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Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article



Additive effects of two agri-environmental schemes on plant diversity but not on productivity indicators in permanent grasslands in Switzerland

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ARTICLE INFO

Handling Editor: Lixiao Zhang

Keywords: Agri-environmental measure Biodiversity conservation Ecological compensation area Ecological focus area Greening Organic farming

ABSTRACT

Different agri-environmental schemes (AES), such as ecological focus areas and organic farming, have been suggested to reduce the impact of intensive agriculture on the environment and to conserve or even restore farmland biodiversity. However, the effectiveness of such schemes, their ability to actually support biodiversity and associated trade-offs with agricultural production are still debated. We analysed a large dataset from the biodiversity monitoring in the Swiss agricultural landscape to assess the effects of two different grassland AES, i. e., *extensively managed ecological focus areas* (EFAs versus non-EFAs) and *organic farming* (versus conventional), on plant diversity, plant community composition and productivity indicators, i.e., weed abundance, forage value and nutrient availability. We also considered environmental factors, i.e., topography and soil conditions, which potentially modulate AES effects on biodiversity. We used in total 1170 plots in permanent grasslands, managed as meadows or pastures.

Both AES had significant positive effects on plant diversity. However, EFAs increased plant richness considerably stronger (+6.6 species) than organic farming (+1.8 species). Effects of the two schemes were additive with organic EFA grasslands exhibiting highest plant diversity. Differences in topography partly explained AES effects on diversity as both AES were associated with differences in elevation and slope. Thus, future assessments of the effectiveness of AES need to consider the non-random placement of AES across heterogeneous landscapes. EFA grasslands revealed a considerably reduced agricultural productivity as shown by low forage values and low nutrient availability. Yet, the abundance of agricultural weeds, i.e., agriculturally undesired plant species, was lower in EFA compared to non-EFA grasslands. Productivity indicators were only weakly affected by organic farming and other than for plant diversity, productivity did not differ between organic and conventional EFA grasslands.

The positive additive diversity effects of EFAs and organic grassland farming underline the potential of both AES to contribute to biodiversity conservation in agricultural landscapes, though to a different extent. Comparing the effects of the two AES revealed that the lower the reduction in agricultural productivity associated with an AES, the smaller the gains in plant diversity, highlighting the inevitable trade-off between productivity and plant diversity in semi-natural grasslands.

1. Introduction

Biodiversity within agricultural landscapes is steadily decreasing, highlighting the need to counteract this ecological degradation with effective agri-environmental policies (Pe'er et al., 2022; Tscharntke et al., 2005). Permanent grassland is a potentially highly multifunctional

and biodiverse ecosystem, but both aspects strongly depend on management intensity (Allan et al., 2014; Schils et al., 2022). Decades of agricultural intensification, conversion and abandonment of grasslands have thus set a focus to the protection and restoration of species-rich grasslands managed at low intensity (Dengler et al., 2014; Isselstein et al., 2005). In many countries, agri-environmental schemes and similar

https://doi.org/10.1016/j.jenvman.2023.119416

Received 8 August 2023; Received in revised form 18 October 2023; Accepted 18 October 2023 Available online 6 November 2023 0301-4797/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

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policy tools have been designed to conserve and enhance biodiversity and gain further positive environmental outcomes within agricultural landscapes. Agri-environmental schemes (AES) can be mandatory to gain eligibility to agricultural subsidies, such as within the CAP of the EU and for the proof of ecological performance in Switzerland, but can also be voluntary such as organic farming (DZV, 2023). Yet, the ecological effectiveness of AES is still debated, and insight in the performance of AES at the landscape scale is urgently needed (Meier et al., 2022; Pe'er et al., 2022).

Grassland AES usually restrict management intensity, especially fertilisation but also other biodiversity-damaging practices such as early harvest dates. Besides, AES often demand a minimum level of land use to inhibit succession (Isselstein et al., 2005; Pornaro et al., 2013). Due to the management restrictions in place, farmers have to accept a lower agricultural productivity such as lower yield quantity and quality, lower soil fertility, and/or an agriculturally non-optimal plant community composition of AES grasslands (Hodgson et al., 2005; Mayer et al., 2008). However, different types of AES exist, with different individual objectives and subsequently different impacts on field and farm management (dos Santos et al., 2015; Wrbka et al., 2008). Yet, combined effects of different AES have rarely been studied, restricting our understanding of how AES impact landscape-scale biodiversity. This limits our potential to optimise these important agricultural policy tools.

In this work, we focus on two different AES (Box 1), one with "strict" regulations, i.e., ecological focus areas (EFAs) of the type extensive grassland management, designed to sustain and create extensive grasslands by a complete ban of fertilisation along other management restrictions (Knop et al., 2006), and a second AES with rather "soft" regulations concerning grassland management, i.e., organic farming (Klaus et al., 2013; Mayer et al., 2008). Although organic farming is a production system and not specifically focused on maximising biodiversity benefits, studies have shown organic farmland to be considerably species-richer than conventional farmland (e.g., Carrié et al., 2022; Mayer et al., 2008). In Switzerland, as in many other places, organic grassland farming cannot use synthetic fertilisers nor pesticides and the maximum use of organic fertilisers per hectare is slightly lower than for non-organic, i.e., conventional agriculture (Box 1; Bio Suisse, 2020). Yet, as national organic farming regulations also prescribe ruminant feed to be organically certified and to originate from Switzerland, with a maximum of 5% of animal dry matter intake being concentrates (Box 1), the quantity and quality of farmyard manures on organic farms is likely significantly lower than for conventional grassland farming, which can have significant effects on farmland biodiversity (Bettin et al., 2023). Similar as for ecological focus areas, Swiss farmers receive per-hectare support payments for organically farmed grassland (DZV, 2023). Previous studies found positive effects of EFAs and similar schemes on different grassland taxa (e.g., Kampmann et al., 2012; Knop et al., 2006), while positive effects of organic farming on grassland biodiversity are still unclear and debated. While Mayer et al. (2008) found organic farming to benefit plant diversity in intensively managed grasslands, Klaus et al. (2013) observed only arthropod but not plant diversity to benefit from organic grassland farming.

Another major aspect of grassland management related to several AES is the harvest type, i.e., grazing versus mowing (Box 1). While farmers are generally free to choose one or the other way to manage their grasslands, topography can considerably restrict how a parcel is managed. For example, livestock grazing is less demanding with regard to an even (micro)topography and a moderate slope than mechanical mowing for silage (Stumpf et al., 2020). In addition, pastures and meadows show partly contrasting plant species composition, mainly due to selective grazing and un-selective mowing favouring different plant traits and species combinations (Busch et al., 2019; Peter et al., 2009). Effects of AES on grassland plant diversity do not only depend on the direct effect of restricting management intensity, but act in concert with other factors such as the local environment, the surrounding landscape setting, and land use history. For example, quick benefits of recently

reduced management intensity can be inhibited by residual nutrient concentrations within the formerly fertilised topsoil (Critchley et al., 2003; Pywell et al., 2002). Thus, to comprehensively assess AES effects on grassland biodiversity, grazing versus mowing as well as major site factors such as local topography need to be included in the analysis.

