






RESEARCH ARTICLE

Experimental extensification of mountain grasslands restores plant species richness but not species composition in the mid-term

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Abstract

1. The traditional grasslands that characterize the cultural landscapes of the Palaearctic mountain massifs represent biodiversity hotspots. Yet, they are currently threatened by the intensification of farming practices, notably excesses in fertilization and irrigation.
2. We experimentally investigated the passive restoration of montane and subalpine hay meadows after 6 years of management intensification, with different levels of fertilization and irrigation, followed by 5 years of release of intensive management, that is, extensification. More specifically, relying on a full randomized block-design replicated at 11 Swiss study sites constituted of extensively managed meadows, we exposed during 6 years (2010–2015) four 20 m diameter plots to three levels of intensification (low, medium and high inputs), while a fourth plot served as a control (no inputs). In the second phase of the experiment (2016–2020), all study meadows underwent farming extensification.
3. We monitored total species richness and plant diversity (Simpson diversity), indicator plant species as well as the composition and variability of the plant communities based on Bray–Curtis dissimilarity distances.
4. We found that total species richness decreased in the most intensified plots after 6 years of intensification, but all plots retrieved their baseline species richness after 5 years of re-extensification. In addition, we found no difference between the years in plant diversity (Simpson diversity) among the treatments. Yet, intensification led to different plants communities' compositions in all three levels of intensification in 2015 compared to the extensive plots, and this structural difference remained after 5 years of re-extensification.
5. *Synthesis and applications.* Land-use intensification induces a rapid impoverishment of the flora of mountain meadows. Our results demonstrate the potential of mountain hay meadows to passively restore plant species richness after

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re-extensification; however, plants communities did not fully recover. We recommend maintaining fertilization inputs as low as possible and operating active restoration on grasslands formerly intensified.

KEYWORDS

agricultural intensification, ecological restoration, functional groups, montane grassland, passive restoration, plant communities, species richness

1 | INTRODUCTION

The decline of semi-natural, cultivated grasslands is one of the primary drivers of biodiversity loss globally (Green et al., 2005; Stoate et al., 2001; Tilman et al., 2001), calling for more sustainable agricultural management capable of retaining plant diversity as an insurance for long-term ecosystem stability (Grime, 1998; Hooper et al., 2012; Soliveres et al., 2016). Anthropogenic disturbances of grassland vegetation originate mostly from the management of grasslands with the aim of producing fodder, with their impact varying depending on the degree of intensification (Humbert et al., 2016; Newbold et al., 2015).

In Western Europe, it has been estimated that more than two-thirds of the previously traditionally managed secondary grasslands have been intensified (Dengler et al., 2020). In montane and subalpine regions of Europe, extensively managed hay meadows, dedicated to fodder production for livestock, as well as pastures have typically dominated the agricultural landscape for centuries (Zabel, 2019). In addition to being emblematic of the cultural landscapes of the Palaearctic, these semi-natural grasslands are recognized as habitats of exceptional biodiversity value (Biurrun et al., 2021; Török & Dengler, 2018; Veen et al., 2009) and the maintenance of high species diversity is essential to maintain stable ecosystem functioning and services (Isbell et al., 2011; Soliveres et al., 2016; Tilman et al., 2006). Yet, the multi-functionality of mountain grassland farming, which was for long economically viable and ecologically sustainable, is nowadays threatened by a rapid expansion of agricultural intensification towards higher elevations (Pecher et al., 2017; Schermer et al., 2016).

Grassland intensification among mountain hay meadows, notably in the Swiss Alps, is achieved through increases in inputs of fertilizers (nowadays in the form of liquid manure, i.e. slurry) and in dry regions combined with irrigation (nowadays using mainly sprinklers) that results in increasing mowing frequency (Britschgi et al., 2006) and altered grazing regimes with higher livestock densities. These marked land-use changes—from extensively to intensively managed grasslands—operate as an environmental filter against biological diversity, whereby generalist species take over other specialists, ultimately leading to a sheer simplification or degradation of ecological communities at all levels of the food chain (Andrey et al., 2016; Boch et al., 2021; Gámez-Virués et al., 2015; Gossner et al., 2016; Klein et al., 2020; Schirpke et al., 2020). Therefore, once species diversity has declined as a result of prolonged high-intensity management, the

grassland ecological community would require a long period of time to recover or ends up with irreversible changes (Isbell et al., 2013), impeding any return to a species-richer stable state as long as the artificially added mineral nutrients remain non-limiting.

