Integrating food production and biodiversity conservation in temperate agricultural landscapes

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Silvia Zingg

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Leiter der Arbeit:

PD Dr. J.-Y. Humbert

Prof. Dr. R. Arlettaz

Institut für Ökologie und Evolution

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SUMMARY

Biodiversity needs space and access to net primary production of ecosystems and therefore often competes with agricultural production. As land is limited and human population rising, this conflict is likely to increase further and calls for more researches on how to better integrate food production and biodiversity conservation in agricultural landscapes.

In the framework of this PhD thesis, we studied the relationships between bird and butterfly communities and different agricultural landscape descriptors in grid cells of 1 x 1 km in the Swiss lowland. We first described how biodiversity changed along three land use intensity gradients, that accounted for land cover (farmed vs. natural areas), crop cover (arable crops vs. permanent grassland) and management intensity (intensively managed vs. extensively managed areas) at landscape scale. Subsequently we focused on the extensively managed wildlife-friendly areas, the so-called biodiversity promotion areas (BPA). We analysed how the composition and configuration of these BPA influenced bird and butterfly communities at landscape scale. Such wider-scale assessments of various types of BPA measures simultaneously implemented, were lacking until now, although many taxonomic groups are ruled by landscape processes rather than mere field-site conditions. Finally, we analyzed the often assumed, trade-off between agricultural productivity and biodiversity. Actual yield figures provided by 299 farmers served to quantify the agricultural production in terms of food energy (in joules), in landscapes with mixed, arable crop and livestock production systems.

Our results confirmed the importance of natural areas, such as forest, hedges and waterbodies, for biodiversity conservation in agricultural landscapes; bird species richness showed a sharp decrease when less than 20% natural areas were present. In addition, natural areas may mitigate the trade-off between agricultural food production and biodiversity, by reducing the negative effect of local high-productive agriculture. Along with natural areas, also BPA proved to considerably enhance bird and butterfly diversity in the surrounding. The target and indicator species of both taxa, defined within the framework of the agriculture-related environmental objectives, positively correlated with BPA. Hereby the amount and quality of BPA habitats contributed more to species richness than their spatial configuration, connectivity included. It became evident that ecological quality of most BPA is low and that generating a momentum for further improving the ecological quality is needed. Finally, there was no *a priori* conflict between biodiversity and food production in mixed temperate agricultural landscapes. Neither farmland birds nor butterflies showed a negative relationship with food energy production. All together the thesis delivers evidence-based prescriptions, for multi-functional temperate agricultural landscapes, integrating production and biodiversity conservation.

GENERAL INTRODUCTION

AGRICULTURAL INTENSIFICATION AND BIODIVERSITY

The ongoing human population growth leads to a constantly increasing demand for food and agricultural products. Between 2005 and 2050, agricultural crop production has to double, to supply the food required by the estimated nine billion people (Tilman *et al.* 2011). So far, this demand has been met mostly by i) developing and intensifying agricultural practices to reach higher yields per area and by ii) converting natural habitats into new agricultural lands. Thereby, productivity increased more significantly than did the area of agricultural land; grain production more than doubled since the 1960s as a consequence of increased use of fertilizers, irrigation, mechanization, pesticides and the development of new varieties and breeds (Robinson & Sutherland 2002), while the total area devoted to arable production only increased by ~ 9% globally (Pretty 2008).

Agricultural intensification radically changed the appearance of farmland ecosystems. At the landscape scale, farms specialized on fewer crops; grasslands and fallow lands were converted to arable fields and natural or edge habitats such as field boundaries and hedges were destroyed (Tscharntke *et al.* 2005). This is a devastating development for farmland biodiversity, as many species require different complementary habitats and a diversity of resources to complete their life cycles (Westphal 2006; Vickery & Arlettaz 2012). Birds, for example, need nesting and feeding sites, while butterflies depend upon specific fodder plants during larval development and nectar sources as adults. The removal of structural landscape elements as described above, therefore impedes resource availability. Not only the loss of natural areas but also the reduction in field borders associated with increased field size negatively affected habitat availability and movement of many farmland species (Smith *et al.* 2014; Batáry *et al.* 2017; Hass *et al.* 2018). At the field scale, mainly the increased use of agrochemicals (e.g. mineral fertilizer and pesticides) impaired biodiversity. Nitrogen input in both, grasslands and arable fields, decreased botanical diversity (Kleijn *et al.* 2009). Therefore, the impoverished plant communities offer fewer host and flowering plants to invertebrates and thus support lower invertebrate diversity (Marini *et al.* 2009; Börschig *et al.* 2013). In addition, the enhanced biomass production, allowed for more frequent harvesting, which are detrimental, not only for vertebrates such as ground-breeding birds, but also for small invertebrates (e.g. Humbert *et al.* 2010). In addition to the direct effects of changes in plant resources, indirect effects also affect upper trophic levels, as for example predators suffer from the decreased availability of invertebrate prey (Vickery *et al.* 2001). On top of that, pesticide applications not only suppresses biodiversity within agricultural fields (Filippi-Codaccioni *et al.* 2010) but also in the wider landscape including natural habitats (Beketov *et al.* 2013).

As a consequence of the changes described above, species occurring in agricultural areas experienced larger population declines than species adapted to other habitat types. In Europe, farmland birds declined by 32 % between 1990 and 2014, whilst for example common forest birds declined only by 12% (Eurostat 2018). 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. Sustainable agricultural production relies on a diverse biological community, that supports a wide range of ecosystem services, such as soil fertility, natural pest control and pollination (Bommarco, Kleijn & Potts 2013). It has for example been shown that biological pest control can improve wheat yields if adjacent wildlife-friendly habitats are promoted (Tschumi *et al.* 2016). Likewise, natural habitats promote pollinators (Ricketts *et al.* 2008), which enhances the yield of arable crops (Bommarco, Marini & Vaissiere 2012). Conservation of farmland biodiversity is therefore important, not only because of its intrinsic value, but also for a sustainable, long term food production (Carvalheiro *et al.* 2011). With the increasing awareness on the consequences of biodiversity loss, and at the same time, the need to produce more food, research on the links between food production and biodiversity considerably intensified in the last two decades. One of the major current challenges, is to describe land use strategies to ensure food production, while minimizing the negative impacts on biodiversity and the ecosystem services it provides (Pretty *et al.* 2010; Balmford, Green & Phalan 2012). In other words, how to integrate food production and biodiversity in agricultural landscapes, if any.

Fig. 1: Agricultural landscapes in the Swiss lowland: fields are relatively small, whilst crop diversity and the proportion of permanent grasslands are high. Shown are two 1km^2 landscape units.

SWISS LOWLAND FARMLAND

Our study was conducted in the Swiss lowland, the lowland region situated between the Jura Mountains and the Alps (mean altitude of 500 m, range 300–800 m). It is the most densely populated region of Switzerland, and its most important agricultural area. Farmland can be cultivated without major difficulties. Management intensity is high, whilst average farms are relatively small (20 ha) with cattle, crop or mixed production systems (Bundesamt für Statistik 2016). Although agriculture was intensified in most European countries, land use and agricultural management practices strongly differ among regions (Sutcliffe *et al.* 2015). Hereby much of the variation is caused by the differences in political systems

(Donald, Green & Heath 2001). In Switzerland, in the early 1990s, increased awareness of the environmental damage caused by farming triggered the transition from a production-oriented towards a multifunctional agricultural policy, which should contribute to the conservation of resources, including biodiversity (Herzog *et al.* 2017). In 1999 integrated production standards were integrated in cross compliance requirements and termed *Proof of Ecological Performance* (PEP) (Herzog *et al.* 2008). The PEP is compulsory for any farmer receiving direct payments, these minimum ecological requirements include among others, a crop rotation, the balanced use of nitrogen and phosphorus fertilizers and at least 7% of the farmed area's being set aside as extensively managed wildlife-friendly habitats, the so-called biodiversity promotion areas (BPA, formerly *ecological compensation areas*) (Bundesrat 2013).

SCOPE OF THE THESIS

The main objective of this thesis was to describe the relationships between land use intensity, agricultural productivity and biodiversity in temperate Swiss landscapes. Squares of 1 km^2 (100 ha) were used as sampling units (Fig. 1) and birds and butterflies as biodiversity indicators. Data on species richness and abundance of the study taxa were provided by the Swiss Biodiversity Monitoring (BDM – Z7 indicator) and the Swiss Ornithological Institute (SOI – Monitoring programme for common breeding birds). For the bird counts, observers choose a trail of approximately 5 km in length and carried out three surveys per year. Butterflies were counted during seven surveys along, a 2.5-km-long transect (see Fig. 2). Method tests have confirmed the reliability of these two monitoring methods; for instance, 90 % of all breeding bird species in a 1km^2 grid cell are typically recorded (BDM Coordination Office 2014). The 1km^2 landscape squares are located on a systematic sampling grid, ensuring an even coverage of the whole study area.

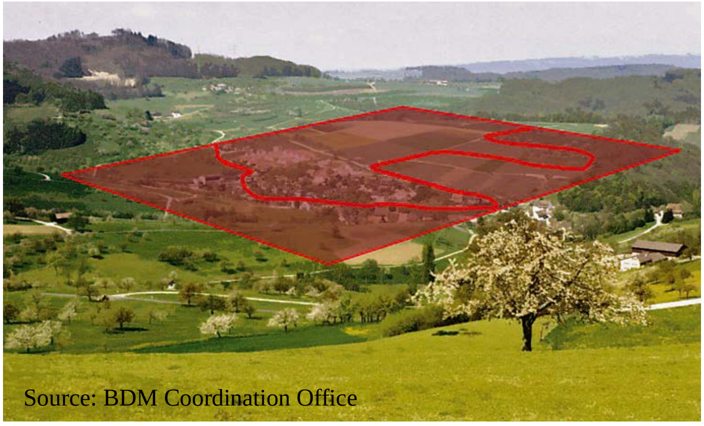

Fig. 2: Transect for the butterfly survey in one of the landscape units (from BDM Coordination Office 2014).

The above described biodiversity data, together with information on land cover (from the cadastral surveys), crop cover (from agricultural surveys) and yield figures (from farmer interviews) were used as database for this thesis. We first assessed how bird and butterfly communities changed along different land use intensity gradients (Herzog *et al.* 2006). Hereby we accounted for differences in land cover (i.e. natural vs. agricultural), but also for changes in agricultural intensity (i.e. intensively vs. extensively managed). European biodiversity conservation being much concerned by the preservation and restoration of fully functional cultural landscapes, we then had a closer look at the effectiveness of agri-environment schemes (AES) (Batáry *et al.* 2015). We analyzed, if AES implemented at the field scale, promote biodiversity in the wider landscape. Third, we included the aspect of agricultural productivity and analyzed, if food energy production (in joules) and biodiversity show the often assumed negative correlation at landscape scale (Cunningham *et al.* 2013). Overall the thesis provides new insights into the relationship between biodiversity and agriculture and it delivers evidence-based prescriptions for a modern multi-functional management of agricultural landscapes.

THESIS OUTLINE

Chapter 1 describes how biodiversity changed in relation to three different land use intensity indicators in 91 - 1 km^2 landscape units. The first indicator was defined as the ratio between utilized agricultural area (UAA) and natural areas, the second as the ratio between arable land and permanent grassland and the third as the ratio between agricultural area and biodiversity promotion areas. Species richness and abundance of birds and butterflies were used as biodiversity indicators and trait-based community indices to describe bird community changes. The results of this chapter show how different species groups react to changes land use, crop cover and management intensity.

Chapter 2 focuses on the effect of biodiversity promotion areas (BPA). BPA are extensively managed, wildlife-friendly farmland habitats, such as hay meadows or traditional orchards and form part of the Swiss agri-environment scheme (AES). We analysed how the landscape composition (e.g. proportion of forest or farmland) and different BPA properties, such as area, mean size, quality or distance, influence bird and butterfly communities in 46 landscapes. The findings of this chapter mirror the general biodiversity response to AES in the wider landscape, and not just locally around BPA measures.

Chapter 3 includes the aspect of agricultural productivity. In this chapter we analyzed the relationship between agricultural production, defined as food energy-equivalent, and bird and butterfly diversity in 49 temperate agricultural landscapes of 1 km^2 each. Food energy was used as common metric of production per unit area, in order, to compare agricultural yields across different crop types in mixed systems. Contrary to other studies, which use reference yield data from agricultural surveys, we collected actual yield data from 299 farmers, over three years. This chapter looks at the productivity-biodiversity frontier under the following over-arching questioning of global relevance: «how to sustainably produce food»?

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Chapter 1

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

Silvia Zingg[1, 2], Jan Grenz[, 2], Jean-Yves Humbert[1]

(1) Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland
(2) School of Agriculture, Forest and Food Sciences, University of Applied Sciences, 3052 Zollikofen, Switzerland

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 km2 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.

Keywords: agriculture, agri-environment schemes, biodiversity, conservation, landscape scale, management

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, Salzmann & Gimmi 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 & Gavin 2012), crop cover (Filippi-Codaccioni *et al.* 2010) or input costs (Teillard, Jiguet & Tichit 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 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, Bengtsson & Smith 2008; Jeliazkov *et al.* 2016). As the study focus 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 & Verburg 2011) and biodiversity (e.g. Baker 2012; Feniuk 2015), but it has also been suggested that for biodiversity conservation actions a landscape perspective needs to be adopted (e.g. Batáry, Baldi & Erdos 2007; 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, Jiguet & Tichit 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.

METHODS

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 x 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).

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.

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).

Agricultural survey data

Detailed information about crop type, field size and biodiversity promotion areas was provided by the cantonal agricultural offices. 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.

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 (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 UAA given that the third crop category, permanent crops, 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 Appendix in Table B.1.

The three indicators showed the following (Pearson) correlations: Indicator 1 & 2, R = 0.18, t = 1.25, df = 48, p-value = 0.22; indicator 1 & 3, R = 0.25, t = 1.82, df = 48, p-value = 0.07; 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-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 = 0.55), but with crop diversity (R = 0.69, t = 6.39, df = 48, p-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 = 0.47), but with mean field size (R = 0.29, t = 2.09, df = 48, p-value = 0.04), indicating that landscapes with less BPA have larger fields.

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 and 5 kilometers (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, Chittaro & Gonseth 2014). Complete species lists with attributed habitats and Red List status can be found in the Appendix (Table A.1. and A.2.).

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 areas (UAA)	Arable land, permanent grasslands and permanent crops	
Natural areas *	Forests (93%), hedges (1%), marshes (0.7%), waterbodies (4%), vegetated roadsides and gravel/rocks (1.3%)	30 ha (± 25.1)
Paved areas	Buildings, streets, railroads, parking lots and other paved areas	8 ha (± 6.4)
Gardens	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 grasslands	Intensively and extensively managed permanent grasslands	42% (± 24.3)
Permanent crops	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 *	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)

** The relative proportions of each type are given in brackets.*

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 Appendix Table A.1.). We adapted the CTI index of Mouysset, Doyen and Jiguet (2012) and Teillard, Jiguet and Tichit (2015) by using four discrete species-specific trophic levels; 1= granivorous; 2 = omnivorous; 3= insectivorous and 4 = carnivorous. The CTI was calculated as follows:

$$CTI = \sum_{i=1}^{n} \frac{Ni}{Ntot} * STI_{\mathrm{i}}$$

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:

$$CNI = \sum_{i=1}^{n} \frac{Ni}{Ntot} * SNI_{\mathrm{i}}$$

$$CMI = \sum_{i=1}^{n} \frac{Ni}{Ntot} * SMI_{\mathrm{i}}$$

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).

Statistical analysis

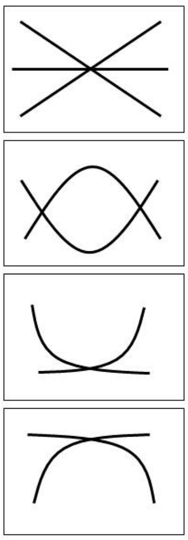
The aim of the statistical analysis was to describe the relationship between the biodiversity indicators and the land use indicators. Species richness and abundance of all, farmland and Red List birds and butterflies and the CTI, CNI and CMI, were used as response variables in the models. In a first step we tested for spatial autocorrelation in the response variables using Moran’s I (R Package ape; Paradis, Claude & Strimmer 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 (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 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).



1) Linear function

```
nls(y ~ a + b*x)
```

2) Quadratic function

```
nls(y ~ a + b*x + c*(x^2))
```

3) Exponential function

```
nls(y ~ a * exp(b*x))
```

4) Saturation function

```
nls(y ~ b *(1- exp(-c*x)))
nls(y ~ a - b * exp(-c*(1-x)))
```

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.

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.2). 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).

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 figure 3 (for birds) and figure 4 (for butterflies).