We assessed the effects of the two previously described grassland AES (i.e., extensive EFA versus intensive non-EFA, and organic versus conventional farming; Box 1) on different measures of plant diversity and agricultural productivity. The latter was estimated by several productivity indicators such as forage value, the abundance of agriculturally undesired weeds and soil nutrient availability. Therefore, we used a large country-level dataset containing 1170 vegetation records compiled by the Swiss biodiversity monitoring in the agricultural landscape. We further included site information such as on soil moisture as well as basic topographical characteristics, i.e., elevation and slope, of the respective land in the analysis. We hypothesized:

- 1) A trade-off exists between plant diversity and productivity indicators in permanent grassland.
- EFA extensive grassland management has a significant positive effect on plant diversity but a strong negative effect on productivity indicators.
- 3) Organic grassland farming results in increased plant diversity but decreased productivity indicators compared to conventional farming.
- 4) EFA extensive management and organic grassland farming do not have an additive effect on plant diversity.
- 5) The effects of both AES, EFA management and organic farming, are consistent in meadows and pastures, but related to differences in topography, i.e., elevation and slope.

2. Material and methods

2.1. Study system and field work

The study area is the Swiss agricultural landscape, of which permanent grasslands make up for approximately 58% (without alpine pastures; BLW, 2021). It encompasses the intensively used Swiss lowlands with elevations between approximately 300 to 700 m a.s.l. and the agriculturally managed areas up to 2000 m a.s.l. in the Pre-Alps and the Jura mountains. Alpine regions and their summer pastures were not included in this study.

Our dataset contains 1170 vegetation records collected within 117 1km² squares, evenly distributed across the different biogeographic and agricultural zones of Switzerland. It encompasses a large gradients of land use and abiotic conditions across the whole country. The 1-km² squares are part of Switzerland's farmland species and habitat monitoring program (http://www.allema.ch). Vegetation records were done within 10 m² circular plots selected from a 50 m \times 50 m sampling grid within the 1-km² squares. The sampling design accounted for a representative sample of the various land use (habitat) types occurring in the 1 km² squares. More than one plot might be located within large grassland parcels, which we consider justified due to the minimum distance of 50 m (or more) between two vegetation records. Plots were visited once between 2015 and 2019 to record the ground cover of all vascular plant species at the peak of flowering according to Braun--Blanquet (1964). Following the guidelines of the monitoring program (Riedel et al., 2018), vegetation records were done when conditions allowed for the identification of occurring plant species, i.e., April to August. Some unidentified species were excluded from the analysis (2.6% of all plot*species records). In total, 701 plant species were identified.

Box 1

Agri-environmental schemes (AES) and harvest types in permanent grasslands as used in this study (Table 1a) and corresponding management requirements for the resulting eight grassland types (Table 1b).

Table 1

Table 1a. Characteristics of two AES (ecological focus area = EFA; organic farming) and the harvest types found in Swiss permanent grasslands. The corresponding management options are presented opposed to each other. All eight combinations of AES and harvest types are possible (Table 1b). Table 1b. Management requirements and resulting intensity levels for the eight permanent grassland management types resulting from a full-factorial combination of the harvest types (meadow versus pasture) under the two AES shown in Table 1a. The sample size of each grassland type in this study is given in brackets.

Ecological focus area (EFA)	biodiversity cons study, the EFA ty meadows" were Switzerland. Reg utilisation per yę delayed date of f application of pe plants can be spr In 2021, extensiv latter also includ 8% of the perma	lements of agri-environ servation in agricultura ypes "extensively used included. They are the ulations specify no fer ear. Regulations furthe first mowing of meado sticides are not allowe ayed. Payments requir yely used meadows an- ling extensively used w	nmental schemes to su al landscapes in Switze pastures" and "extens e most frequent grassla triliser input but at lear r restrict management ws. Mulching and broo ed, but some specific si e a contract duration o d extensively used pas vooded pastures) made Switzerland, respectiv	pport rland. In this ively used nd EFAs in st one , e.g., a ad-scale ingle weed f eight years. tures (the e up 14% and	 or Non-EFA (intensive management) Classical grassland management for intensive forage production. Management intensity is not restricted but the general Swiss agricultural guidelines on fertilizer use and nutrient balances apply, the so-called "Proof of Ecological Performance" as described below (DZV, 2023). Farmers are free to choose an intensity level. These grasslands are usually considerably fertilised to produce high-quality forage for ruminants for meat or dairy production. or Conventional Conventional, i.e., non-organic grasslands are managed according to the "Proof of Ecological Performance" (PEP) guidelines, which is the classical farming system in Switzerland. PEP guidelines need to be followed to be eligible for receiving agricultural direct payments. Their standards are based on the concept of integrated production and require, for example, a balanced nutrient budget for phosphorus and nitrogen at the farm level. There are no direct restrictions on ruminant feeding. Upper limits for total fertiliser applications per farm apply, such as on average 162 kg available nitrogen per hectare and year across all intensive conventional grasslands (at low elevations; DZV, 2023). 					
Organic farming	organic farming a balanced nutric use of synthetic f restrictions apply animal feeding. F only contain up limits for total or 135 kg available elevations) are lu permanent grass 2023).	in Switzerland and res ent budget at farm level fertilizers and syntheti y regarding the trade of Geed for ruminants need to 5% concentrate (bas ganic fertiliser applica nitrogen per hectare a ower than in conventio	e according to the regu pective baseline regula l (Bio Suisse, 2020; DZV ic pesticides is forbidde of fertilisers among far ds to be grass-based for sed on dry matter intal tions per fertilizable far and year on average at onal systems. In 2021, nd was organically farm	lations of titions such as V, 2023). The en. Further ms and on 75% and can ke). Upper rm area (e.g., ! low 21.5% of the med (FiBL,						
Harvest type	silage. Grazing is	s possible and often pr	y or, if intensively mana acticed for the later re ivity and fertilization in	aged, also for growth. The	or Pasture Pastures are grasslands that are predominantly grazed by livestock, in Switzerland mostly by cattle (BLW, 2020). Mowing is also allowed and practiced for cleaning cuts but also for occasional silage and haymaking, feasible. Grazing intensities and schemes vary widely and include variou types such as continuous or rotational grazing.					
Туре	Meadow				Pasture					
	Non-EFA (intensive) EFA (extensive)				Non-EFA (inter	nsive)	EFA (extensive)			
	Conventional $(n = 461)$	Organic (n = 162)	Conventional (n = 167)	Organic (n = 158)	Conventional $(n = 171)$	Organic $(n = 42)$	Conventional (n = 71)	Organic (n = 38)		
Harvest methods	Mainly mowing	Mainly mowing	Mainly mowing	Mainly mowing	Mainly grazing	Mainly grazing	Mainly grazing	Mainly grazing		
First date of harvest	No restriction	No restriction	Delayed first cut	Delayed first cut Bannod	No restriction	No restriction	No restriction	No restriction Reprod		
Fertilisation	Allowed	Allowed but no synthetic fertiliser	Banned	Banned	Allowed	Allowed but no synthetic fertiliser	Banned	Banned		
Synthetic pesticides	Allowed	Banned	Single plant application upon request	Banned	Allowed	Banned	Single plant application upon request	Banned		
Allowed maximum intensity level	+++	++(+)	+	+	+++	++(+)	+	+		