To remedy grassland degradation, various restoration techniques are currently proposed or under development (e.g. Hedberg & Kotowski, 2010; Jongepierová et al., 2007; Kiehl et al., 2010; Královec et al., 2009; Ludewig et al., 2021; Wagner et al., 2021). Their aim is to reinstate stable assemblages of plants comparable to their non-intensified counterparts (vanandel & Aronson, 2012), further offering room for other associated living forms (Schaffers et al., 2008; Scherber et al., 2010). The capacity of a degraded semi-natural grassland to be reconverted into an integral system is generally greater if the surrounding matrix is made up of a complex and rich plant community (Johanidesová et al., 2015; Lencová & Prach, 2011; Török et al., 2018) and if the exposure to a perturbation has been brief (Bekker et al., 1997). However, any effort towards the retro-conversion target may be compromised by the dynamic of the interspecific interactions taking place in the community, notably those revolving around species dominance and outcompetition that may eventually lead to a total shift in community composition (Fynn et al., 2005; Zhou et al., 2020). Given this complexity, evaluating the appropriateness of different grassland restoration techniques necessitate truly controlled, replicated experiments. Unfortunately, most insights so far came from purely empirical studies carried out mostly at only one site. This is what decided us to launch a long-term research programme on grassland restoration in mountain agro-ecosystems.

The potential for self-recovery of montane grassland communities is likely to be greater than in monotonous landscape matrices where fields are subjected to long-term high-intensity agriculture. This is due to the capacity of a grassland that was species rich in the past but has suffered from a change in its management to recover without any action beyond halting the disturbance. Although most studies have investigated the shifts in plant communities in species-poor, over-simplified landscapes (e.g. grasslands in the lowland), we still lack investigations that experimentally tested the response of montane meadow plant communities to the release of management intensity in traditional, complex agricultural landscapes.

In this context, we experimentally investigated the passive restoration of montane hay meadows (800–1800m a.s.l.), embedded in a naturally richly structured agricultural Alpine landscape, 4 years

after intensive agricultural management had been halted. In particular, we investigated the response of total species richness and plant diversity (Simpson diversity). In addition, we looked at indicator plant species, the relative species abundance and community structure because they reflect long-term ecosystem stability (Foley et al., 2005; Ives et al., 2003; Ives & Carpenter, 2007). We designed a full randomized block-design experiment split in two phases. During the first phase (2010–2015), three randomly chosen plots, within 11 extensively managed hay meadows scattered across the south-western Swiss Alps, were exposed to different degrees of intensification, while a fourth plot serving as a control was not subjected to intensification at all. In the second phase (2016–2020), intensification was totally halted, allowing the plant community to reconstitute. Vegetation relevés were conducted in 2010, 2015 and 2020 to measure, via longitudinal data, the response of plants to releasing management intensity, that is, the restoration potential of montane grasslands.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

In 2010, 11 extensively managed meadows (>4000m² each) were selected as study sites in Valais, SW Swiss Alps (800–1800m elevation; Table S1). Each meadow had been extensively managed (no or very low levels of fertilizer, only in the form of organic solid manure) for at least 10 years prior to the onset of the experiment. Within each meadow, four circular plots of 20m diameter were delimited, their edges being 5 m distant at their closest proximity. Three different experimental treatments matching a gradient of fertilization plus irrigation in combination, as well as a control (no such inputs, i.e. extensive management; hereafter C-plot) were randomly allocated to the four plots of a meadow (Figure S1). The treatment plots received low, medium or high inputs, corresponding to a combination of aerial irrigation (sprinklers) and fertilization (slurry) that mimicked a gradient of intensification, with, respectively, 1/3 (low intensity; I+F 1/3), 2/3 (mid intensity; I+F 2/3) and 3/3 (high intensity; I+F 3/3) of the quantity of inputs that would be necessary to achieve the maximum local hay yield in a given meadow according to its agronomic properties. The exact amount of slurry applied per plot are presented in Table S2, and in Andrey et al. (2014, 2016) and Lessard-Therrien et al. (2017). Mowing regimes had to be adapted to phytomass production to simulate local farming practice: C- and I+F 1/3 plots were mown once a year, the other plots twice a year (see Andrey et al., 2014, 2016; Lessard-Therrien et al., 2017 for details). From 2016 onwards, we stopped fertilization and watering operations, that is, totally released intensification, thus eliciting a phase of 're-extensification'.

All farmers granted us access to their meadows for the duration of the study. No other authorization was required to conduct the fieldwork.

