




Experiment-based recommendations for biodiversity-friendly management of mountain hay meadows

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Keywords

Biodiversity; Conservation; Fertilization; Functional groups; Grasslands; Irrigation; Phylogenetic diversity; Species richness

Abbreviations

F = Fertilization; I+F = Irrigation and fertilization; I = Irrigation.

Nomenclature

Lauber et al. (2012)

Received 28 July 2016

Accepted 16 February 2017

Co-ordinating Editor: Beth Middleton

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Introduction

For centuries, grasslands below the tree line of European mountain ranges have been managed traditionally, creating diverse, biodiversity-rich cultural landscapes (Poschlod & Wallis de Vries 2002). These grasslands result from a long history of human exploitation for hay production, which varied according to local culture and natural context (Fischer & Wipf 2002; Väre et al. 2003; Baur et al. 2006).

Abstract

Question: The biodiversity of mountain hay meadows has historically been maintained through traditional, low-intensity farming practices. In recent decades, however, agricultural intensification for hay production has led to dramatic declines in their biodiversity. This study asks: which management practices can contribute to maintaining the biodiversity value of mountain hay meadows without jeopardizing agricultural revenue?

Location: Eleven semi-natural meadows, canton of Valais, inner Alps, south-west Switzerland.

Methods: We experimentally measured the effects of various intensities of fertilization (slurry) and aerial irrigation (sprinklers) on the taxonomic, phylogenetic and functional diversity of plants. The experiment consisted of six different treatments, each randomly applied to one of six plots within a meadow. A plot therefore was (1) not irrigated and only fertilized with slurry, (2) not fertilized and only irrigated with a sprinkler, (3–5) receiving low, medium or high amounts of both fertilizer and water, respectively, or (6) receiving no input of irrigation or fertilizer (control plots).

Results: After 4 yr, all biodiversity metrics were negatively impacted under the highest management intensity (irrigation combined with fertilization at concentrations corresponding to the input necessary to achieve maximum local hay yield, i.e. three-thirds of inputs). In contrast, at low- and mid-intensity management levels (irrigation combined with fertilization at one-third and two-thirds of the maximum concentration, respectively) most diversity metrics did not differ from the controls, except for forb species richness, which was already reduced under mid-intensity management compared to low-intensity and control plots. Neither irrigation nor fertilization alone had a negative impact on plant biodiversity.

Conclusions: Low to moderate agricultural intensification of hay production does not appear to be detrimental to plant biodiversity among mountain meadows. These results suggest that sustainable management would be obtained via irrigation and fertilization corresponding to one-third to two-thirds of the quantity necessary to achieve maximum local hay yield.

These semi-natural grasslands were all characterized by low-intensity management involving mostly limited inputs of solid manure obtained from the farmer's own livestock (Maurer et al. 2006). However, in drier mountain regions, such as the inner Rhône and Rhine valleys, grasslands exploited for hay were also irrigated to reduce stress caused by drought, using a network of open water channels which distributed water to the meadows by gravity (Crook & Jones 1999; Leibundgut 2004).

In recent decades, many of these semi-natural mountain hay meadows have been abandoned in difficult terrain that is inaccessible to agricultural machinery, which has led to progressive encroachment by woody plants and eventually, reverting to forest (e.g. Gellrich et al. 2008; Graf et al. 2014). Yet, in more accessible areas, the meadows have been farmed more intensively in the quest for higher forage production (Tasser & Tappeiner 2002). Throughout Europe, these changes have provoked a dramatic decline of traditionally managed, biodiversity-rich meadows (Poschold & Wallis de Vries 2002; Tasser & Tappeiner 2002; Fischer et al. 2008; Niedrist et al. 2009). In the Swiss Alps, for example, approximately 95% of the area of dry meadows and pastures were lost between 1900 and 2010 (Lachat et al. 2010). Grassland management intensification in alpine regions involves fertilization with slurry (compound fertilizer from livestock wastes composed mostly of N, P and K), and irrigation via sprinklers (Crook & Jones 1999). These modern practices alter plant community composition because some species profit from enhanced nutrient and water supply, increasing biomass production (Fischer & Wipf 2002; Bassin et al. 2012), whereas others disappear through competitive exclusion (Grime 1973). This phenomenon is well explained by the hump-shaped model, which posits that plant diversity peaks at intermediate levels of productivity (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015). At low productivity levels, where soil nutrients are deficient, only a few species can tolerate environmental stress, whereas at high productivity levels, only a few highly competitive species dominate. To date, the coupling of irrigation and fertilization along an intensification gradient has not been addressed experimentally in mountain grassland systems, which hinders the formulation of clear management recommendations for sustainable farming practices.