2.2. Grassland types and agri-environmental schemes

From all vegetation surveys, we selected the 1170 belonging to the eight main management types of permanent grassland occurring in Switzerland outside alpine areas (Box 1). These eight types are the result of a full-factorial design of (i) ecological focus areas (EFAs) of the type *extensive grassland management* versus intensive management, (ii) organic versus conventional management, and (iii) the harvest type

meadow (predominantly mown) versus *pasture* (predominantly grazed). The grassland types in our study comprise EFAs (extensive and unfertilised) and intensively used meadows and pastures. All extensively used grasslands belong to the Swiss AES of *ecological focus areas* (EFAs; Box 1). They must not be fertilised and can be specified as two sub-types of EFAs, i.e., extensively used meadows and extensively used pastures. These extensive grasslands are compared to their intensively managed counterparts, which can generally be fertilised (Table 1b). Note that the information on the grassland types originate from the parcel-scale agricultural statistics of Switzerland. Thus, we do not have further details on management practices such as amount of fertilizer applied, actual livestock densities and sward age. Yet, the typology used here has successfully been used by previous studies with a different or more reginal focus (Kampmann et al., 2012; Meier et al., 2022; Ravetto Enri et al., 2020). Although we lack specific information on the livestock type, most pastures will be grazed by cattle because 90% of the ruminant livestock units in 2019 in Switzerland were cattle (BLW, 2020). Yet, horses, sheep, goats and rarer livestock species such as water buffaloes also occur.

Extensively used meadows are cut at least once each year, albeit not earlier than a set date depending on agricultural zone (linked to elevation, e.g., June 15th in the lowlands). Autumn grazing of extensively used meadows is permitted from September to end of November. Extensively used pastures are also utilised at least once each year by grazing livestock. Additional feeding of grazing animals is not allowed onsite. Extensively used pastures can, and often do, contain up to 20% of unproductive land such as rocks or shrubs. Certain exclusion criteria exist for extensively used pastures: (i) more than 20% of the parcel area is dominated by productive and ecologically undesirable species such as perennial ryegrass (Lolium perenne), white clover (Trifolium repens), rough meadow-grass (Poa trivialis) or creeping buttercup (Ranunculus repens), and (ii) more than 10% of the parcel area is dominated by species indicating excessive nutrient enrichment or mismanagement such as common nettle (Urtica dioica) and broad-leaved dock (Rumex obtusifolius). No restrictions on the date or frequency of grazing are in place for extensively used pastures. Cleaning cuts are allowed.

We removed all plots for which the vegetation surveys indicated a

high prevalence of trees and shrubs (>40% cover) and also those few cases for which the grassland type was not defined in the agricultural statistics. In total, within the 117 squares, 1170 plots were retained for further statistical analyses (Supplemental Material Table S1), with 1–21 plots per square (mean 10). In the whole dataset there were more meadows (72%) than pastures, more intensively managed grasslands (72%) than EFAs (extensive), and more conventional (74%) than organic grasslands. Still, even for the least represented grassland type, i. e., organic EFA (extensive) pasture, 38 plots were included.

2.3. Plant diversity measures, species composition and indicators

From the vegetation data, two measures of plant diversity, i.e., the *number of all vascular plant species* and the *number of policy-relevant target plant species*, were calculated per 10 m² survey. Policy-relevant species comprised a list of plant species representative for the conservation and promotion of species and their habitats across the whole elevational gradient, within the framework of the agriculture-related environmental objectives of Switzerland (species list given in Supplemental Material Table S2; Walter et al., 2013). The underlying idea was to have a set of target species to inform policy-makers about trends in species and habitat diversity within the agricultural landscape. We further categorised species according to their *plant functional types* (i.e., grasses, legumes, and non-legume forbs) and calculated their cover sums per plot, as these are potentially affected by AES and related to plant diversity (Pallett et al., 2016).

Several indicators for the field-scale agricultural productivity of the grasslands were analysed. First, abundance sums were calculated for all undesired and poisonous plant species (i.e., cover sums of agricultural



Fig. 1. DCA biplot of grassland plant communities with overlay (blue arrows) of plant species richness, plant functional groups, topography and indicators values. In total, 701 plant species were included in the ordination. The widely overlapping black and red ellipses refer to the harvest type, i.e., meadow (mostly mown) or pasture (mostly grazed). Extensive = EFA = ecological focus area, nutrient supply/availability = mean Landolt indicator value for nutrients, soil moisture = mean Landolt indicator value for soil moisture, forage value = mean Briemle indicator for forage quality, weeds = agriculturally undesired plant species. Axes length in SD units and Eigenvalues of first and second axis: 5.7 and 0.44, 5.4 and 0.25, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Results of linear mixed models testing the effects of the two AES (i.e., extensive EFA versus intensive non-EFA and organic versus conventional farming), harvest type (i.e., meadow versus pasture), with and without topographical factors (i.e., slope and elevation) on plant diversity (i.e., total and policy-relevant plants), abundance of undesired plant species (i.e., cover sum of agricultural weeds), forage quality (mean Briemle indicator value), and environmental conditions (Landolt indicators for soil moisture and for nutrient availability), with survey square as random factor to account for differences in local species pools and regional climate. Two models were run per dependent variable, a reduced model only including the two grassland AES and meadow versus pasture, and a full model additionally including elevation and slope. Note that using survey square as random factor accounted for among-square but not within-square variation in elevation and slope. Thus, results only show the relevance of variation in elevation and slope within the squares. Significant factors (p < 0.05) in bold. Further note that the number of plots differs between grassland types (Table 1b).

