Biological Conservation 304 (2025) 111027

Contents lists available at ScienceDirect

Biological Conservation

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

Relaxation of management intensity promotes butterfly communities in mountain grasslands☆

Isabelle Arnold *, Gaëtan Marchand, Aline Hayoz-Andrey, Alberto Serres-Hänni, Raphaël Arlettaz, Jean-Yves Humbert

Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

ARTICLE INFO

Dataset link: Data for relaxation of management intensity promotes butterfly communities in mountain grasslands (Original data)

Keywords:
Passive restoration
Fertilisation reduction
Vegetation
Hay meadow
Lepidoptera
Conservation

ABSTRACT

Semi-natural mountain grasslands are currently threatened by either land abandonment or management intensification, which calls for evidence-based recommendations for sustainable and biodiversity-friendly farming of these valuable biodiversity hotspots in the long run. We investigated the effects of the relaxation of the management intensity on their plant and butterfly communities, via an experimental reduction of fertiliser inputs. In 2019, 13 study sites were selected in the SW Swiss Alps, each including three meadows that had been intensively managed for at least the previous 20 years. Adopting a randomised block design, two out of three meadows per study site were restored by shifting their mode of exploitation towards low-intensity (1/3 of the fertiliser dose applied beforehand) or extensive management (cessation of fertilisation), respectively, while the third continued to be managed intensively, serving as control. After four years (2023), plant species richness had increased by 9.3 % in extensively managed meadows compared to baseline. Yet, butterfly abundance was more than twice greater (112 %) and species richness 81 % higher in extensively managed meadows compared to controls. A higher butterfly abundance and species richness following management relaxation was mostly driven by a decrease in vegetation density and an increase in forb cover. Extensively managed meadows also exhibited higher conservation values, harbouring comparatively more threatened butterfly species, whilst no change was observed in low-intensity meadows. Altogether these results indicate that the butterfly communities of mountain hay meadow respond rapidly and massively to a relaxation of management intensity.

1. Introduction

Semi-natural temperate grasslands belong to the richest ecosystems worldwide, exhibiting a high intrinsic nature value (Veen et al., 2009; Wilson et al., 2012). For centuries, their rich biodiversity had been maintained by traditional, extensive management practices, notably haymaking, seasonal grazing and occasional fertilisation with organic manure (Ellenberg and Leuschner, 2010; Poschlod and WallisDeVries, 2002). This specific ecosystem is nowadays globally threatened by rapid changes in land-use: land abandonment, on the one hand, and agriculture intensification, on the other (Dengler et al., 2020; Lachat et al., 2011; Newbold et al., 2016). Such transformations have dramatic consequences on the rich plant and animal communities typically inhabiting these grasslands (e.g. Green et al., 2005; Stoate et al., 2009), impacting ecosystem dynamics and ecological functioning (e.g. Felipe-Lucia et al., 2020; Tilman et al., 2014).

In mountainous regions of the Old World, grassland abandonment takes place mostly in remote areas offering limited access to agricultural machinery, whilst farming intensification spreads in places more accessible to vehicles (Graf et al., 2014; Strijker, 2005; Tasser and Tappeiner, 2002). Land abandonment typically leads to shrub encroachment, triggering vegetation succession, which negatively affects open-habitat species (e.g. Baur et al., 2006; Koch et al., 2015). Grassland management intensification, characterised by higher fertiliser inputs, enhances phytomass production which allows for a higher mowing frequency and/or grazing intensity. Yet, this enhanced phytomass production negatively impacts plant diversity, in particular of flowering plants (Boch et al., 2021; Humbert et al., 2016; Marini et al., 2009), with cascading effects to higher trophic levels up to insectivorous vertebrates (Andrey et al., 2016; Brambilla et al., 2021; Britschgi et al.,

☆ This article is part of a special issue entitled: Palaearctic grasslands published in Biological Conservation.

* Corresponding author at: Institute of Ecology and Evolution, Division of Conservation Biology, Baltzerstrasse 6, CH-3012 Bern, Switzerland.
E-mail address: isabelle.arnold@unibe.ch (I. Arnold).

https://doi.org/10.1016/j.biocon.2025.111027
Received 31 October 2024; Received in revised form 28 January 2025; Accepted 10 February 2025
Available online 21 February 2025
0006-3207/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

2006; Humbert et al., 2021; Lessard-Therrien et al., 2018).

As typical inhabitants of flower-rich, semi-natural grasslands, butterflies are particularly affected by the decline and degradation of that key habitat (Sánchez-Bayo and Wyckhuys, 2019; Thomas et al., 2004; Van Swaay and Warren, 2006). If nearly 20 % of butterfly species are threatened or near threatened in Europe (Van Swaay et al., 2010), the situation is even worse in Switzerland, with 34.5 % of species red-listed as threatened and 19.5 % as near threatened, a majority being grassland specialists (Wermeille, 2014). A general decrease in plant diversity caused by an augmented phytomass productivity negatively impacts butterfly species richness and abundance (e.g. Marini et al., 2009; Roth et al., 2021). It leads to a pronounced homogenisation of their communities in favour of mobile generalist species, while specialist species, which are bound to micro-habitat heterogeneity and require species-specific hostplants, vanish (Börschig et al., 2013; Guariento et al., 2023). While the negative impacts of agriculture intensification on grassland biodiversity have been extensively documented, research on the effects of extensification, i.e. on the relaxation of management intensity, notably via a reduction of fertiliser inputs, is still lacking.

Studies in the field of restoration ecology that aim at regenerating biodiversity-rich grasslands have been carried out mostly in lowland regions, i.e. in those very areas that have undergone the most severe landscape and habitat homogenisation following decades of intensive management. In such simplified landscape structure, it has been demonstrated that only active restoration strategies, such as reseeding, allow achieving biodiversity objectives (Pywell et al., 2002; Slodowicz et al., 2023; Walker et al., 2004). In contrast, in mountain areas, a more traditional and sustainable land-use by farmers has somehow persisted, providing a more favourable heterogenous landscape structure. Indeed, the uplands are often characterised by a mosaic of small-sized fields interspersed with natural habitats that can typically support the natural dispersal of organisms (Mitchley et al., 2012; Rudmann-Maurer et al., 2008). Under these circumstances, passive restoration (also termed "natural restoration"; Atkinson and Bonser, 2020) can still occur in the sense that these ecosystems have the potential to recover spontaneously, following a mere reduction of anthropogenic pressure. For instance, Helbing et al. (2023) have established that newly created grasslands are readily recolonised by leafhoppers, true bugs and grasshoppers when they are embedded in an overall species-rich network. An apparent similar resilience has been demonstrated for the flora of mountain hay meadows in the European Alps (Humann-Guilleminot et al., 2023). However, that experiment on the effects of relaxing farming intensity had been performed at plot-scale (20 m diameter) after a six-year period of intensification in formerly biodiversity-rich meadows that had been managed extensively over decades. Hence, one still lacks information about the spontaneous resilience of mountain grassland biodiversity at field rather than plot scale in the long run, and for organisms other than plants, i.e. for other trophic levels than primary producers.

In this study, we aimed at investigating whether the relaxation of farming intensity by a reduction of fertiliser inputs suffices to reinstate a biodiversity-rich plant and butterfly community among formerly intensively managed mountain grasslands. We focused on fertiliser reduction because it is by far the main driver of farming intensity in temperate mountain grasslands and a common form of extensification promoted by agri-environmental schemes (Batáry et al., 2015; Klaus et al., 2024). Using a randomised block design, we conducted an experiment in which two out of three meadows (the third one was a control) at thirteen study sites across the Swiss Alps were passively restored by reducing or cessing fertiliser inputs since 2019. We assessed vegetation composition every second year from the onset of the experiment (2019, 2021, 2023) and sampled butterfly along fixed transect-lines after four years (2023). We selected butterflies as an invertebrate taxon because they readily respond to environmental change, being both short-lived and relatively mobile (e.g. Bruppacher et al., 2016; Thomas, 2005). Yet, their response to the relaxation of farming intensity in mountain grasslands has never been experimentally tested. Based on previous research results, our predictions were that relaxing farming intensity would lead to increasing plant species richness and boosting the presence of forbs, which should translate into more speciose, more abundant and more specialised butterfly communities.