			Indicator 1			**XY coordinates**			**adj. R^2**
			edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Bird	Species	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	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

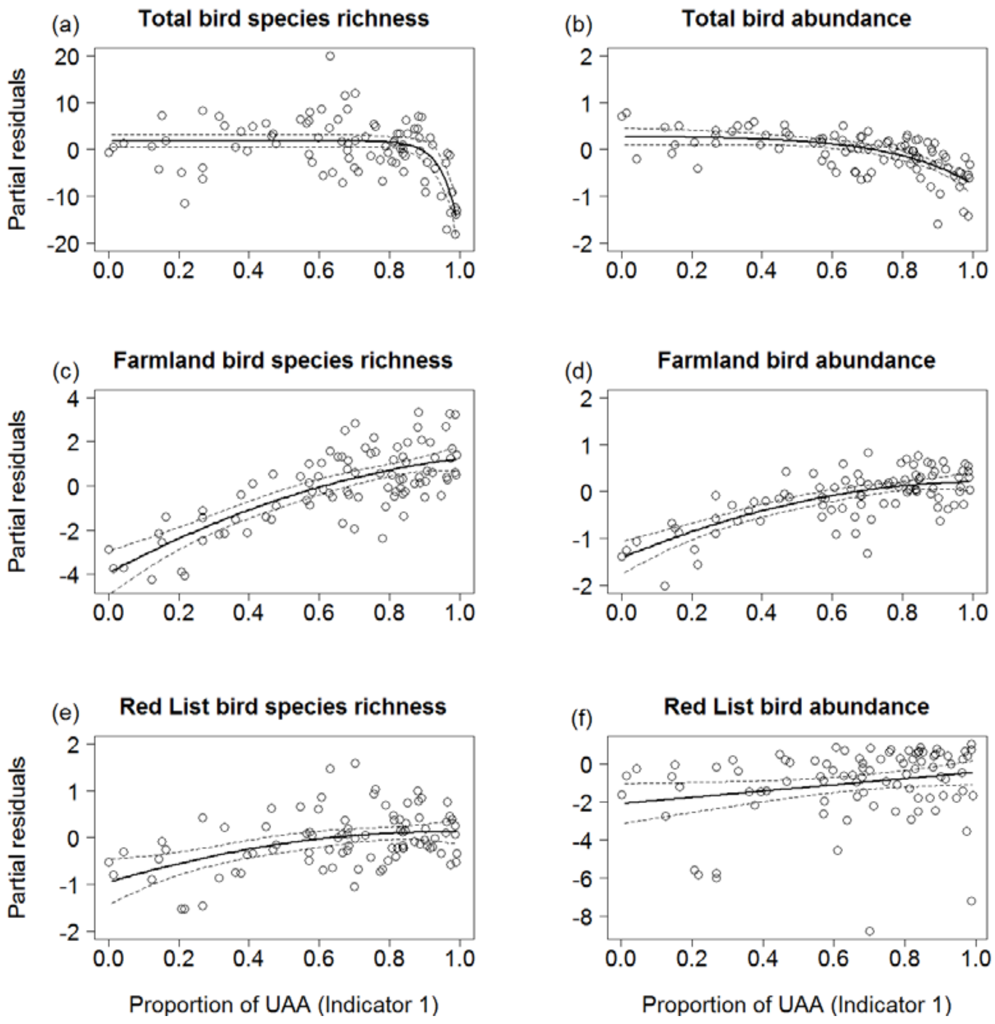


Fig. 3: Bird species richness and abundance along the land use intensity gradient of indicator 1 (n = 91) for: all- (a and b), farmland- (c and d) and Red List birds (e and f). Partial residuals and predictions with 95% confidence intervals from the best fitting curves are shown. Graphs b), d), e) and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

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 Appendix).

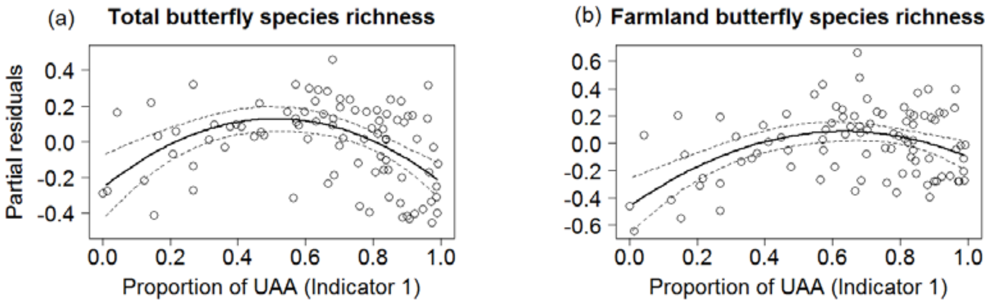


Fig. 4: Total (a) and farmland (b) butterfly species richness along the land use intensity gradient of indicator 1 (n = 91). Partial residuals on the log scale and predictions with 95% confidence intervals from the best fitting curves are shown.

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 and 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)

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 landscapes, 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 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.3 and Fig. B.4 in the Appendix).

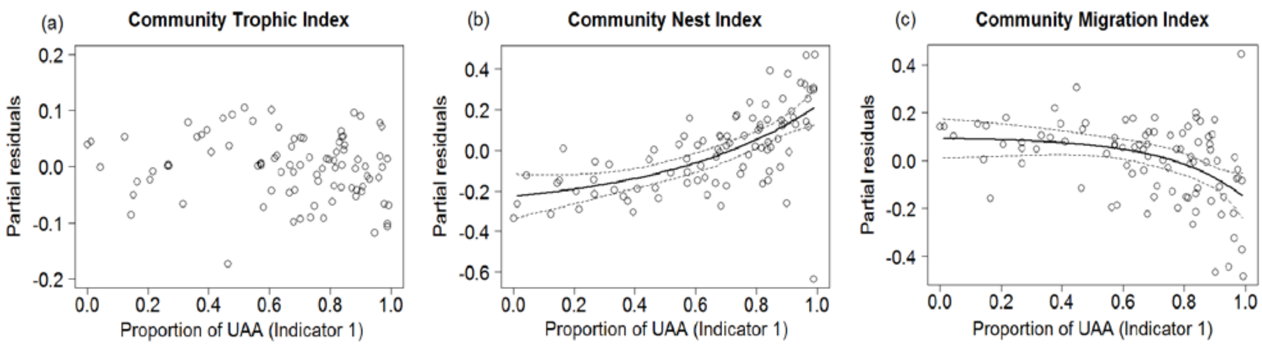


Fig. 5: Bird community composition changes along the land use intensity gradient of indicator 1 (n = 91). The CTI (a) did not show a significant change, the CNI (b) showed a non-linear increase and the CMI (c) a non-linear decrease. Partial residuals and predictions with 95% confidence intervals from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

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 figure 6.

			Indicator 1			**Indicator 2**			**Indicator 3**			**XY coordinates**			**adj. R2**
			edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	edf	F/Chi	Sign.	
Bird	Species	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	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

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.

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 & 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 & 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 & Kuussaari 2012), in our landscapes the proportion of BPA was the most important predictor for butterfly species richness (see also Jeanneret *et al.* 2003).

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. In general, permanent grasslands are associated with decreased agricultural intensity and arable land with increased agricultural intensity (but see Persson *et al.* 2010; Teillard, Jiguet & Tichit 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 arable/permanent grassland, without considering management intensity, may not be a good predictor for land use intensity (Teillard, Jiguet & Tichit 2015).

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 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 & 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 2012; Prince & 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).

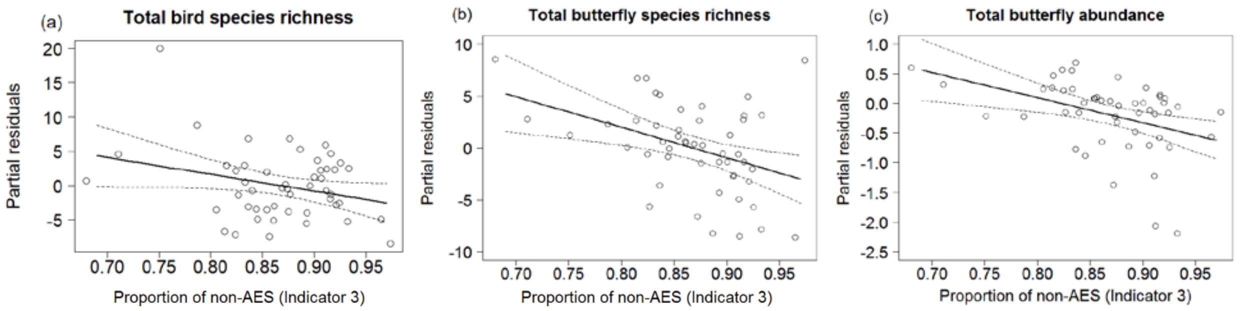


Fig. 6: Decreasing total bird (a) and butterfly (b) species richness and butterfly abundance (c) with decreasing proportion of BPA (indicator 3) in the landscape (n = 50). Partial residuals from the GAM and predictions with 95% confidence intervals from the best fitting curve are shown. Figure (c) is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

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, Jiguet & Tichit 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, Renard & Jiguet 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).

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

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	Habitat	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

Table B.1. 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.2. 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).

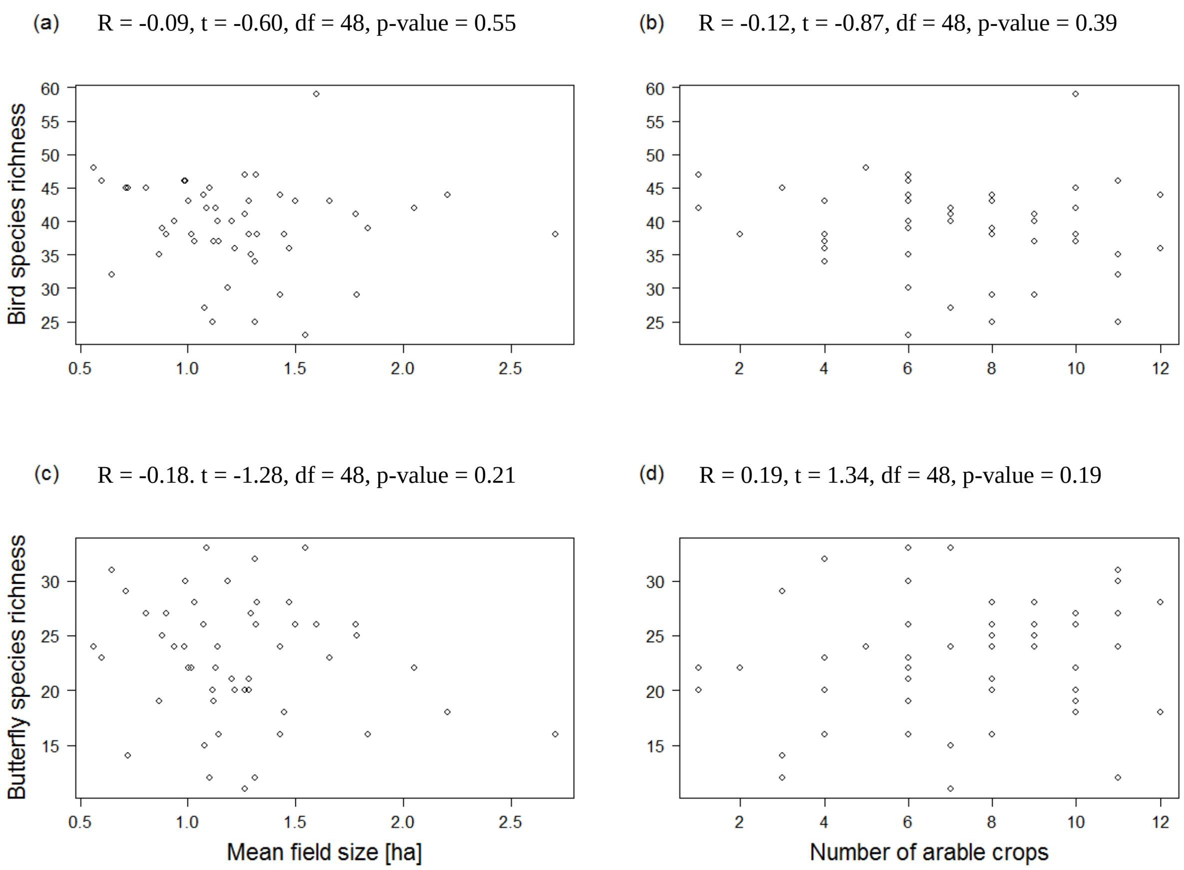


Table B.3. Field size and proportion of non-BPA

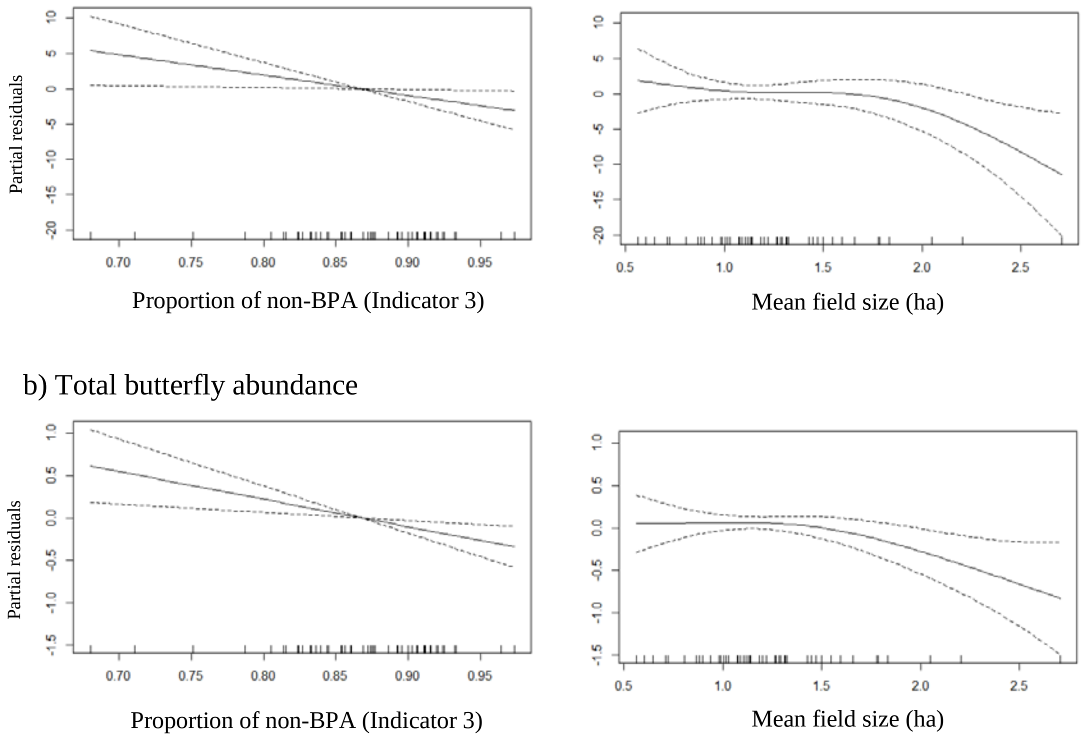
Field size and proporiton of non-BPA (Indicator 3) were positively correlated (R = 0.29, t = 2.09, df = 48, p-value = 0.04), indicating that landscapes with larger fields had less biodiversity promotion areas (BPA). We included mean field size as additional variable in the GAM, to ensure that the observed 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.4.

	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.4. 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).

a) Total butterfly species richness



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).

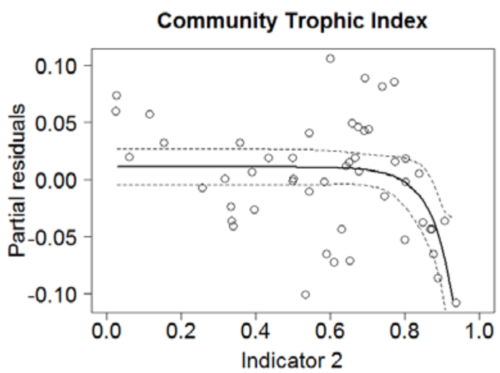
The table below contains the summary of the GAM models showing the relation between the community trophic index (CTI), the community nest index (CNI), the community migration index (CMI) and the land use indicators. The three models under a) included only indicator 1 and the XY coordinates as fixed effects (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.

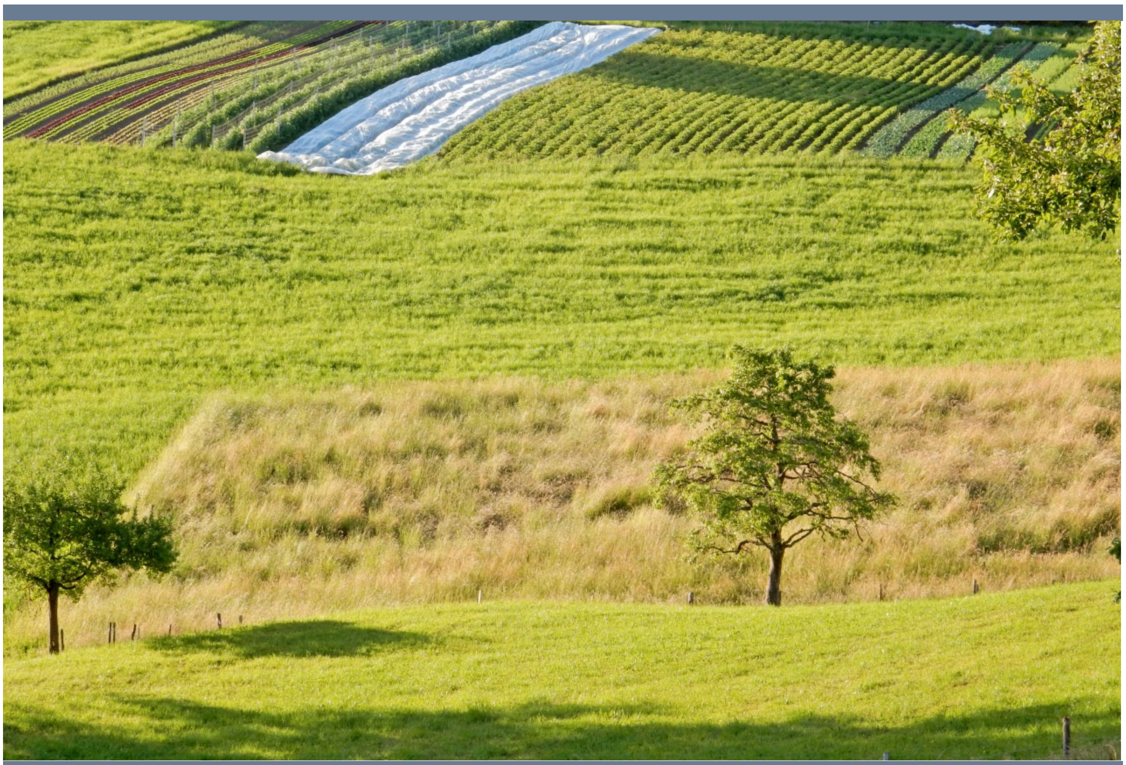
a)	Indicator 1			XY Coordinates			adj. R2
	edf	F	Sign.	edf	F	Sign.	
CTI	1.4	0.7	ns	5.9	1.5	ns	0.13
CNI	1.8	21.1	***	3.2	1.5	ns	0.40
CMI	1.7	7.0	**	2.0	0.5	ns	0.15

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.