2.2 | Vegetation relevés

In each circular treatment plot, a permanent subplot of 2×4 m was placed at a distance of 4 m from the plot centre, with the rectangle being oriented longitudinally parallel to the slope axis (see figure 1 in Andrey et al., 2016 and Figure S1). The upper proximal corner of the subplot was permanently marked belowground with a nail enabling that the sampling area could subsequently be retrieved. Baseline vegetation relevés have been conducted prior to treatments, in 2010 and in the last year with experimental inputs, in 2015. In June 2020, we conducted new vegetation relevés, following the exact same procedure as in 2010 and 2015, at nine of the 11 study sites (two meadows having in-between unfortunately been converted into other land-uses). Plant species richness was assessed from field vegetation relevés while the cover of each species within the plot was estimated visually before the first mowing in June–July. Plant species covering only <0.1% were arbitrarily attributed a percentage of 0.03.

2.3 | Statistical analyses

All analyses were performed using R v. 3.5.3 (R Core Team, 2020).

2.3.1 | Treatment effects on plant species richness, diversity and cover

First, we tested the effect of the three experimental treatments against control with a four-level factorial analysis (low, mid- and high intensity, i.e. I+F 1/3, I+F 2/3, I+F 3/3). Second, we tested the difference between sampling dates, that is, 2010–2015, 2010–2020 and 2015–2020 with a three-factorial analysis and by changing the contrast. For both analyses, the response variables were as follows: (1) plant species richness and (2) plant diversity as measured by Simpson's diversity (D_1) where $D_1 = 1 - \sum p_i^2$, with p_i being the cover of each species i (Morris et al., 2014). Additional analyses on (3) species richness of three different functional groups (legumes, forbs and grasses) and (4) cover of the three functional groups are presented in the supplemental results of the supporting information. We opted for a combination of species richness and Simpson diversity indices in order to account for biases typically induced by either rare or abundant plant species (Morris et al., 2014).

We ran linear mixed-effects models (LMMs), with restricted maximum likelihood for parameter estimation, using the *lmer* function from the *lme4* R package (Bates et al., 2015). The validity of each LMM was verified by comparing the Akaike information criterion (AIC) of the full model against the AIC of the null model (intercept only), using the maximum likelihood estimation function (Forstmeier & Schielzeth, 2011). Modelling assumptions (normality and homoscedasticity of residuals, homogeneity of variance and normality of random effect) were further validated by visual inspection using

the *check_model* function of the *PERFORMANCE* R package (Lüdecke et al., 2021). Variables were transformed when necessary (indicated in the respective summary Tables 1 and 2 and Tables S4–S7).

For facilitating the interpretation of the results and because the design and the inclusion of random factors rendered insufficient degrees of freedom to run a full model fitting an interaction term *treatment* × *year*, that would include both the repeated measures in each plot and the study sites as random intercepts, we first ran separate models for each year with study site included as a random intercept. We then ran separate models for each treatment but including all 3 years with study site included as a random intercept. To avoid inflating the family-wise type I rate from multiple models testing the same hypothesis, we controlled the false discovery rate, that is, the proportion of incorrect rejections among all rejections of the null hypothesis (Benjamini & Hochberg, 1995), and corrected all *p*-values with the *fdr* method of the *p.adjust* function (*STATS* package; R Core Team, 2020). All linear mixed model outputs, variable transformation and Δ AIC are reported in Tables 1 and 2 and Tables S4–S7.

2.3.2 | Multivariate analyses of plant community composition and variability

All multivariate analyses were performed using the *VEGAN* R package (Oksanen et al., 2020). Here again, for an easier interpretation of the results and due to a lack of degrees of freedom to run a full model

including an interaction term *treatment* × *year*, we ran separate models for each year of sampling.

We tested the effect of treatment on plant community composition with a permutational analysis of variance (*permanova*; 999 permutations) using Bray–Curtis dissimilarity with the function *adonis*. It tests the null hypothesis that the centroids and dispersion of the species (as defined by the measure of space) within each group (i.e. treatment) are equivalent. A rejection of the null hypothesis means that either the centroid and/or the spread of the species is different between groups. To compare specific groups, we ran pairwise analyses between each experimental treatment and the control and corrected *p*-values applying the false discovery rate (*p.adjust*) as described above.