In order to understand some of the impacts of modern agricultural practices in this system, our study examines the influence of the addition of water (irrigation via sprinklers) and/or compound organic fertilizer (slurry, i.e. liquid cattle manure) on the plant communities of species-rich montane and sub-alpine hay meadows in the Swiss Alps. Our experimental design included a gradient of management intensity (four levels) as well as a factorial design that allowed testing for the individual effects of irrigation and fertilization. Four years after the onset of the experimental manipulation, we measured how management intensity affects various metrics of plant biodiversity, including species richness, Shannon index, as well as phylogenetic and functional diversity (grasses, legumes and forbs).

Based on the hump-shaped model (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015), our broad hypothesis was that conventional plant biodiversity metrics (species

richness and diversity) would show the largest values at moderate management intensity (typical of traditional, low-intensity management), and the lowest values at maximum management intensity (modern approach to maximize hay production). Although the impact of fertilization on grasslands has received considerable attention, changes in irrigation techniques (i.e. from traditional irrigation with open gravity channels to the use of sprinklers) are little documented. In two studies, the type of irrigation did not affect plant biodiversity in mountain areas (Riedener et al. 2013; Melliger et al. 2014). Given data scarcity for both the impact of irrigation, and of irrigation combined with fertilization, we designed an experiment that merged different intensities of fertilization and irrigation, thereby mimicking different options for modern hay production intensification.

In addition to those traditional biodiversity metrics, we also relied on phylogenetic information, most commonly referred to as phylogenetic diversity. This is a measure of the proportion of evolutionary history (i.e. how species are related to each other, measured by the distance between them in a phylogenetic tree) represented within a given community (Faith 1992). This approach provides information on the evolutionary trajectory of the species pool, and its evolutionary potential and functional diversity, as most traits are phylogenetically conserved (Purvis & Hector 2000; Cadotte & Davies 2010). Therefore, phylogenetic diversity represents a separate and distinct measure of biodiversity that supplements conventional information derived from mere taxonomy-based analyses. More specifically, we hypothesized that high management intensity reduces phylogenetic diversity, predicting that plant communities in highly productive meadows are composed of closely related species (Grime 1973; Harvey & Pagel 1991).

Finally, we also looked at the responses of various functional groups to management intensity (Mountford et al. 1993; Leto et al. 2008; Onipchenko et al. 2012). In general, abundance of grass species is expected to increase with nutrient input, mainly as a consequence of N addition, while legume species, which have symbiotic relationships with N fixers, would benefit from nutrient input only if P and K are also included. Forbs with faster growth rates and large aerial structures are expected to respond positively to fertilization, but small forb species with slow growth rates and/or occupying specific microhabitats (Grime 1998) are generally expected to decline in cover, contributing significantly to an overall decline in species richness (Kirkham et al. 1996). We thus predicted contrasting responses in change of percentage cover between these different functional groups to experimental intensification of management. Ultimately, the aim of this study is to identify the optimal trade-off for the conservation of

plant biodiversity with hay production in the context of modern meadow management.

Methods

Study sites

In 2010, 11 traditionally managed hay meadows were selected within the canton of Valais, in the inner Alps of southwest Switzerland (Fig. 1). The region is characterized by a continental climate with cool and wet winters, as well as warm and dry summers. Average monthly ambient temperature (2004–2014) in the valley at 482 m a.s.l. ranged from a minimum of 0.3 °C in Jan to a maximum of 20.5 °C in Jul (Federal Office of Meteorology and Climatology 2016). The 11 meadows were situated within the montane and sub-alpine belts, between 880 and 1770 m a.s.l. (Table 1). These meadows have been extensively managed for at least 10 yr preceding the experiment. The extensive management consisted of no ($n = 8$ meadows) or low amounts of fertilization once per year (three meadows), no (five meadows) or some irrigation during droughts (six meadows), as well as one harvest of hay per year in all meadows.