	Reduced mod	del (n = 1049)		Full model ($n = 1047$)				
Total plant richness			R ² _{adi}	= 0.37			R ² _{adi.} =	= 0.84
No transformation	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	20.92	0.693	30.2	<0.001	10.19	1.133	9.0	<0.001
Organic	1.79	0.732	2.4	0.015	1.22	0.680	1.8	0.072
EFA	6.60	0.669	9.9	<0.001	5.75	0.625	9.2	< 0.001
Organic:EFA	0.29	1.190	0.2	0.809	0.00	1.117	0.0	0.999
Meadow (vs. pasture)	-3.08	0.555	-5.6	< 0.001	-1.02	0.543	-1.9	0.060
Elevation	-	-	-	-	0.01	0.001	7.0	<0.001
Slope		-		-	0.18	0.016	11.2	< 0.001
Policy-plant richness			R ² _{adj.}	= 0.20			R _{adj.} =	= 0.42
No transformation	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	0.87	0.061	14.3	<0.001	-0.11	0.101	-1.1	0.267
Organic	0.23	0.062	3.7	< 0.001	0.19	0.058	3.3	0.001
EFA	0.76	0.057	13.4	< 0.001	0.69	0.053	13.1	< 0.001
Organic:EFA	-0.12	0.101	$^{-1.2}$	0.227	-0.16	0.095	-1.7	0.094
Meadow (vs. pasture)	-0.20	0.047	-4.3	< 0.001	-0.03	0.046	-0.6	0.525
Elevation	-	-	-	-	0.00	0.000	7.5	< 0.001
Slope	-	-	-	-	0.01	0.001	11.1	< 0.001
Abundance undesired specie	s		R ² _{adj.}	= 0.04			R _{adi.} =	= 0.13
Transf. = log	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	2.25	0.087	25.9	<0.001	2.93	0.176	16.7	< 0.001
Organic	-0.17	0.102	-1.6	0.102	-0.12	0.101	-1.2	0.241
EFA	-0.39	0.094	-4.1	< 0.001	-0.32	0.092	-3.5	< 0.001
Organic:EFA	0.04	0.168	0.2	0.825	0.08	0.165	0.5	0.627
Meadow (vs. pasture)	0.22	0.078	2.8	0.006	0.04	0.080	0.5	0.602
Elevation	_	_	_	_	-0.00	0.000	-2.4	0.017
Slope	-	-	-	-	-0.02	0.002	-6.7	< 0.001
Forage quality indicator			P ²	= 0.13			P ²	= 0.21
No transformation	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	6.76	0.076	88.6	< 0.001	7.49	0.150	50.1	< 0.001
Organic	-0.14	0.098	-1.4	0.159	-0.08	0.095	-0.8	0.426
EFA	-0.96	0.090	-10.7	< 0.001	-0.89	0.088	-10.1	< 0.001
Organic:EFA	-0.08	0.162	-0.5	0.630	-0.03	0.157	-0.2	0.870
Meadow (vs. pasture)	0.20	0.075	2.7	0.007	0.01	0.076	0.2	0.864
Elevation	_	_	_	_	-0.00	0.000	-3.0	0.003
Slope	-	-	-	-	-0.02	0.002	-7.4	<0.001
Nutrient availability indicate	or		R ² _{adj.}	= 0.16			R _{adj.} =	= 0.33
No transformation	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	3.65	0.029	127.9	<0.001	4.02	0.048	84.2	<0.001
Organic	-0.09	0.039	-2.4	0.017	-0.06	0.035	-1.8	0.075
EFA	-0.38	0.036	-10.7	< 0.001	-0.33	0.033	-10.1	< 0.001
Organic:EFA	-0.00	0.065	-0.1	0.952	0.02	0.059	0.3	0.745
Meadow (vs. pasture)	0.15	0.030	5.1	< 0.001	0.03	0.029	1.0	0.331
Elevation	-	-	-	-	-0.00	0.000	-3.3	0.001
Slope	-	-	-	-	-0.01	0.001	-13.5	<0.001
Soil moisture indicator			R _{adi}	= 0.08			R _{adi} =	= 0.18
Transf. $= \log$	Value	SE	t-value	p-value	Value	SE	t-value	p-value
Intercept	1.13	0.006	178.7	<0.001	1.17	0.013	90.2	< 0.001
Organic	-0.02	0.009	-2.2	0.032	-0.01	0.008	-1.6	0.104
EFA	-0.05	0.008	-6.4	< 0.001	-0.04	0.008	-5.3	<0.001
Organic:EFA	0.01	0.014	0.5	0.616	0.01	0.014	0.7	0.467
Meadow (vs. pasture)	0.03	0.007	4.3	<0.010	0.01	0.007	0.9	0.395
Elevation	-	-	-	-	0.00	0.000	0.2	0.819
Elevation								

weeds) according to Swiss recommendations for grassland management (AGFF, 2008). The majority of the weed species listed are nutrient demanding and thus frequent in fertilised swards (see list of species in Supplemental Material Table S3). Second, we calculated the *forage quality value* based on the eponymous indicator according to Briemle

et al. (2002). Moreover, to inform about *soil nutrient availability* and *soil moisture*, the eponymous indicator values according to Landolt et al. (2010) were considered. All three indicator values used in this study were weighted by species abundance per plot. When the abundance sum did not match 100%, species abundances were adjusted to achieve



Fig. 2. Richness of a) all vascular plant species and b) policy-relevant plant species in response to two agri-environmental schemes, i.e., organic versus conventional and extensive (EFA) versus intensive (non-EFA) management, separately for meadows (predominantly mown) and pastures (predominantly grazed). Significant differences between permanent grassland types derived from pairwise (uncorrected) Wilcoxon tests. The horizontal line indicates the median. Note that number of plots differ between grassland types (Table 1b). Significant levels: *** = p < 0.001, ** = p < 0.01, * = p < 0.05, "n.s." = p > 0.05. See Table 2 for results of corresponding mixed models.

exactly 100% cover per plot. Site information was further completed with topographical information about *elevation* and *slope*. For each plot, the respective values were calculated based on a digital elevation model with 25 m \times 25 m resolution (Swisstopo, 2005).

2.4. Statistical analyses

For the analyses, the vegetation data according to the scale of Braun-Blanquet (1964) were transformed into values of percent cover (r = 0.01%, + = 0.5%, 1 = 3%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 =87.5%). To explore patterns in species composition and diversity, and to relate these to the indicators of agricultural productivity and site information, a detrended component analysis (DCA) was conducted. This was done using a presence-absence matrix and the function decorana within the package vegan 2.6-4 (Oksanen, 2017). The total inertia of the dataset was 23.1. The axis length and Eigenvalues of the first, second, and third axes were 5.7 and 0.44, 5.4 and 0.25, 2.8 and 0.18, respectively. Pearson correlations were used to assess relationships between selected variables such as plant diversity and topography. Next, to test for significant differences in plant diversity, community composition and agricultural productivity among grassland types, mixed linear regression models were run using the *lme* function of the *nlme* package (Pinheiro and Bates, 2023). An adjusted R² was derived with the rsq function from the rsq package (Zhang, 2020). To test for these differences with and without potentially covarying topographic factors, two sets of models were run. The first, reduced model tested for a significance of only EFA, organic farming and the harvest type (i.e., lme(y \sim organic*EFA + harvest type, random = ~ 1 |square_ID). The second, full model then also included elevation and slope (i.e., lme(y ~ organic*EFA + harvest type + elevation + slope, random = ~ 1 |square_ID), which potentially covary with the factors included in the first model. Information on this covariance can inform about a spatial targeting of farmers placing AES grasslands and harvest types within the landscape. To keep models simple and focus on the main factors, the only interaction included in the models was that of the two AES, i.e., EFA and organic. All models further included the survey square, the primary design unit of the sampling scheme, as random factor to account for inter-regional differences such as in climate and species pool. Thus, this random factor also accounted for among-square but not within-square variation in elevation and slope. To reveal potential differences in AES effects in predominately grazed (pastures) versus mown grasslands (meadows), violin plots, trimmed to the actual data, with pairwise (uncorrected) Wilcoxon tests were created with ggplot2 (Wickham, 2016). Finally, we assessed direct and indirect effects of the two AES, topography (slope, elevation), soil moisture (mean Landolt F indicator), and nutrient availability (mean Landolt N indicator) on total plant richness via structural equation modelling (SEM) using the *lavaan* package (Rosseel, 2012). Note that for the SEM, we did not account for the monitoring design, i.e., plots being nested in the 1-km² survey squares, so that the effects of slope and elevation become more apparent in the SEM compared to the mixed linear regression with square as random factor. All statistical analyses were preformed using R (version 4.2.2; R Core Team, 2022).

3. Results

3.1. Gradients in plant diversity and species composition

Total plant species richness in the studied 1170 grasslands ranged from 2 to 67, with on average 24.2 \pm 10.25 species per 10 m^2 plot. The number of policy-relevant plant species ranged from 0 to 30, with a mean of 3.9 \pm 5 species. Total plant species richness and the richness of policy-relevant plants were closely correlated ($r_{Pearson}=0.83,\ p<0.001$).