Chapter 2

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

Silvia Zingg [1, 2], Eva Ritschard [1], Raphaël Arlettaz [1, 3], Jean-Yves Humbert [1]

(1) Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland
(2) School of Agriculture, Forest and Food Sciences, University of Applied Sciences, 3052 Zollikofen, Switzerland
(3) Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, 1950 Sion, Switzerland

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 increases by 22% and 60%, respectively, when the proportion of BPA in the landscape increases from 5% to 15%. Likewise, bird species richness increased, but to a lesser extent, with the proportion of BPA in the landscape. For birds, but not for butterflies, the proportion of BPA characterized by a high ecological quality played a role in promoting both priority-farmland and red-listed species. Interestingly, 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 field scale have positive effects on spatially-mobile biodiversity that are noticeable at 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.

Keywords: Agriculture, biodiversity conservation, landscape composition, habitat quality, restoration

INTRODUCTION

Since the second half of the 20th century, agricultural practices have been considerably intensified, particularly in the Western World lowlands (e.g. Robinson & Sutherland 2002). Agricultural intensification includes not only the increase of fertiliser 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 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 AES-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 (Birrer *et al.* 2007; Arponen *et al.* 2013), 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 field scale, usually focusing on only one type of AES measure at a time (Batáry *et al.* 2015). In contrast, wider-scale assessments of the effects of various types of measures simultaneously implemented are still lacking although 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. Westphal, Steffan-Dewenter & Tscharntke 2006; Concepción & Díaz 2011). 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 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 landscape scale. These two taxa were selected as study models because their life cycles mostly require habitat complementarity, thus operating at landscape scale (e.g. Concepción & 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 was also considered in our assessment, such as the proportion of forests and waterbodies in the landscape. As former evaluation studies, carried out at 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 landscape scale (Henderson *et al.* 2012). Secondly, we predicted that BPA habitat quality, assessed through botanical diversity, promote the two study taxa (Birrer *et al.* 2007; Aviron *et al.* 2011). Our third prediction was that habitat fragmentation and distance between BPA can negatively influence their effectiveness (Bailey *et al.* 2010; Knop 2010) and could play a role even in more mobile species such as birds and butterflies (Krauss, Steffan-Dewenter & Tscharntke 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 landscape scale (Haynes, Diekötter & Crist 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. Benton, Vickery & Wilson 2003; Diacon-Bolli *et al.* 2012). Actually, they provide birds and butterflies with the necessary habitat complementarity, notably shelter, food supply and corridors for movement (e.g. Siriwardena 2012; Coulthard, McCollin & Littlemore 2016). As our study focuses on the intensively-cultivated Swiss lowlands, its outcomes bear relevance for other European highly productive agricultural regions, if not beyond that region, and may thus assist in refining future AES.

METHODS

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 characterised 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 less than 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).

Biodiversity

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 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 and 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).

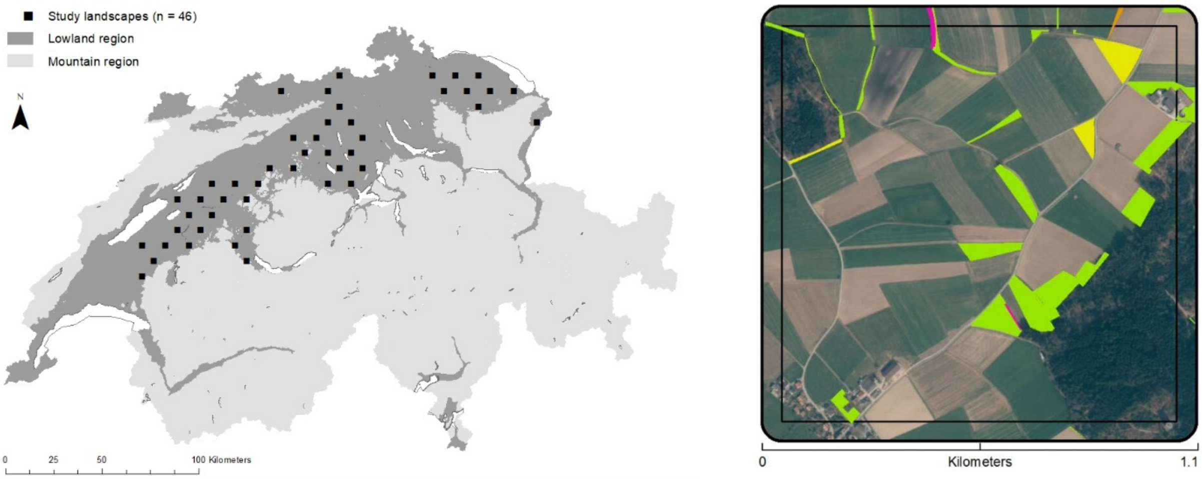


Fig. 1: Map of Switzerland with the 46 1-km^2 selected study landscapes and one landscape with different BPA types: extensively-managed meadows (green), low-intensity meadows (yellow), hedges (purple) and wildflower strips (orange). As the immediate surrounding of the landscapes may influence the bird and butterfly counts, we added a 50m broad buffer to all landscape squares for all analysis.

Butterfly and bird species were classified into four main groups: total, farmland, AEO priority and red listed species (see Table A.1 and A.2). The so-called AEO priority species include the target and indicator species defined within the framework of the agriculture-related environmental objectives (AEO species) 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, Chittaro & Gonseth 2014).

In an attempt to gain information on the effect of AES on ecosystem 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). Life-history traits for butterfly species were derived from (Settele, Feldman & Reinhardt 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 A.1 and A.2).

BPA and land-use

Land-use maps were obtained from the Swiss cadastral survey of 2014 (Swisstopo). From them we derived the proportions of utilized agricultural area (UAA), forests, hedges, waterbodies, impervious, 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 with respect to 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. 1). Detailed information on all BPA types can be found in Table 1 (see also Caillet-Bois *et al.* 2018).

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).

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 50m.	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.	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 and/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)

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 (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 2003). The general formula of 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. 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).

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 [%]**
UAA	Arable land, permanent grasslands, permanent crops and BPA	66.1 (± 13.5)
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 (± 1’576.9)
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)

RESULTS

Overall, 59 different 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 Appendix Table A.1 and A.2). The main land-use types in the landscapes were (mean ± SD) farmland (66.1% ± 13.5) and forest (18.2% ± 14.7, Table 2). On average, 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 1% (± 4%)

of the farmed area (UAA). Two landscapes were outstanding, with BPA exhibiting ecological quality covering 16% and 18% of the farmland area, respectively.

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. 2). 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 species), but regarding specialist butterflies (14 species) only abundance responded positively to the fraction of BPA in the landscape (Appendix Table B.1). 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.

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. 2). 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 40 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, this positive effect of BPA with ecological quality was strongly influenced by the two outstanding study landscapes harbouring high proportions of BPA with quality (Fig. 2f). 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 (Appendix Table B.2).

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 '***' 0.001 '**' 0.01 '*' 0.05 '.' 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	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
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	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
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		

DISCUSSION

Biodiversity promotion areas (BPA) are wildlife-friendly managed farmland habitats such as semi-natural grasslands, traditional 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 landscape scale that disentangles the effects of landscape composition (e.g. proportion of forest 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 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).

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 & 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 landscape scale. If a positive effect of extensively-managed grasslands and wildflower strips was already demonstrated at 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, Heliölä & Kuussaari 2010), it is therefore important that agri-environment schemes support this group (see also Krauss, Steffan-Dewenter & Tscharntke 2003; Bruppacher *et al.* 2016). 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).

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 2012; Prince & Jiguet 2013). Birds in general and hedge/tree or cavity breeding species particularly profit from AES-BPA measures such as extensively managed meadows and 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 2011). For example, extensively-managed grasslands provide invertebrate prey supplies for insectivores while hedges and high-stem orchards nesting sites.

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 '***' 0.001 '**' 0.01 '*' 0.05 '.' 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	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
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	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
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		

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 (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 (16% and 18%) are behind the significance of the observed pattern (Fig. 2f), 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).

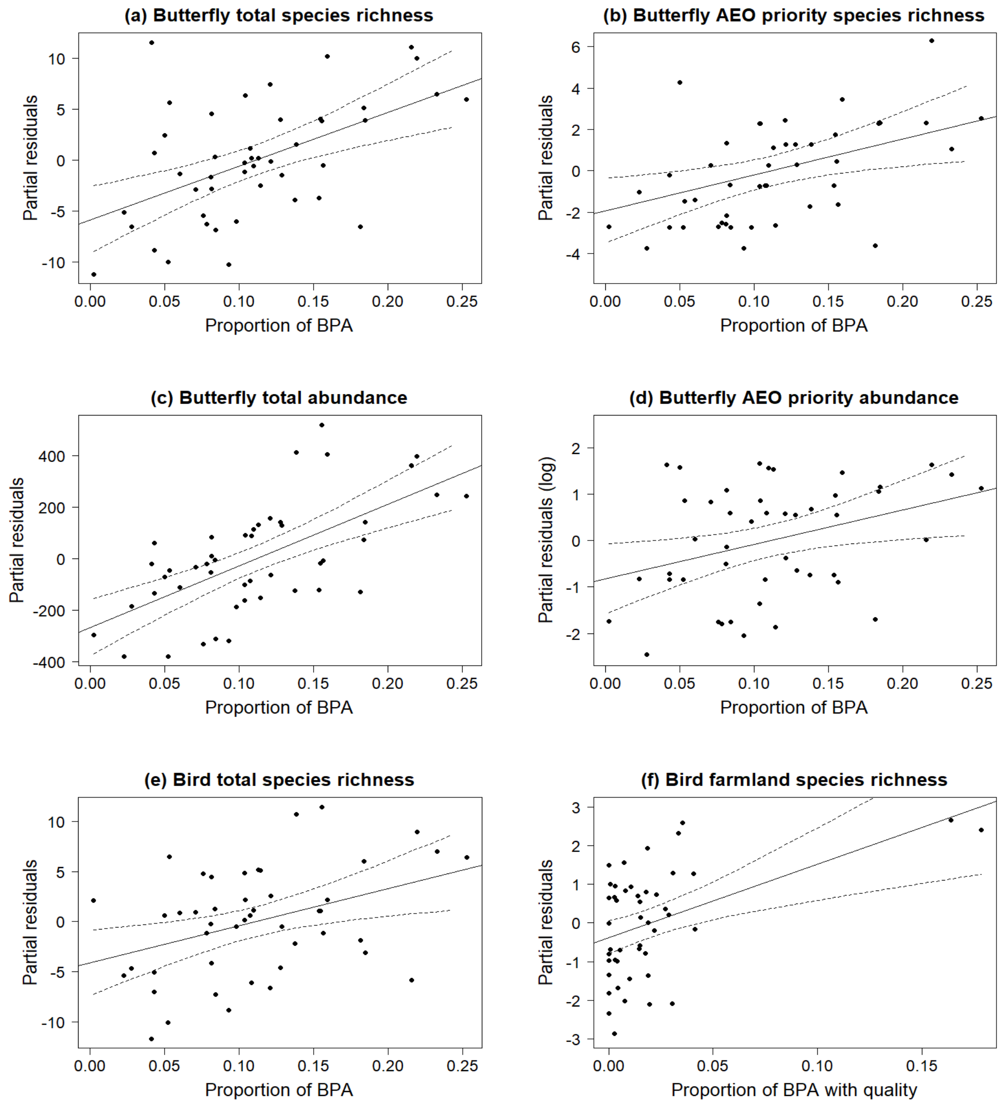


Fig. 2: Relationships between species richness and abundance of different butterfly (a-d) and bird groups (e-f) vs the proportion of BPA per UAA. The so-called AEO-priority species include the target and indicator species defined within the framework of the agriculture-related environmental objectives. Partial residuals and predictions with 95% confidence intervals from the final model are shown.

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 characterised by a high-intensity but small-scaled farming system. In effect, 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 influenced neither by distance, diversity, spatial configuration, nor 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 enough habitat continuum for our two mobile taxa. In support of it, Brückmann, Krauss and Steffan-Dewenter (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, Herzog & Schmid 2011). Despite the fact that the species-area relationship (island biogeography theory) is a central concept in conservation biology (Bender 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 non-monotonous cultivated landscapes typical of the Swiss lowlands (Helzer & Jelinski 1999; Öckinger & Smith 2006; Perović *et al.* 2015).

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 landscape scale. As 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, generating a momentum for 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 (Humbert *et al.* 2010; Schmiede, Otte & Donath 2011; Bruppacher *et al.* 2016; Buri *et al.* 2016). 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

Table A.1. Butterfly species list

Overall 59 different butterfly species were observed in the 46 study landscapes. On average 22.6 ± 6.1 (mean ± SD) species, including 15 ± 4 farmland, 4 ± 3 priority and 1 ± 1 red list species were observed per landscape. Total butterfly abundance ranged from 90 to 1007 individuals with a mean of 409 (± 216) including 36 (± 36) priority and 8 (± 11) red list individuals. The table shows the complete species lists including group affiliations. Specialists were defined as resident species with a mono- or oligophagous diet (caterpillars feed on a single plant genus or family) and a maximum of two generations per year. Life-history traits derived from Settele, Feldmann & Reinhardt (1999). Priority species were defined as such within the framework of the agriculture-related environmental objectives of the Swiss government (Walter et *al.* 2013) and species listed as near threatened (NT), vulnerable (VU) or critically endangered (CR), were defined as red listed species (Wermeille, Chittaro & Gonseth 2014).

English name	**Latin name**	**Farmland**	**Red list**	**Priority**	**Specialist**
Marbled white	*Melanargia galathea*	yes	no	yes	yes
Meadow brown	*Maniola jurtina*	yes	no	no	no
Old world swallowtail	*Papilio machaon*	yes	no	no	no
Small white	*Pieris rapae-Komplex*	NA	no	no	no
Large white	*Pieris brassicae*	yes	no	no	no
Green-veined white	*Pieris napi-Komplex*	NA	no	no	no
Wall brown	*Lasiommata megera*	yes	no	yes	no
Queen of Spain fritillary	*Issoria lathonia*	yes	no	yes	no
Clouded yellow	*Colias croceus*	yes	no	no	no
Red admiral	*Vanessa atalanta*	yes	no	no	no
Six-spot burnet	*Zygaena filipendulae*	yes	no	no	no
Common blue	*Polyommatus icarus*	yes	no	no	no
Small tortoiseshell	*Aglais urticae*	yes	no	no	no
Ringlet	*Aphantopus hyperantus*	yes	no	no	no
Pale clouded yellow	*Colias hyale-Komplex*	NA	no	no	no
Small heath	*Coenonympha pamphilus*	yes	no	no	no
Mallow skipper	*Carcharodus alceae*	yes	yes	yes	no
Silver-washed fritillary	*Argynnis paphia*	no	no	no	no
Large skipper	*Ochlodes venata*	yes	no	no	no
Meadow fritillary	*Melitaea parthenoides*	yes	yes	yes	yes
Provencal short-tailed blue	*Cupido alcetas*	yes	yes	no	no
Speckled wood	*Pararge aegeria*	no	no	no	no
Marbled fritillary	*Brenthis daphne*	no	no	no	yes
Map	*Araschnia levana*	no	no	no	no
Small skipper	*Thymelicus sylvestris*	yes	no	yes	yes
European peacock	*Inachis io*	no	no	no	no

English name	Latin name	Farmland	Red list	Priority	Specialist
White admiral	*Limenitis camilla*	no	no	no	no
Large tortoiseshell	*Nymphalis polychloros*	no	no	no	no
Common copper	*Lycaena phlaeas*	yes	no	yes	no
Short-tailed cupid	*Cupido argiades*	yes	yes	no	yes
Orange tip	*Anthocharis cardamines*	yes	no	no	yes
Comma	*Polygonia c-album*	no	no	no	no
Great banded grayling	*Brintesia circe*	yes	yes	yes	no
Painted lady	*Vanessa cardui*	yes	no	no	no
Chapman's blue	*Polyommatus thersites*	yes	yes	yes	no
Southern small white	*Pieris mannii*	yes	yes	yes	no
Violet fritillary	*Boloria dia*	yes	yes	yes	yes
Brown argus	*Aricia agestis-Komplex*	NA	no	yes	no
Essex skipper	*Thymelicus lineola*	yes	no	yes	yes
Common brimstone	*Gonepteryx rhamni*	no	no	no	no
Mazarine blue	*Polyommatus semiargus*	yes	no	yes	yes
Holly blue	*Celastrina argiolus*	no	no	no	no
Brown hairstreak	*Thecla betulae*	no	no	yes	no
Grizzled skipper	*Pyrgus malvae-Komplex*	yes	no	no	no
Wood white	*Leptidea sinapis-Komplex*	yes	no	no	no
Large wall brown	*Lasiommata maera*	yes	no	yes	no
Red-underwing skipper	*Spialia sertorius*	yes	yes	yes	no
Heath fritillary	*Melitaea athalia*	yes	no	yes	yes
Lulworth skipper	*Thymelicus acteon*	yes	yes	yes	no
Adonis blue	*Polyommatus bellargus*	yes	no	yes	yes
Dingy skipper	*Erynnis tages*	yes	no	no	yes
Sooty cooper	*Lycaena tityrus*	yes	no	yes	yes
Purple emperor	*Apatura iris*	no	yes	no	no
Small blue	*Cupido minimus*	yes	no	yes	no
High brown fritillary	*Argynnis adippe*	yes	no	yes	no
Large grizzled skipper	*Pyrgus alveus-Komplex*	NA	no	yes	yes
Arctic skipper	*Carterocephalus palaemon*	yes	no	no	no
Oberthür's grizzled skipper	*Pyrgus armoricanus*	NA	yes	yes	no
False heath fritillary	*Melitaea diamina*	yes	yes	yes	no

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Table A.2. Bird species list

In total 99 different bird species were observed in the 46 study landscapes. On average 39 ± 7 (mean ± SD) bird species were detected per landscape, including 8 ± 2 farmland, 7 ± 3 priority and 4 ± 2 red list species. Mean abundance (number of breeding pairs) was 309 ± 116 ranging from a minimum of 95 to a maximum of 580. Abundance of farmland 44 ± 19, priority 25 ± 15 and red list birds 13 ± 12 were lower. The table shows the complete species list including group affiliations. Species allocation to the different feeding (Food) and nesting (Nest) guilds and the category farmland was done in accordance with the Swiss Ornithological Institute. Priority species were defined as such within the framework of the agriculture-related environmental objectives by the Swiss government (Walter et al. 2013) and species listed as near threatened (NT), vulnerable (VU) or critically endangered (CR) were defined as red listed species (Keller et al. 2010). Feeding and nesting abbreviations are: c = carnivorous; g = granivorous; i = insectivorous; o = omnivorous; a = above ground (hedge/tree); b = building; c = cavity; g = ground; and r = reed breeder.