2. Materials and methods

2.1. Study sites

The study area was located in the canton of Valais, an inner valley of the Swiss Alps which experiences a continental climate due to high mountain ranges all around, with mean annual ambient temperature and precipitation of 11.1 °C and ca 556 mm, respectively (2010–2020; Sion weather station, 482 m a.s.l.). We selected 13 sites in the montane and subalpine altitudinal belts, along an elevation gradient ranging from 892 to 1664 m a.s.l. (Fig. 1; Table A.1). Each site included three hay meadows that had been intensively managed – i.e. frequently fertilised with liquid (slurry) or solid manure, mown at least twice a year and regularly used as pastures in autumn – for at least 20 years before the onset of the experiment. The average size of a meadow was 0.34 ha (range: 0.16–0.82 ha). To ensure consistency in management history and minimise potential confounding effects, the three meadows of a given site were all located within a 500-m radius and managed by the same farmer.

2.2. Experimental design

From 2019, three different experimental treatments, mimicking contrasted farming practices, were randomly allocated to the three meadows of a site, and consistently applied during four successive years until 2023. In the first meadow of a trio, the previous intensive management mode was continued unchanged and served as a control (hereafter abbreviated H, for high-intensity management). The two other meadows were passively restored by simply relaxing the farming intensity into 1) low-intensity management, specifically with the fertiliser input corresponding to one third of the dose applied beforehand (hereafter abbreviated L, for low-intensity management), and 2) extensive management, i.e. cessation of any fertiliser input (abbreviated E). On average, H-meadows received the equivalent of 74 ± 10 (mean ± SE) kg of nitrogen (N) per ha and year, whereas L-meadows received, on average, 26 ± 4 kg N ha^{-1} and year. Farmers were free to decide about the timing and number of mowing events per year to operate in their meadows, according to site vegetation phenology and phytomass productivity, but also based on their own farm organisation. On average, H-meadows were cut 1.9 ± 0.5 times a year (mean 2019–2023 ± SD), L-meadows 1.9 ± 0.5 and E-meadows 1.8 ± 0.5. In addition, most fields were used as autumn pastures.

2.3. Vegetation surveys

In each meadow, we set two permanent vegetation plots of 2 × 4 m (Fig. A.1). The corner of the first plot was randomly determined so as to ensure a distance of at least 10 m from meadow edge, i.e. defining a wide buffer zone to avoid as much as possible spill-over effects from neighbouring habitats, while the second plot was placed at 8 m distance from the first plot in a random cardinal direction. The two vegetation plots were furthermore orthogonally positioned so as to capture the small-scale heterogeneity of vegetation patterns.

The vegetation composition was assessed at the start of the experiment, in spring 2019, and again after two and four years of passive restoration, in spring 2021 and 2023, respectively. In these two permanent plots, we identified all vascular plants and estimated their percentage cover. Additionally, we estimated the percentage cover of bare ground, litter and mosses. Finally, we estimated phytomass productivity and density of each meadow, relying merely on species-specific ecological indicator values of the weighted-mean of the plant

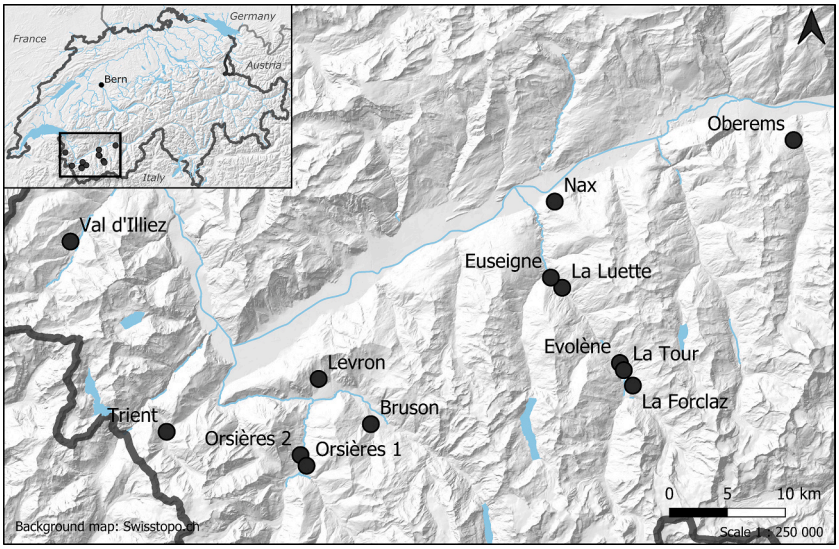

Fig. 1. Location of study sites in the Valais Alps, SW Switzerland. A study site consists of three meadows, each subjected to a different farming regime (high-intensity, low-intensity and extensive management). Exact coordinates can be found in the supplementary materials Table A.1.

community in terms of soil nutrient content and light preferences (Landolt et al., 2010). Due to logistic issues, we could not sample two meadows in 2023 (H-meadow in Bruson and L-meadow in La Forclaz).

2.4. Butterfly sampling

In summer 2023, butterflies (including day-flying moths of the Zygaenidae family) were surveyed along fixed line-transects. For each meadow, depending on its size and shape, we defined the longest line-transect possible (from 60 m to 120 m in length; Fig. A.2), excluding a 7.5 m buffer zone from the edge of the meadow for the same reasons as above (see Fig. A.1). However, in some small meadows, we had to survey two or three smaller line-transects, separated by at least 15 m, instead of a single linear transect.

We conducted five sampling sessions, spaced by at least two weeks, during the main butterfly flight season (May to September). Butterfly sampling took place between 10 am and 5 pm on warm and sunny days, with a minimal ambient temperature of 13 °C and a maximal wind speed of 5 on Beaufort's scale (Sevilleja et al., 2019). We used the Pollard walk method, i.e. walked the transects at a slow and constant walking speed, counting all butterflies within an imaginary box of 2.5 m on each transect side, and 5 m in front and above (Pollard and Yates, 1993; Sevilleja et al., 2019). We visually identified all butterflies to species according to Baudraz and Baudraz (2021). In case of ambiguities in the identification, individuals were caught with a butterfly net, identified and immediately released. We always sampled all the three meadows of a site on the same day in a random sequence. In each meadow, at least one sampling session was performed prior to the first seasonal mowing. The first post-mowing sampling took place on average 10 days after each mowing event (range 1–30 days; average number of days in H-meadows = 9.9, L-meadows = 10.7, E-meadows = 9.8).

Six butterfly ecological and life-history traits were considered, based on literature information (Settele et al., 2015; Settele et al., 1999): 1) dispersal capacity (from sedentary to migratory); 2) trophic specialisation (nectar sources from one flower genus to several plant families); 3) host plant specificity (one genus to several families); 4) number of generations per year; 5) flight period in months; and 6) overwintering stage (egg, larva, imago). Categorical traits were transformed into ordinal values prior to statistical analysis (e.g. trophic specialisation scaled from 1 to 3: feeding on one plant genus, one plant family or several families, respectively; Table A.2). Accordingly, butterfly species were further classified as either specialists or generalists, with specialists defined by a low dispersal capacity (site loyal), a narrow trophic niche (one plant genus or family as nectar resource) and reduced host plant dependence (one genus or family), a maximum of two generations per season, and overwintering as egg or caterpillar, never as imago. We computed one community-weighted mean for each trait and specialisation category per meadow. We also computed a conservation index, following the approach proposed by Hannappel and Fischer (2020), by summing the Swiss red list status scores for all species recorded in a given meadow (least concern = 1; near threatened = 5; vulnerable = 10; endangered = 20) according to Wermeille (2014). For more details on traits see Table A.2 and A.3 in supplementary materials.

2.5. Statistical analysis

In all statistical analyses, the data from the two vegetation plots in a given meadow were pooled together as were the records from the five seasonal butterfly surveys. Additionally, we transformed the plant cover estimates into relative cover (summing to 100 %).