To test for homogeneity of dispersion among groups (i.e. beta diversity), we created a distance matrix with a square-root transformed Bray–Curtis dissimilarity index using *vegdist* and performed an analysis of multivariate homogeneity of group dispersions using the *betadisper* function. This function calculates the average distance of group constituents (plant species within each treatment) to the group spatial median in a multivariate space. To test if one or more levels of our experimental treatment is/are more variable than the other(s), we performed a permutation test (ANOVA; 999 permutations) of the distances to group spatial medians under the null hypothesis of no difference in dispersion between the four levels of the experimental treatment. Statistical significance was obtained from post-hoc

TABLE 1 Linear mixed model outputs testing for an effect of the three levels of intensification on total plant species richness and Simpson diversity fitted using a restricted maximum likelihood function. Transformation of the response variable is indicated in the estimate column and corresponding year. All the *p*-values presented are corrected for the false discovery rate. Significant effects (*p* < 0.05) are in bold. The difference between the AIC of each full model against the AIC of the null model (intercept only) is indicated in the Δ AIC column, a negative Δ AIC meaning that the full model better explains the data

	Plant species richness					Simpson diversity				
	Estimate	SE	df	<i>p</i>	Δ AIC	Estimate	SE	df	<i>p</i>	Δ AIC
2010					0.300					−0.300
Intercept (control)	47.455	2.593	21.257	<0.001		0.819	0.030	19.260	<0.001	
I+F 1/3	4.727	2.481	30.000	0.199		0.032	0.027	30.000	0.305	
I+F 2/3	3.364	2.481	30.000	0.556		−0.021	0.027	30.000	0.443	
I+F 3/3	4.522 E-15	2.481	30.000	1.000		−0.031	0.027	30.000	0.388	
2015					−6.000	<i>Logit</i>				1.600
Intercept (control)	48.091	2.678	28.960	<0.001		1.251	0.237	38.806	<0.001	
I+F 1/3	−0.455	3.039	30.000	0.882		0.475	0.318	30.000	0.305	
I+F 2/3	−2.455	3.039	30.000	0.638		0.310	0.318	30.000	0.443	
I+F 3/3	−9.727	3.039	30.000	0.010		−0.101	0.318	30.000	0.753	
2020					4.700					2.100
Intercept (control)	47.889	2.777	18.533	<0.001		0.847	0.031	30.838	<0.001	
I+F 1/3	−0.667	2.798	24.000	0.882		0.044	0.042	24.000	0.305	
I+F 2/3	−0.889	2.798	24.000	0.753		0.071	0.042	24.000	0.304	
I+F 3/3	−2.889	2.798	24.000	0.468		0.067	0.042	24.000	0.357	

TABLE 2 Linear mixed model outputs testing for an effect of each year on total plant species richness and Simpson diversity. Transformation of the response variable is indicated in the estimate column and corresponding treatment. All the p -values presented are corrected for the false discovery rate. Significant effects ($p < 0.05$) are in bold and marginally non-significant effects ($0.05 < p < 0.1$) in italics. The difference between the AIC of each full model against the AIC of the null model (intercept only) is indicated in the Δ AIC column, a negative Δ AIC meaning that the full model better explains the data

	Plant species richness					Simpson diversity				
	Estimate	SE	df	p	Δ AIC	Estimate	SE	df	p	Δ AIC
Control	Log					3.400				
Intercept (2010)	3.846	0.067	18.236	<0.001		0.819	0.049	17.688	<0.001	
2015 vs. 2010	0.009	0.065	17.720	0.888		-0.070	0.048	16.804	0.358	
2020 vs. 2010	-0.041	0.069	18.221	0.577		-0.001	0.051	17.343	0.981	
Intercept (2015)	3.855	0.067	18.236	<0.001		0.749	0.049	17.688	<0.001	
2020 vs. 2015	-0.050	0.069	18.221	0.958		0.069	0.051	17.343	0.199	
I + F 1/3	Log					0.700				
Intercept (2010)	3.944	0.059	22.838	<0.001		0.850	0.025	26.181	<0.001	
2015 vs. 2010	-0.107	0.067	18.519	0.167		-0.026	0.032	18.719	0.577	
2020 vs. 2010	-0.103	0.071	19.221	0.326		0.042	0.034	19.651	0.309	
Intercept (2015)	3.836	0.059	22.838	<0.001		0.825	0.025	26.181	<0.001	
2020 vs. 2015	0.004	0.071	19.221	0.958		0.068	0.034	19.651	0.081	
I + F 2/3	Log					0.000				
Intercept (2010)	3.915	0.048	24.330	<0.001		1.258	0.047		<0.001	
2015 vs. 2010	-0.103	0.053	20.397	0.156		-0.029	0.054		0.587	
2020 vs. 2010	-0.090	0.056	21.132	0.326		-0.155	0.054		0.018	
Intercept (2015)	3.812	0.048	24.330	<0.001		1.229	0.046		<0.001	
2020 vs. 2015	0.014	0.056	21.132	0.958		-0.126	0.054		0.039	
I + F 3/3	Log					-4.300				
Intercept (2010)	3.843	0.057	27.299	<0.001		1.311	0.090		<0.001	
2015 vs. 2010	-0.221	0.076	15.907	0.043		0.095	0.071		0.358	
2020 vs. 2010	-0.046	0.081	17.145	0.577		-0.139	0.068		0.083	
Intercept (2015)	3.622	0.057	27.299	<0.001		1.405	0.092		<0.001	
2020 vs. 2015	0.175	0.081	17.145	0.179		-0.234	0.071		0.004	

*GLMM applied.

tests of pairwise differences using the Tukey Honest Significant Differences test with *TukeyHSD*.