English name	Latin name	Farmland	Red list	Priority	Nest	Food
Great spotted woodpecker	*Dendrocopos major*	no	no	no	c	o
European goldfinch	*Carduelis carduelis*	no	no	yes	a	g
Common kestrel	*Falco tinnunculus*	yes	yes	yes	a	c
Common wood pigeon	*Columba palumbus*	no	no	no	a	g
European greenfinch	*Carduelis chloris*	no	no	no	a	g
Black kite	*Milvus migrans*	no	no	no	a	c
Common buzzard	*Buteo buteo*	yes	no	no	a	c
Black redstart	*Phoenicurus ochruros*	no	no	no	c	i
European pied flycatcher	*Ficedula hypoleuca*	no	no	no	c	i
White wagtail	*Motacilla alba*	no	no	no	b	i
Great tit	*Parus major*	no	no	no	c	o
Firecrest	*Regulus ignicapilla*	no	no	no	a	i
Eurasian tree sparrow	*Passer montanus*	yes	no	no	c	o
Eurasian jay	*Garrulus glandarius*	no	no	no	a	o
Eurasian blackcap	*Sylvia atricapilla*	no	no	no	a	o
Common blackbird	*Turdus merula*	no	no	no	a	o
Fieldfare	*Turdus pilaris*	yes	yes	yes	a	o
Winter wren	*Troglodytes troglodytes*	no	no	no	g	i
Hooded crow	*Corvus corone*	yes	no	no	a	o
Common chiffchaff	*Phylloscopus collybita*	no	no	no	g	i
Yellowhammer	*Emberiza citrinella*	yes	no	yes	a	o
Eurasian magpie	*Pica pica*	no	no	no	a	o
Red kite	*Milvus milvus*	yes	no	yes	a	c
Mallard	*Anas platyrhynchos*	no	no	no	g	o
Blue tit	*Parus caeruleus*	no	no	no	c	o
Coal tit	*Parus ater*	no	no	no	c	o
European robin	*Erithacus rubecula*	no	no	no	g	o

English name	Latin name	Farmland	Red list	Priority	Nest	Food
European crested tit	*Parus cristatus*	no	no	no	a	o
Common chaffinch	*Fringilla coelebs*	no	no	no	a	o
Eurasian treecreeper	*Certhia familiaris*	no	no	no	a	i
Common starling	*Sturnus vulgaris*	yes	no	no	c	o
northern raven	*Corvus corax*	no	no	no	c	o
Eurasian nuthatch	*Sitta europaea*	no	no	no	c	o
House sparrow	*Passer domesticus*	no	no	no	c	o
Red crossbill	*Loxia curvirostra*	no	no	no	a	g
Common linnet	*Carduelis cannabina*	yes	yes	yes	a	g
Mistle thrush	*Turdus viscivorus*	no	no	no	a	o
Song thrush	*Turdus philomelos*	no	no	no	a	o
Long-tailed bushtit	*Aegithalos caudatus*	no	no	no	a	i
Hawfinch	*Coccothraustes coccothraustes*	no	no	no	a	o
Spotted flycatcher	*Muscicapa striata*	no	no	no	a	i
Marsh tit	*Parus palustris*	no	no	no	c	o
Black woodpecker	*Dryocopus martius*	no	no	no	c	i
European honey buzzard	*Pernis apivorus*	no	yes	no	a	i
European green woodpecker	*Picus viridis*	no	no	yes	c	i
Goldcrest	*Regulus regulus*	no	no	no	a	i
Common quail	*Coturnix coturnix*	yes	no	yes	g	o
Stock dove	*Columba oenas*	no	no	no	c	g
Eurasian skylark	*Alauda arvensis*	yes	yes	yes	g	o
Eurasian collared dove	*Streptopelia decaocto*	no	no	no	b	o
Short-toed treecreeper	*Certhia brachydactyla*	no	no	yes	c	i
Common house martin	*Delichon urbicum*	no	yes	no	c	i
Feral pigeon	*Columba livia domestica*	no	no	no	b	o
Barn swallow	*Hirundo rustica*	yes	no	yes	b	i
Common swift	*Apus apus*	no	yes	no	c	i
Eurasian reed warbler	*Acrocephalus scirpaceus*	no	no	no	r	i
Marsh warbler	*Acrocephalus palustris*	no	no	yes	r	i
Common moorhen	*Gallinula chloropus*	no	no	no	r	o
Garden warbler	*Sylvia borin*	no	yes	yes	a	i
Eurasian stonechat	*Saxicola rubicola*	yes	yes	yes	g	i
Great crested grebe	*Podiceps cristatus*	no	no	no	r	c
Long-eared owl	*Asio otus*	yes	yes	yes	a	c
European serin	*Serinus serinus*	no	no	no	a	g
Common reed bunting	*Emberiza schoeniclus*	no	yes	no	r	o
Common cuckoo	*Cuculus canorus*	no	yes	yes	a	i
Eurasian coot	*Fulica atra*	no	no	no	r	o
European turtle dove	*Streptopelia turtur*	yes	yes	yes	a	g
Red-backed shrike	*Lanius collurio*	yes	no	yes	a	c
Common nightingale	*Luscinia megarhynchos*	no	yes	yes	a	i
White-throated dipper	*Cinclus cinclus*	no	no	no	c	i
Northern goshawk	*Accipiter gentilis*	no	no	no	a	c
Dunnock	*Prunella modularis*	no	no	no	a	o

English name	Latin name	Farmland	Red list	Priority	Nest	Food
Willow tit	*Parus montanus*	no	no	no	c	o
Eurasian bullfinch	*Pyrrhula pyrrhula*	no	no	no	a	g
Wood warbler	*Phylloscopus sibilatrix*	no	yes	no	g	i
Grey wagtail	*Motacilla cinerea*	no	no	no	c	i
Eurasian hobby	*Falco subbuteo*	no	yes	no	a	i
Lesser spotted woodpecker	*Dendrocopos minor*	no	no	yes	c	i
Eurasian sparrowhawk	*Accipiter nisus*	no	no	no	a	c
Common redstart	*Phoenicurus phoenicurus*	yes	yes	yes	c	i
Grey heron	*Ardea cinerea*	no	no	no	a	c
Middle spotted woodpecker	*Dendrocopos medius*	no	yes	no	c	i
Willow warbler	*Phylloscopus trochilus*	no	yes	no	a	i
Western jackdaw	*Corvus monedula*	yes	yes	yes	c	o
Yellow-legged gull	*Larus michahellis*	no	no	no	g	o
Savi's warbler	*Locustella luscinioides*	no	yes	no	r	i
Mute swan	*Cygnus olor*	no	no	no	g	o
Northern lapwing	*Vanellus vanellus*	yes	yes	yes	g	o
Tawny owl	*Strix aluco*	no	no	no	c	c
Greylag goose	*Anser anser*	no	no	no	g	o
Eurasian golden oriole	*Oriolus oriolus*	no	no	no	a	o
Common kingfisher	*Alcedo atthis*	no	yes	no	c	c
White stork	*Ciconia ciconia*	yes	yes	yes	b	c
Water rail	*Rallus aquaticus*	no	no	no	r	c
Little grebe	*Tachybaptus ruficollis*	no	yes	no	r	c
Grey-headed woodpecker	*Picus canus*	no	yes	yes	c	i
Western yellow wagtail	*Motacilla flava*	yes	yes	yes	g	i
Common pheasant	*Phasianus colchicus*	yes	no	no	g	o
Icterine warbler	*Hippolais icterina*	no	yes	no	a	i

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

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APPENDIX B

Table B.1. Results butterfly functional groups

Summary output of the final models predicting butterfly generalist and specialist species richness and abundance. Shown are parameter estimates (Est.), standard errors (SE) and significance (p-value < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '), as well as the adjusted R^2 of the respective model. Abbreviations: BPA = biodiversity promotion areas; PAR = perimeter area ratio; UAA = utilized agricultural area.

Butterfly species richness	Generalists			Specialists		
	Est.	SE	Sign.	Est.	SE	Sign.
Intercept	25.5	3.5	***	1.9	0.6	**
BPA proportion	27.1	12.0	*	8.8	5.8	
BPA quality				17.1	9.5	.
BPA mean size	-0.0	0.0	*			
BPA mean distance	-0.0	0.0	.			
BPA diversity						
BPA PAR						
UAA	-8.9	4.5	.			
Forest				3.4	1.8	.
Waterbodies						
Hedges						
Vegetated						
Non-vegetated						
Altitude						
Adj. R-squared	0.31			0.16		

Butterfly abundance	Generalists			Specialists (log)		
	Est.	SE	Sign.	Est.	SE	Sign.
Intercept	323.2	63.6	***	2.2	0.4	***
BPA proportion	2361.0	503.3	***	7.7	3.4	*
BPA quality	-1697.0	809.7	*			
BPA mean size	0.05	63.6	**			
BPA mean distance						
BPA diversity						
BPA PAR						
UAA						
Forest						
Waterbodies	-1180.0	667.3	.			
Hedges						
Vegetated				-6.7	3.0	*
Non-vegetated						
Altitude						
Adj. R-squared	0.38			0.13		

Table B.2. Results bird functional groups

Summary output of the final models predicting different bird functional groups. Shown are parameter estimates (Est.), standard errors (SE) and significance (p-value < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ') as well as the adjusted R^2 of the respective model. Abbreviations: BPA = biodiversity promotion areas; PAR = perimeter area ratio; UAA = utilized agricultural area.

Bird species richness	Insectivorous			Omnivorous			Hedge/tree breeders			Cavity breeders		
	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
Intercept	6.6	1.1	***	21.4	1.6	***	16.8	1.2	***	9.3	0.8	***
BPA proportion	14.3	7.4	.				17.5	8.1	*	13.5	5.3	*
BPA quality												
BPA mean size												
BPA mean distance												
BPA diversity												
BPA PAR				-12.2	6.1	*						
UAA												
Forest	10.2	2.9	**	9.7	2.6	***	6.9	3.4	*	9.0	2.1	***
Waterbodies	28.9	11.5	*	25.7	10.0	*						
Hedges	203.0	62.4	**				210.8	64.8	**			
Vegetated							-18.3	7.7	*			
Non-vegetated												
Altitude												
Adj. R-squared	0.41			0.29			0.36			0.34		

Bird abundance	Insectivorous			Omnivorous			Hedge/tree breeders			Cavity breeders		
	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.	Est.	SE	Sign.
Intercept	39.3	7.6	***	405.2	50.5	***	77.6	13.0	***	130.5	32.6	***
BPA proportion										191.3	113.2	.
BPA quality												
BPA mean size												
BPA mean distance												
BPA diversity												
BPA PAR												
UAA				-307.0	73.2	***						
Forest	113.9	28.5	***				301.8	50.2	***			
Waterbodies	243.5	111.7	*									
Hedges	1378.9	596.9	*	3163.7	1393.2	*	3294.4	1040.0	**			
Vegetated										325.3	98.0	**
Non-vegetated												
Altitude										-0.1	0.1	.
Adj. R-squared	0.32			0.34			0.47			0.27		

Chapter 3

The productivity-biodiversity frontier in mixed temperate agro-ecosystems

Silvia Zingg [1, 2], Jan Grenz [2], Raphaël Arlettaz [1, 3], Jean-Yves Humbert [1]

(1) Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland
(2) School of Agriculture, Forest and Food Sciences, University of Applied Sciences, 3052 Zollikofen, Switzerland
(3) Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, 1950 Sion, Switzerland

ABSTRACT

Preserving farmland biodiversity requests sufficient amount of habitat, where net primary productivity is not directed, solely towards human exploitative use, but devoted to the development of flora and fauna. Yet, offering space for biodiversity will irremediably compete against agricultural production, which represents a real challenge in a World, with a naturally limited farmland area and a steadily growing human population to be fed. We thus need more landscape-scale research on the ability of agro-ecosystems to sustain both agriculture and biodiversity, which has rarely been attempted, in mixed farming systems with arable and livestock production, that are typically encountered in temperate biomes. This study was carried out in 49 1-km^2 such mixed-production landscapes. We compared their biodiversity value, agricultural productivity and landscape composition – notably in terms of proportion of farmland. Yield figures provided by 299 farmers served to quantify a common metric of energy-equivalents of food production (in joules) across crop types within the 49 landscapes. Species richness and abundance of all birds, of birds typical of farmland, and of all butterflies were assessed by repeated transect counts performed within our landscapes. We found a negative relationship between bird species richness and abundance and food energy in landscapes exhibiting great proportions of farmland (i.e. $\geq$ 80 ha), but a neutral relationship in landscapes with lower farmland proportions (i.e. $\leq$ 60 ha). In contrast, neither typical farmland birds nor butterflies showed any significant relationship with food energy production. We conclude that mixed agricultural landscapes are not characterized by a mere monotonous negative productivity-biodiversity relationship. Much depends on the proportion of non-farmed areas, supposable the fraction of natural areas. This study suggests that if the latter make up a large fraction of the cultivated landscape matrix, they might compensate for, otherwise locally intensive production.

Keywords: agricultural productivity, birds, butterflies, conservation, farmland, landscape scale, multiple imputation

INTRODUCTION

The ongoing human population growth leads to a constantly increasing demand for food and agricultural products Tilman *et al.* (2011). As a consequence agricultural practices were intensified and natural areas converted to new agricultural land; thereby crop production more than doubled since the 1960s, while the total area devoted to arable production increased by ~ 9 % globally (Pretty 2008). Far-reaching land use changes came along with the rise of agricultural production. At field scale, the increased use of agrochemicals (e.g. mineral fertilizer and pesticides), mechanisation and the use of high-yielding varieties increased productivity. While at landscape scale, farms specialized on few crops, grasslands were converted to arable fields, fallow lands disappeared and natural or edge habitats such as field boundaries and hedges were destroyed (Tscharntke *et al.* 2005). The above described land use changes, reduced, not only the biodiversity of natural habitats and traditional, low-intensity agroecosystems, but also the flora and fauna of intensively used agroecosystems (Tscharntke *et al.* 2005; Donald *et al.* 2006; Sutcliffe *et al.* 2015).

Agricultural production relies on a diverse biological community that supports a wide range of ecosystem services, such as soil fertility, natural pest control and pollination (Bommarco, Kleijn & Potts 2013). Farmland biodiversity is therefore an important component for a sustainable, long term food production (Carvalheiro *et al.* 2011). With the increasing awareness of the consequences of biodiversity loss, and at the same time, the need to produce more food, research on the agricultural productivity-biodiversity frontier considerably intensified in the last two decades. Hereby it became evident, that complex ecological interactions do occur at landscape scale, as many taxonomic groups are ruled by landscape processes rather than mere field-site conditions (Tscharntke *et al.* 2012). Agricultural land use changes, influences habitat availability, complementarity or connectivity for many species at large scales (Vickery & Arlettaz 2012; Smith *et al.* 2014), calling for more research on the productivity-biodiversity relationship at landscape scale (Mattison & Norris 2005).