To test for any year-to-year trends on total plant species richness and species richness of grasses (i.e. graminoids including *Poaceae*, *Cyperaceae* and *Juncaceae*) and forbs (all other vascular plants including legumes), we used linear mixed-effects models (*lme4* package; Bates et al., 2015). Specifically, we ran different models for each management regime and set year as a fixed categorical factor (3 levels) and study site (13 levels) as random intercept. Furthermore, we tested for the effects of management intensity on the vegetation and butterfly communities for each sampling year separately (vegetation: 2019, 2021 and 2023; butterfly: 2023) by means of linear mixed-effects models. We set the levels of management intensity (3 levels) as a fixed categorical factor and study site as random intercept. Concerning vegetation, the response variables were: plant species richness; species richness and relative cover of grasses and forbs; cover of bare ground and the community-weighted means of the Landolt indicator for soil nutrient and light preference. Response variables for butterflies were: abundance per 100 m of transect; species richness; conservation value; and the community-weighted means of the ecological and life-history traits (i.e. dispersal capacity, trophic specialisation, host plant specificity, number of generations per year, flight period, and overwintering stage), and the community-weighted mean of specialisation category (i.e. generalists vs specialists). We used the total number of butterfly species recorded in each meadow as species richness. While transect lengths varied between the single meadows, mean transect length did not differ between the three

management regimes (Fig. A.2), meaning that any difference between experimental treatments and control cannot be due to transect length. Species rarefaction curves furthermore clearly reached an asymptote in all three management regimes (Fig. A.3).

To test for differences in vegetation and butterfly community composition between management intensities, we computed a multivariate analysis (permutational analysis of variance, permanova; 999 permutations) using Bray-Curtis dissimilarity. We used the function *adonis2* (*vegan* package; Oksanen et al., 2022), setting the study site as strata. We tested the homogeneity of dispersion among groups, i.e. management intensities, with the function *betadisper* (same package) and tested its significance using an ANOVA. To visualise the differences in community composition, we used non-metric multidimensional scaling (NMDS) to account for the semi-metric nature of the Bray-Curtis dissimilarity. To assure a good and interpretable visual representation, we assessed the goodness of fit of the ordination (NMDS) by means of the Shepard diagram and the stress value.

We tested species-specific responses to management intensities by means of a model-based community analysis using the function *manyglm* (*mvabund* package; Wang et al., 2012). This function fits a generalised linear model (GLM) to a matrix of abundance (percentage cover for vegetation and abundance per 100 m transect for butterflies). We conducted the test with species occurring in at least eight sites out of 13, which yielded a total of 38 plant and 10 butterfly species. The management intensities and sites were set as fixed factors and we fitted a negative binomial error distribution.

Finally, we tested for relationships between selected vegetation variables – accounting for the vegetation density (i.e. bare ground cover and Landolt light index), total plant species richness, and species richness and cover of grasses and forbs – vs butterfly species richness and abundance per 100 m transect, respectively, using linear mixed-effects models with site set as random intercept.

We performed all statistical tests using R, version 4.3.2 (R Team Core, 2023). Model assumptions were checked by visually assessing the normality and homoscedasticity of residuals. If assumptions on the distribution were not satisfied, we log or square-root transformed the corresponding response variable (which performed better than using a Poisson models). For testing the effects of the management intensity and year, we relied on the function *relevel* so as to obtain pairwise comparisons between levels.

3. Results

3.1. Plant community responses

Over the three years of sampling (2019, 2021 and 2023), 204 plant species belonging to 33 families were recorded, including five species red-listed in Switzerland (Bornand et al., 2016).

We found no difference in the plant species richness between management intensities at the onset of the experiment in 2019 (Table B.1). After four years, in 2023, only the extensively managed meadows (E-meadows) showed an increase in species richness by 9.3 %, on average, corresponding to 3–4 new species (Fig. 2; Table B.2). That same year, the difference between extensively managed meadows (E-meadows), which harboured, on average (± SE), 41 ± 2 plant species, and intensive meadows (H-meadows; our control), with 37 ± 3 plant species, was only marginally significant ($P = 0.058$). In contrast, no significant difference was observed between E-meadows and low-intensity meadows (L-meadows; 40 ± 3; Table B.1).

Multivariate analyses showed no difference between management intensities in terms of community composition at the onset of the experiment, but a significant difference between the E-meadows and the two regimes with fertilisation (L- and H-meadows) after two (2021) and four years (2023), respectively (Fig. 3; Table B.3). Yet, these differences in plant community remained small, with management intensity being responsible for only 5 % of the variation observed in the plant community in 2023. At the 2023 vegetation sampling, the cover of grass species was lower by 32.8 % and 30.1 %, pairwisely (E vs H; E vs L), respectively, whilst the cover of forb species was higher by 35.8 % and 31.5 % (E vs H; E vs L) respectively, on E-meadows compared to both H-meadows and L-meadows. This is well reflected in the model-based community analysis that points out to a recovery of forb species characteristic of extensively managed meadows such as *Leontodon hispidus*, *Picris hieracioides*, *Plantago lanceolata*, *Rhinanthus alectorolophus* and *Silene vulgaris*, paralleled by a decrease of grasses, notably *Poa trivialis*, *Poa pratensis* and *Dactylis glomerata* decreased (Fig. B.1).

Vegetation productivity and density were also lower in extensively managed meadows compared to fertilised meadows, as indicated by a lower Landolt index for soil nutrient content (E vs H, −10.9 %; E vs L, −5.9 %), a higher index for light preference (E vs H, +4.0 %; E vs L, not significant), and higher bare ground cover (E vs H, +54.0 %; E vs L, +42.6 %; Table B.4). Additionally, the productivity (nutrient index) was significantly 5.3 % lower in L-meadows than in H-meadows.

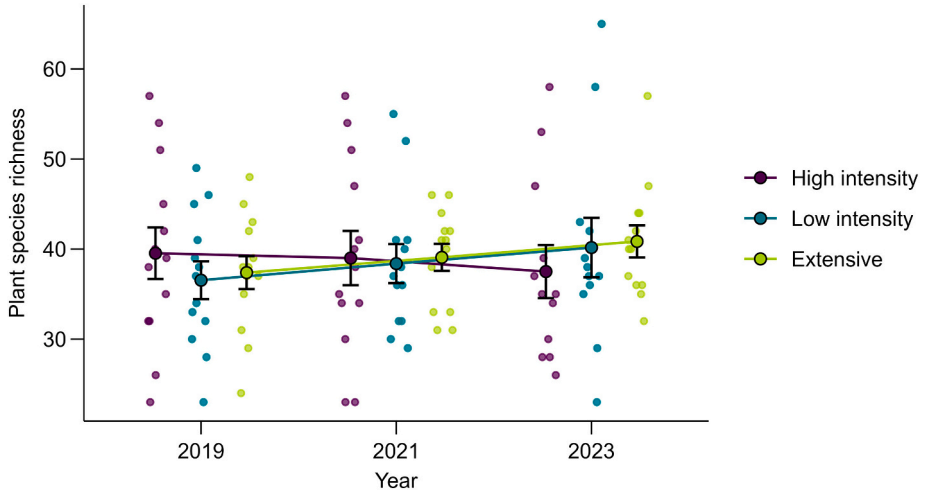

Fig. 2. Plant species richness (with means ± SEM) with respect to management regime at the onset of the experiment (in 2019), and after two (2021) and four years (2023). Linear mixed-effects models showed a significant trend only for the extensive management between 2019 and 2023 ($P = 0.040$; Table B.2).