To account for our full block design, that is, we tested the effect of treatment within each study site, permutation tests were performed within experimental sites (i.e. meadows) but never across them. Restricted permutation could be achieved by setting a strata directly on the model generated, either using the function *adonis* from the *VEGAN* package or with the function *how* from the package *PERMUTE* (Simpson, 2019).

To visualize the plants community composition and homogeneity (i.e. beta diversity), we extracted the scores of each site of the groups as well as the distances to their centroids (medians) along the first two main axes of a principal coordinates analysis and displayed the four treatments with different colours (Figure 2). All summary statistics of both analyses are reported in Table 3 and Table S8.

2.3.3 | Indicator species analysis

We ran an indicator species analysis (*multipatt* function of the *INDIC-SPECIES* package; Cáceres & Legendre, 2009) to identify which species (1) reflect the biotic or abiotic state of the local environment; (2) provide evidence for the impact of changes resulting from the experimental treatments and (3) best predict overall plant species diversity within the treatment plots (Cáceres & Legendre, 2009). We further relied on a correlation index to assess the positive or negative ecological preference of a plant species for a given treatment; the statistical significance of these relationships was tested via permutation tests of the underlying plant abundance matrix (999 permutations). Corrections for multiple testing (i.e. multiple species tested) were applied using the false discovery rate (*p.adjust*) described above. Summary statistics of the indicator species analysis are reported in Table S9.

FIGURE 1 Effects of different levels of combined irrigation and fertilization (I+F, with 1/3, 2/3 and 3/3 corresponding to low-, medium- and high-intensity management, respectively) on plants species richness and Simpson diversity index in 2010, 2015 and 2020 as measured from vegetation relevés carried out on a reference area of 8 m² per plot. Non-significant differences between treatments and control are indicated by the annotation 'NS' and significant effects are indicated by asterisks (***p* ≤ 0.01).

