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Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale

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ABSTRACT

The intensification of agricultural practices that Western nations have experienced after World War II has led to an alarming decline in farmland biodiversity. With the aim of stopping and even reversing this decline, agri-environment schemes (AES) have been implemented in many European countries since the 1990s. In Switzerland, farmers are required to manage at least 7% of their land in the form of biodiversity promotion areas (BPA), which are extensively managed, wildlife-friendly farmland habitats such as hay meadows and traditional orchards. We investigated how the occurrence and characteristics of these BPA influence birds and butterflies in the Swiss lowlands. Butterfly species richness and abundance increased by 22% and 60%, respectively, when the proportion of BPA in the landscape increased from 5% to 15%. Likewise, bird species richness increased, but to a lesser extent, with the proportion of BPA in the landscape. For birds, the proportion of BPA characterized by a high ecological quality played a role in promoting both priority-farmland and red-listed species. For both taxonomic groups, the amount and quality of BPA habitats contributed more to species richness than their spatial configuration, connectivity included. This study shows that AES measures implemented at the field scale have positive effects on mobile species that are noticeable at the landscape scale, and that the fraction of AES in the cultivated landscape matters more than their spatial configuration, which has strong implications for designing multi-functional agro-ecosystems.

1. Introduction

Since the second half of the 20th century, agricultural practices have been considerably intensified, particularly in the Western World lowlands (Robinson and Sutherland, 2002). Agricultural intensification includes not only the increase of fertilizer and agrochemicals, but also the removal of natural structural landscape elements such as hedges and waterbodies (Stoate et al., 2001). Consequently, the amount of semi-natural habitats has dramatically decreased over time, with a wide range of species typical of extensively-managed farmland being on the brink of extinction in today's agroecosystems (Donald et al., 2006; Sutcliffe et al., 2015). As early as the 1990s, the European Union started to implement agri-environment schemes (AES) with the objective to stop and reverse this decline of farmland biodiversity. AES financially support farmers to adopt more environment-friendly management practices (e.g. organic farming) and to maintain or restore semi-natural habitats, such as hedgerows, field margins and traditionally managed grasslands. Biodiversity promotion areas (BPA; formerly called ecological compensation areas) are a major component of the Swiss AES policy. They have been introduced in 1993 by the Swiss government. Habitats typically falling under these BPA schemes are wildflower strips, hedges, high-stem orchards and extensively managed grasslands (i.e. with no fertilizer and pesticide application, see Table 1). BPA measures have to cover at least 7% of the land managed by a farmer and must stay in place for a minimum of eight consecutive years (Bundesrat, 2013). Despite high efforts and considerable flow of money into these schemes, farmland biodiversity is still in a deep crisis in Switzerland, as it is throughout Western Europe (Fischer et al., 2015). The reasons of the low effectiveness of these schemes are manifold, for example: lack of spatial connectivity between AES measures (Arponen et al., 2013; Birrer et al., 2007), poor ecological quality of the measures and insufficient fraction of farmland under AES (Birrer et al., 2007; Kleijn et al., 2011). AES effectiveness has been mostly evaluated at a field scale, usually focusing on only one type of AES measure at a time (Batáry et al., 2015; but see Bright et al., 2015; Davey et al., 2010). In contrast, wider-scale assessments of the effects of various types of

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Table 1
Description and occurrence of the biodiversity promotion areas (BPA) present in the 46 study landscapes. BPA 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 or 2 years.

BPA type	Management requirements and quality criteria	Mean area (± SD) per UAA [%]
Extensively managed meadows	At least one cut per year, first cut not before 15 June. No fertilizer and pesticide use (except single plant application). Quality: At least six indicator plant species.	6.3 (± 4.7)
Orchards	Fruit, walnut and chestnut trees, with a minimal stem height of 1.20/1.60 m. Quality: 30–100 trees/ha, > 0.2 ha with > 10 trees, in combination with another BPA within 50 m.	1.9 (± 2.2)
Less intensively managed meadows	At least one cut per year, first cut not before 15 June. Fertilization with 30 kg N/ha/year in form of solid manure is allowed, no pesticide use (except single plant application). Quality: At least six indicator plant species.	0.7 (± 1.5)
Extensively managed pastures	At least one use per year. No fertilizer and pesticide use (except single plant application) allowed. Quality: At least six indicator plant species and/or structural elements.	0.6 (± 1.3)
Litter meadows	First cut not before 1 September. No fertilizer and pesticide use allowed. Quality: At least six indicator plant species.	0.5 (± 1.9)
Hedges	Hedges with vegetated buffer strips of 3–6 m width. Quality: Only native species, > 2 m width, > 5 tree/shrub species per 10 m length, > 20% of thorny shrubs or one native tree every 30 m.	0.4 (± 0.5)
Wildflower strips	Sown wildflower strips on arable land without pesticide and fertilizer.	0.4 (± 1.6)
Field margins	Extensively managed field margins from arable crops without pesticide and fertilizer.	0.1 (± 0.2)