Experimental design

Within each of the 11 meadows, six management treatments were randomly assigned to 20-m diameter plots, with at least 5 m separating the boundaries of adjacent plots. The same treatment was applied consistently each

year. The first treatment served as a control (no input: C-plot) while the second was irrigated with sprinklers (I-plot; see Table 2 for irrigation level) weekly from May until mid-Sept, except when there was heavy rainfall (>20 mm water during the previous week). The third plot was fertilized with slurry twice during the summer, once in the spring and a second time after the first hay harvest (F-plot). The three other plots received a combination of fertilization and irrigation at three levels, which corresponded to 1/3, 2/3 or 3/3 of the amount required to achieve the maximum local hay yield (I+F 1/3-, I+F 2/3-, I+F 3/3-plots, respectively) according to Sinaj et al. (2009). This design allowed us to test the different influences of irrigation and fertilization along a gradient of management intensification. All plots were mown twice during the growing season, except the C-plots, which were mown once to simulate local standards for extensively managed meadows. The fertilizer consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, CH) and mineral potassium-sulphate (K_2SO_4) dissolved in water so as to reach the viscosity of standard farm slurry (Sinaj et al. 2009). A total of 1 m³ of this solution contained 2.4 kg of available N, 0.87 kg of P and 6.64 kg of K. The amount of slurry applied per plot depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site elevation (see appendix A in Andrey et al. 2016). Study sites were therefore divided into categories of similar potential productivity (Table 1), which correlates strongly with elevation, with the amount of added fertilizer adjusted accordingly (Table 2).

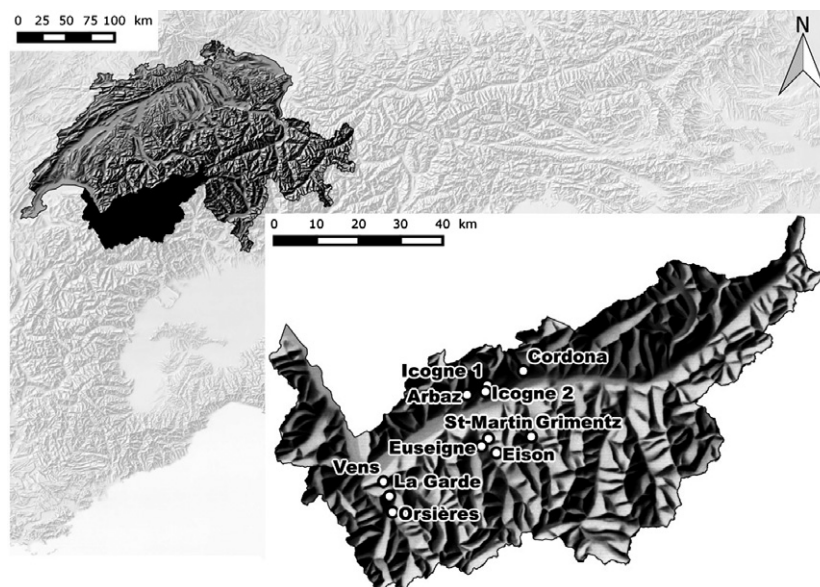


Fig. 1. Location of the 11 meadows used as study sites in the canton of Valais (outlined in black on the country map), southwest Switzerland.

Table 1. Description of study meadows in the inner Alps of southwest Switzerland by typical productivity type (A: higher elevation and lower productivity; B: mid-elevation and intermediate productivity; C: lower elevation and higher productivity with fertilizer amount adjusted for each category; Table 2), elevation and geographic coordinates.

Number	Meadow	Productivity Type	Elevation (m a.s.l.)	Coordinates	
				Latitude	Longitude
1	Icogne 2	C	880	46°17'6" N	7°26'10" E
2	La Garde	B	980	46°3'45" N	7°8'35" E
3	Orsières	C	1022	46°1'44" N	7°9'8" E
4	Euseigne	C	1028	46°10'9" N	7°25'27" E
5	Cordona	B	1153	46°19'45" N	7°33'8" E
6	Icogne 1	B	1200	46°17'56" N	7°26'31" E
7	Arbaz	B	1270	46°16'42" N	7°22'47" E
8	Vens	B	1373	46°5'7" N	7°7'24" E
9	St-Martin	A	1589	46°11'8" N	7°26'43" E
10	Grimontz	A	1738	46°11'22" N	7°34'35" E
11	Eison	A	1768	46°9'18" N	7°28'10" E

Vegetation survey

In each plot, one permanently marked subplot of 2 m × 4 m was established randomly, either on the right or left of the centre when facing upslope. Vegetation surveys were conducted during Jun and Jul 2014. In each subplot, all individuals were identified to species level and their percentage cover was visually estimated by two observers, and averaged if different. The species were further classified according to functional groups: graminoids (Poaceae, Cyperaceae and Juncaceae; hereafter referred to as grasses), legumes (Fabaceae) and forbs (other families). Tree and shrub species seedlings were excluded from the analysis.