Current literature reveals that most landscape scale studies either describe neutral, negative, or more complex hump-shaped productivity-biodiversity relationships. Neutral relationships were found in tropical agroforestry systems, where coffee and cacao are produced under shade trees. Thereby, agricultural production and biodiversity are spatially combined in a complex habitat structure, which can provide both high yield and high biodiversity (Gordon *et al.* 2007; Clough *et al.* 2011; but see De Beenhouwer, Aerts & Honnay 2013). Negative relationship between productivity and biodiversity were evidenced in temperate arable and livestock production systems (Dross, Jiguet & Tichit 2017). In such agricultural systems, namely monocultures of grasslands and arable fields, yields are maintained at a high level through agricultural inputs, which at the same time decrease biodiversity (Kleijn *et al.* 2009). The often assumed, trade-off between production and biodiversity has been repeatedly demonstrated in tropical regions, where agricultural management has in general detrimental effects on species from pristine forests (e.g. Phalan et al. 2011). However, many species are adapted to open or semi-open habitats, such as grasslands or savannahs (Fischer *et al.* 2008; Godfray 2011). Studies from tropical, extensive livestock systems confirmed the assumption, that more complex productivity-biodiversity curves occur, if agricultural landscapes provided ecological niches for forest and open habitat species. Consecutively, hump-shaped (inverse quadratic) productivity-biodiversity curves were observed, showing that biodiversity is highest at intermediate productivity levels and decreases at lower and higher levels (Mastrangelo & Gavin 2012; Macchi *et al.* 2013).

Although Europe is characterized by a wide range of productions systems, from managed grasslands and mixed farmland mosaics to monoculture of high-input arable crops, landscape scales studies from mixed production systems are still rare (but see Feniuk 2015). In addition most studies either focused on the extension of farmland, or on the per unit area productivity, without disentangling the two (e.g. Dross *et al.* 2018). In this study, we analyzed the relationship between agricultural productivity, defined as food energy per landscape, and bird and butterfly diversity in 49 temperate agricultural landscapes of 1 km^2 each. In order to compare agricultural yields across grasslands and different arable crops, food energy, instead of yield, was used as a common metric of production per unit area (Dross *et al.* 2018). Contrary to other studies, which use reference yield data from agricultural surveys (e.g. Dross, Jiguet & Tichit 2017), we collected actual yield data from 299 farmers, over three years. Birds and butterflies were selected as model taxa because they react to different aspects of agricultural production and landscape composition (e.g. Rundlof, Bengtsson & Smith 2008; Jeliazkov *et al.* 2016).

In Europe, agricultural landscapes have developed over centuries (Burgi, Salzmann & Gimmi 2015) and typically hold species dependent upon open and semi-open landscapes (Fischer *et al.* 2008). Nonetheless, in such landscapes, productivity often increases at the expense of biodiversity (Gabriel *et al.* 2013; Dross, Jiguet & Tichit 2017). In our temperate study system, we therefore expected negative linear, or concave biodiversity-productivity relationships. Productivity at landscape level is strongly influenced by the share of farmland (Tscharntke *et al.* 2005), which, if increased at the expense of natural areas, negatively impacts biodiversity (Zingg, Grenz & Humbert unpubl.). Even butterflies, which typically depend upon farmland habitats (Wermeille, Chittaro & Gonseth 2014), show highest overall diversity in landscapes with a combination of farmed and natural areas (Ouin & Burel 2002). The same is valid for birds, as many species require different habitats and a diversity of resources to complete their life cycles (Vickery & Arlettaz 2012). Increased crop productivity often relates to the intensity of agricultural practices, such as the amounts of fertilizers and pesticides used (Flynn *et al.* 2009) with negative effects on birds and butterflies (Jeliazkov *et al.* 2016). High fertilizer input reduces the botanical diversity of grasslands and arable fields (Kleijn *et al.* 2009), as a consequence the impoverished plant communities offer fewer host and flowering plants to invertebrates, such as butterflies (Marini *et al.* 2009; Börschig *et al.* 2013). In addition, the indirect effects can affect birds, as they suffer from the decreased availability of invertebrate prey (Vickery *et al.* 2001).

METHODS

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, ranging from 400 to 800 m). It is the most densely populated region of Switzerland, and its most important agricultural area. The Biodiversity Monitoring Switzerland (BDM) conducts repeated biodiversity surveys in 520 systematically distributed landscape grid cells of 1 x 1 km across Switzerland (BDM Coordination Office 2014). For this study, 49 BDM landscapes located on the Swiss Plateau, with less than 25 ha of water bodies and paved areas were selected (Fig. 1). For each of the 49 landscape grid cells (hereafter called landscapes), digitized information on land use was provided by the Swiss cadastral survey in 2014. The supplied GIS polygon layers were controlled and completed where necessary, using satellite images in ArcGIS (Version 10.2.2). Crop cover maps were provided by the cantonal agricultural offices in 2014. Because such maps were not available for the cantons of Aargau and Vaud, these landscapes (n = 16) were visited and crops were mapped in summer 2016 (Fig. 2).

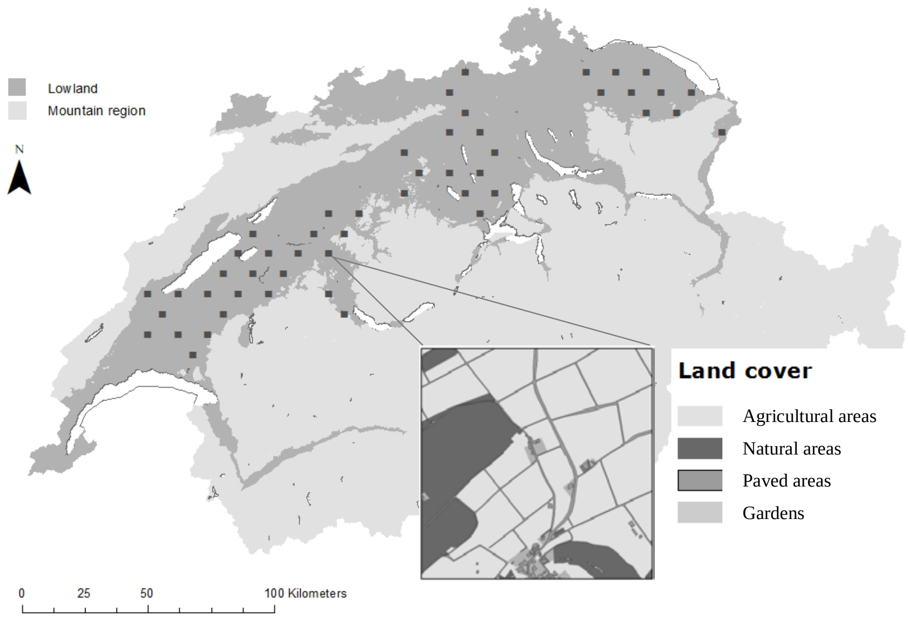


Fig. 1: Map of Switzerland with the lowland landscape 1 x 1 km grid cells selected in this study (n = 49). The insert shows the detailed configuration of one landscape as an example.

Biodiversity

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 2012 to 2016. 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, and 5 km, respectively (BDM Coordination Office 2014). For data analysis, birds and butterflies were classified into two groups: 1) all species pooled within the corresponding taxonomic group; and 2) typical farmland species. 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). Complete species lists can be found in the Appendix (Table A.1). As total and farmland butterfly species richness and abundance were highly correlated (Pearson correlation coefficient > 0.9), results are only shown for total butterfly species richness and abundance.

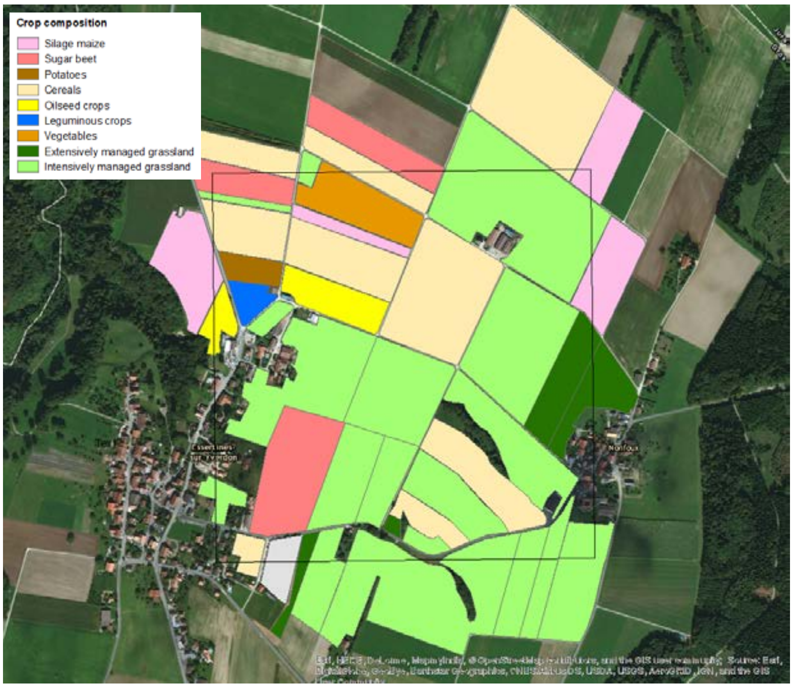


Fig. 2: Example of a study landscape 1 x 1 km grid cell showing the variegated spatial agriculture configuration. To obtain accurate data on agricultural yield, all farmers in the landscape grid cell were contacted. To assess butterflies and birds, surveys along 2.5 and 5 km transects, respectively, were conducted (BDM Coordination Office 2014).

Productivity

In order, to estimate agricultural productivity, interviews with 299 farmers (in person or via questionnaires) in 49 landscapes were conducted. Farmers were asked to provide information on crop area, production system, yield (biomass), as well as the frequency of use (number of cuts and grazing) for grasslands, over a three-year period (e.g. 2012 – 2014 or 2013 – 2015).

Estimate missing yield values using Multiple Imputation

Unfortunately, yield estimates were not available for all fields, either because farmers were not willing to participate in the survey, or because yields were unknown. Before the statistical analysis, we therefore processed our incomplete yield dataset using Multiple Imputation (MI). As an advanced procedure for handling missing data, MI consists of estimating the missing data multiple times to create several complete versions of an incomplete dataset. We used predictive mean matching (PMM) from the R Package *mice* to impute the missing yield values and to create 50 completed datasets (van Buuren 2011). The PMM procedure subsamples from the observed data and predicts the value of the target variable Y according to the specified imputation models:

i) Grassland yield ~ Grassland category + Frequency of use + Management + Year + Landscape + Region + Altitude
ii) Arable yield ~ Crop category + Management + Year + Landscape + Region + Altitude

We used separate imputation models to predict grassland and arable yields and included the following predictors: grassland or crop category (see Table 1), the frequency of use for grasslands (number of cuts and grazing sessions), the management (organic, extensive or conventional) and the year (2012 to 2015), based on the farmer interviews. In addition, landscape (ID), altitude (meter above sea level), and the region (Swiss canton) were included. Because MI can generate implausible values (e.g. 120 dt/ha for wheat), we restricted the yield values after the imputation (post-processing), to the ranges given by farmers (see Appendix, Figure C.2).

Calculate food energy per landscape

For each of the 50 completed datasets, we calculated the mean crop yield per hectare, averaging over all three sampling years and fields, within each landscape. Using this, we calculated the total food energy production *P* (in GJ year $^{-1}$), in each landscape for each imputed dataset *k* as follows:

$$P_{jk} = \sum_{i=1}^{n} X_{ijk}\, A_{ij}\, CF_i\, ME_i$$

where, *j* refers to the study landscape and *i* to the crop category. *X* is the averaged crop yield (dt ha^{-1} year $^{-1}$) from the imputed dataset, *A* the crop area (ha) from the agricultural survey or crop mapping, *CF* the conversion factor, which accounts for the losses during food processing or conversion (see Table 1) and *ME* the content of metabolizable energy per unit weight of edible portion (GJ dt $^{-1}$) from the Swiss Food Composition Database (FSVO 2017). Instead of using gross energy (measured by completely burning the dried crop in a bomb calorimeter), we used metabolizable energy (ME), which accounts for fecal losses and represents the energy that enters blood after digestion. Crop areas (*A*) were calculated based on agricultural survey data from 2014 or crop mapping in 2016. The crop areas did not account for changes of crop cover over time, due to crop rotation. However, as crop rotation is on a farm scale, we considered inter-annual fluctuations to be low within landscapes, as crops may change between fields, but proportions at landscape scale remain similar. Non-edible crops, such as ornamental plants (e.g. Christmas trees), by-products such as straw, or and non-harvested crops such as biodiversity promotion areas (e.g. hedges or wildflower strips) were attributed a food energy content of zero. In general, we accounted for one main crop per year, while catch crops covering the soil during winter were not included in the productivity estimates. In vegetable production, we always accounted for two harvests per year.

Define crop use scenarios

We calculated total food energy production per landscape for two scenarios; for *scenario 1* we assumed that all crops would be converted into an edible form and be directly consumed by humans (FAO 2011). Energy yield of fodder crops (in scenario 1 only silage maize and grass) was expressed as the energy-equivalent of edible meat (in GJ), produced per unit weight of crop. For *scenario 2*, we accounted for the fact, that edible crops (e.g. cereals) are not always directly consumed by humans, but also used as animal feed: In cereals, for example, a share of 42 % is used as animal feed, mostly to produce meat (BFS 2016). Because the food energy values from the two scenarios were highly correlated (Pearson's correlation coefficient R = 0.99), we only present the results from scenario 2.

For both scenarios, we assumed that beef cows would be the only recipients of fodder crops. This is a simplification, as other farm animals such as milk cows, poultry or pigs also receive fodder crops. In alternative crop use scenarios (e.g. milk instead of meat energy-equivalent), the food conversion factors would change, but hardly the conclusions, as already scenario1 and 2 were highly correlated. Information on the use of the crops in the two scenarios and the energetic values of the products can be found in Table 1. Detailed information on the conversion from crop to meat energy-equivalent can be found in the Appendix, Table B.1.

Statistical analysis

Relationship between biodiversity and agricultural productivity

We used regression models to describe the relationship between the biodiversity and the productivity indicators at landscape scale. Species richness and abundance of birds and butterflies were used as response variables. Food energy production per landscape in gigajoule (GJ) and the proportion of utilized agricultural area (UAA) in hectare (ha) were included as explanatory variables. We used the following generalized linear models with Poisson (for species richness) and negative binomial (for abundance) distributions and the log link function:

i) glm (Biodiversity indicator ~ Food energy per landscape (GJ) * UAA (ha))

The interaction term was removed if not significant, and we also tested whether there were significant quadratic relationships, which was not the case. The regression models were fitted to the n (= 50) imputed datasets and the model results were pooled using the R Package *mitools* (Lumley 2015). Hereby, for logistic regression modelling in combination with MI, the pooled regression coefficients

Table 1: Food energy content of edible portions per crop category. In the first column the crop categories and corresponding crops species are given. We always used the most common crop and its edible form as representatives for each category (e.g. wheat for cereals). Hereby the conversion factor (CF) determines the part of the agricultural product that is edible, or retained during food processing (e.g. sugar extraction). Energy contents are from the Swiss food composition database (FSVO 2017). Information on the crop use scenarios can be found in the method section and on the conversion from crop, to the food energy-equivalent of beef in Table B.1. Abbreviations: GJ = gigajoule, ME = metabolizable energy, DM = dry matter, FM = fresh matter, CF = conversion factor, 🐄 = used as cattle fodder to produce beef, 🧍 = used for human consumption, * edible by-product used as cattle fodder.

Crops	Food/fodder	CF	Food conversion	Source	ME GJ t^{-1} edible portion	ME GJ t^{-1} FM (1)	Use in Scenario 1	Use in Scenario 2
Cereals: wheat, barley, oat, rye, sorghum, spelt and triticale	Wheat grains	0.780	edible portion	FAO, 2011	13.70	10.69	100% 🧍	58% 🧍
	Wheat grains	0.094	conversion to beef	Table B.1	5.64	0.53		42% 🐄
Fruits and berries: berries, fruit orchards	Apple, raw	0.750	edible portion	FAO, 2011	2.32	1.74	100% 🧍	100% 🧍
Oilseed crops: rapeseed, soja, sunflower	Rapeseed oil	0.370	oil extraction	SwissOlio, 2016	33.30	12.32	100% 🧍	100% 🧍
	Rapeseed cake*	0.087	conversion to beef	Table B.1	5.64	0.49	63% 🐄	63% 🐄
Potato	Potato peeled, raw	0.900	edible portion	FAO, 2011	3.20	2.88	100% 🧍	100% 🧍
Sugar beet: sugar and fooder beet	Sugar, white	0.180	sugar extraction	SVZ, 2016	17.00	3.06	100% 🧍	100% 🧍
	Pressed pulp *	0.022	conversion to beef	Table B.1	5.64	0.12	24% 🐄	24% 🐄
	Molasse*	0.076	conversion to beef	Table B.1	5.64	0.43	4% 🐄	4% 🐄
Vegetables: indoor and outdoor vegetables	Carrot, raw	0.900	edible portion	FAO, 2011	1.58	1.42	100% 🧍	100% 🧍
Grain maize	Sweet maize, raw	0.790	edible portion	FAO, 2011	3.90	3.08	100% 🧍	
	Graine maize	0.096	conversion to beef	Table B.1	5.64	0.54		100% 🐄
Silage maize	Silage maize	0.077	conversion to beef	Table B.1	5.64	0.43	100% 🐄	100% 🐄
Leguminous crops: field bean, leguminous and protein pea	Green beans	0.900	edible portion	FAO, 2011	1.29	1.16	100% 🧍	
	Pea seeds	0.088	conversion to beef	Table B.1	5.64	0.50		100% 🐄
Extensively managed grasslands: meadows and pastures	Hay	0.043	conversion to beef	Table B.1	5.64	0.24	100% 🐄	100% 🐄
Intensively managed grasslands: meadows and pastures	Green, silage fodder	0.069	conversion to beef	Table B.1	5.64	0.39	100% 🐄	100% 🐄

(1) given in DM for silage maize, extensively and intensively managed grasslands

and standard errors were obtained by using Rubin's Rule (Rubin 1976). The pooled coefficient is derived by averaging the regression coefficient estimates from each complete data analysis result across the imputed datasets. The standard error is obtained by pooling the variance between as well as within imputations, which account for sampling and imputation uncertainty, respectively (see also Eekhout 2017). The variability between the imputations reflects the uncertainty of the actual value (van Buuren 2012).