measures simultaneously implemented are still lacking although distribution and population dynamics of many taxonomic groups are ruled by landscape processes rather than mere field-site conditions, notably due to the habitat complementarity that organisms require to complete their life cycle (e.g. Concepción and Díaz, 2011; Westphal et al., 2006). If the availability of digital maps of land use and AES measures has so far represented a serious impediment to such landscape-scale analyses, recent technology developments opened new avenues for research on the effects of AES at the landscape scale.

The main goal of this study was to investigate the influence of Swiss AES (BPA) on bird and butterfly species richness and abundance at the landscape scale. These two taxa were selected as model groups because their life cycles mostly require habitat complementarity, thus operating at a landscape scale (e.g. Concepción and Díaz, 2011). Seven different landscape-scale BPA properties were analysed: the proportion of BPA, the proportion of BPA with ecological quality according to Swiss agri-environmental policy standards (see Table 1), the BPA mean size, the mean minimal distance between individual BPA, the diversity and the configuration of BPA. Besides these BPA-related variables, the wider landscape composition, such as the proportion of forests and water-bodies in the landscape, was also considered. As former evaluation studies, carried out at the field scale, have demonstrated enhancement of farmland biodiversity in response to AES measures (Batáry et al., 2015), we predicted, firstly, that positive effects of the proportion of BPA on birds and butterflies should also be noticeable at the landscape scale (Henderson et al., 2012). Secondly, we predicted that BPA habitat quality, assessed through botanical diversity, promotes the two study taxa (Aviron et al., 2011; Birrer et al., 2007). Our third prediction was that habitat fragmentation and distance between BPA can negatively influence their effectiveness (Bailey et al., 2010; Knop et al., 2011) and could play a role even in mobile species such as birds and butterflies (Krauss et al., 2003). Fourthly, the spatial association between different types of BPA (e.g. hedges and extensively managed meadows) may provide complementary resources, meaning that BPA diversity may have a favourable effect that should be detectable at the landscape scale (Haynes et al., 2007). Beside these various and direct potential effects of BPA, we also expected that the wider non-agricultural landscape impacts biodiversity. In particular, forests, hedges and water bodies are natural features, among agroecosystems, known to promote biodiversity (e.g. Diacon-Bolli et al., 2012; Zingg et al., 2018). Actually, they provide birds and butterflies with the necessary habitat complementarity, notably shelter, food supply and corridors for movement (e.g. Coulthard et al., 2016; Siriwardena et al., 2012). As our study focuses on the intensively-cultivated Swiss lowlands, its outcomes bear relevance for other highly productive agricultural regions in Europe and may thus assist them in refining future agricultural policy.

2. Material and methods

2.1. Landscape selection

This study was conducted on the Swiss Plateau, a lowland region situated between the Alps and the Jura mountain ranges. It is the most densely populated region of Switzerland and characterized by high-intensity agriculture. The Biodiversity Monitoring Switzerland (BDM) conducts repeated biodiversity surveys, using a systematic sampling grid with 520 landscapes of 1 km^2 across Switzerland (BDM Coordination Office, 2014). For this study, 46 such 1 km^2 squares were selected in the Swiss lowlands (average elevation of 560 m a.s.l., range: 320–780 m). Termed “landscapes”, the selected 1 km^2 squares all stemmed from cantons for which digitalised maps of the BPA were available. All selected landscapes had < 25% cover of water bodies and impervious areas, and at least 40% of utilized agricultural area (UAA). These study landscapes were at least 12 km apart and scattered across the Swiss lowlands (Fig. 1).

2.2. Biodiversity

Data on species richness and abundance of birds and butterflies was provided by the Swiss Biodiversity Monitoring (BDM – Z7 indicator) and the Swiss Ornithological Institute (SOI – Monitoring programme for common breeding birds). All selected landscapes were surveyed once in the years 2010–2014. Most bird surveys were carried out in 2014 (33 out of 46), whereas butterfly counts were equally distributed over all five sampling years. Surveys consisted of within-year repeated counts along transects of 2.5 km, with 7 and 3 surveys a year for butterflies and birds, respectively (BDM Coordination Office, 2014). Ornithologists estimated number of breeding bird territories based on their field observations, while butterfly specialists counted numbers of individuals, at the species or species-complex level. Note that for large groups of butterflies (> 20 individuals), abundance was estimated in a semi-quantitative way (21–40, 41–100 and > 100).

