LC	1	1	1
Erynnis tages	A	LC	1	28	12
Euphydryas aurinia	A	EN	1	1	1
Gonepteryx rhamni	O	LC	1	35	47
Hesperia comma	A	LC	1	1	1
Inachis io	O	LC	1	11	65
Issoria lathonia	A	LC	1	28	20
Lasiommata maera	A	LC	1	1	1

Lasiommata megera	A	LC	1	36	68
Leptidea sinapis-Komplex	A	LC	1	79	40
Limenitis camilla	O	LC	1	21	29
Lopinga achine	O	EN	4	4	1
Lycaena phlaeas	A	LC	1	10	21
Lycaena tityrus	A	LC	1	10	14
Maculinea alcon-Komplex	NA	VU	1	1	1
Maniola jurtina	A	LC	1	550	75
Melanargia galathea	A	LC	1	94	57
Melitaea athalia	A	LC	1	19	6
Melitaea cinxia	A	VU	1	1	1
Melitaea diamina	A	NT	1	7	2
Melitaea parthenoides	A	VU	1	16	4
Neozephyrus quercus	O	LC	1	2	2
Nymphalis polychloros	O	LC	1	1	1
Ochlodes venata	A	LC	1	38	64
Papilio machaon	A	LC	1	15	50
Pararge aegeria	O	LC	1	111	71
Pieris brassicae	A	LC	1	26	75
Pieris mannii	A	NT	1	43	6
Pieris napi-Komplex	NA	LC	6	328	91
Pieris rapae-Komplex	NA	LC	1	296	91
Plebeius argus	A	NT	1	35	2
Polygonia c-album	O	LC	1	23	62
Polyommatus bellargus	A	LC	2	15	5
Polyommatus coridon	A	LC	24	24	1
Polyommatus icarus	A	LC	1	132	85
Polyommatus semiargus	A	LC	1	55	72
Polyommatus thersites	A	VU	1	1	1
Pyrgus alveus-Komplex	NA	LC	1	4	3
Pyrgus armoricanus	NA	NT	1	1	1
Pyrgus malvae-Komplex	A	LC	1	3	12
Satyrium w-album	O	LC	1	2	4
Spialia sertorius	A	NT	1	4	3
Thecla betulae	O	LC	1	1	3
Thymelicus acteon	A	EN	2	2	1
Thymelicus lineola	A	LC	1	223	26
Thymelicus sylvestris	A	LC	1	39	23
Vanessa atalanta	A	LC	1	29	80
Vanessa cardui	A	LC	1	24	61
Zygaena ephialtes	A	VU	1	1	1
Zygaena filipendulae	A	LC	1	160	38

Wermeille, Chittaro & Gonseth 2014: Rote Liste Tagfalter und Widderchen. Gefährdete Arten der Schweiz, Stand 2012. Bundesamt für Umwelt, Bern, und Schweizer Zentrum für die Kartografie der Fauna, Neuenburg. Umwelt-Vollzug, 1403, 97.

Benz *et al.* 1987: Tagfalter und ihre Lebensräume. Schweizerischer Bund für Naturschutz, Basel.

Appendix B

Figure B.1. Agricultural survey data

The information on crop cover and biodiversity promotion areas were derived from the cantonal agricultural surveys. These data were available for the cantons Thurgau, St. Gallen, Fribourg, Bern, Luzern and Zürich (not available for Aargau, Vaud and Baselland). Hereby only landscapes with comprehensive data (missing data < 15% of utilized agricultural area UAA) and at least 30 ha of UAA were considered (n = 50). The figure below shows one of these landscape squares including the agricultural fields for which management data was available. Fields at the edge of the 1-km^2 landscape (black line) were considered if > 50% of the area, or > 1ha was located inside the square.