Relationship between agricultural productivity, crops and land use

To describe which crop and land use properties correlate with food energy, we fitted a series of univariate linear models with gaussian distributions. The models were fitted using all 50 imputed datasets and results were pooled as described above. We included food energy per landscape as response variable and the following explanatory variables; area of forest, hedges, waterbodies, farmland, paved and non-vegetated zones given in hectares per landscape. In addition, area and mean yield per landscape for cereals, grasslands, vegetables, potatoes, sugar beet, fruits, oilseeds, legumes and non-edible crops, intensively and extensively managed grasslands. All significant variables from the univariate models were included in the full model. We reduced the full model with backward stepwise selection, by removing the variables with the largest relative standard error (i.e. standard error/estimate).

RESULTS

Biodiversity

In the 49 landscapes, 99 bird species were recorded. Per landscape, an average (± SD) 39 (± 6.6) bird species were detected, including 8 (± 1.9) farmland species. The bird abundance (i.e. number of breeding pairs per landscape) was, on average, 344 (± 126), ranging from 93 to 714. Farmland bird abundance ranged from 5 to 88, with a mean of 39 (± 18). In total 60 butterfly species were detected, on average 24 (± 6.4) species and 443 (± 241) individuals were observed per landscape (range 95 – 1123).

Productivity

In our 49 selected landscapes, farmers cultivated 30 different crops out of 12 crop categories. Cereals, intensively managed grasslands and silage maize were the most abundant crop categories in our landscapes, which were characterized by mixed production systems with arable and livestock production. An overview on the composition of all landscapes can be found in the Appendix, Figure C.1. Most yield estimates from farmers were for wheat (n = 696), intensively managed grasslands (n = 213) and silage maize (n = 187, see Figure C.2). The highest-yielding crops, in terms of dry mass per area, were sugar beet, silage and grain maize, followed by intensively managed grasslands (Table C.4). Study landscapes had, on average (mean ± SD), 68 ± 16 ha of farmland and the total produced food energy (scenario 2) averaged to 3'679 GJ (± 2'403) per landscape or 53 GJ per ha (± 34). Hereby, highly

Table 3: Summary of the models showing the relationships between bird and butterfly abundance and species richness, and agricultural productivity given as total produced food energy from scenario 2. The results are based on the pooled model outcomes from the 50 imputed datasets. For each model, the estimates, including confidence intervals, are given on a log scale and significant effects are shown in bold. Abbreviations: AB = abundance, SP = species richness, UAA = utilized agricultural area, GJ = gigajoule, ha = hectare.

Response	**Intercept**			**Food energy (GJ)**			**UAA (ha)**			**Food energy (GJ) * UAA (ha)**		
	Est.	(Lower	Upper)	Est.	(Lower	Upper)	Est.	(Lower	Upper)	Est.	(Lower	Upper)
Total bird SP	3.75	3.47	4.03	1.03E-04	2.20E-05	1.84E-04	-1.03E-03	-5.52E-03	3.46E-03	**-1.47E-06**	**-2.66E-06**	**-2.85E-07**
Farmland bird SP	1.80	1.34	2.25	1.92E-06	-4.13E-05	4.51E-05	4.66E-03	-2.15E-03	1.15E-02			
Total bird AB	6.35	5.83	6.86	2.02E-04	5.68E-05	3.47E-04	-8.76E-03	-1.68E-02	-7.48E-04	**-3.08E-06**	**-5.14E-06**	**-1.03E-06**
Farmland bird AB	3.41	2.97	3.85	2.61E-05	-1.75E-05	6.98E-05	4.74E-03	-2.04E-03	1.15E-02			
Total butterfly SP	3.39	3.14	3.65	9.91E-06	-1.61E-05	3.59E-05	**-4.07E-03**	**-8.07E-03**	**-6.92E-05**			
Total butterfly AB	6.08	5.38	6.78	2.79E-05	-4.25E-05	9.83E-05	-1.21E-03	-1.21E-02	9.63E-03			

productive landscapes, in terms of food energy in joules, were characterized by high proportions of cereals, potatoes, sugar beets, and high yields of sugar beet and vegetables (Table 2). Proportion of farmland did not correlate with total produced food energy (see also Figure 3).

Table 2: Crop and land use variables correlated with total produced food energy (scenario 2) at landscape scale. The results are based on the pooled model outcomes from the 50 imputed datasets. For each model, the estimates, including confidence intervals, are given. Only variables with significant effects (CI not overlapping zero) were kept in the final model.

Total produced food energy (GJ)	Est.	(Lower	Upper)
Intercept	1098.06	388.81	1807.30
Cereal area (ha)	46.71	2.60	90.83
Sugar beet area (ha)	156.02	21.44	290.60
Potato area (ha)	198.69	19.38	377.99
Sugar beet yield (ha)	7.62	2.43	12.80
Vegetable yield (dt/ha)	17.37	5.03	29.71

The relationship between biodiversity and productivity

We observed a correlation between total bird abundance, species richness and total produced food energy per landscape, which was influenced by the proportion of farmland. More specifically, there was a negative relationship between food energy and bird species richness and abundance in landscapes with high proportions of farmland, but a neutral one in landscapes with lower proportions of farmland (Fig. 3). Neither typical farmland birds, nor butterflies did show any relationship with total produced food energy (Table 3).

DISCUSSION

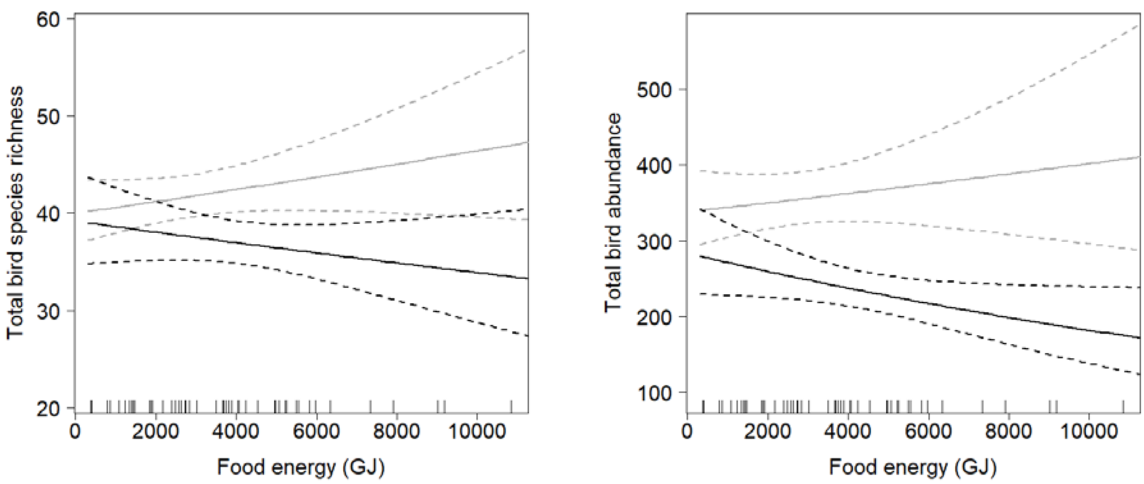
This study investigated how the diversity of birds and butterflies relates to agricultural productivity, measured as total food energy production, in 49 1-km^2 landscape grid cells. Landscapes were dominated by mixed arable and livestock farming systems, with varying proportions of farmland (range 27 to 94 ha). We found that there is no simple negative relation between agricultural production and biodiversity at landscape scale. Interactive effects between the proportion of farmland and the productivity influenced the relationship with bird species richness and abundance. Surprisingly, neither typical farmland bird, nor butterfly species richness, or abundance correlated with food energy at landscape scale.

While the aspects of productivity and farmland extension, are in general separately assessed (e.g. Jeliazkov *et al.* 2016; Dross, Jiguet & Tichit 2017), we show here, that there is an interaction between them (see Fig. 4). Bird species richness and abundance were negatively correlated with food energy in landscapes dominated by farmland (i.e. 80 ha UAA and 20 ha non-farmed), whereas there was no relationship in landscapes with less farmland (i.e. 60 ha farmland and 40 ha non-farmed). In our study landscapes, non-farmed habitats were mainly (mean ± SD) forests (15 ± 13 ha), impervious (e.g. settlements and streets, 8 ± 6 ha) and vegetated areas (e.g. gardens, 3 ± 7 ha), and to a lesser extent, waterbodies, hedges and unvegetated areas (e.g. gravel, rock, sand). It has been shown that for bird conservation in agricultural landscapes, at least 20 % natural areas, such as forests, hedges and waterbodies, need to be present (Zingg, Grenz & Humbert unpubl.). Such structurally complex landscapes may not only enhance local diversity in agroecosystems, but also compensate for local high intensity management (Tscharntke *et al.* 2005), which could explain the absence of a correlation in landscapes with *enough* non-farmed habitats. Nonetheless we observed a negative correlation between bird species richness and abundance and agricultural productivity in landscapes dominated by farmland (i.e. 80 ha UAA). Such simple landscapes, which are dominated by agricultural areas provide few habitat elements and resources for birds (Vickery & Arlettaz 2012). If the agricultural areas are, in addition, intensively managed, food and nesting resources are further depleted (Wilson *et al.* 1999; Vickery *et al.* 2001), which may lead to the observed negative correlation between agricultural productivity and bird species richness and abundance, in farmland-dominated landscapes.

We found no correlation between typical farmland bird or butterfly species richness, or abundance and food energy production at landscape scale. This came as a surprise, as neutral biodiversity–productivity relationships have rarely been observed, particularly in temperate agro-ecosystems. It is often assumed that the presence of natural, or wildlife friendly areas and low intensity management practices, promote biodiversity at the cost of agricultural productivity (e.g. Gabriel *et al.* 2013). Nonetheless, there is evidence for biodiversity-mediated benefits to agricultural production; wildlife-friendly habitats which promote pollinators and other beneficial organisms can increase total yield, even when land is taken out of production (Carvalheiro *et al.* 2011; Pywell *et al.* 2011). It has for example been shown, that biological pest control can improve wheat yields if adjacent wildlife-friendly habitats are promoted (Tschumi *et al.* 2016). Likewise, natural habitats promote pollinators (Ricketts *et al.* 2008), which enhances productivity of arable crops (Bommarco, Marini & Vaissiere 2012). Hereby, butterflies are recognized as being good indicators of other invertebrate groups, including bees and flies, which include the most important pollinators worldwide (Thomas 2005; Rader *et al.* 2016). Agricultural policy in Switzerland follows the framework of ecological intensification (Bundesrat 2013). Management practices such as intercropping, crop rotations or reduced agrochemical use, shall promote ecosystem services and endorse production (Bommarco, Kleijn & Potts 2013). This policy framework may temper the productivity-biodiversity trade-off (Kovacs-Hostyanszki *et al.* 2017). In addition, the comparison with other European studies shows, that our productivity gradient encompasses mostly intermediate landscapes, without the very low-productivity traditional (Feniuk 2015), nor the very high-productivity, industrialized, monocultural systems (Dross, Jiguet & Tichit 2017). In such intermediate productivity landscapes, the productivity-biodiversity trade-off may be less pronounced.

Although we described how bird and butterfly communities changed along a productivity gradient, it is hardly meaningful, to derive conservation recommendations, based on our results. It is not productivity per se, but agricultural practices associated with the crops which have an effect on biodiversity (Kremen 2015). In our mixed agricultural landscapes, productivity increased, with the share of crops, with high energetic values and high yields (i.e. sugar beet, potatoes and cereals), hereby high productivity does not imply high management intensity (e.g. quantity of pesticide application or fertilization). To provide conservation measures, we should refer to agricultural practices instead of productivity, this in order to reduce the inherent confusion which is created by considering productivity as a measure of biodiversity (un-)friendliness (Kremen 2015). However, there is one study by Feniuk (2015), analyzing biodiversity and food energy in mixed arable and livestock production systems. Comparing the two studies, it becomes apparent that in the Swiss lowland, very low-intensity, traditional agricultural systems, still present in Poland, don't exist anymore. Bird species adapted to low-productivity agriculture had their highest population densities below 33 GJ ha^{-1} $year^{-1}$, in return our mean (± SD) productivity was with 53 GJ ha^{-1} $year^{-1}$ (± 34) well above this threshold. Consequently, farmland bird or butterfly species associated with such low-intensity habitat types in Switzerland, as for example the whinchat (*Saxicola rubetra*) or the woodchat shrike (*Lanius senator*) already disappeared from our study area in the last decades. From a conservation perspective, to promote such farmland species, measures such as nature reserves with very low intensive management may be needed (Feniuk 2015).

Fig. 4: The relationship between bird species richness, abundance and food energy-equivalents (scenario 2) depends on the amount of farmland (UAA) within the landscape grid cell. The figure shows the predicted regression lines for landscapes with 60 ha (grey) and 80 ha UAA (black); respectively. Shown are pooled predictions with 95% confidence intervals from the n (= 50) models. The means of the imputed food energy values are shown at the bottom.



CONCLUSIONS

It seems that in temperate mixed agricultural systems, high agricultural production, in term of joules produced per 100 ha landscapes, is not fully incompatible with biodiversity. Whilst birds were negatively correlated with productivity in landscapes dominated by farmland, we observed an absence of relationship in landscapes with more non-farmed habitats. In addition, neither farmland birds, nor butterflies were correlated with food energy production. Although it is not possible to establish any causality from our analysis, non-farmed areas such as forest, hedges or gardens seem to be able to mitigate the negative influence of high productive fields in agricultural landscapes. As the main purpose of agriculture is to produce food for human (and domestic animal) consumption, it is good news, that there is *a priori* no conflict between biodiversity and food production in mixed temperate agricultural landscapes. It is therefore possible to start designing the multi-functional agro-ecosystems of the future that will account for both, biodiversity and agricultural food productivity.

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APPENDIX A

Table A.1. Species list

Minimal and maximal abundance per landscape and the number of landscape grid cells out of 49 (N_{lan}) in which a given species was observed. Information on habitat was obtained from the Swiss Ornithological Institute (Benz et *al.* 1987 and the Red List status from Keller *et al.* 2010 and Wermeille et *al.* 2014). Abbreviations: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, NA = not available

Taxa	**Latin name**	**Farmland**	**Red list**	**Min. abund.**	**Max. abund.**	**Mean abund.**	**N_{lan}**
Bird	*Accipiter gentilis*	No	LC	1	1	1	1
Bird	*Accipiter nisus*	No	LC	1	1	1	2
Bird	*Acrocephalus palustris*	No	LC	1	8	4	40
Bird	*Acrocephalus scirpaceus*	No	LC	1	25	11	20
Bird	*Aegithalos caudatus*	No	LC	1	3	1	1
Bird	*Alauda arvensis*	Yes	NT	1	35	8	1
Bird	*Alcedo atthis*	No	VU	1	2	1	29
Bird	*Anas platyrhynchos*	No	LC	1	14	3	43
Bird	*Anser anser*	No	NA	1	1	1	1
Bird	*Apus apus*	No	NT	1	7	3	40
Bird	*Apus melba*	No	NT	30	30	30	3
Bird	*Asio otus*	Yes	NT	1	1	1	36
Bird	*Buteo buteo*	Yes	LC	1	4	2	14
Bird	*Carduelis cannabina*	Yes	NT	1	8	3	17
Bird	*Carduelis carduelis*	No	LC	1	13	4	1
Bird	*Carduelis chloris*	No	LC	1	44	7	3
Bird	*Certhia brachydactyla*	No	LC	1	12	5	1
Bird	*Certhia familiaris*	No	LC	1	10	3	44
Bird	*Ciconia ciconia*	Yes	VU	1	1	1	5
Bird	*Cinclus cinclus*	No	LC	1	2	1	7
Bird	*Coccothraustes coccothraustes*	No	LC	1	4	2	49
Bird	*Columba livia domestica*	No	NA	1	5	2	2
Bird	*Columba oenas*	No	LC	1	3	1	12
Bird	*Columba palumbus*	No	LC	1	22	7	2
Bird	*Corvus corax*	No	LC	1	1	1	49
Bird	*Corvus corone*	Yes	LC	1	18	7	3
Bird	*Corvus monedula*	Yes	VU	6	6	6	4
Bird	*Coturnix coturnix*	Yes	LC	1	3	2	47
Bird	*Cuculus canorus*	No	NT	1	4	1	32
Bird	*Cygnus olor*	No	NA	1	3	2	6
Bird	*Delichon urbicum*	No	NT	1	48	11	16
Bird	*Dendrocopos major*	No	LC	1	8	4	37
Bird	*Dendrocopos minor*	No	LC	1	1	1	37
Bird	*Dryocopus martius*	No	LC	1	3	1	1
Bird	*Emberiza calandra*	Yes	VU	5	5	5	3