Butterfly and bird species were classified into four main groups: total, farmland, AEO priority and red listed species (see Table S1 and S2). The so-called AEO priority species include the target and indicator species defined within the framework of the agriculture-related environmental objectives by the federal offices of environment and agriculture (Walter et al., 2013). These species are currently the focus of national farmland conservation programmes. Our red-listed species belong to the categories near threatened, vulnerable, or critically endangered sensu IUCN criteria (Keller et al., 2010; Wermeille et al., 2014).

In an attempt to gain information on the effect of AES on ecosystem

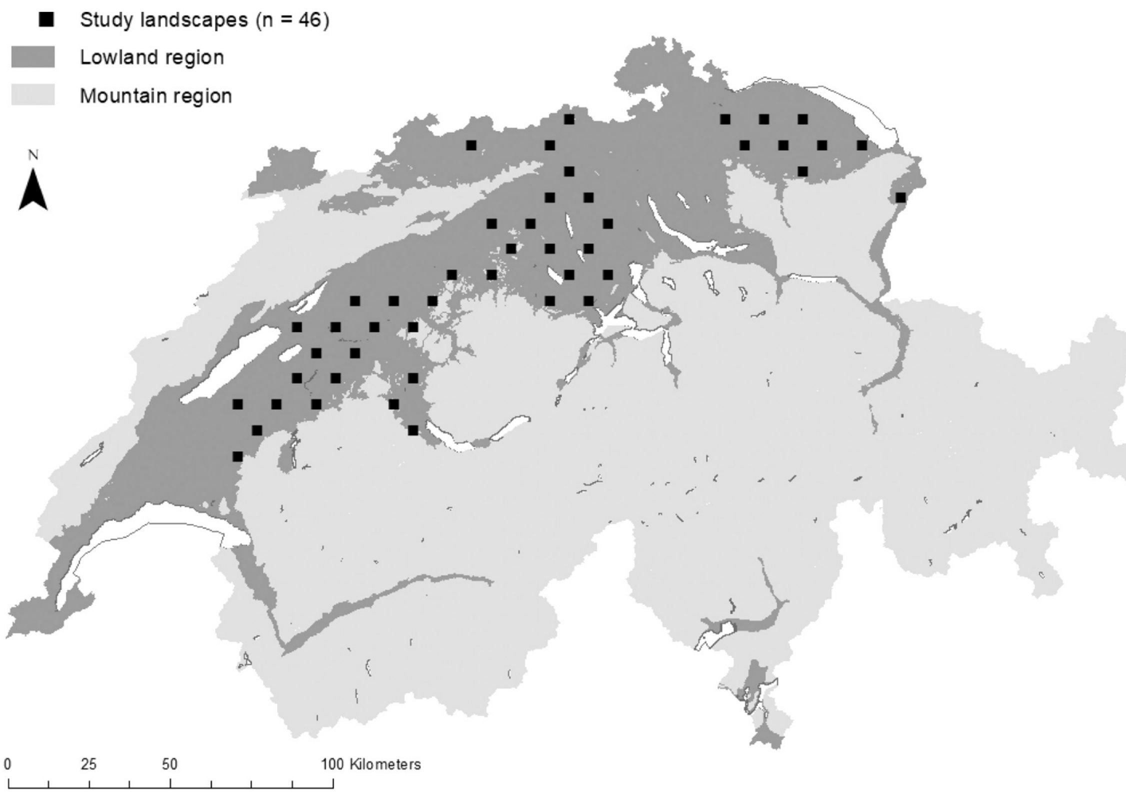

Fig. 1. Map of Switzerland with the 46 1-km^2 selected study landscapes.

functionality (beyond species richness), we first classified butterflies into specialists or generalists, with specialists being resident species with a mono- or oligophagous diet (caterpillars feeding on a single plant species, genus or family) and a maximum of two generations per year (see also Bruppacher et al., 2016). We derived life-history traits for butterfly species from (Settele et al., 1999). Second, we grouped birds into functional groups, or guilds, according to their foraging and nesting characteristics: granivorous, insectivorous, carnivorous (i.e. raptors preying mostly on small mammals and birds) and omnivorous species; building breeders, cavity breeders (nesting in artificial or natural cavities), ground breeders, hedge/tree breeders (nesting aboveground in wooden structures, i.e. outside tree cavities) and reed breeders (Tables S1 and S2).