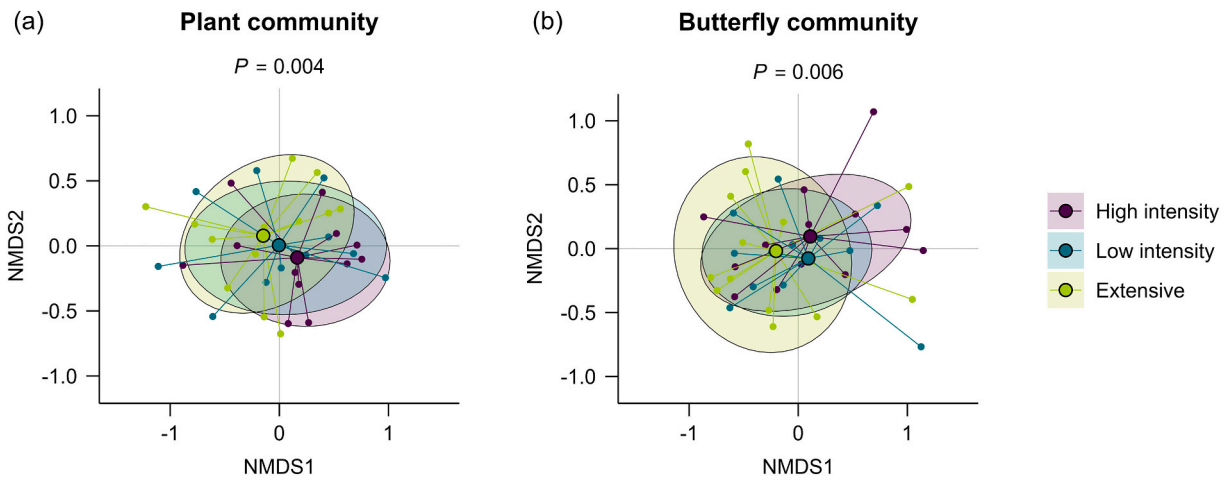

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of the plant (a) and the butterfly (b) communities, based on Bray-Curtis distance, showing differences between management regimes in 2023, i.e. four years of the onset of passive restoration (relaxation of intensification). Small coloured circles represent the centroids for each management intensity and the corresponding ellipses 75 % confidence intervals. *P*-values are from a PERMANOVA analysis (site as strata) testing differences between management regimes.

3.2. Butterfly community responses

We recorded a total of 1276 butterfly individuals from 66 species representing five butterfly families and one moth family: Hesperiidae (*n* = 6 species); Lycaenidae (16); Nymphalidae (25); Papilionidae (4); Pieridae (11); Zygaenidae (4). Three species accounted for half of the records: *Maniola jurtina* (22.0 % of total number of individuals), *Melanargia galathea* (19.8 %) and *Coenonympha pamphilus* (12.1 %). Ten species recorded were listed as near threatened, eleven as vulnerable and one as endangered (*Phengaris alcon*; Table A.3).

After four years of restoration, butterfly species richness and abundance were significantly higher on extensively managed meadows (E-meadows: 14 ± 1 species and 55 ± 7 individuals per 100 m; mean ± SE) compared to fertilised meadows (L-meadows: 9 ± 1 species and 35 ± 6 individuals; H-meadows: 8 ± 1 species and 26 ± 4 individuals; Fig. 4; Table B.5). No significant difference was observed between L-meadows and H-meadows.

Multivariate analyses showed a significant difference between the butterfly communities occurring in extensively managed meadows and fertilised meadows (Fig. 3; Table B.3). However, similarly to plant community results, this difference remained low, with 6 % of the total variance explained by management intensity. The model-based community analysis showed that *Pieris brassicae*, *Cyaniris semiargus* and *Colias crocea* were more frequent in E-meadows compared to H-meadows (Fig. B.2).

The analysis of ecological and life-history traits did not yield any significant differences between management regimes (Table B.6). The average conservation value estimated from the red list scores was significantly higher in E-meadows (31.5 ± 5.8; mean ± SE) compared to H-meadows (15.8 ± 2.9; Fig. 4; Table B.5). L-meadows (22.4 ± 3.8) showed no significant differences compared to E- and H-meadows.

3.3. Butterfly vs vegetation relationships

Butterfly abundance per 100 m of survey transect increased with the total and functional groups (grasses and forbs) plant species richness, whereas we found no significant relation between butterfly species richness and the same vegetation variables (Fig. 5; Table B.7; Figs. B.3 and B.4). Butterfly abundance per 100 m and species richness were consistently positively related to forb cover, Landolt index for light preference as well as percentage of bare ground cover, and negatively related to Landolt index for soil nutrient content (Fig. 5; Table B.7).

4. Discussion

This study demonstrates that the relaxation of management intensity via a reduction of fertiliser inputs triggers positive effects on plant communities of semi-natural mountain grasslands in the short- and mid-term, prompting in turn a fairly rapid recovery of butterfly communities. To the best of our knowledge, this is the first research that has experimentally (applying a completely randomised block design) tested under real field conditions the effects of passive restoration on the plant and butterfly communities of mountain grasslands. A fully controlled experimental approach has enabled us to circumvent any potential confounding effects, such as the influence of topography and surrounding landscape configuration, providing accurate and reliable evidence-based information for guiding grassland restoration action. This is a timely and pressing issue because mountain grasslands are currently undergoing massive intensification wherever mechanisation allows (Graf et al., 2014; Strijker, 2005; Tasser and Tappeiner, 2002). In effect, if nothing is undertaken to reverse this antagonistic change, these biodiversity hotspots of the Alps, may rapidly lose their natural and conservation value (Maurer et al., 2006; Veen et al., 2009).

4.1. Plant community responses

In 2023, four years after the cessation of fertilisation, there was only a marginal difference ($P = 0.058$) in plant species richness between hay meadows subjected to extensive (E) vs high-intensity (H, control) management regimes, whereas low-intensity meadows (L) did not differ from controls (H). Nonetheless, the 2019–2023 trend showed a significant 9.3 % positive trend in plant species richness for E-meadows, the most extensive treatment. This is in line with earlier findings that plant species richness can apparently be restored fairly quickly to its initial state, after only five years of cessation of intensive management (Humann-Guilleminot et al., 2023). One can conclude that there exists definitely some potential for spontaneous (i.e. passive) restoration of mountain grasslands once farming intensity is relaxed.

At a first glance, an increase by 9.3 % might seem negligeable, but it must be kept in mind that our E-meadows already harboured a high plant species richness at the onset of the experiment, with, on average (± SE), 37 ± 2 species per 16 m^2. We expect that this positive trend will continue unabated with the progressive depletion of soil nutrient content following the termination of fertilisation (Clark et al., 2009). In effect, this will allow the establishment of new less nitrophilous species that are otherwise eliminated via competitive exclusion (Rajaniemi,