Bird	*Emberiza citrinella*	Yes	LC	1	13	6	15
Bird	*Emberiza schoeniclus*	No	VU	1	1	1	5
Bird	*Erithacus rubecula*	No	LC	1	31	10	22
Bird	*Falco subbuteo*	No	NT	1	1	1	2
Bird	*Falco tinnunculus*	Yes	NT	1	3	1	1
Bird	*Ficedula hypoleuca*	No	LC	1	9	2	47
Bird	*Fringilla coelebs*	No	LC	5	56	27	40
Bird	*Fulica atra*	No	LC	1	13	6	29
Bird	*Gallinula chloropus*	No	LC	1	2	1	14
Bird	*Garrulus glandarius*	No	LC	1	7	3	5
Bird	*Hippolais icterina*	No	VU	4	4	4	48
Bird	*Hirundo rustica*	Yes	LC	1	26	8	46
Bird	*Lanius collurio*	Yes	LC	1	3	2	43
Bird	*Larus michahellis*	No	LC	1	1	1	14
Bird	*Locustella luscinioides*	No	NT	2	2	2	48
Bird	*Loxia curvirostra*	No	LC	1	4	2	8
Bird	*Luscinia megarhynchos*	No	NT	1	4	2	7
Bird	*Milvus migrans*	No	LC	1	2	1	7
Bird	*Milvus milvus*	Yes	LC	1	3	1	40
Bird	*Motacilla alba*	No	LC	1	12	4	2
Bird	*Motacilla cinerea*	No	LC	1	2	1	1
Bird	*Motacilla flava*	Yes	NT	1	1	1	30
Bird	*Muscicapa striata*	No	LC	1	15	4	1
Bird	*Oriolus oriolus*	No	LC	1	9	3	42
Bird	*Parus ater*	No	LC	1	22	7	30
Bird	*Parus caeruleus*	No	LC	1	27	11	2
Bird	*Parus cristatus*	No	LC	1	7	2	41
Bird	*Parus major*	No	LC	1	36	17	49
Bird	*Parus palustris*	No	LC	1	11	3	30
Bird	*Passer domesticus*	No	LC	1	96	33	37
Bird	*Passer montanus*	Yes	LC	1	24	8	5
Bird	*Pernis apivorus*	No	NT	1	1	1	5
Bird	*Phasianus colchicus*	Yes	NA	2	2	2	1
Bird	*Phoenicurus ochruros*	No	LC	1	27	10	21
Bird	*Phoenicurus phoenicurus*	Yes	NT	1	1	1	9
Bird	*Phylloscopus collybita*	No	LC	1	32	10	39
Bird	*Phylloscopus sibilatrix*	No	VU	1	1	1	46
Bird	*Phylloscopus trochilus*	No	VU	1	4	2	1
Bird	*Pica pica*	No	LC	1	9	3	3
Bird	*Picus canus*	No	VU	1	1	1	15
Bird	*Picus viridis*	No	LC	1	3	1	27
Bird	*Podiceps cristatus*	No	LC	1	4	2	3
Bird	*Prunella modularis*	No	LC	1	13	3	20
Bird	*Pyrrhula pyrrhula*	No	LC	1	1	1	1
Bird	*Rallus aquaticus*	No	LC	1	1	1	27
Bird	*Regulus ignicapilla*	No	LC	1	28	8	24

Bird	*Regulus regulus*	No	LC	1	24	5	49
Bird	*Saxicola rubicola*	Yes	NT	1	2	2	7
Bird	*Serinus serinus*	No	LC	1	11	4	16
Bird	*Sitta europaea*	No	LC	1	12	5	41
Bird	*Streptopelia decaocto*	No	LC	1	7	2	7
Bird	*Streptopelia turtur*	Yes	NT	1	1	1	7
Bird	*Strix aluco*	No	LC	1	1	1	11
Bird	*Sturnus vulgaris*	Yes	LC	1	29	11	2
Bird	*Sylvia atricapilla*	No	LC	1	71	25	35
Bird	*Sylvia borin*	No	NT	1	12	3	5
Bird	*Sylvia communis*	Yes	NT	1	2	2	45
Bird	*Tachybaptus ruficollis*	No	VU	1	4	3	4
Bird	*Troglodytes troglodytes*	No	LC	1	39	11	1
Bird	*Turdus merula*	No	LC	2	88	25	3
Bird	*Turdus philomelos*	No	LC	1	25	7	48
Bird	*Turdus pilaris*	Yes	VU	1	12	4	48
Bird	*Turdus viscivorus*	No	LC	1	8	3	44
Bird	*Vanellus vanellus*	Yes	CR	2	2	2	1
Butterfly	*Aglais urticae*	Yes	LC	1	74	10	2
Butterfly	*Anthocharis cardamines*	Yes	LC	1	15	4	18
Butterfly	*Apatura iris*	No	NT	1	2	1	49
Butterfly	*Aphantopus hyperantus*	Yes	LC	2	222	32	16
Butterfly	*Aporia crataegi*	Yes	NT	3	3	3	6
Butterfly	*Araschnia levana*	No	LC	1	35	8	21
Butterfly	*Argynnis adippe*	Yes	LC	1	1	1	6
Butterfly	*Argynnis paphia*	No	LC	1	23	4	13
Butterfly	*Aricia agestis-Komplex*	No	LC	1	6	2	14
Butterfly	*Boloria dia*	Yes	NT	1	7	3	14
Butterfly	*Brenthis daphne*	No	LC	1	5	2	7
Butterfly	*Brenthis ino*	No	NT	1	1	1	28
Butterfly	*Brintesia circe*	Yes	NT	1	1	1	1
Butterfly	*Carcharodus alceae*	Yes	NT	1	16	3	1
Butterfly	*Carterocephalus palaemon*	Yes	LC	1	1	1	17
Butterfly	*Celastrina argiolus*	No	LC	1	12	3	29
Butterfly	*Coenonympha pamphilus*	Yes	LC	1	79	21	2
Butterfly	*Colias croceus*	Yes	LC	1	47	10	47
Butterfly	*Colias hyale-Komplex*	No	LC	1	130	13	4
Butterfly	*Cupido alcetas*	Yes	NT	1	12	5	1
Butterfly	*Cupido argiades*	Yes	NT	1	48	10	23
Butterfly	*Cupido minimus*	Yes	LC	1	1	1	39
Butterfly	*Erynnis tages*	Yes	LC	1	35	8	1
Butterfly	*Gonepteryx rhamni*	No	LC	1	13	3	39
Butterfly	*Inachis io*	No	LC	1	11	3	2
Butterfly	*Issoria lathonia*	Yes	LC	1	9	3	1
Butterfly	*Lasiommata maera*	Yes	LC	1	1	1	32
Butterfly	*Lasiommata megera*	Yes	LC	1	36	6	44
Butterfly	*Leptidea sinapis-Komplex*	Yes	LC	1	39	7	4

Butterfly	*Limenitis camilla*	No	LC	1	20	5	16
Butterfly	*Lycaena phlaeas*	Yes	LC	1	18	3	6
Butterfly	*Lycaena tityrus*	Yes	LC	1	2	2	1
Butterfly	*Maniola jurtina*	Yes	LC	1	550	87	49
Butterfly	*Melanargia galathea*	Yes	LC	1	103	20	35
Butterfly	*Melitaea athalia*	Yes	LC	1	2	2	41
Butterfly	*Melitaea diamina*	Yes	NT	1	1	1	1
Butterfly	*Melitaea parthenoides*	Yes	VU	9	9	9	39
Butterfly	*Ochlodes venata*	Yes	LC	1	42	6	4
Butterfly	*Papilio machaon*	Yes	LC	1	15	3	12
Butterfly	*Pararge aegeria*	No	LC	1	64	14	1
Butterfly	*Pieris brassicae*	Yes	LC	1	23	6	42
Butterfly	*Pieris mannii*	Yes	NT	8	43	20	27
Butterfly	*Pieris napi-Komplex*	No	LC	4	328	83	3
Butterfly	*Pieris rapae-Komplex*	No	LC	4	296	80	1
Butterfly	*Plebeius argus*	Yes	NT	1	1	1	23
Butterfly	*Polygonia c-album*	No	LC	1	12	4	35
Butterfly	*Polyommatus bellargus*	Yes	LC	2	2	2	37
Butterfly	*Polyommatus icarus*	Yes	LC	1	132	29	1
Butterfly	*Polyommatus semiargus*	Yes	LC	1	50	10	47
Butterfly	*Polyommatus thersites*	Yes	VU	1	1	1	30
Butterfly	*Pyrgus alveus-Komplex*	No	LC	1	4	2	43
Butterfly	*Pyrgus armoricanus*	No	NT	1	1	1	32
Butterfly	*Pyrgus malvae-Komplex*	Yes	LC	1	2	1	48
Butterfly	*Satyrium w-album*	No	LC	1	2	2	1
Butterfly	*Thecla betulae*	No	LC	1	1	1	1
Butterfly	*Thymelicus lineola*	Yes	LC	1	223	31	11
Butterfly	*Thymelicus sylvestris*	Yes	LC	2	26	10	12
Butterfly	*Vanessa atalanta*	Yes	LC	1	29	6	3
Butterfly	*Vanessa cardui*	Yes	LC	1	19	5	21
Butterfly	*Zygaena filipendulae*	Yes	LC	1	160	28	45

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

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

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APPENDIX B

As crops and crop by-products are often used as cattle feed, we calculated the amount of meat, produced with a given crop type. Swiss standards were used for the calculations, the values may change in systems where fattening is either very intensive or very extensive. We assumed that a cow would gain on average 1.1 kg per day (intermediate fattening intensity), for which an average daily food energy input of 39 MJ NEV (net energy meat) is required (Agroscope 2013). Consecutively, within one year (365 days), a cow gains 401.5 kg and uses 14’235 MJ NEV to attain the slaughter weight of 466.5 kg (assuming 65 kg were the start weight of the calf). From this 466.5 kg animal only around 35% are consumed by humans (Agridea 2014). Non-used and uneatable parts such as bones, fibers or cuts are eliminated during processing. Given our assumptions 14’235 MJ NEV were used to produce 163.3 kg beef, which means that with 87.2 MJ NEV, 1 kg beef can be produced.

Table B.1. Conversion from crop to meat

The table below shows how much edible meat is produced with 1 kg of a given crop or by-product. NEV energetic values for ruminants were obtained from the Swiss feed database. The feed conversion factor equals the amount of edible meat (in kg) which is produced per unit weight of a given crop. A cow would for example need 11 kg leguminous crops or 23 kg hay from extensively managed meadows to obtain enough energy to produce 1 kg beef. Abbreviations: NEV = net energy meat, MJ = megajoule, DM = dry matter, FM = fresh matter.

Crop category	Cattle feed	NEV MJ	per kg	NEV MJ needed for 1kg meat	Conversion factor
Cereals	Wheat, whole grain	8.23	FM	87.2	0.094
Oilseed crops	Rapeseed cake	7.55	FM	87.2	0.087
Sugar beet	Pressed pulp, fresh	1.94	FM	87.2	0.022
	Molasses	6.60	FM	87.2	0.076
Grain maize	Maize, grains	8.34	FM	87.2	0.096
Silage maize	Silage maize	6.69	DM	87.2	0.077
Leguminous crops	Protein pea seeds	7.71	FM	87.2	0.088
Extensively managed grassland	Hay (1)	3.75	DM	87.2	0.043
Intensively managed grassland	Hay, green and silage fodder (2)	6.02	DM	87.2	0.069

(1) Average energetic value for mixed grassland communities harvested at growth stages 6 - 7 (late use)

(2) Average energetic value for mixed grassland communities with raygras harvested at growth stages 1 - 5 (early use)

Agridea (2014): Direktvermarktung von Fleisch. Agridea Lindau.

Agroscope (2013): Fütterungsempfehlungen für Wiederkäuer (Grünes Buch). Posieux.

Agroscope & University of Zürich (2017): Feedbase. The Swiss feed database. Available online at https://www.feedbase.ch, checked on 7/27/2017.

APPENDIX C

Figure C.1. Landscape composition

The figure below shows the landscape grid cell compositions in number of ha per crop category. Abbreviations: Ext. = extensively managed, Int. = intensively managed.

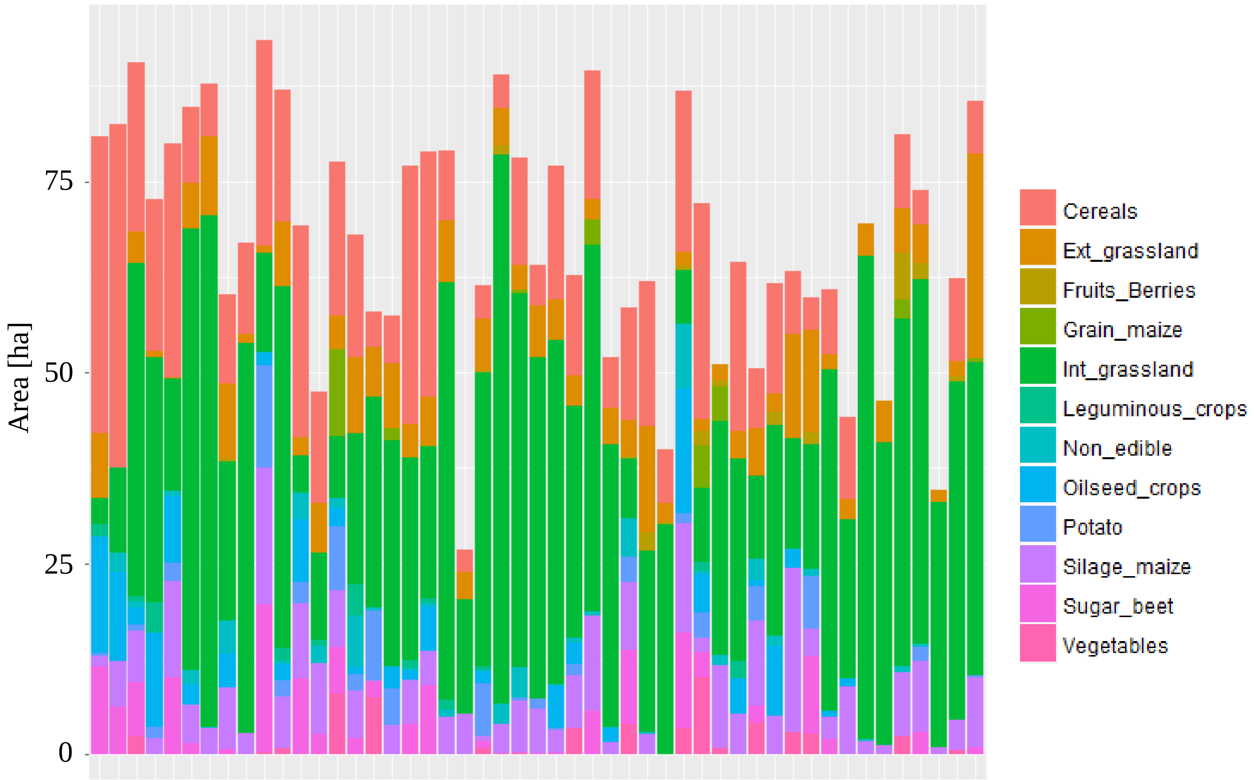
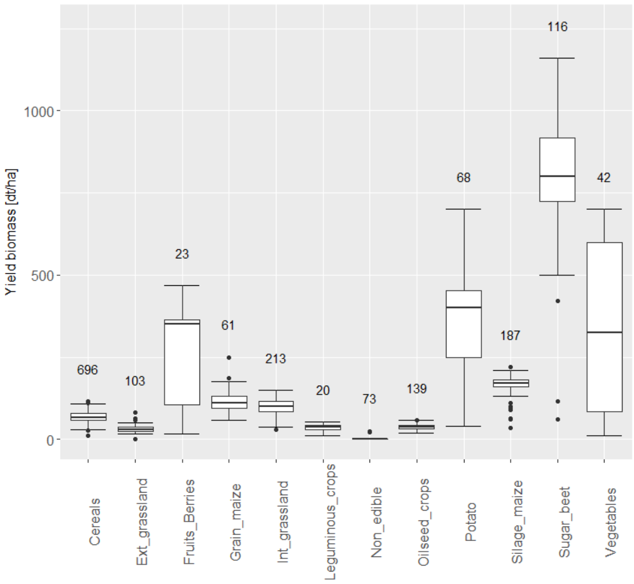


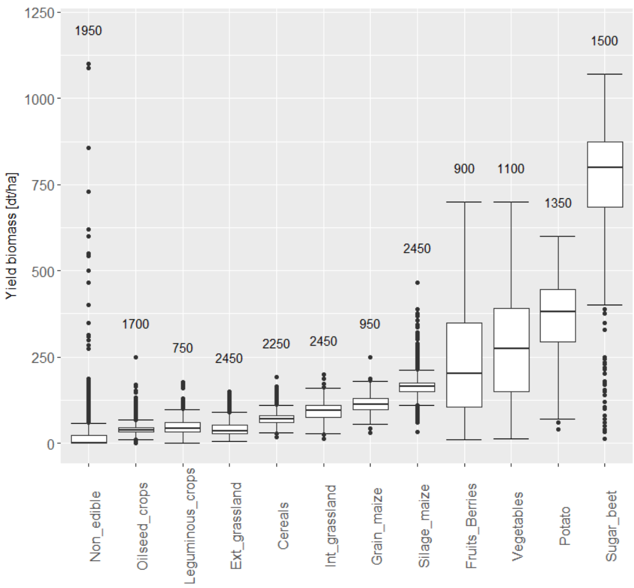
Figure C.2. Imputation of yield values

The figure below shows the raw data from farmer interviews (a) and the imputed yield values before (b) and after processing (c). Because multiple imputation can generate implausible values, the yield values were processed after imputation to increase credibility; they were i) squeezed into the range of minimum and maximum yields reported by the farmers and ii) vegetable yields were doubled (to account for multiple harvests per season). Grassland and silage maize yields are given in dry matter (DM), all others in fresh matter (FM). Shown are the medians, quartiles, outliers and the number of observations (above the bars). The summary statistics of the post-processed imputed yield values can be found in Table C.3.

a) Raw data



b) Imputed values



c) Post-processed imputed values

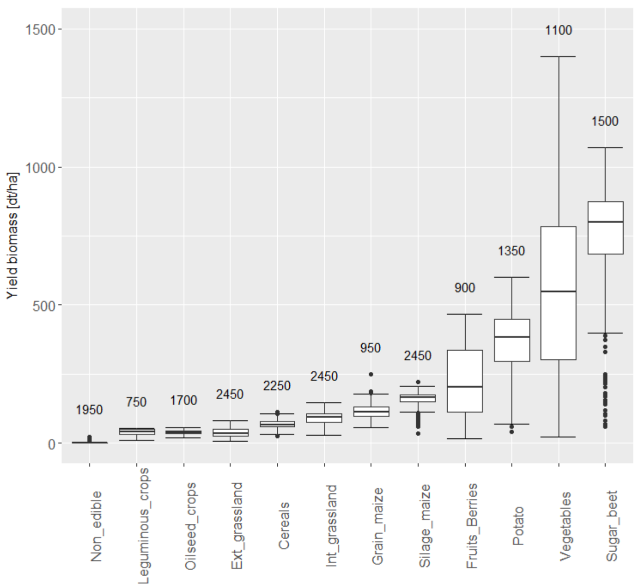


Table C.3. Summary statistics of yield values

Summary statistics on the dry matter (DM) yield of different crop types. Shown are the means and the standard deviation (sd) from the 50 imputed datasets. In order, to standardize the values, yield was converted, if necessary, from fresh to dry matter. We assumed the following dry matter contents (Agroscope 2009); sugar beet (22% DM), silage maize (100% DM), grain maize (85% DM), intensively and extensively managed grasslands (100% DM), vegetables (11% DM), potatoes (18% DM), cereals (85% DM), oilseed crops (90% DM), leguminous crops (85% DM), fruits and berries (15% DM), non-edible (100% DM).