The first DCA axis mainly depicts a gradient of increasing elevation and, weaker, also decreasing soil fertility of the plots (Fig. 1). Along this first axis, a strong trade-off between plant species richness on the one hand and agricultural productivity, e.g., forage value, nutrient availability and grass cover, can be found. Increasing plant species richness along gradients of elevation and slope highlights the relevance to include these two environmental factors as covariates in the further analyses (see also Supplemental Material Fig. S1). The second axis represents mainly a gradient in increasing soil moisture. Most of the plots clumped on the left-hand side of the biplot, showing floristically rather homogeneous grasslands with high forage value and a high prevalence of grasses at high nutrient availability. On the opposite side of the plot, species-rich grasslands associated with low nutrient availability spread out, indicating grasslands with a higher compositional



Fig. 3. Indicators for agricultural productivity and site environmental conditions of permanent grassland in response to two agri-environmental schemes separated into meadows and pastures. Agricultural productivity was assessed by a) forage quality (mean Briemle indicator for forage quality value), and b) agriculturally undesired species (listed in Supplemental Material Table S3). Site conditions assessed by c) nutrient availability (mean Landolt indicator for nutrients), and d) soil moisture (mean Landolt indicator for soil moisture). AES are organic (Org.) versus conventional farming (Conv.), and extensive (= ecological focus area, EFA) versus intensive (non-EFA) management. Significant differences between grassland types derived from pairwise (uncorrected) Wilcoxon tests. The horizontal line indicates the median. Note that the number of plots differs between grassland types (Table 1b). Significance levels: *** = p < 0.001, ** = p < 0.01, * = p < 0.05, "n.s." = p > 0.05. See Table 2 for results of corresponding mixed models.

heterogeneity.

Pastures had higher total as well as policy-plant richness than meadows, but this effect decreased strongly when topographical information was included in analysis, highlighting the interrelatedness of harvest type and topography (Table 2). Pastures and meadows tended to overlap in the DCA biplot, indicating basically similar species composition along the two main gradients (Fig. 1).

3.2. Effects of agri-environmental schemes on plant diversity and functional types

Total plant species richness was significantly increased by the two AES and also by their combination (Fig. 2), even when (within-square) variation in elevation and slope was included in the models (Table 2). However, EFA (extensive) management had a considerably stronger effect on total plant richness (+6.6 species) than organic farming (+1.8 species), with the latter being only marginally significant in the model including topography. As there was no significant interaction of the two AES (Table 2), organic farming led to increased plant diversity in EFA (extensive) and non-EFA (intensive) grasslands. In meadows, total plant richness showed significant pairwise differences between all grassland types (Fig. 2a), while pairwise differences between intensive organic versus intensive conventional pastures and between intensive organic versus EFA (extensive) conventional pastures were not significant.

Similarly, the number of policy-relevant plant species was significantly higher for the two AES and their combination (Table 2). When including slope and elevation in the analysis, the main effects of the AES again remained highly significant. All pairwise comparisons also yielded significant results, with the exception of a non-significant pairwise difference between intensive organic versus EFA (extensive) conventional pastures (Fig. 2b). The two AES affected the cover of the plant functional types differently (Supplemental Material Table S4). Grass cover decreased slightly under organic farming and also, in the full model only, under EFA management. Legume cover was significantly increased by organic farming but decreased by EFA management. Cover of nonlegume forbs was hardly affected by organic farming but increased by EFA management (Supplemental Material Table S4).



Fig. 4. Structural equation model revealing direct and indirect effects of topography, soil moisture and agri-environmental schemes (extensive EFA versus intensive non-EFA and organic versus conventional farming) via changes in nutrient availability on total vascular plant richness of 1170 permanent grasslands. Arrow thickness according to standardized path coefficients. Dotted blue lines indicate decreasing, solid green lines increasing effects. Extensive = EFA = ecological focus area, soil moisture = mean Landolt indicator for soil moisture, nutrient availability = mean Landolt indicator for nutrients. Three non-significant paths have been removed from the figure to ease readability: elevation to soil moisture (p > 0.1), slope to organic (p > 0.1), and organic to nutrient availability (p > 0.05). All studied grasslands were included, both meadows and pastures. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. Effects of agri-environmental schemes on indicators for agricultural productivity

EFA extensive management had a significant negative effect on forage quality but at the same time also on the cover of agricultural weeds, which was true for both meadows and pastures (Fig. 3a and b; Table 2). On the contrary, organic farming had no overall effect on forage quality and agricultural weeds in the regressions (Table 2). Yet, according to the pairwise tests, intensive organic meadows showed a tendency to lower forage quality compared to intensive conventional meadows, while intensive organic meadows and pastures revealed lower weed cover compared to their conventional counterparts (Fig. 3b). Note that in this study, agricultural weeds do not only include poisonous weeds and thistles but also low-performing species typical for strongly or even overly fertilised swards (Supplemental Material Table S3).

Nutrient availability and soil moisture were both significantly lower in EFA (extensive) grasslands than in intensive ones (Fig. 3c and d; Table 2). Weak but significant effects of organic farming on nutrient availability and soil moisture were found only in the model without slope and elevation, indicating that differences in topography were likely responsible for changes in soil conditions under organic farming. The indication of considerably drier soils of EFA grasslands fits well to their position on steeper slopes (Fig. 4).

3.4. Joint analysis of AES and site effects on plant diversity

Because the effects of the two AES on plant diversity were generally highly similar for meadows and pastures, we ran only one SEM over all plots to identify direct and indirect effects of potential drivers of total plant species richness, yielding an R² of 0.43 (Fig. 4). Except organic farming, which affected total plant richness only directly, all drivers included in the model had significant direct and indirect effects on plant species richness. Thus, the SEM revealed close connections among all factors included in its vertical structure. Specifically, the model showed a non-random placement of AES in the landscape by significant effects of slope and elevation on both AES. In the case of slope, this topographical effect on EFA and organic grasslands acted (partly) via soil moisture, with slope decreasing soil moisture that was in turn negatively related to registering land for EFA (extensive) management and organic farming. In short, grasslands of both AES were placed on drier terrain with steeper slopes. In line with the linear regressions (Table 2), EFA (extensive) management had a considerably stronger effect on total plant richness than organic farming, because besides a positive direct effect, EFA management also increased total plant richness via decreasing nutrient availability. Contrary to extensive EFA grasslands, organic farming was not significantly linked to nutrient availability in this model (p > 0.05, Fig. 4).

4. Discussion

Using 1170 plots in permanent grasslands across the Swiss agricultural landscape, we identified a strong trade-off between plant diversity on the one hand and forage value and nutrient availability on the other hand, confirming our first hypothesis. This trade-off was essentially related to the diversity-promoting effects of the two agri-environmental schemes (AES), i.e., ecological focus areas (EFAs) with extensive management and organic farming. Such a trade-off was previously found for AES in arable ecosystems (Gong et al., 2022). The positive effects of the two AES on plant diversity confirmed our second and third hypothesis, but they differed considerably in strength, with smaller increases in diversity but smaller decreases in forage value in organic compared to EFA grasslands. Contrary to our fourth hypothesis, the effects of both AES on plant diversity were additive, with organic EFA grasslands exhibiting highest diversity. AES effects were widely consistent for meadows and pastures, confirming our fifth hypothesis. Yet, meadows showed a slightly stronger response to AES.