2.3. BPA and land-use

Land-use maps were obtained from the Swiss cadastral survey of 2014 (Swisstopo). We derived the proportions of utilized agricultural area (UAA), forests, hedges, waterbodies, impervious surfaces, vegetated and non-vegetated areas per landscape. Maps of BPA were provided by the cantonal agricultural offices for 2013 and 2014. From them, we could extirpate seven BPA properties for every study landscape: 1) total area of BPA within the 1 km^2; 2) proportion of BPA per UAA; 3) mean BPA size; 4) proportion of BPA with ecological quality per UAA; 5) mean distance between BPA; 6) BPA diversity and 7) mean BPA perimeter area ratio (PAR). We used the two-dimensional projected areas to calculate properties 1–3. Property 4 refers to the ecological quality criteria as defined by the Swiss Ordinance on Direct Payments, which comprise both the presence of particular indicator plant species and a diversified vegetation structure (see Table 1). Mean distance between BPA (property 5) was defined as the mean minimal distance to the nearest BPA. Property 6 corresponds to a Shannon diversity index calculated from the various types of BPA found within a 1-km^2 landscape square:

$$BPA\ diversity = -\sum_{i=1}^{N} p_i \times \ln(p_i)$$

where N is the total number of BPA types and p_i the proportion of the BPA type i in the landscape square. Property 7 was calculated as the mean perimeter area ratio (PAR) of the BPAs and is a measure for the configurational heterogeneity of the BPAs within a landscape (Perović et al., 2015). All spatial analyses were conducted in ArcGIS (Version 10.2.2) with a buffer of 50 m added to each landscape square of 1 km^2 (Fig. 2). Detailed information on all BPA types can be found in Table 1 (see also Caillet-Bois et al., 2018).

2.4. Data analysis

Species richness and abundance of all, farmland, AEO priority and Red List birds and butterflies and different functional groups and guilds were used as response variables in the models. Functional bird groups were only analysed if they included at least 20 species. To meet model assumptions regarding normal distribution of residuals, abundance of farmland (only birds), AEO priority and red-listed birds and butterflies had to be log-transformed. Correlations between all explanatory variables were assessed using Pearson's correlation coefficient (r_s). Strong positive correlations ($r_s \geq 0.7$) were found between the total area of BPA and the proportion of BPA per UAA ($r_s = 0.91$), total area of BPA with ecological quality and BPA with quality per UAA ($r_s = 0.99$) and, finally, the proportion of impervious (e.g. settlements, roads) and vegetated areas (e.g. gardens, vegetated roadsides). Therefore, total area of BPA, total area of BPA with ecological quality and impervious areas were excluded from the modelling process (Table 2). A three-step model selection approach adapted from Potts et al. (2009) was then applied. Three different model sets were fitted using linear models: Model 1 included all BPA-related variables and Model 2 included all land-use related variables and altitude. Altitude was added to account for climatic differences between the landscapes, potentially influencing the biodiversity indicators (Mac Nally et al., 2003). The general formula of

Fig. 2. Example of a 1 km × 1 km study landscape showing different BPA types: extensively-managed meadows (green), low-intensity meadows (yellow), hedges (purple) and wildflower strips (orange). As the immediate surrounding of the landscapes may influence the bird and butterfly counts, we added a 50 m broad buffer to all landscape squares for all analyses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the first two linear models was:

Model 1:

lm (y~BPA proportion + BPA quality + BPA mean size + BPA mean distance + BPA diversity + BPA PAR)

Model 2:

lm (y~UAA + forest + hedges + waterbodies + vegetated + non_vegetated+altitude)

Additionally, several two-way interactions were tested in bivariate models (i.e. BPA proportion ∗ BPA mean distance, BPA proportion ∗ BPA quality and BPA mean size ∗ distance) and the interaction was included in the model selection process only if it was significant in the bivariate model. Automated model selection, using the *dredge* function from the R Package *MuMIn* (Bartón, 2017) was performed to find the most parsimonious model. Hereby all possible combinations of explanatory variables are fitted and ranked according to the AICc. Only the explanatory variables retained in the best models 1 and 2 were afterwards combined in a new third model that had the same structure as the two previous models (see Table S3). Again, automated model selection was applied to obtain the final models. Normality, homogeneity and spatial independence of the residuals were visually checked using QQ plots and the graph of residuals versus fitted values and XY coordinates. All statistical analyses were performed using R version 3.4.5 (R Core Team, 2017).

3. Results

Overall, 59 butterfly species were observed, of which 41 were categorized as farmland, 26 as AEO-priority and 13 as red-listed species. For birds, 99 species including 22 farmland, 26 AEO-priority and 28 red-listed species, were observed (see also Table S1 and S2).

Table 2
Land-use and BPA properties in our 46 study landscapes. UAA stands for utilized agricultural area.