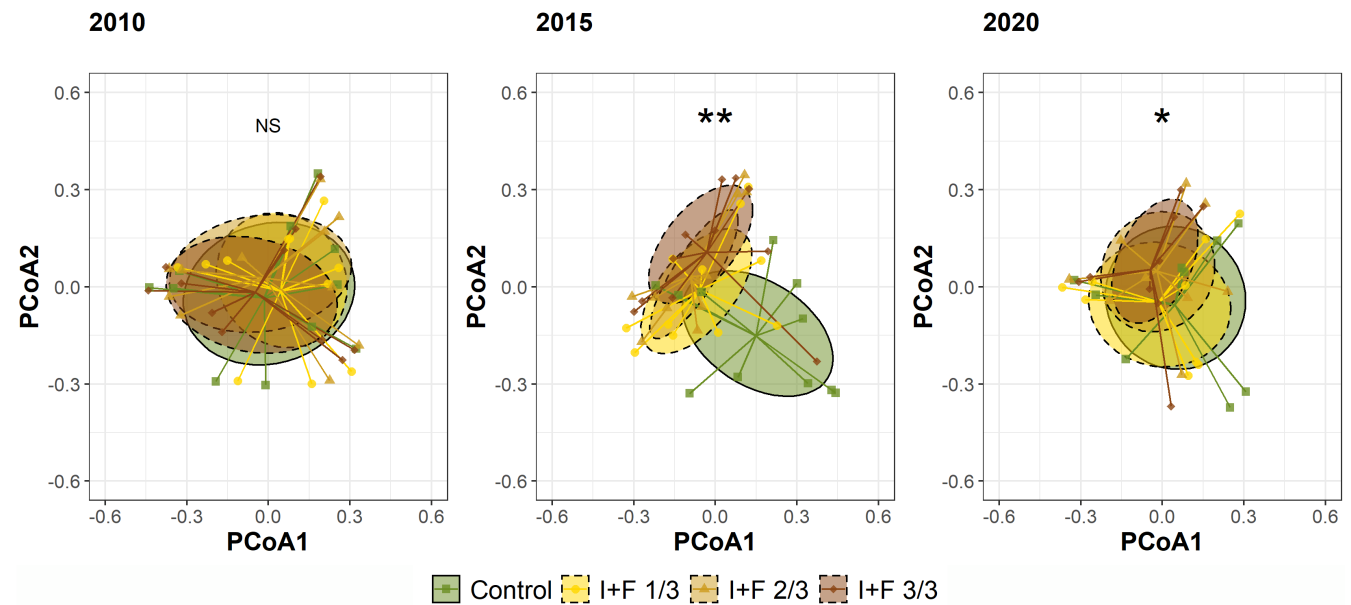
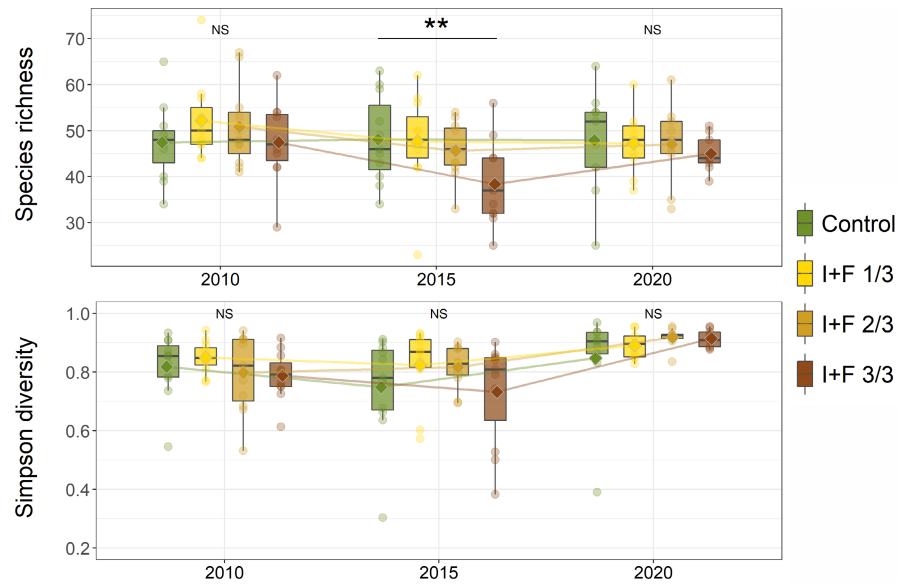


FIGURE 2 Principal coordinates analysis (PCoA) ordination plot of the first two axes based on Bray–Curtis dissimilarities of plants community variabilities among the three levels of intensification (see legend of Figure 1 for more details) in 2010, 2015 and 2020. Non-significant differences between treatments and control are indicated by the annotation 'NS' and significant effects are indicated by asterisks (**p* ≤ 0.05, ***p* ≤ 0.01).

3 | RESULTS

We recorded a total of 310 species of plants from 39 families over the three sampling dates and treatments. All recorded species and respective cover are presented in the Dryad Digital Repository (Humann-Guillemint et al., 2022). Basic descriptive statistics are presented in Table S3.

3.1 | Treatment effects on plant species richness and diversity

At the onset of the experiment, in 2010, there were no statistically significant differences in plant species richness and diversity (Simpson D₁ index) between any of the experimental treatments and the controls (Table 1, Figure 1), indicating that the random allocation

TABLE 3 Summary statistics of permutational multivariate analysis of variance using the Bray–Curtis distance indices testing the effects of experimental management treatment on plant community composition. Presented are degrees of freedom, variance explained (R^2), F -values and p -values. Significant effects ($p < 0.05$) are in bold and marginally non-significant effects ($0.05 < p < 0.1$) in italics. p -values from the pairwise analyses are presented with the false discovery rate correction

	df	F-value	R^2	p
2010				
Treatment	3	0.574	0.041	0.089
Control vs. I + F 1/3	1	0.626	0.030	0.154
Control vs. I + F 2/3	1	0.352	0.017	0.390
Control vs. I + F 3/3	1	0.419	0.021	0.317
2015				
Treatment	3	1.671	0.111	0.001
Control vs. I + F 1/3	1	1.997	0.091	0.002
Control vs. I + F 2/3	1	2.883	0.126	0.002
Control vs. I + F 3/3	1	2.797	0.123	0.002
2020				
Treatment	3	0.726	0.064	0.011
Control vs. I + F 1/3	1	0.452	0.032	0.467
Control vs. I + F 2/3	1	1.014	0.066	0.015
Control vs. I + F 3/3	1	1.156	0.079	0.015

of treatments and control to plots induced no bias. In 2015, we found a significant decrease (by 20.2%) in plant species richness of the most intensified (I + F 3/3) plots, compared to the control plots, but no difference as regards the Simpson diversity (Table 1, Figure 1). In 2020, after 5 years of re-extensification, there was no statistically significant difference anymore between any of the three levels of intensification and the controls, neither for plant species richness nor for diversity (Table 1, Figure 1).