AES effects were clearly interlinked with differences in elevation and slope, highlighting the non-random placement of AES at the landscape. Thus, future assessments of AES effects on biodiversity need to consider the non-random placement of AES by farmers across heterogeneous landscapes. Although our models for plant diversity yielded high proportions of explained variance, further factors, which have not been studied, will be responsible for the remaining unexplained variance. These are, for example, variability in management within grassland types such as in fertilisation intensity, sward age, duration of AES management and potential ecological restoration measures such as the use of species-rich seed mixtures (Freitag et al., 2021; Isselstein et al., 2005; Klaus et al., 2011).

4.1. Effects of extensive ecological focus areas

The EFA (extensive) grasslands had on average 6.6 more species per 10 m² than intensive non-EFA grasslands, which represents an increase of +32% in total plant richness. This positive effect on plant diversity is in line with previous studies assessing former versions of this scheme (Kampmann et al., 2012; Knop et al., 2006) and the current scheme within a regionally restricted context (Meier et al., 2023; Ravetto Enri et al., 2020). Requirements of extensive EFAs, designed to mimic the historic way of grassland management without fertilisation and, for meadows, with a delayed first cut, were shown to also benefit invertebrates (Humbert et al., 2012; Buri et al., 2016). For plant diversity, the ban of fertilisation, the interconnected decrease in overall management intensity and nutrient availability, and the ban of broad-scale application of pesticides were certainly among the most beneficial aspects of EFA management (Knop et al., 2006; Klimek et al., 2008; Socher et al., 2013). On the other hand, the low management intensity resulted in considerably reduced productivity indicators as shown by low forage values, low soil fertility (i.e., nutrient availability), and related changes in plant community composition. This reduction is in line with previous studies on extensive grassland management (Klaus et al., 2011; Pallett et al., 2016) and can be seen as a justification for linking this type of AES to agricultural support payments (Isselstein et al., 2005). Comparable strong EFA effects were found for both harvest types, meadows and pastures, indicating that EFAs work well for biodiversity conservation in mown and in grazed grasslands across the Swiss agricultural landscape. Interestingly, EFA grasslands exhibited a considerably lower abundance of agriculturally undesired "weed" plants when compared to intensive stands.

Due to their wide range in species richness, reaching from less than 10 to more than 60 plant species per 10 m², EFA grasslands were likely a mixture of old, ecologically highly valuable and species-rich grasslands and species-poor, recently extensified grasslands. Low nutrient availability and an outstandingly high richness of more than 50 species per 10 m² indicate very old semi-natural grasslands that were most likely never intensified (Fagan et al., 2008; Gustavsson et al., 2007). In addition, some EFA grasslands might have become species-rich only after the ban of fertilisation, potentially leading to a significant increase in plant diversity in formerly intensively managed stands (Pallett et al., 2016). However, there were also species-poor grasslands among extensive EFA grasslands. These stands might either be recently converted from intensive management or suffer from issues such as a depleted local species pool (Concepcion et al., 2012; Knop et al., 2008), thick layers of litter due to underutilisation or residual soil nutrient loads, which all have lasting detrimental effects on plant diversity (Clark and Tilman, 2010; Fagan et al., 2008).

We found positive direct effects of slope and elevation on plant diversity, which is in line with previous studies (Kampmann et al., 2012; Klimek et al., 2008; Socher et al., 2013). As these two aspects of topography were also related to preferentially registering land for extensive EFAs, some of these particularly sloping EFA grasslands have likely never been intensified before. However, compared to intensive non-EFA grasslands, EFAs were also found to be placed at slightly lower mean elevation, which might result from the obligation to have 7% of the farmland registered as any kind of EFA to be eligible for direct payments in Switzerland. While the steeper slope position indicated farmers preferentially registered land less suitable for intensive farming to become extensive EFA, there are actually no regulations on the spatial positioning of EFA grasslands, except that they cannot be further away from the farm than 15 km (DZV, 2023). This situation has likely led to a certain proportion of ecologically less valuable, species-poor EFA grasslands in areas highly suitable for intensive agriculture.

4.2. Effects of organic grassland farming

Organic farming significantly though weakly increased plant

diversity in both meadows and pastures. Organic grasslands had on average 1.8 more species than conventional grasslands, depicting an increase of +9% in total plant richness. This positive response of plant diversity to organic farming is not self-evident, because organic grassland farming guidelines only softly restrict grassland management (Box 1; Bio Suisse, 2020). While synthetic pesticides and fertilisers are prohibited, organic farming still allows for intensive organic fertilisation and other practices detrimental to plant diversity such as sward renewal. This widely explains the considerably smaller effect of organic farming on plant diversity and indicators of agricultural productivity compared to EFA regulations. While the positive effect of organic grassland farming on plant diversity contradicts Schneider et al. (2014) regarding their results from intensive grasslands in Norway, Switzerland and the UK, it is in line with findings from Germany (Mayer et al., 2008), the UK (Pallett et al., 2016) and the Netherlands (van Dobben et al., 2019), and also fits the (partly insignificant) trends observed in Bettin et al. (2023), Carrié et al. (2022) and Klaus et al. (2013).

The mechanisms behind the increase in plant diversity as observed here are not completely clear. Klaus et al. (2013) and van Dobben et al. (2019) found considerably lower fertilisation intensity in organic compared to conventional grasslands, which could also apply to the grasslands in this study and would certainly benefit plant diversity. Yet, details of management practices and intensities are unknown for our dataset. However, due to restrictions on ruminant feeding and feed purchase in Swiss organic farming (Bio Suisse, 2020), there is highly likely a lower quantity and/or quality of fertilisers available on organic than on conventional farms, which relates to the link between low concentrate feeding and higher plant diversity on cattle farms observed in Germany (Bettin et al., 2023). In addition, the ban of synthetic herbicides might have increased plant diversity (only) due to higher numbers of weed species. This is, however, contradicted by the fact that undesired species cover was not higher but rather lower in organic than in conventional grasslands, most likely because the application of herbicides is generally rare in all types of grassland (Schneider et al., 2014). Moreover, organic farming considerably increased the number of policy-relevant plant species. Thus, the effect of organic farming might be small, but appeared to be relevant since it encompassed ecologically valuable and not "just some" species.

Similar to EFA extensive management, organic grassland farming was found to be related to topographical factors, especially to higher elevations. Thus, landscape composition and related factors might also be responsible for the positive effect on plant diversity, particularly since the effect of organic was additive to the effect of extensive EFA management (see 4.3). Similarly, van Dobben et al. (2019) found the landscape context to be important for difference in plant diversity in organic versus conventional grasslands. In that study, organic grasslands were more frequent in locations of high soil moisture, which restricts management intensity and supports plant diversity. Yet, future research still needs to further clarify the underlying mechanisms and evaluate the set of plant species benefiting from organic grassland farming.

Forage quality was not generally lower under organic farming but appeared to be slightly reduced in intensive organic meadows compared to their conventional counterparts. This might be associated with somewhat lower grass but higher legume cover in organic grasslands. Together with the finding of rather small reductions in yields in organic versus conventional grasslands, spanning a range from 0 to 20% (Klaus et al., 2013, and references therein), our results indicate that organic grassland farming can contribute to some extent to the conservation of plant species in both intensive and extensive grasslands, while only weakly decreasing field-scale productivity.