Land-use		Mean area (± SD) per landscape [%]
Forest	Forest	18.2 (± 14.7)
Impervious	Buildings, streets, railroads, parking lots and other impervious areas	7.8 (± 5.7)
Vegetated	Gardens, roadsides and other green areas	5.7 (± 6.6)
Waterbodies	Lakes, ponds, rivers and reed	1.7 (± 3.8)
Hedges	Hedges (not BPA) and planted roadsides	0.4 (± 0.7)
Non-vegetated	Landfils, gravel, rock and other non-vegetated areas	0.1 (± 0.7)
Biodiversity promotion areas (BPA)		**Mean value (± SD) per landscape**
BPA area	Total area of BPA in m^2	87'715 (± 46'043)
BPA proportion	Proportion of BPA per UAA in %	11.1 (± 5.7)
BPA quality	Proportion of BPA with quality per UAA in %	2.0 (± 3.5)
BPA mean size	Mean BPA size in m^2	3'168 (± 1'577)
BPA mean distance	Mean distance between BPA in m	64.4 (± 161.7)
BPA diversity	Shannon's diversity index of BPA types	0.82 (± 0.36)
BPA PAR	Mean perimeter area ratio of BPA	0.24 (± 0.06)

Table 3
Summary output of the final models predicting total, farmland, AEO priority and red list butterfly species richness and abundance. Shown are parameter estimates (Est.), standard error (SE) and significance (*** p-value < 0.001, ** $p < 0.01$, * $p < 0.05$, . $p < 0.1$) for all variables retained in the final models, as well as the adjusted R^2.

Butterfly species richness	Total			Farmland			AEO-priority			Red list		
	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Intercept	17.4	2.3	***	7.1	2.7	*	2.8	0.8	**	1.2	0.2	***
BPA proportion	52.9	14.0	***	36.1	10.0	***	17.3	6.3	**			
BPA quality												
BPA mean size	−0.0	0.0	.									
BPA mean distance												
BPA diversity												
BPA PAR				14.5	9.3							
UAA												
Forest	12.6	5.3	*									
Waterbodies							−21.5	9.5	*			
Hedges												
Vegetated												
Non-vegetated										52.8	28.6	.
Altitude												
Adj. R-squared	0.30			0.21			0.18			0.05		

Butterfly abundance	Total			Farmland			AEO-priority (log)			Red list (log)		
	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Intercept	345.0	68.2	***	192.4	62.1	**	2.3	0.4	***	1.1	0.2	***
BPA proportion	2390.0	540.2	***	1466.0	431.2	**	7.4	3.0	*			
BPA quality	−1364.0	869.1										
BPA mean size	−0.0	0.0	*	−0.0	0.0	*						
BPA mean distance												
BPA diversity												
BPA PAR												
UAA												
Forest												
Waterbodies	−1378.0	716.3	.	−1127.0	635.4	.	−11.6	4.6	*			
Hedges												
Vegetated												
Non-vegetated										47.3	23.1	*
Altitude												
Adj. R-squared	0.36			0.25			0.18			0.07		