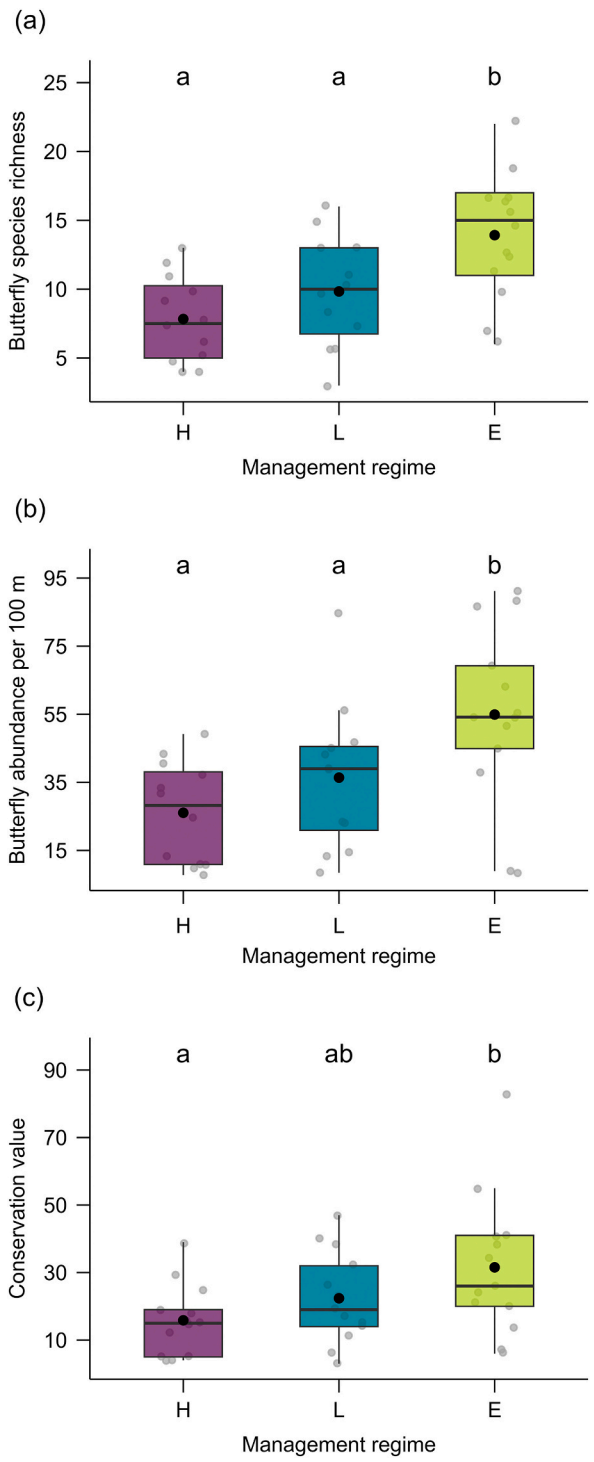

Fig. 4. Effect of management regime (H = high intensity; L = low intensity; E = extensive) in 2023 on butterfly species richness (a), butterfly abundance per 100 m survey transect (b), and the conservation value estimated from the cumulated species-specific red list scores per meadow (c). Different letters on frame top indicate significant differences between management regimes ($P \leq 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2002). However, the success of this process may be constrained by the available seed sources in the surrounding landscape (Bakker et al., 1996). Previous, longer-term investigations have stressed that the full recovery of species richness after the relaxation of grassland fertilisation may take decades, mainly because of a kinetic response of soil nutrient content after cessation of fertiliser input (Hrevušová et al., 2009; Královec et al., 2009; Semelová et al., 2008). What is also clear from our experiment, despite a non-significant trend partly due to a high inter-sites variance, is that a reduction of fertilisation to one third of the initial fertiliser input (our low-intensity, L-meadow) could possibly lead to some similar ameliorations of plant diversity, but over a much longer period of time (see parallel trajectories in Fig. 2). Our observations seem to contradict the view by Isbell et al. (2013) that even low but unabated fertiliser inputs, in the range of 20–54 kg N ha^{-1} $year^{-1}$, will jeopardise any chance of recovery of the vegetation diversity.

The multivariate analysis of community structure showed noticeable differences between the extensive and the two intensive management regimes four years after the cessation of fertilisation. Given the small differences in species richness discussed above, these changes in the plant communities were mainly driven by shifts in species abundance. Characteristic was in particular the decrease of tall grass species such as *Dactylis glomerata* and *Poa pratensis*, agronomically considered as highly productive. This allowed more forbs to enter the game, i.e. the sympatric coexistence of a more complex vegetation cohort, with fewer nitrophilous plants thanks to a reduced asymmetric light competition at the understorey level (Hautier et al., 2009). This is mirrored in higher indicator values for light preference and lower indicator values for soil nutrient content (Landolt et al., 2010), while higher cover of bare ground was also evidenced in unfertilised, extensively managed meadows. Overall, this denotes a drop in vegetation productivity and density in extensively farmed compared to fertilised meadows. As a matter of fact, Boch et al. (2021) have showed that fertilised meadows (40–80 kg N ha^{-1} $year^{-1}$) in the Swiss Alps yield about twice the phytomass of unfertilised meadows (see also Pallett et al., 2016). We expect a similar decrease in yield in our restored meadows in the long run.

4.2. Butterfly community responses

Butterflies responded faster and stronger than vegetation to the relaxation of management intensity, with 81 % more species and twice more abundant communities in extensively managed compared to high-intensity meadows. This corroborates the general view that butterflies are extremely reactive to environmental change, in either direction: degradation or amelioration (Bruppacher et al., 2016; Thomas et al., 2004). Butterfly species richness and abundance was positively associated with both the proxy for plant light preference and the cover of bare ground, but negatively with the proxy for soil nutrient content. This demonstrates that relaxing management intensity improves habitat quality for butterflies, notably via a reduction of vegetation density that procures more heterogenous micro-habitats as well as warmer and more luminous conditions (Dennis, 1992; Roy and Thomas, 2003). Indeed, fertilisation enhances phytomass production and boosts vegetation height, leading to moister and cooler microclimates in the grassland understorey (Humbert et al., 2021), which impede butterfly larval development (Roth et al., 2021; WallisDeVries and Van Swaay, 2006). Following the decrease in phytomass production after fertiliser cessation, some of the farmers involved in this study (3/13) reduced the number of annual mowing events, which could further improve ecological conditions for butterflies (Fumy et al., 2023; Hudewenz et al., 2012). Beyond vegetation structure, fertilisation also alters plant tissue chemistry, thereby diminishing the quality of the host plants for herbivores in general and impacting the survival of butterfly larvae (Prudic et al., 2005; Kurze et al., 2018). These per se may explain the differences in butterfly population sizes observed between our different experimental treatments. Contrary to the study of Marini et al. (2009) in the Italian Alps, we did not find any effect of plant species richness on butterfly species richness, either overall or considering the two main functional groups separately (i.e. grasses or forbs), although the relative cover of forbs was larger on E-meadows. Host plant availability was maybe not a limiting factor in our experiment, possibly due to a comparatively higher floral diversity (40 ± 9 plant species; mean ± SD)

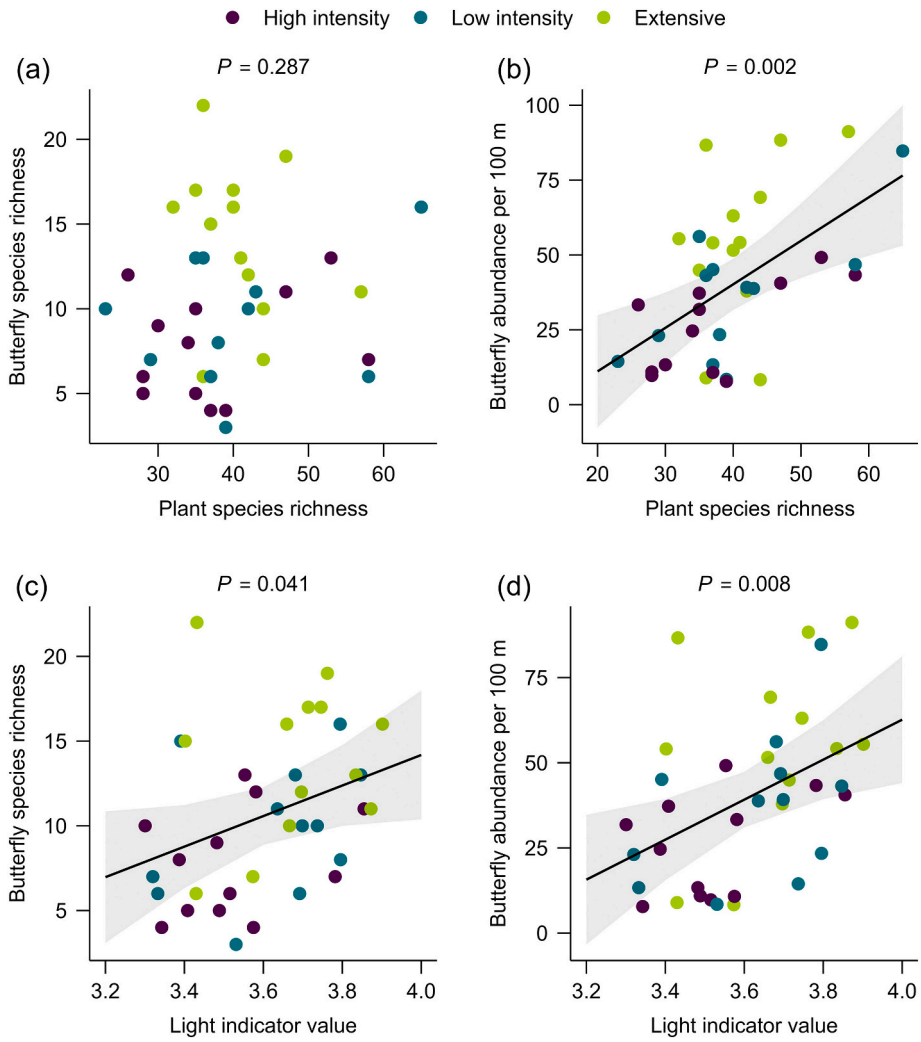

Fig. 5. Relationships between butterfly species richness (left graphs, a and c) and abundance per 100 m survey transect (right graphs, b and d) vs plant species richness and the light index (plant ecological indicator based on Landolt et al. (2010) and used as a proxy for vegetation density). Data are from the year 2023. The regression line stems from the linear mixed-effects model outputs with 95 % confidence intervals. P-values are given on graph tops.