As in Switzerland organic farming is a whole-farm AES (Bio Suisse, 2020), there might be further biodiversity-related effects of this farming system beyond the field scale. For example, Mack et al. (2020) found Swiss organic farms to have a higher share of land managed as EFA compared to conventional farms. However, studying farm- and landscape-scale effects of organic farming requires to comprehensively

consider the spatial placement of this AES in the landscape (Meier et al., 2022), as less productive sites at higher and steeper locations and at places of high soil moisture were preferentially converted to organic farming (this study and van Dobben et al., 2019).

4.3. Combined effect of the two schemes

Against our expectations, the effects of EFA and organic farming on plant diversity were additive, meaning EFAs on organic farms were more diverse than EFAs on conventional farms. This result contradicts findings of Carrié et al. (2022), who did not find differences in plant diversity in semi-natural grasslands in Sweden, and cannot be attributed to recent grassland management, because regulations of extensive EFA management overrule organic farming guidelines in almost every aspect, except the possibility of single-plant herbicide treatments in conventional EFA grasslands. Thus, organic EFAs will benefit from either land use history, in that organic EFAs were potentially older and more continuously managed at low intensity than their conventional counterparts, or from the spatial setting, with organic EFAs being located in landscapes with higher connectivity and a larger species pool. Both aspects have been shown to benefit plant diversity (Gaujour et al., 2012; Gustavsson et al., 2007) and both are likely to play a role in explaining the observed effects as well as deviations from previous findings. Yet, neither nutrient availability nor soil moisture or forage value differed considerably between organic and conventional EFA grasslands. Generally, this finding highlights the need to not only assess assumed effects due to direct AES regulations but also the effects of their realisation in the landscape, to comprehensively understand AES effects on biodiversity. In addition, there might be further explanations for the additive effect of the two AES, such as organic farmers being particularly aware of issues of biodiversity conservation and thus being more open to ecological measures (Gabel et al., 2018, and references therein). Thus, we cannot exclude an effect of organic farmers being more committed than conventional farmers to, for example, actively promoting plant diversity such as via measures of ecological grassland restoration (Freitag et al., 2021; Pywell et al., 2002).

5. Conclusions

The positive effects of EFA extensive management and organic farming on grassland plant diversity underline the potential of both AES to contribute to biodiversity conservation within agricultural landscapes. Comparing the effects of the two AES revealed that the lower the reduction in agricultural productivity, the smaller the gains in plant diversity, highlighting the unavoidable trade-off in productivity versus plant diversity in agriculturally managed permanent grasslands. Yet, positive effects of AES on biodiversity conservation could be used as a sales argument for respective products from organic and extensive grassland farming to further support biodiversity-friendly dairy and meat production.

Authors contributions

VHK, AJ and GL conceived the idea. EK manages the ALL-EMA project. AJ, FR and VHK analysed the data with input from GL. All authors contributed to discussing the results and to revising the manuscript, which was written by VHK.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: no competing interests.

Data availability

Data will be made available on request.

Acknowledgements

VKH acknowledges funding by the Agroscope research program *Indicate* and by the Mercator Foundation Switzerland. This research was conducted in cooperation with the ALL-EMA monitoring project, funded by the Federal Office for the Environment and the Federal Office for Agriculture. We further thank the ALL-EMA field teams for gathering vegetation data across Switzerland, and we thank Olivier Huguenin-Elie for sharing his expertise in grassland fertilisation and management types in Switzerland. Finally, we also thank five anonymous reviewers for providing comments on a previous version of this publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.119416.

References

- AGFF, 2008. Merkblatt 4 Regulierung von Unkräutern und Ungräsern in Naturwiesen. Zürich.
- Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., et al., 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proc. Natl. Acad. Sci. USA 111, 308–313.
- Bettin, K., Komainda, M., Tonn, B., Isselstein, J., 2023. Relationship between concentrate feeding strategy and grassland phytodiversity on dairy farms. Agric. Ecosyst. Environ. 344, 108293.
- Bio Suisse, 2020. Richtlinien für die Erzeugung, Verarbeitung und den Handel von Knospe-Produkten. Bio Suisse, Basel
- BLW, 2020. 2020 Agrarbericht. https://2020.agrarbericht.ch/de/betrieb/strukturen/ti ere. (Accessed 19 September 2023).
- BLW, 2021. Agrarbericht 2022. Available at: https://www.agrarbericht.ch. (Accessed 16 May 2022).
- Braun-Blanquet, J., 1964. Pflanzenphysiologie. 3. Springer.
- Briemle, G., Nitsche, S., Nitsche, L., 2002. Nutzungswertzahlen f
 ür Gef
 ä
 ßpflanzen des Gr
 ünlandes. Schr. Veg. 38, 203–225.
- Buri, P., Humbert, J.Y., Stańska, M., Hajdamowicz, I., Tran, E., Entling, M.H., Arlettaz, R., 2016. Delayed mowing promotes planthoppers, leafhoppers and spiders in extensively managed meadows. Insect Conserv. Diver. 9, 536–545.
- Busch, V., Klaus, V.H., Schäfer, D., Prati, D., Boch, S., Müller, J., et al., 2019. Will I stay or will I go? Plant species-specific response and tolerance to high land-use intensity in temperate grassland ecosystems. J. Veg. Sci. 30, 674–686.
- Carrié, R., Ekroos, J., Smith, H.G., 2022. Turnover and nestedness drive plant diversity benefits of organic farming from local to landscape scales. Ecol. Appl. 32, e2576.
- Clark, C.M., Tilman, D., 2010. Recovery of plant diversity following N cessation: effects of recruitment, litter, and elevated N cycling. Ecology 91, 3620–3630.
- Concepcion, E.D., Diaz, M., Kleijn, D., Baldi, A., Batary, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695–705.
- Critchley, C.N.R., Burke, M.J.W., Stevens, D.P., 2003. Conservation of lowland seminatural grasslands in the UK: a review of botanical monitoring results from agrienvironment schemes. Biol. Conserv. 115, 263–278.
- Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agric. Ecosyst. Environ. 182, 1–14.
- dos Santos, R.F., Antunes, P., Ring, I., Clemente, P., 2015. Engaging local private and public actors in biodiversity conservation: the role of agri-environmental schemes and ecological fiscal transfers. Environ. Policy Gov. 25, 83–96.
- DZV, 2023. Verordnung über die Direktzahlungen an die Landwirtschaft (Direktzahlungsverordnung, DZV) vom 23. Oktober 2013 (Stand am 1 Januar 2023) [Swiss council regulation no. 910.13: ordinance on Direct Payments of 23 October 2013 (as of 1 January 2021)]. In: Swiss Federal Office for Agriculture. Berne, Switzerland.
- Fagan, K.C., Pywell, R.F., Bullock, J.M., Marrs, R.H., 2008. Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. J. Appl. Ecol. 45, 1293–1303.
- FiBL, 2023. Zahlen zum Schweizer Biolandbau interaktiv aufbereitet. https://www.bioa ktuell.ch/grundlagen/zahlen-und-fakten-biolandbau/infografiken-biolandbau-sch weiz. (Accessed 20 September 2023).
- Freitag, M., Klaus, V.H., Bolliger, R., Hamer, U., Kleinebecker, T., Prati, D., et al., 2021. Restoration of plant diversity in permanent grassland by seeding: assessing the limiting factors along land-use gradients. J. Appl. Ecol. 58, 1681–1692.
- Gabel, V.M., Home, R., Stolze, M., Pfiffner, L., Birrer, S., Köpke, U., 2018. Motivations for Swiss lowland farmers to conserve biodiversity: identifying factors to predict proportions of implemented ecological compensation areas. J. Rural Stud. 62, 68–76.