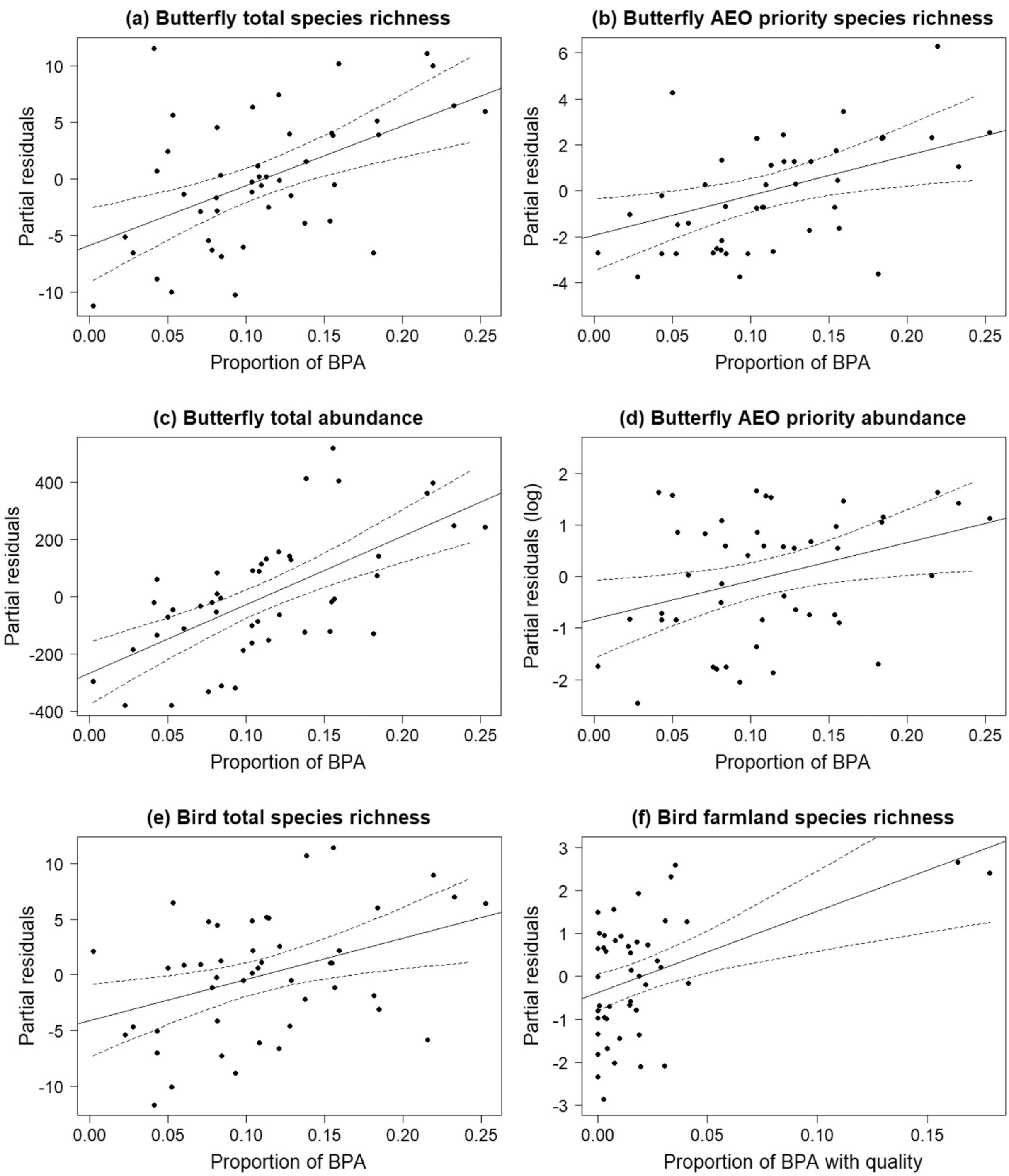

Fig. 3. Relationships between species richness and abundance of different butterfly (a-d) and bird groups (e-f) vs the proportion of BPA per UAA. The so-called AEO-priority species include the target and indicator species defined within the framework of the agriculture-related environmental objectives. Partial residuals and predictions with 95% confidence intervals from the final model are shown.

The main land-use types in the landscapes were farmland and forest (Table 2). On average (mean ± SD), 11% (± 6) of the farmland (UAA) was managed as BPA, which equates to 8.8 ha (± 4.6) per landscape square. The most common BPA types were extensively-managed meadows and traditional high-stem orchards (Table 1). The proportion of BPA with ecological quality was very low and accounted for only 2% (± 4%) of the UAA. Two landscapes were outstanding, with BPA exhibiting ecological quality covering 16% and 18% of the farmland area, respectively.

3.1. Effects of BPA and land-use on butterflies

The best models predicting total, farmland and AEO-priority butterfly species richness and abundance always included the proportion of BPA per UAA, which had a significant positive effect (Table 3 and Fig. 3). An increase of the BPA fraction of UAA from 5% to 15% was accompanied, on average, by an additional 5 butterfly species (+22%, from an average of 23 species per landscape) and by an increase of 242 individuals (+60%, from an average abundance of 409 individuals per landscape). The same trends were found for generalist butterflies (45

Table 4
Summary output of the final models predicting total, farmland, AEO priority and red list bird species richness and abundance. Shown are parameter estimates (Est.), standard error (SE) and significance (*** p-value < 0.001, ** p < 0.01, * p < 0.05, p < 0.1), for all variables retained in the final models, as well as the adjusted R^2.

Bird species richness	Total			Farmland			AEO-priority			Red list		
	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Intercept	29.2	2.0	***	3.7	1.0	***	4.6	0.6	***	−0.6	1.2	
BPA proportion	37.3	13.7	**				12.7	5.3	*			
BPA quality				19.0	5.6	**	17.8	8.8	*	17.1	6.7	*
BPA mean size												
BPA mean distance												
BPA diversity												
BPA PAR												
UAA				5.6	1.4	***				4.1	1.7	*
Forest	19.7	5.4	***									
Waterbodies	55.6	21.3	*				26.4	7.2	***	28.9	6.2	***
Hedges	349.8	115.1	**	90.6	27.6	**	103.2	38.9	*	159.2	33.1	***
Vegetated												
Non-vegetated				54.0	27.4	.						
Altitude												
Adj. R-squared	0.44			0.40			0.54			0.61		