Table B.2. Biodiversity promotion areas

Description of the biodiversity promotion areas BPA (formerly called *ecological compensation areas*) present in our study landscapes. BPA are wildlife-friendly managed farmland habitats such as semi-natural grasslands, high-stem orchards and wildflower strips. They remain in general for eight consecutive years on the same field. Exceptions are BPA on arable land (e.g. wildflower strips) where the farmer can change the location every 1 - 2 years (see Caillet-Bois et *al.* 2017).

Type	**Management requirements***	**Proportion**
Extensively managed meadows	At least one cut per year, first cut not before the 15th of June. No fertilizer and pesticide use (except single plant application).	51 %
Orchards	Fruit, walnut and chestnut trees, with a minimal stem height of 1.20/1.60m.	22 %
Less intensively managed meadows	At least one cut per year, first cut not before the 15th of June. Fertilization with 30kg N/ha/year in form of solid manure is allowed, no pesticide use (except single plant application).	6 %
Extensively managed pastures	At least one use per year. No fertilizer (except from grazing livestock) and pesticide use (except single plant application) allowed.	10 %
Litter meadows	First cut not before the 1st of September. No fertilizer and pesticide use allowed.	5 %
Hedges	Hedges with vegetated buffer strips of 3 - 6m width.	3 %
Wildflower strips	Sown wildflower strips on arable land without pesticide and fertilizer.	2 %
Others	Extensively managed field margins from arable crops without pesticide and fertilizer, landscape elements such as single trees, pile of stones or ponds…	2 %

Caillet-Bois, D., Weiss, B., Benz, R. & Stäheli, B. (2017) Biodiversitätsförderung auf dem Landwirtschaftsbetrieb - Wegleitung. 5. Auflage 2017, **Agridea,** Lindau.

Figure B.3. Field size and crop diversity

There were no linear correlations (Pearson's correlation coefficient R) between mean field size or crop diversity (defined as number of arable crops), per landscape, and species richness of birds (a, b) or butterflies (c, d). Field size and crop diversity were not correlated (R = -0.01, t = -0.07, df = 48, p-value = 0.95).