Species richness significantly decreased by 5.2% in the high-intensive treatment between 2010 and 2015 (Table 2, Figure 1). However, we did not find any other significant results regarding the species richness between any years (Table 2, Figure 1). We found a significant and marginally non-significance difference in Simpson diversity between 2015 and 2020 in the mid- and high-intensive and low-intensive treatments, respectively (Table 2, Figure 1). There was no statistical difference in Simpson diversity in any of the treatments between 2010 and 2015 nor 2010 and 2020.

Results on the effects of treatments on plant species richness and cover of the three functional groups are presented in the supplementary Results and Discussion, and in Tables S4–S7 and Figures S2 and S3.

3.2 | Treatment effects on plant community composition and variability

While the permutational multivariate analysis of variance using Bray–Curtis distance index did not detect any significant effect of

our experimental treatment on plant species composition in 2010, there was a significant effect of treatment in 2015 and 2020. More specifically, our experimental treatments explained 11% and 6% of the compositional variance in 2015 and 2020, respectively (Table 3, Figure 2). When conducting pairwise comparisons between the three levels of intensification and the control plots, we found that, in 2015, the plant species composition of all three intensification levels differed from that of the control plots, with our treatment explaining 9%–13% of the compositional variance (Table 3, Figure 2). Moreover, in 2020, the mid-intensive plots and the high-intensive plots significantly differed from the control plots in terms of plant species composition, with our experimental treatment explaining 7% and 8% of the compositional variance, respectively. Yet, plant species composition was not significantly different between the low-intensive and the control plots (Table 3, Figure 2).

The analysis of multivariate homogeneity of group dispersions using Bray–Curtis distance index did not reveal any significant effect of our experimental treatment on the variability of plant communities, neither in 2010, 2015 nor in 2020 (Table S8, Figure 2).

Results of the indicator species analysis are presented in the supplementary Results and Discussion, and in Table S9.

4 | DISCUSSION

The effects of land-use intensification and re-extensification upon grassland biodiversity are still poorly documented, which represents an impediment to the development of sound grassland restoration strategies. Our long-term, spatially replicated field experiment, which involved 6 years of farming intensification (with slurry addition and aerial irrigation), followed by 5 years of re-extensification, established that plant species richness of Alpine hay meadows dramatically declined under the highest level of agricultural intensification, but was passively restored 5 years after intensification had been halted. In contrast, plant diversity (Simpson D_1 index) showed no significant pattern all along years and across treatments and controls. After 6 years of intensification followed by 5 years of re-extensification, however, the composition of the plant communities still remained affected by intensification. Plant communities had not fully returned to their initial composition, suggesting some mid-term retention of the effects of formerly intensified farming practices. We shall first discuss these findings in the light of the extant literature, before drawing preliminary recommendations for biodiversity-friendly management of mountain hay meadows.

Intensification induces a rapid impoverishment of the flora of montane and subalpine meadows in the short term (Andrey et al., 2014) and mid-term (Boch et al., 2021; Lessard-Therrien et al., 2017), as demonstrated by our earlier work within the same experimental set up and corroborated in this study. In addition, effects of intensification are more pronounced in species-rich grasslands (e.g. extensive grasslands) compared to species-poor grasslands because species-rich grasslands are home to a larger number of rare species, more vulnerable to increasing land-use intensity (Kleijn

et al., 2009; Suding et al., 2005). Although plant species richness could be passively reversed after 5 years of re-extensification, plant communities' compositions were not completely restored. The analyses of the composition of the plant communities (i.e. beta diversity) and of the relative species-specific abundances show that intensification did not affect the floral composition but influenced their relative abundance. In effect, fairly similar across all plots in 2010, the relative species-specific abundances started to diverge after 5 years of intensification, with a legacy effect still observable in the mid- and the high-intensive plots in 2020, that is, after 5 years of re-extensification. Nonetheless and in contrast, these differences have vanished already in 2020 in low-intensive plots, compared to control plots, exemplifying the potential resilience of the hay meadow plant community to mid-term intensification of management and mid-term re-extensification, provided that the amount of fertilizer applied remained low. In addition, the indicator species analysis revealed that plant species with a propensity to grow in nitrogen-rich soils (e.g. *Taraxacum officinale* aggr., *Trifolium repens* or *Ranunculus acris*) were more abundant in 2015 and 2020 in the plots that had received mid to high amounts of fertilizers and irrigation before 2016 (see supplementary Discussion for details). This suggests that the environmental conditions in the two most intensified plots were not fully restored after 5 years: the accumulation of nutrients in the soil was still impacting plant communities after 5 years of re-extensification, engendering a mid-term legacy effect of intensive agricultural management. The rapid convergence in species richness and slow convergence in species composition has also been found in other grassland experiments where communities were allowed to passively reassemble after manipulation of the initial plant community composition (Fukami et al., 2005; Roscher et al., 2009).