Bird abundance	Total			Farmland (log)			AEO-priority (log)			Red list (log)		
	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Intercept	564.8	73.4	***	3.9	0.2	***	3.9	0.4	***	3.0	0.5	***
BPA proportion				−0.04	1.2							
BPA quality				−16.8	7.5	*	4.4	2.1	*	5.4	3.5	
BPA mean size												
BPA mean distance												
BPA diversity												
BPA PAR										−4.0	1.9	*
BPA prop. * BPA quality				87.3	33.4	*						
UAA	−417.6	106.5	***									
Forest				−0.8	0.4	*						
Waterbodies										7.4	3.1	*
Hedges	4572.2	2026.3	*									
Vegetated							−2.2	1.1	.			
Non-vegetated												
Altitude							−0.0	0.0	*			
Adj. R-squared	0.32			0.20			0.21			0.19		

species), but regarding specialist butterflies (14 species) only abundance responded positively to the fraction of BPA in the landscape (Table S4). Other BPA properties (ecological quality, size, distance, diversity or spatial BPA configuration) showed no significant effects. As for land-use variables, the only significant (positive) correlation was between total butterfly species richness and the area of forest.

3.2. Effects of BPA and land-use on birds

Total bird species richness showed a positive correlation with the proportion of BPA, whereas farmland, AEO-priority and red-listed species richness increased also with the proportion of BPA with ecological quality (Table 4 and Fig. 3). An increase in the proportion of BPA from 5% to 15% led to a predicted increase of 4 bird species (or 10%), from an average of 39 per landscape. Similarly, an increase in the proportion of BPA with ecological quality from 0% to 5% led to a predicted increase of farmland species richness by 1 species (or 13%) from an average of 8. There was a significant interaction between the effect of BPA proportion and BPA quality on farmland bird abundance; the higher the proportion of BPA with quality, the stronger the positive effect of increasing BPA proportion was. However, the positive effect of BPA with ecological quality was strongly influenced by the two outstanding study landscapes harbouring high proportions of BPA with quality (Fig. 3f). When these two landscapes were excluded from the analyses, the proportion of BPA with quality had no significant effect on bird species richness anymore.

The analysis furthermore revealed that species richness of hedge/tree and cavity breeders were positively correlated with the proportion of BPA. The abundance of the different functional groups and guilds did not significantly change with respect to BPA-related variables, but only with some land-use variables: the abundance of insectivorous birds increased with the proportion of forest, while the abundance of omnivorous birds increased with the proportion of UAA within the landscape (Table S5).

4. Discussion

Biodiversity promotion areas (BPA) are wildlife-friendly managed farmland habitats such as semi-natural grasslands, high-stem orchards and wildflower strips that form part of the Swiss AES. This study conducted in 46 1-km^2 landscapes across the Swiss lowlands is one of the first carried out at the landscape scale that disentangles the effects of landscape composition (e.g. proportion of forests or farmland) and BPA availability on biodiversity. It shows that BPA have broad-scale positive effects on birds and butterflies. As bird and butterfly surveys were conducted along transects that were not specifically located to record the fauna of the BPA areas themselves, these findings are likely to mirror the general biodiversity response to BPA in the wider modern Swiss lowland landscape, and not just local aggregations around BPA measures. We therefore conclude that the increased number of species and individuals were not due to concentration effects (attraction of individuals) but due to population level responses (see Le Féon et al., 2013).

4.1. Effects of BPA and land-use on butterflies

The proportion of BPA in the landscape proved to be the most important property of this Swiss AES measure for butterfly species richness and abundance. This was regardless of BPA quality, size, distance, diversity, configuration, and landscape composition. Total, farmland and AEO-priority butterfly species were all positively correlated with the proportion of BPA. Most butterflies depend on grassland habitats, especially flower-rich meadows that offer variegated plant hosts and nectar sources. They are therefore favoured by low-input management practices (Ekroos and Kuussaari, 2012) as typically encountered among BPA meadows. Extensively-managed and low-intensity BPA meadows account for 63% of all BPA fields in our study landscapes. It is thus not surprising that butterflies showed such a strong response to the implementation of BPA at the landscape scale. If a positive effect of extensively-managed grasslands and wildflower strips was already demonstrated at the field scale (e.g. Aviron et al., 2011), the present study is the first to establish clear effects at the wider landscape scale. In addition, we found that increasing the proportion of BPA promotes existing population of butterfly specialists by increasing their abundance. Specialist species are known to be strongly affected by agriculture intensification, such as landscape simplification and habitat fragmentation (Ekroos et al., 2010), it is therefore important that agri-environment schemes support this group (see also Bruppacher et al., 2016; Krauss et al., 2003). In contrast, red-listed butterflies were almost absent (on average only 1 ± 1 species) in our study landscapes and thus don't seem to benefit from BPA, probably because most need species-specific habitat restoration measures (Kleijn et al., 2006).