and a more heterogenous and extensively managed surrounding than in the Italian study (26 ± 9; Habel et al., 2019). Nevertheless, butterfly communities might benefit from a higher presence of nectar resources on forb-dominated E-meadows (WallisDeVries et al., 2012).

Our butterfly communities differed markedly between management regimes despite a low explanatory power of management intensity (6 % of total variance). As we did not observe any difference in butterfly life-history traits between management regimes, it is likely that passive restoration promoted a broad butterfly community. However, we could not demonstrate a positive response of specialists, while the three most abundant species in E-meadows were common generalists. It is known that agricultural intensification leads to a rapid habitat deterioration (Andrey et al., 2014) that is particularly detrimental to specialised butterflies, especially those with low dispersal ability (Börschig et al., 2013; Habel et al., 2016). One can conclude that farming extensification, i.e. the relaxation of management intensity, as investigated in the present research, is at least not detrimental to generalists, on the contrary. Moreover, the absence of an effect of farming extensification on specialists should be tempered by the observation that the conservation index for threatened butterfly species was twice higher on E-meadows than on H-meadows. Hence, relaxing management intensity definitely promotes rare species, highlighting again the high nature and conservation value of traditionally managed mountain grasslands.

4.3. Conclusions and conservation implications

If most studies of grassland biodiversity have focused on the negative impact of land-use intensification (e.g. Gossner et al., 2016), our experiment demonstrates the great potential of passive restoration for both plant and butterfly communities of mountain grasslands. Plant species richness increased as early as four years after the cessation of fertiliser inputs. Relaxing management intensity favoured a more open and forb-dominated vegetation which in turn promoted a more abundant and species-rich butterfly community, including a greater number of threatened species. Yet, we have to stress that such a rapid response might be context-dependent, i.e. related to overall habitat quality of the surroundings, and region-dependent as mountain area differ from the lowlands, notably in terms of land-use history (Habel et al., 2019; Woodcock et al., 2021). It is likely that farming extensification promotes also other wildlife among meadows, with expected cascading effects at the upper levels of the food chain, but further research is needed. Sustainable farmland management requires a delicate balance between agricultural production, biodiversity conservation and the maintenance of key ecosystem services (Rasmussen et al., 2024). In this respect, mountain farming systems, maybe more than any other agroecosystem due to their high intrinsic nature conservation potential, would benefit from a multifunctional approach that accounts for trade-offs between farmers' livelihoods, agricultural production, biodiversity preservation,

landscape protection and tourism (Chapman and Deplazes-Zemp, 2023; Dick et al., 2017). This study is an ecological contribution to these challenging issues of the future.

CRediT authorship contribution statement

Isabelle Arnold: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis. **Gaëtan Marchand:** Writing – original draft, Investigation, Formal analysis. **Aline Hayoz-Andrey:** Methodology, Investigation. **Alberto Serres-Hänni:** Investigation. **Raphaël Arlettaz:** Writing – review & editing, Funding acquisition, Conceptualization. **Jean-Yves Humbert:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Funding

This project was financially supported by the canton of Valais and the Swiss National Science Foundation (grant number 310030_215272 to Raphaël Arlettaz and Jean-Yves Humbert).

Declaration of competing interest

We declare that we do not have competing interests.

Acknowledgements

We would like to thank Silja Eller and Ségolène Humann-Guilleminot for field assistance, our colleagues at the Division of Conservation Biology, University of Bern, as well as the members of the project accompanying group. We are also thankful to the farmers for their collaboration.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111027.

Data availability

Data are freely available on the Mendeley Data repository.

Data for relaxation of management intensity promotes butterfly communities in mountain grasslands (Original data) (Mendeley Data)

References

Andrey, A., Humbert, J., Pernollet, C., Arlettaz, R., 2014. Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. Ecol. Evol. 4, 2610–2623. https://doi.org/10.1002/ece3.1118.

Andrey, A., Humbert, J.-Y., Arlettaz, R., 2016. Functional response of leaf- and planthoppers to modern fertilisation and irrigation of hay meadows. Basic Appl. Ecol. 17, 627–637. https://doi.org/10.1016/j.baae.2016.07.002.

Atkinson, J., Bonser, S.P., 2020. "Active" and "passive" ecological restoration strategies in meta-analysis. Restor. Ecol. 28, 1032–1035. https://doi.org/10.1111/rec.13229.

Bakker, J., Poschlod, P., Strykstra, R., Bekker, R., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Bot. Neerlandica 45, 461–490. https://doi.org/10.1111/j.1438-8677.1996.tb00806.x.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of Agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. https://doi.org/10.1111/cobi.12536.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Baudraz, V., Baudraz, M., 2021. Guide d'identification des papillons de jour de Suisse. Société Vaudoise des Sciences Naturelles, Lausanne, Switzerland.

Baur, B., Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Stoll, P., Erhardt, A., 2006. Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania. Romania. Biol. Conserv. 132, 261–273. https://doi.org/10.1016/j.biocon.2006.04.018.

Boch, S., Kurtogullari, Y., Allan, E., Lessard-Therrien, M., Rieder, N.S., Fischer, M., Martínez De León, G., Arlettaz, R., Humbert, J.-Y., 2021. Effects of fertilization and irrigation on vascular plant species richness, functional composition and yield in mountain grasslands. J. Environ. Manag. 279, 111629. https://doi.org/10.1016/j.jenvman.2020.111629.

Bornand, C., Gygax, A., Juillerat, P., Jutzi, M., Möhl, A., Rometsch, S., Sager, L., Santiago, H., Eggenberg, S., 2016. Liste rouge Plantes vasculaires: Espèces menacées en Suisse. L'environnement pratique. Federal Office for Environment; Info Flora, Bern, Switzerland.

Börschig, C., Klein, A.-M., Von Wehrden, H., Krauss, J., 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Basic Appl. Ecol. 14, 547–554. https://doi.org/10.1016/j.baae.2013.09.002.

Brambilla, M., Gubert, F., Pedrini, P., 2021. The effects of farming intensification on an iconic grassland bird species, or why mountain refuges no longer work for farmland biodiversity. Agric. Ecosyst. Environ. 319, 107518. https://doi.org/10.1016/j.agee.2021.107518.

Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the whinchat Saxicola rubetra: lessons for overall alpine meadowland management. Biol. Conserv. 130, 193–205. https://doi.org/10.1016/j.biocon.2005.12.013.

Bruppacher, L., Pellet, J., Arlettaz, R., Humbert, J.-Y., 2016. Simple modifications of mowing regime promote butterflies in extensively managed meadows: evidence from field-scale experiments. Biol. Conserv. 196, 196–202. https://doi.org/10.1016/j.biocon.2016.02.018.

Chapman, M., Deplazes-Zemp, A., 2023. 'I owe it to the animals': the bidirectionality of Swiss alpine farmers' relational values. People Nat. 5, 147–161. https://doi.org/10.1002/pan3.10415.