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Gaujour, E., Amiaud, B., Mignolet, C., Plantureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands - a review. Agron. Sustain. Dev. 32, 133-160.

Gong, S., Hodgson, J.A., Tscharntke, T., Liu, Y., van der Werf, W., Batáry, P., et al., 2022. Biodiversity and yield trade-offs for organic farming. Ecol. Lett. 25, 1699-1710.

Gustavsson, E., Lennartsson, T., Emanuelsson, M., 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biol. Consverv. 138, 47-59.

Hodgson, J.G., Montserrat-Marti, G., Tallowin, J., Thompson, K., Díaz, S., Cabido, M., et al., 2005. How much will it cost to save grassland diversity? Biol. Consverv. 122, 263-273.

Humbert, J.Y., Pellet, J., Buri, P., Arlettaz, R., 2012. Does delaying the first mowing date benefit biodiversity in meadowland? Environ. Evid. 1, 1-13.

Isselstein, J., Jeangros, B., Pavlu, V., 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe-a review. Agron. Res. 3, 139-151. Kampmann, D., Lüscher, A., Konold, W., Herzog, F., 2012. Agri-environment scheme

protects diversity of mountain grassland species. Land Use Pol. 29, 569-576. Klaus, V.H., Kleinebecker, T., Prati, D., Gossner, M.M., Alt, F., Boch, S., et al., 2013. Does organic grassland farming benefit plant and arthropod diversity at the expense of yield and soil fertility? Agric. Ecosyst. Environ. 177, 1-9.

Klaus, V.H., Kleinebecker, T., Hölzel, N., Blüthgen, N., Boch, S., Müller, J., et al., 2011. Nutrient concentrations and fibre contents of plant community biomass reflect species richness patterns along a broad range of land-use intensities among agricultural grasslands. Perspect. Plant Ecol. Evol. Systemat. 13, 287–295.

Klimek, S., Marini, L., Hofmann, M., Isselstein, J., 2008. Additive partitioning of plant diversity with respect to grassland management regime, fertilisation and abiotic factors. Basic Appl. Ecol. 9, 626-634.

Knop, E.V.A., Kleijn, D., Herzog, F., Schmid, B., 2006. Effectiveness of the Swiss agrienvironment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120–127.

Knop, E., Schmid, B., Herzog, F., 2008. Impact of regional species pool on grasshopper restoration in hay meadows. Rest. Ecol. 16, 34-38.

Landolt, E., Bäumler, B., Ehrhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Wohlgemuth, T., 2010. Flora indicativa: Okologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt.

Mack, G., Ritzel, C., Jan, P., 2020. Determinants for the implementation of action-, result-and multi-actor-oriented agri-environment schemes in Switzerland. Ecol. Econ. 176, 106715.

Mayer, F., Heinz, S., Kuhn, G., 2008. Effects of agri-environment schemes on plant diversity in Bavarian grasslands. Community Ecol. 9, 229-236.

Meier, E.S., Lüscher, G., Knop, E., 2022. Disentangling direct and indirect drivers of farmland biodiversity at landscape scale, Ecol. Lett. 25, 2422-2434. Oksanen, J., 2017. Vegan: an Introduction to Ordination.

Pallett, D.W., Pescott, O.L., Schäfer, S.M., 2016. Changes in plant species richness and productivity in response to decreased nitrogen inputs in grassland in southern England, Ecol. Indicat, 68, 73-81.

Pe'er, G., Finn, J.A., Díaz, M., Birkenstock, M., Lakner, S., Röder, N., et al., 2022. How can the European Common Agricultural Policy help halt biodiversity loss? Recommendations by over 300 experts. Conserv. Lett. 15, e12901.

Peter, M., Gigon, A., Edwards, P.J., Lüscher, A., 2009. Changes over three decades in the floristic composition of nutrient-poor grasslands in the Swiss Alps. Biodivers. Conserv. 18, 547-567.

Pinheiro, J., Bates, D., R Core Team, 2023. Nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-162. https://CRAN.R-project.org/package=nlme.

Pornaro, C., Schneider, M.K., Macolino, S., 2013. Plant species loss due to forest succession in Alpine pastures depends on site conditions and observation scale. Biol. Conserv. 161, 213-222.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. J. Appl. Ecol. 39, 294-309.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project. org/

Ravetto Enri, S., Nucera, E., Lonati, M., Alberto, P.F., Probo, M., 2020. The Biodiversity Promotion Areas: effectiveness of agricultural direct payments on plant diversity conservation in the semi-natural grasslands of the Southern Swiss Alps. Biodivers. Conserv. 29, 4155-4172.

Riedel, S., Meier, E., Buholzer, S., Herzog, F., Indermauer, A., Lüscher, G., et al., 2018. Methodenbericht ALL-EMA Arten und Lebensräume Landwirtschaft – espèces et milieux agricoles. Agroscope Science 57, 1-31.

Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. J. Stat. Software 48, 1-36.

Schils, R.L., Bufe, C., Rhymer, C.M., Francksen, R.M., Klaus, V.H., Abdalla, M., et al., 2022. Permanent grasslands in Europe: land use change and intensification decrease their multifunctionality. Agric. Ecosyst. Environ. 330, 107891.

Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., et al., 2014. Gains to species diversity in organically farmed fields are not propagated at the farm level. Nat. Commun. 5, 4151.

Socher, S.A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., et al., 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic Appl. Ecol. 14, 126-136.

Stumpf, F., Schneider, M.K., Keller, A., Mayr, A., Rentschler, T., Meuli, R.G., Liebisch, F., 2020. Spatial monitoring of grassland management using multi-temporal satellite imagery. Ecol. Indicat. 113, 106201.

Swisstopo, 2005. DHM25 - das digitale Hoehenmodell der Schweiz [DHM25 - digital terrain model of Switzerland]. http://www.swisstopo.admin.ch/internet/sw sstopo/d.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8, 857-874.

van Dobben, H.F., Quik, C., Wamelink, G.W., Lantinga, E.A., 2019. Vegetation composition of Lolium perenne-dominated grasslands under organic and conventional farming. Basic Appl. Ecol. 36, 45–53.

Walter, T., Eggenberg, S., Gonseth, Y., Fivaz, F., Hedinger, C., Hofer, G., Klieber-Kühne, A., Richner, N., Schneider, K., Szerencsits, E., Wolf, S., 2013. Operationalisierung der Umweltziele Landwirtschaft: bereich Ziel- und Leitarten, Lebensräume (OPAL). ART-Schriftenreihe 18, 1–138.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wrbka, T., Schindler, S., Pollheimer, M., Schmitzberger, I., Peterseil, J., 2008. Impact of the Austrian Agri-Environmental Scheme on diversity of landscapes, plants and birds. Community Ecol. 9, 217–227.

Zhang, D., 2020. Coefficients of Determination for Generalized Linear Mixed Models, vols. 20-01. Department of Statistics, Purdue University. Technical Report.

Meier, E. S., Lüscher, G., Herzog, F., Knop, E., 2023. Collaborative approaches at the landscape scale increase the benefits of agri-environmental measures for farmland biodiversity. Agric. Ecosyst. Environ., submitted.