4.2. Effects of BPA and land-use on birds

The proportion of BPA in the landscape as well as their ecological quality were the two main drivers of bird species richness in the otherwise fairly intensively-cultivated Swiss lowlands, which is in line with previous findings (Baker et al., 2012; Prince and Jiguet, 2013). Birds in general and hedge/tree, or cavity breeding species particularly profit from AES-BPA measures such as extensively managed meadows or hedges (see also Bright et al., 2015; Zellweger-Fischer et al., 2018). BPA and natural areas increase the functional heterogeneity of the cultivated landscape, which is likely to provide a better habitat complementarity for accomplishing the different phases of bird life cycle (Fahrig et al., 2011). For example, extensively-managed grasslands provide invertebrate prey supplies for insectivores while hedges and high-stem orchards provide nesting sites. The benefits of farmland habitat heterogeneity for enriching bird communities became evident when land-use properties beyond AES-BPA measures were accounted for, as formerly stated by Siriwardena et al. (2012) and Vickery and Arlettaz (2012). Yet, birds of conservation concern (farmland, priority and red-list species) were mainly positively correlated with the proportion of BPA with ecological quality. Notwithstanding the fact that two outstanding landscape squares with a high fraction of BPA with quality (16% and 18%) are behind the significance of the observed pattern (Fig. 3f), our findings corroborate the view that commonly implemented AES have only moderate effects if any upon red list and farmland birds. More demanding AES or specific action plans that go beyond the standard AES measures are necessary to maintain and restore farmland bird communities (Breeuwer et al., 2009; Meichtry-Stier et al., 2014).

4.3. BPA properties and effectiveness

It is an ongoing debate under which agricultural intensities and landscape compositions and configurations AES work best (Batáry et al., 2015). We show here that the Swiss AES can effectively promote biodiversity in Central European lowland regions characterized by a high-intensity but small-scaled farming system. In our study area fields have a relatively small size (mean ± SD: 1.25 ± 0.4 ha), while arable crop diversity is high (7 ± 3 per 1 km^2) and patches of natural habitats often present. This setting corresponds to an agricultural landscape of intermediate complexity, where AES measures are likely to provide the best biodiversity benefits (Concepción et al., 2012; Tscharntke et al., 2012). In contrast to our hypothesis, BPA effectiveness was not influenced by distance, diversity, spatial configuration, or by size of individual BPAs. However, it is important to note that connectivity (or fragmentation) is inherently linked to the proportion of available habitat (Fahrig, 2003). If habitat cover reaches a certain threshold, distance between patches becomes fairly irrelevant (Thomas et al., 2001). In our landscapes, BPA covered, on average, 11% of farmed area while mean distance between BPA patches was 64 m. This probably provided sufficient habitat continuum for our two mobile taxa. In support of it, Brückmann et al. (2010) showed that connectivity was an important predictor for butterflies and plants typical of calcareous grasslands where this habitat covered only 0.01–2.2% of the farmed landscape. However, for less mobile species or bad dispersers, connectivity between BPA may still be of importance (Knop et al., 2011). Despite the known positive species-area relationship from island biogeography theory (see also Bender et al., 1998), we could not evidence any effect of BPA size or perimeter-area ratio on species richness and abundance. Again, this could be due to the study of highly mobile taxa in the heterogeneous cultivated landscapes typical of the Swiss lowlands (Helzer and Jelinski, 1999; Öckinger and Smith, 2006; Perović et al., 2015).

4.4. Conclusions and management recommendations

Our results provide strong evidence for the beneficial effects of Swiss AES (BPA) on bird and butterfly communities and populations at the landscape scale. As BPA proportion and quality were by far the most important properties for efficient BPA, farmland biodiversity could be further promoted by, firstly, increasing the proportion of BPA in the cultivated landscape and, secondly, further improving the ecological quality of the BPA. Methods to enhance BPA quality already exist: the floral diversity of low-quality hay meadows can for example be boosted through reseeding (Kiehl et al., 2010). In addition, delaying the first mowing date or maintaining uncut grass refuges has been shown to benefit invertebrate biodiversity (Bruppacher et al., 2016; Buri et al., 2016; Humbert et al., 2010; Schmiede et al., 2011). Yet, we have to recognize, that biodiversity in the Swiss lowlands is generally depauperated. Any slight enhancement of ecological conditions might thus have had positive effects on it, which is probably why we could evidence so clear positive effects of BPA. Our findings on the effectiveness of the Swiss BPA system bear relevance beyond Switzerland, notably for improving the often criticized ecological focus areas, which are part of the greening measures of the current EU Common Agricultural Policy (Pe'er et al., 2016).

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Appendix A. Supplementary data

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