Clark, C.M., Hobbie, S.E., Venterea, R., Tilman, D., 2009. Long-lasting effects on nitrogen cycling 12 years after treatments cease despite minimal long-term nitrogen retention. Glob. Chang. Biol. 15, 1755–1766. https://doi.org/10.1111/j.1365-2486.2008.01811.x.

Dengler, J., Biurrun, I., Boch, S., Dembicz, I., Török, P., 2020. Grasslands of the Palaearctic biogeographic realm: Introduction and synthesis. In: Encyclopedia of the World's Biomes. Elsevier, Oxford, United Kingdom, pp. 617–637. https://doi.org/10.1016/B978-0-12-409548-9.12432-7.

Dennis, R.L.H., 1992. The Ecology of Butterflies in Britain. Oxford science publications, Oxford University Press, Oxford, United Kingdom.

Dick, M., Rous, A.M., Nguyen, V.M., Cooke, S.J., 2017. Necessary but challenging: multiple disciplinary approaches to solving conservation problems. FACETS 1, 67–82. https://doi.org/10.1139/facets-2016-0003.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. UTB.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., Fischer, M., Ammer, C., Boch, S., Boeddinghaus, R.S., Bonkowski, M., Buscot, F., Fiore-Donno, A.M., Frank, K., Goldmann, K., Gossner, M.M., Hölzel, N., Jochum, M., Kandeler, E., Klaus, V.H., Kleinebecker, T., Leimer, S., Manning, P., Oelmann, Y., Saiz, H., Schall, P., Schloter, M., Schöning, I., Schrumpf, M., Solly, E.F., Stempfhuber, B., Weisser, W.W., Wilcke, W., Wubet, T., Allan, E., 2020. Land-use intensity alters networks between biodiversity, ecosystem functions, and services. Proc. Natl. Acad. Sci. 117, 28140–28149. https://doi.org/10.1073/pnas.2016210117.

Fumy, F., Schwarz, C., Fartmann, T., 2023. Intensity of grassland management and landscape heterogeneity determine species richness of insects in fragmented hay meadows. Glob. Ecol. Conserv. 47, e02672. https://doi.org/10.1016/j.gecco.2023.e02672.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S.C., Sikorski, J., Wubet, T., 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540, 266–269. https://doi.org/10.1038/nature20575.

Graf, R., Müller, M., Korner, P., Jenny, M., Jenni, L., 2014. 20% loss of unimproved farmland in 22 years in the Engadin, Swiss Alps. Agric. Ecosyst. Environ. 185, 48–58. https://doi.org/10.1016/j.agee.2013.12.009.

Green, R.E., Cornell, S.J., Scharlemann, J.P., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550–555. https://doi.org/10.1126/science.1106049.

Guariento, E., Rüdisser, J., Fiedler, K., Paniccia, C., Stifter, S., Tappeiner, U., Seeber, J., Hilpold, A., 2023. From diverse to simple: butterfly communities erode from extensive grasslands to intensively used farmland and urban areas. Biodivers. Conserv. 32, 867–882. https://doi.org/10.1007/s10531-022-02498-3.

Habel, J.C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W.W., Schmitt, T., 2016. Butterfly community shifts over two centuries. Conserv. Biol. 30, 754–762. https://doi.org/10.1111/cobi.12656.

Habel, J.C., Ulrich, W., Biburger, N., Seibold, S., Schmitt, T., 2019. Agricultural intensification drives butterfly decline. Insect Conserv. Divers. 12, 289–295. https://doi.org/10.1111/icad.12343.

Hannappel, I., Fischer, K., 2020. Grassland intensification strongly reduces butterfly diversity in the Westerwald mountain range. Germany. J. Insect Conserv. 24, 279–285. https://doi.org/10.1007/s10841-019-00195-1.

Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for light causes plant biodiversity loss after eutrophication. Science 324, 636–638. https://doi.org/10.1126/science.1169640.

Helbing, F., Fartmann, T., Morkel, C., Poniatowski, D., 2023. Rapid response of vascular plants and insects to restoration of montane grasslands. Front. Ecol. Evol. 11, 1148266. https://doi.org/10.3389/fevo.2023.1148266.

Hrevušová, Z., Hejcman, M., Pavlů, V.V., Hakl, J., Klaudisová, M., Mrkvička, J., 2009. Long-term dynamics of biomass production, soil chemical properties and plant species composition of alluvial grassland after the cessation of fertilizer application in the Czech Republic. Agric. Ecosyst. Environ. 130, 123–130. https://doi.org/10.1016/j.agee.2008.12.008.

Hudewenz, A., Klein, A.-M., Scherber, C., Stanke, L., Tscharntke, T., Vogel, A., Weigelt, A., Weisser, W.W., Ebeling, A., 2012. Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. Biol. Conserv. 150, 42–52. https://doi.org/10.1016/j.biocon.2012.02.024.

Humann-Guilleminot, S., Boch, S., Martínez-De León, G., Lessard-Therrien, M., Hayoz-Andrey, A., Serres-Hänni, A., Humbert, J., 2023. Experimental extensification of mountain grasslands restores plant species richness but not species composition in the mid-term. J. Appl. Ecol. 60, 530–540. https://doi.org/10.1111/1365-2664.14344.

Humbert, J.-Y., Delley, S., Arlettaz, R., 2021. Grassland intensification dramatically impacts grasshoppers: experimental evidence for direct and indirect effects of fertilisation and irrigation. Agric. Ecosyst. Environ. 314, 107412. https://doi.org/10.1016/j.agee.2021.107412.

Humbert, J.-Y., Dwyer, J.M., Andrey, A., Arlettaz, R., 2016. Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: a systematic review. Glob. Chang. Biol. 22, 110–120. https://doi.org/10.1111/gcb.12986.

Isbell, F., Tilman, D., Polasky, S., Binder, S., Hawthorne, P., 2013. Low biodiversity state persists two decades after cessation of nutrient enrichment. Ecol. Lett. 16, 454–460. https://doi.org/10.1111/ele.12066.

Klaus, V.H., Richter, F., Lüscher, A., Buchmann, N., Delore, J.-M., le Clec'h, S., 2024. Organic farming is more related to topography than to soil characteristics in extensively and intensively managed grasslands in Switzerland. Agric. Ecosyst. Environ. 376, 109242. https://doi.org/10.1016/j.agee.2024.109242.

Koch, B., Edwards, P.J., Blanckenhorn, W.U., Walter, T., Hofer, G., 2015. Shrub encroachment affects the diversity of plants, butterflies, and grasshoppers on two Swiss subalpine pastures. Arct. Antarct. Alp. Res. 47, 345–357. https://doi.org/10.1657/AAAR0013-093.

Královec, J., Pocová, L., Jonášová, M., Macek, P., Prach, K., 2009. Spontaneous recovery of an intensively used grassland after cessation of fertilizing. Appl. Veg. Sci. 12, 391–397.

Kurze, S., Heinken, T., Fartmann, T., 2018. Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. Oecologia 188, 1227–1237. https://doi.org/10.1007/s00442-018-4266-4.

Lachat, T., Pauli, D., Gonseth, Y., Klaus, G., Scheidegger, C., Vittoz, P., Walter, T., 2011. Evolution de la biodiversité en Suisse depuis 1900: Avons-nous touché le fond? Bristol-Schriftenreihe, Haupt, Bern, Switzerland.

Landolt, E., Bäumler, B., Ehrhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F., Theurillat, J., 2010. Flora indicativa: Okologische Zeigerwerte und Biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt, Bern.

Lessard-Therrien, M., Humbert, J.-Y., Hajdamowicz, I., Stańska, M., Klink, R.V., Lischer, L., Arlettaz, R., 2018. Impacts of management intensification on ground-dwelling beetles and spiders in semi-natural mountain grasslands. Agric. Ecosyst. Environ. 251, 59–66. https://doi.org/10.1016/j.agee.2017.08.025.