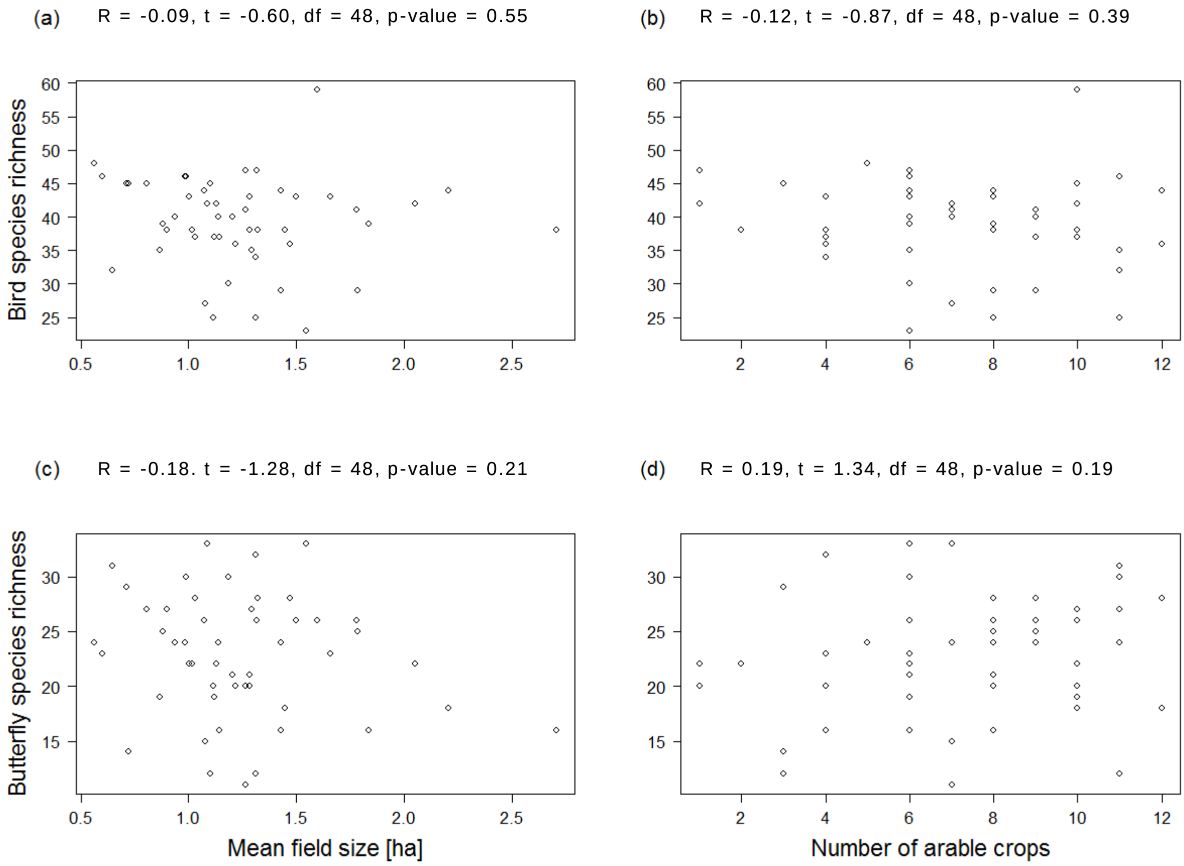


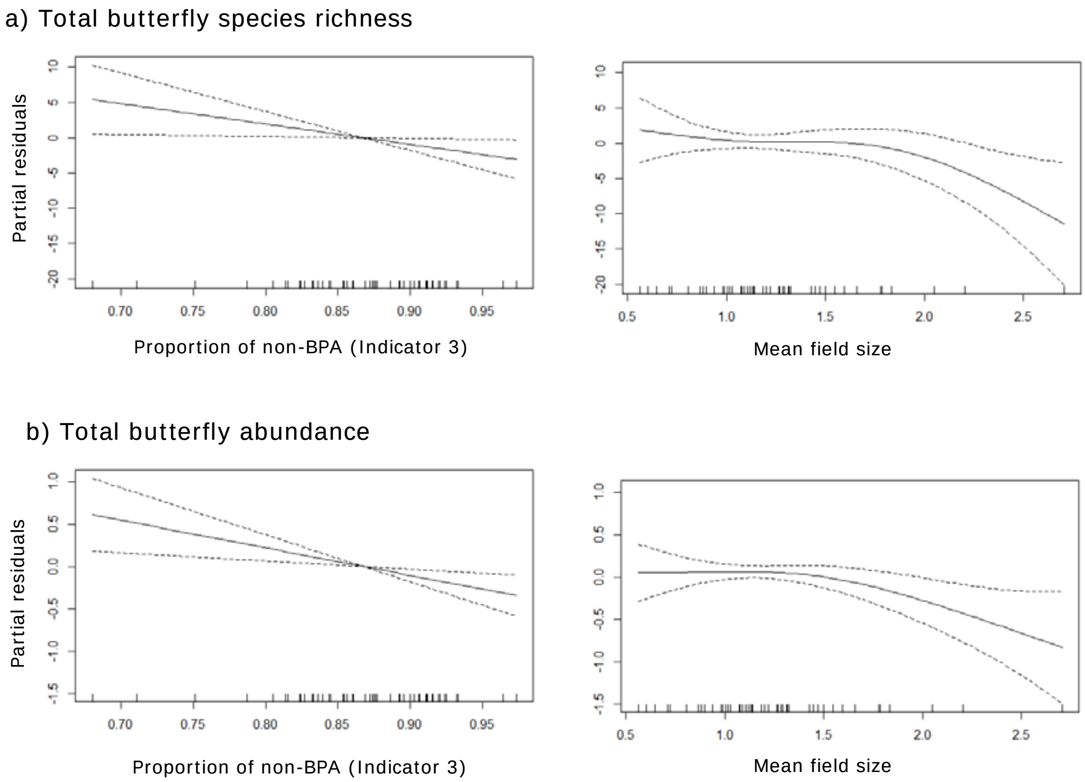
Table B.4. Field size and proportion of non-BPA