In the light of this contrasted pattern, two main questions emerge. First, did the fairly short periods of intensification (6 years) and re-extensification (5 years) of our experiment explain the high mid-term resilience of our plant species richness and diversity to farming intensification? Second, did the embedment of our meadows among heterogeneous and naturally richly structured farmed landscapes, natively particularly rich in biodiversity, contribute to enhance the recovery of the hay meadow flora, thanks to what has been termed an insurance effect (Yachi & Loreau, 1999)? The short-term history of grasslands intensification and the landscape matrix itself may play a decisive role when it comes to regeneration. Intensified mountain meadows are most of the time embedded in a heterogeneous environment that still consists of small fields, subjected to various levels of management intensity, interspersed with natural structures such as hedges, stone walls, etc. A greater landscape heterogeneity involves an increased number of potential sources of plant species via the dispersion of propagules over sometimes long distances (Geertsema et al., 2002). It may therefore increase the regional species pool, enhance colonization probability of the target grassland and likely contributed to the partial recovery of our experimental plots (Bakker & Berendse, 1999; Bekker et al., 1997; Benton et al., 2003; Lencová & Prach, 2011; Riedener

et al., 2015; Török et al., 2018; Wagner & Edwards, 2001). However, the establishment of species adapted to disturbed environments is a slow process and species sometimes need several decades to establish even when the seed pool is available in the immediate vicinity (Berendse et al., 2021; Isbell et al., 2013). Although grasslands can eliminate accumulated nitrogen following fertilization episodes, full recovery may take several years before formerly fertilized soils return to concentrations similar to that of unfertilized grasslands (Clark et al., 2009; Stevens, 2016). Furthermore, the recovery of species richness does not necessarily predict the restoration of species composition, that may take centuries to recover once the grasslands are destroyed (Isbell et al., 2019; Nerlekar & Veldman, 2020). To fasten the process of grassland restoration, multiple reliable approaches for active restoration are available. Methods include, for instance, the addition of hay or seeds collected from a species-rich donor grassland (Bischoff et al., 2018; Slodowicz et al., 2019; Valkó et al., 2022), topsoil transfer from a species-rich donor grassland or topsoil removal from the degraded grassland (Buisson et al., 2022; Piqueray et al., 2020; Rasran et al., 2007) or the activation of the soil seed bank (Klaus et al., 2018; Ludewig et al., 2021). So far, seed addition via hay transfer appears to be an effective measure for grassland restoration, provided that the donor sites are sufficiently species rich and close enough to the receiver grassland to ensure compatibility (Albert et al., 2019; Durbecq et al., 2022; Valkó et al., 2022).

The present robust experimental study, because spatially replicated and fully controlled, demonstrates the potential of montane and subalpine hay meadows to passively restore the flora species richness in the mid-term. However, it also demonstrates that more time is needed for intensified meadows to retrieve their original plants composition. We therefore recommend keeping grasslands management as extensive as possible while maintaining a surrounding undisturbed area. When considering the recovery of former intensified montane and subalpine grasslands, we recommend operating active restoration of grasslands by means of a relaxation of farming intensification, together with a transfer of hay from adjacent species-rich donor meadows, which are still readily available in the Alps.

AUTHOR CONTRIBUTIONS

Jean-Yves Humbert conceived the study. Jean-Yves Humbert, Aline Hayoz-Andrey, Malie Lessard-Therrien and Ségolène Humann-Guillemot designed the study. Ségolène Humann-Guillemot, Malie Lessard-Therrien, Aline Hayoz-Andrey, Alberto Serres-Hänni, Steffen Boch, Gerard Martinez-De León and Jean-Yves Humbert conducted the experiment and collected the data. Ségolène Humann-Guillemot performed the statistical analyses and wrote the manuscript. All authors read and approved the manuscript.

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CONFLICT OF INTEREST

The authors bear sole responsibility for the content and declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.ksn02v787> (Humann-Guillemint et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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