Marini, L., Fontana, P., Battisti, A., Gaston, K.J., 2009. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland–forest mosaic: a multi-scale approach. Insect Conserv. Divers. 2, 213–220. https://doi.org/10.1111/j.1752-4598.2009.00053.x.

Maurer, K., Weyand, A., Fischer, M., Stöcklin, J., 2006. Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. Biol. Conserv. 130, 438–446. https://doi.org/10.1016/j.biocon.2006.01.005.

Mitchley, J., Jongepierová, I., Fajmon, K., 2012. Regional seed mixtures for the re-creation of species-rich meadows in the white Carpathian Mountains: results of a 10-yr experiment. Appl. Veg. Sci. 15, 253–263. https://doi.org/10.1111/j.1654-109X.2012.01183.x.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L., Hoskins, A.J., Lysenko, I., Phillips, H.R., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353, 288–291. https://doi.org/10.1126/science.aaf2201.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2022. Vegan: community ecology package.

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. Indic. 68, 73–81. https://doi.org/10.1016/j.ecolind.2015.12.024.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation: The Britisch Butterfly Monitoring Scheme, 1st ed. Chapman & Hall.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. Biol. Conserv. 104, 361–376. https://doi.org/10.1016/S0006-3207(01)00201-4.

Prudic, K.L., Oliver, J.C., Bowers, M.D., 2005. Soil nutrient effects on oviposition preference, larval performance, and chemical defense of a specialist insect herbivore. Oecologia 143, 578–587. https://doi.org/10.1007/s00442-005-0008-5.

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. https://doi.org/10.1046/j.1365-2664.2002.00718.x.

R Team Core, 2023. R: a language and environment for statistical computing.

Rajaniemi, T.K., 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. J. Ecol. 90, 316–324. https://doi.org/10.1046/j.1365-2745.2001.00662.x.

Rasmussen, L.V., Grass, I., Mehrabi, Z., Smith, O.M., Bezner-Kerr, R., Blesh, J., Garibaldi, L.A., Isaac, M.E., Kennedy, C.M., Wittman, H., Batáry, P., Buchori, D., Cerda, R., Chará, J., Crowder, D.W., Darras, K., DeMaster, K., Garcia, K., Gómez, M., Gonthier, D., Guzman, A., Hidayat, P., Hipólito, J., Hirons, M., Hoey, L., James, D., John, I., Jones, A.D., Karp, D.S., Kebede, Y., Kerr, C.B., Klassen, S., Kotowska, M., Kreft, H., Llanque, R., Levers, C., Lizcano, D.J., Lu, A., Madsen, S., Marques, R.N., Martins, P.B., Melo, A., Nyantakyi-Frimpong, H., Olimpi, E.M., Owen, J.P., Pantevez, H., Qaim, M., Redlich, S., Scherber, C., Sciligo, A.R., Snapp, S., Snyder, W. E., Steffan-Dewenter, I., Stratton, A.E., Taylor, J.M., Tscharntke, T., Valencia, V., Vogel, C., Kremen, C., 2024. Joint environmental and social benefits from diversified agriculture. Science 384, 87–93. https://doi.org/10.1126/science.adj1914.

Roth, T., Kohli, L., Rihm, B., Meier, R., Amrhein, V., 2021. Negative effects of nitrogen deposition on Swiss butterflies. Conserv. Biol. 35, 1766–1776. https://doi.org/10.1111/cobi.13744.

Roy, D., Thomas, J., 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. Oecologia 134, 439–444. https://doi.org/10.1007/s00442-002-1121-3.

Rudmann-Maurer, K., Weyand, A., Fischer, M., Stöcklin, J., 2008. The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps. Basic Appl. Ecol. 9, 494–503. https://doi.org/10.1016/j.baae.2007.08.005.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020.

Semelová, V., Hejcman, M., Pavlů, V., Vacek, S., Podrázský, V., 2008. The Grass garden in the Giant Mts.(Czech Republic): residual effect of long-term fertilization after 62 years. Agric. Ecosyst. Environ. 123, 337–342. https://doi.org/10.1016/j.agee.2007.07.005.

Settele, J., Feldmann, R., Reinhardt, R., 1999. Die Tagfalter Deutschlands. Ulmer Verlag, Stuttgart, Germany.

Settele, J., Steiner, R., Reinhardt, R., Feldmann, R., Hermann, G., 2015. Schmetterlinge. Ulmer Verlag, Stuttgart, Germany, Die Tagfalter Deutschlands.

Sevilleja, C., Van Swaay, C.A.M., Bourn, N., Collins, S., Settele, J., Warren, M., Wynhoff, I., Roy, D., 2019. Butterfly transect counts: manual to monitor butterflies (No. 16), report VS2019.

Slodowicz, D., Durbecq, A., Ladouceur, E., Eschen, R., Humbert, J., Arlettaz, R., 2023. The relative effectiveness of different grassland restoration methods: a systematic literature search and meta-analysis. Ecol. Solut. Evid. 4, e12221. https://doi.org/10.1002/2688-8319.12221.

Stoate, C., Baldi, A., Beja, P., Boatman, N., Herzon, I., Van Doorn, A., De Snoo, G., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe–a review. J. Environ. Manag. 91, 22–46.

Strijker, D., 2005. Marginal lands in Europe : causes of decline. Basic Appl. Ecol. 6, 99–106. https://doi.org/10.1016/j.baae.2005.01.001.

Tasser, E., Tappeiner, U., 2002. Impact of land use changes on mountain vegetation. Appl. Veg. Sci. 5, 173–184. https://doi.org/10.1111/j.1654-109X.2002.tb00547.x.

Thomas, J.A., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos. Trans. R. Soc. B Biol. Sci. 360, 339–357. https://doi.org/10.1098/rstb.2004.1585.

Thomas, J.A., Telfer, M., Roy, D.B., Preston, C.D., Greenwood, J., Asher, J., Fox, R., Clarke, R., Lawton, J., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879–1881. https://doi.org/10.1126/science.1095046.

Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. 45, 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917.

Van Swaay, C.A.M., Warren, M.S., 2006. Prime butterfly areas of Europe: an initial selection of priority sitesfor conservation. J. Insect Conserv. 10, 5–11. https://doi.org/10.1007/s10841-005-7548-1.

Van Swaay, C.A.M., Cuttelod, A., Collins, S., Maes, D., Munguira, M.L., Šašić, M., Settele, J., Verovnik, R., Verstrael, T., Warren, M., Wiemer, M., Wynhof, I., 2010. European Red List of Butterflies. Publications Office of the European Union, Luxembourg, Luxembourg.

Veen, P., Jefferson, R., De Smidt, J., Van der Straaten, J., 2009. Grasslands in Europe: Of High Nature Value. KNNV Publishing, Zeist, Netherlands.

Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biol. Conserv. 119, 1–18. https://doi.org/10.1016/j.biocon.2003.10.020.

WallisDeVries, M.F., Van Swaay, C.A.M., 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Glob. Chang. Biol. 12, 1620–1626. https://doi.org/10.1111/j.1365-2486.2006.01202.x.

WallisDeVries, M.F., Van Swaay, C.A.M., Plate, C.L., 2012. Changes in nectar supply: a possible cause of widespread butterfly decline. Curr. Zool. 58, 384–391. https://doi.org/10.1093/czoolo/58.3.384.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. Mvabund–an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474.

Wermeille, E., Suisse. Office fédéral de l'environnement, Centre suisse de cartographie de la faune, Chittaro, Y., Gonseth, Y., Birrer, S., 2014. Liste rouge Papillons diurnes et zygènes: Espèces menacées en Suisse, état 2012, L'environnement pratique. Federal Office for Environment ; Swiss Center for Faunal Cartography, Bern, Switzerland.

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x.

Woodcock, B.A., Pywell, R.F., Macgregor, N.A., Edwards, M.E., Redhead, J., Ridding, L. E., Batáry, P., Czerwiński, M., Duffield, S., 2021. Historical, local and landscape factors determine the success of grassland restoration for arthropods. Agric. Ecosyst. Environ. 308, 107271. https://doi.org/10.1016/j.agee.2020.107271.