Field size and proporiton of non-BPA (Indicator 3) were positively correlated (R = 0.29, t = 2.09, df = 48, p-value = 0.04), indicating that landscapes with larger fields had less biodiversity promotion areas (BPA). We included mean field size as additional variable in the GAM, to ensure that the observed effect of Indicator 3 was not due to its correlation with field size. The table below contains the summary of the models showing the relation between total bird and butterfly species richness and butterfly abundance, and the significant variables from the full model (see main text Table 3). For each model the estimated degrees of freedom (edf), F statistic (F) and approximate significance of smooth terms (Sign.) are given. The adjusted R2-value (adj. R2) is the proportion of variance explained by the model. The partial residual plots are shown in figure B.5.

	Indicator 1			**Indicator 3**			**XY Coordinates**			**Mean field size**			**adj. R2**
Bird (total)	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Species richness	3.8	8.5	***	3.8	4.5	**				1.0	1.3	ns	0.57
Butterfly (total)	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Species richness				1.0	4.9	*	5.6	4.3	**	2.5	2.4	.	0.42
Abundance				1.0	8.1	**	2.0	25.8	***	2.0	7.1	*	0.27

Figure B.5. Field size and proportion of non-BPA

Total butterfly species richness (a) and abundance (b) along the land use intensity gradient of indicator 3 and the mean field size (n = 50). Partial residuals plots (log scale for abundance) from the GAM models are shown (the xy coordinates were also in the model, but not shown here).



Appendix C

Table C.1. Community weighted means

The community trophic index (CTI) ranged from 2.01 to 2.3 with a mean (± SD) of 2.19 (± 0.06). The community nest index (CNI) was 2.26 (± 0.21) with a minimum of 1.58 and a maximum of 2.71. The community migration index (CMI) ranged from 1.83 to 2.76 with a mean of 2.30 (± 0.17).

The table below contains the summary of the GAM models showing the relation between the community trophic index (CTI), the community nest index (CNI), the community migration index (CMI) and the land use indicators. The three models under a) included only indicator 1 and the XY coordinates as fixed effects (n = 91). Models under b) considered all three indicators and the XY coordinates (n = 50). For each model the estimated degrees of freedom (edf), F statistic (F) and approximate significance of smooth terms (Sign.) are given. The adjusted R2-value (adj. R2) is as usual the proportion of variance explained by the model. All models were fitted with a gaussian distribution and identity link function.

a)	**Indicator 1**			**XY Coordinates**			**adj. R2**
	edf	F	Sign.	edf	F	Sign.	
CTI	1.4	0.7	ns	5.9	1.5	ns	0.13
CNI	1.8	21.1	***	3.2	1.5	ns	0.40
CMI	1.7	7.0	**	2.0	0.5	ns	0.15

b)	**Indicator 1**			**Indicator 2**			**Indicator 3**			**XY Coordinates**			**adj. R2**
	edf	F	Sign.	edf	F	Sign.	edf	F	Sign.	edf	F	Sign.	
CTI	1.7	3.2	.	3.6	3.0	*	2.0	2.1	ns	5.6	1.8	ns	0.51
CNI	2.7	29.1	***	1.7	3.4	*	3.6	4.7	**	7.8	2.9	*	0.76
CMI	1.0	29.9	***	1.0	0.3	ns	3.5	2.7	*	7.4	3.4	**	0.58

Figure C.2. Community trophic index

The CTI changed along with indicator 2, the proportion of arable land within the agricultural areas. The partial residual plots indicate a decrease of the CTI with an increase of the proportion of arable land (n = 50 landscapes).