	Yield DM [dt/ha]	
	Mean	**SD**
Sugar beet	175	45
Silage maize	160	34
Grain maize	101	31
Int. grassland	94	35
Vegetables	71	44
Potato	69	26
Cereals	57	18
Ext. grassland	40	21
Oilseed crops	34	10
Leguminous crops	32	11
Fruits, berries	31	24
Non edible	2	7

Agroscope (2009): GRUDAF 2009. Grundlagen für die Düngung im Acker- und Futterbau. In Agrarforschung Schweiz 16 (2).

General discussion

Main findings

In chapter 1 we showed how the diversity of birds and butterflies changed in relation to three different land use intensity indicators. The first indicator was defined as the ratio between utilized agricultural area (UAA) and natural areas (mainly forest), the second as the ratio between arable land and permanent grassland and the third as the ratio between agricultural area and biodiversity promotion areas (BPA).

We showed that biodiversity of both taxa was highest in landscapes with a mix of farmed and natural areas. 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. 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. It also emphasizes the importance of natural habitats such a forests, waterbodies and hedges for bird diversity (Vickery & Arlettaz 2012). None of the species groups was significantly correlated with the proportion of arable land versus permanent grassland. We explained this result with the fact, that most of our permanent grasslands were intensively managed, with frequent fertilizer inputs and 4-6 cuts (or grazing events) per year. Finally, total bird species richness, butterfly species richness and abundance increased with the proportion of biodiversity promotion areas in the landscape. This emphasizes, that BPA can effectively foster birds (Baker 2012; Prince & Jiguet 2013) and butterflies (Aviron *et al.* 2011), not only at field, but also at landscape scale.

In chapter 2 we focused on the above, mentioned BPA, which are extensively managed, wildlife-friendly farmland habitats, such as hay meadows or traditional orchards and form part of the Swiss agri-environment scheme (AES). The proportion of BPA in the landscape proved to be the most important BPA property for butterfly species richness and abundance. 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 & Kuussaari 2012) as typically encountered among BPA meadows. 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 2012; Prince & Jiguet 2013). Interestingly, for both taxonomic groups, the amount and quality of BPA habitats contributed more to species richness than their spatial configuration, connectivity included. Our landscapes probably provided enough habitat continuum for our two mobile taxa, explaining why distance was irrelevant (Thomas *et al.* 2001). This chapter showed that AES measures implemented at field scale have positive effects on spatially-mobile species that are noticeable at landscape scale, and that the fraction of BPA in the cultivated landscape matters more than their spatial configuration in our system.

In Chapter 3 we investigated how biodiversity relates to agricultural productivity, given as total food energy production in 49 landscape units. Interactive effects between the proportion of farmland and the productivity, influenced the relationship with bird species richness and abundance. Hereby birds were negatively correlated with food energy production in landscapes dominated by farmland (i.e. 80 ha UAA), but there was a neutral relationship in landscapes with less farmland (i.e. 60 ha UAA). Structurally complex landscapes, with a certain amount of non-farmed habitat, may not only enhance local diversity in agroecosystems, but also compensate for local high intensity management (Tscharntke *et al.* 2005). Surprisingly, neither farmland bird nor butterfly species richness or abundance correlated with food energy production at landscape scale. Biodiversity loss, is not directly coupled with high agricultural production, but with specific agricultural processes and methods (Kremen 2015). As the main purpose of agriculture is to produce food for human (and domestic animal) consumption, it is good news, that there is *a priori* no conflict between biodiversity and food production in mixed temperate agricultural landscapes.

Local and regional characteristics

This thesis presents results on the relationship between agriculture and biodiversity in temperate, mixed production systems. Our results were shaped by regional characteristics, as not all management or land-use changes are equivalent in their impact on biodiversity under different biogeographic, political or ecological circumstances (Cunningham *et al.* 2013). Hereafter we discuss some of the regional characteristics and their influence on the results.

Tropical and temperate systems

So far, most landscape scale studies on the relationship between agricultural productivity (e.g. yield) and biodiversity have been conducted in tropical ecosystems. In these regions, the trade-off between agriculture and biodiversity has been repeatedly demonstrated, as agricultural management has in general detrimental effects on species from pristine forests (e.g. Green *et al.* 2005; Phalan *et al.* 2011). In Europe, agricultural landscapes have developed over centuries, being influenced by long-term historical management (Burgi, Salzmann & Gimmi 2015) and species that typically depend upon open and semi-open landscapes (Fischer *et al.* 2008). In Switzerland from the 199 common breeding birds, 42 are considered as typical farmland species (Keller *et al.* 2010). Other taxa depend even more on human-shaped farmland habitats; in butterflies for example, 80% of the species are bound to open grassland areas (Wermeille, Chittaro & Gonseth 2014). In the context of European cultural landscapes, the conservation value of farmland has been recognized and the biodiversity promotion focuses on keeping biodiversity within farmed landscapes. As such, conservation objectives, community composition and species responses to agricultural management, differ between regions and illustrate the need for local adapted land use strategies for production and biodiversity.

Large-scaled monocultural and small-scaled mixed production systems

Also within regions large differences between production systems can be observed (Fox 2004). Our study landscapes were characterized by relatively small fields, high crop diversity and patches of natural habitats and permanent grasslands, contrasting with industrialized monocultural systems from other European countries (FAO 2018). The described agricultural landscape composition and configuration may mitigate the negative effect of increased agricultural expansion and productivity and promote the effectiveness of AES in our study system (Concepción *et al.* 2012; Tscharntke *et al.* 2012; Batáry *et al.* 2015). It has for example been shown, that field size, has an influence on biodiversity and thereof on the effect of agricultural management (Batáry *et al.* 2017; Hass *et al.* 2018). The production system impacts, how management intensity and land use changes effect biodiversity (Dross *et al.* 2018). In monocultural systems, high productivity is generally attained, with high-input, impairing biodiversity (Gabriel *et al.* 2013). However, in mixed production system, crop identity is an important predictor for productivity and for management intensity (Hass *et al.* 2018), making conclusion on the relationship between agriculture and biodiversity, across production systems thereof difficult (Dross *et al.* 2018).

CAP and PEP

Agricultural policy strongly influences the environmental impacts of farming, including biodiversity. Switzerland is not a member of the European Union and the implemented Agri-environment measures, are more strict than the cross-compliance requirements of the EU countries (Stoate *et al.* 2009). Swiss agricultural policy is defined by a high level of domestic producer support: in 2016, 63.4 % of total agricultural production value was based on political subsidies, compared to 38.8 % in the EU-28 (Bundesamt für Statistik 2017). All farmers receiving direct payments need to fulfil the proof of ecological performance PEP. These minimum ecological requirements include among others, a crop rotation, the balanced use of nitrogen and phosphorus fertilizers and at least 7% of the farmed area’s being set aside as BPA (Bundesrat 2013). It has been demonstrated that PEP measures can mitigate harmful agricultural practices, for example, between 1990/92 and 2005 a 78% reduction in the P surplus of the Swiss agriculture was reached (Herzog et al. 2008). Overall, policy rules, particularly within the framework of ecological intensification, are important in mitigating negative effects management practices (Kovacs-Hostyanszki *et al.* 2017).

Conclusion

Temperate mixed agricultural landscapes are not characterized by a mere monotonous negative relationship between agriculture and biodiversity. Natural areas within cultural landscapes are crucial to mitigate the negative effects of farmland expansion and agricultural productivity. In addition, biodiversity promotion areas, managed under the Swiss Agri-environment scheme, effectively promoted biodiversity, not only locally, but at landscape scale. To start designing multi-functional agro-ecosystems for biodiversity and agricultural food production, the angle of view needs to be widened. Social, economic and political circumstances need to be considered, as they drive decision-making processes and the effect of land use changes on production and biodiversity (Cunningham *et al.* 2013). Future work should ideally include these aspects, examine a wide range of taxa, including metrics for functional biodiversity and ecosystem services.

Management recommendations

Based on the results of this thesis, we suggest, that to promote biodiversity in cultural landscapes, natural areas, such as forests, hedges and waterbodies, should always cover at least 20% of agricultural landscapes. At landscape scale, both, natural areas and extensively managed farmland habitats under Agri-environment schemes (AES) are important for birds and butterfly. Swiss biodiversity promotion areas (BPA) can effectively promote overall biodiversity and even more importantly, species defined within the framework of the agriculture-related environmental objectives (AEO species) and specialists. Because proportion and quality were by far the most important BPA properties, the focus should be on increasing the proportion of BPA in the cultivated landscape and particularly, further improving their ecological quality.

However, red-listed species, particularly butterflies, were almost absent in our study landscapes. Past land use changes, especially agricultural intensification, led to the disappearance of these species in the last decades (Lachat *et al.* 2010). Hereby common AES have only moderate effects, if any, upon red listed species and not broad AES, but species-specific restoration measures are needed (Kleijn *et al.* 2006). In addition, to reinstate populations of such farmland species, alternative approaches, for example creating nature reserves with very low-intensity agriculture may be needed (Feniuk 2015).

Finally, our findings bear relevance beyond Switzerland, notably for improving the often criticized greening measures of the new European Common Agricultural Policy (Pe'er *et al.* 2016). The CAP greening measures were criticized as they lack specific management guidelines to promote high-value permanent grasslands (Pe'er *et al.* 2014). We confirmed that the presence of permanent grassland *per se*, has no positive effect on biodiversity. We emphasize, that strict management guidelines are needed to restore semi-natural conditions that favor biodiversity. In addition, we suggest, that the form and management requirements of the Swiss AES and BPA especially, may be used to improve the criticized ecological focus areas, which also from part of the new CAP greening measures (Pe'er *et al.* 2016).

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Declaration of consent

on the basis of Article 28 para. 2 of the RSL05 phil.-nat.

Name/First Name: Zingg Silvia

Matriculation Number: 04-124-772

Study program: Ecology and Evolution

Bachelor □ Master □ Dissertation √

Title of the thesis: Integrating food production and biodiversity conservation in temperate agricultural landscapes

Supervisor: PD Dr. J.-Y. Humbert and Prof. Dr. R. Arlettaz

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 para. 1 lit. r of the University Act of 5 September, 1996 is authorised to revoke the title awarded on the basis of this thesis. I allow herewith inspection in this thesis.

Place/Date: Bern, 04/08/2018

Signature:

Curriculum Vitae

Name:	Silvia Zingg
Address:	Schoren 97 3215 Gempenach
Telephone:	0041 79 613 70 72
Email:	silvia.zingg@bfh.ch
Date of birth:	1. May 1984
Place of origin:	Bussnang/Rothenhausen TG

Academic education

2013 - 2018	PhD Thesis: Integrating food production and biodiversity conservation in temperate agricultural landscapes. Supervision: PD Dr. J.Y. Humbert and Prof. Dr. R. Arlettaz, Conservation Biology, University of Bern, J. Grenz, HAFL.
2007 - 2009	*Master of Science in Ecology and Evolution* MSc Thesis: Nestbox design influences territory occupancy and reproduction in a declining, secondary cavity-breeding bird. Conservation Biology, University of Bern
2004 - 2007	*Bachelor of Science in Biology* BSc Thesis: Postglacial recolonization of the south-eastern Alps by *Microtus arvalis*. Division of Population Genetics, University of Bern
Sept. 2006 – Feb. 2007	Erasmus, Universidad Autónoma de Madrid

Professional experience

Since August 2018	Lecturer in Biology and Ecology at the University of Applied Sciences HAFL
Jan. 2016 – July 2018	Representative in the teaching committee at the University of Applied Sciences HAFL
Jan. 2012 – July 2018	Research and teaching associate in Biology, Dr. R. Debernardi, Bern University of Applied Sciences HAFL, CH-3052 Zollikofen
Nov. 2010 – Dec. 2011	Teaching assistant in Biology, Dr. R. Debernardi, Bern University of Applied Sciences HAFL

Sept. – Nov. 2010	Research assistant at the division of Plant Ecology, Prof. Dr. M. Fischer, University of Bern
May – Oct. 2009	Internship at WWF Bern
April – May 2009	Research assistant at the division of Conservation Biology, Prof. Dr. R. Arlettaz, Conservation Biology, University of Bern
2010 – 2014	Project leader SMARAGD at the WWF Bern
2009 – today	Excursion leader for Pro Natura, Nature reserve Auried
2008 – 2016	Board and Committee WWF Bern
2007 – 2009	Research assistant at the division of Plant Ecology, Prof. Dr. M. Fischer, University of Bern (temporary staff)

Further education

16. – 19.5.2017	Research Exchange, Prof. Dr. A. Balmford, Department of Zoology, Cambridge University
08. – 12.5.2017	Statistics course: Introduction to Regression Models with Spatial and Temporal Correlation, Highland Statistics, Genova University
13.10. – 06.11.18	Research Exchange, Prof. Dr. H. Smith, Department of Biology, Lund University
Aug. 2013 – Feb. 2018	CUSO Doctoral Program in Ecology and Evolution, Neuchâtel
Oct. 2012 – Aug. 2013	CAS Hochschuldidaktik und E-Learning, BFH Bern
Jan. 2011 – Juny 2012	Field ornithology course, Birdlife Aargau
Nov. 2009 – Sept. 2010	Traveling in South and Central America, training as a dive master in the Dominican Republic
04.12.2008	Course: Heckenpflege, Technik Aufwertung Wirkung, Ökobüro Jaques Studer, Freiburg
12.06.2007	Course: Identifikation mit der Landschaft, Sanu, Bern

Teaching experience

Since 2010 teaching in German and French at the Bern University of Applied Sciences (level of employment 50 %): School of Agricultural, Forest and Food Sciences (HAFL) in the following courses:

- Biology (BUUx020)
- Plant biology (BUUb026 / BLFf014)
- Ecology (BUUb014 / BUUb046)
- Ecological excursions (BUUx052)

- Aquatic ecology (BLAx272)
- Land Use and Biodiversity (MLST7 / BUUk054)
- Supervision of Bsc and Msc thesis

Peer-reviewed publications

In progress

Zingg, S., Ritschard, E., Arlettaz, R., Humbert, J.-Y. Increasing the area and quality of land under agri-environment schemes promotes bird and butterfly biodiversity at landscape scale. *Submitted to Biological Conservation*.

Zingg, S., Grenz, J., Humbert, J.-Y. Landscape-scale effects of land use intensity on birds and butterflies. *Resubmitted to Agriculture, Ecosystem and Environment*.

Published

2018 **Zingg, S**., Dolle, P., Voordouw, M.J., Kern, M. (2018) The negative effect of wood ant presence on tick abundance. Parasites & Vectors. doi.org/10.1186/s13071-018-2712-0

2016 Pe'er, G., Zinngrebe, Y., Hauck, J., Schindler, S., Dittrich, A., **Zingg, S**., Tscharntke, T., Oppermann, R., Sutcliffe, L. M.E., Sirami, C., Schmidt, J., Hoyer, C., Schleyer, C. and Lakner, S. (2016), Adding Some Green to the Greening: Improving the EU's Ecological Focus Areas for Biodiversity and Farmers. *Conservation Letters*. doi:10.1111/conl.12333

2010 **Zingg, S.**, Arlettaz, R. & Schaub, M. (2010) Nestbox design influences territory occupancy and reproduction in a declining, secondary cavity-breeding bird. *Ardea*, 98, 67-75.

Contributions at international conferences

2018 Talk: Landscape-scale effects of agricultural productivity on birds and butterflies
Agricultural productivity and biodiversity. Students conference on conservation biology, Cambridge UK

2016 Poster: Integrating biodiversity conservation in temperate agricultural landscapes. Eco Summit 2016, Montpellier FR

2015 Talk: Agri-environment schemes in agricultural landscapes: the importance of area, quality and connectivity for birds and butterflies. ICCB-ECCB 2015, Montpellier FR