Phylogenetic reconstruction

Phylogenetic relationships between all the plant species found in the study meadows (Appendix S1) were retrieved

from a well resolved and dated phylogeny of 4685 European species (Durka & Michalski 2012). This phylogeny was constructed by manually combining sub-trees from recent molecular studies of recognized family relationships, dated with the most recent fossil records (Durka & Michalski 2012). An ultrametric phylogenetic tree was calculated so that distances from the root to every branch tip (current species) were equal. We pruned this phylogeny to match the species pool found in all our sites using the R-package *ape* (Paradis et al. 2004).

Statistical analysis

The effects of irrigation, fertilization and the gradient of irrigation and fertilization combined (C, I, F, I+F 1/3, I+F 2/3 and I+F 3/3) on biodiversity metrics (species richness and diversity, phylogenetic diversity and functional group species richness and cover) were tested with linear mixed effects models (LMMs) using the R-package *lme4* (Bates et al. 2015). Species richness was defined as the total number of vascular plant species recorded in each subplot. The Shannon-Wiener index of diversity (Spellerberg & Fedor 2003), hereafter referred to as the Shannon index, was computed using the *diversity* function from the *vegan* R-package. Phylogenetic diversity was calculated from the phylogenetic tree described in the *Phylogenetic reconstruction* section associated with the evolutionary distance matrix built from our plant community data. As phylogenetic diversity is positively correlated with species richness (Kembel 2009), we used the standardized effect size of phylogenetic diversity. We applied the function *ses.pd* from the R library *picante* (Kembel et al. 2010), which compares the observed phylogenetic diversity to that expected from a null model that would consist of sampling the same number of species at random. By doing so, it is possible to identify communities with phylogenetic diversity higher or lower than expected, given the number of species in the community (Moullot et al.

Table 2. Experimental management treatments of study meadows by elevation and productivity type (see Table 1). Treatment abbreviations are as follows: (C) control; (I) irrigated, (F) fertilized, and (I+F) irrigated and fertilized. I+F 3/3 corresponds to the quantity of fertilizer input necessary to achieve the local maximum hay yield; I+F 1/3 and I+F 2/3 refer to one-third and two-thirds of this quantity, respectively, following Sinaj et al. (2009).

Treatment	No. Cuts per Year	Slurry Fertilization (kg·ha ⁻¹ ·yr ⁻¹)									Sprinkler Irrigation (mm·wk ⁻¹)
		Category A			Category B			Category C			
		N	P	K	N	P	K	N	P	K	
C	1	0	0	0	0	0	0	0	0	0	0
I	2	0	0	0	0	0	0	0	0	0	20
F	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	0
I+F 1/3	2	13.3	4.8	36.9	20	7.3	55.4	26.7	9.7	73.8	10
I+F 2/3	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	20
I+F 3/3	2	40.0	14.5	110.6	60	21.8	166.0	80	29.1	221.4	30

2011). Phylogenetic diversity is measured in units of SD. The relationship between species richness and phylogenetic diversity was measured using Pearson correlation, with the *cor.test* function. The cover of functional groups was log-transformed to respect normality assumptions in the distribution of residuals in the model. All models included the management treatments as fixed effects (i.e. a six-level categorical variable; C, I, F, I+F 1/3, I+F 2/3 and I+F 3/3) and study sites as random effects. The *relevel* function in R, which allows changing the reference level of the fixed effects, was used to carry out comparisons among treatments when performing the LMMs. All analyses were conducted using R statistical software, v 3.1.2 (R Core Team 2015).

Results

A total of 197 vascular plant species belonging to 34 families were recorded (Appendix S2). Species richness per subplot (8 m²) ranged from a minimum of 25 in the most intensive (I+F 3/3) treatment in Euseigne at 1028 m a.s.l. to a maximum of 66 in the low intensive (I+F 1/3) treatment in Grimentz at 1738 m a.s.l. (mean \pm SE: 46.8 ± 2.18 in C-plots). Overall, only the I+F 3/3 treatment (38.2 ± 2.67 species) harboured significantly fewer species than the other treatments (Fig. 2a, Table 3). Species diversity (Shannon index) was significantly lower in I+F 3/3-plots (2.4 ± 0.15) than in I+F 1/3-plots (2.8 ± 0.15), while there was no difference between the other treatments (Fig. 2b, Table 3). As for species richness, phylogenetic diversity was significantly lower in I+F 3/3-plots (-0.2 ± 0.52) than in C-plots (1.4 ± 0.52), with no other differences between treatments (Fig. 2c, Table 3). A negative value indicates that the plant community encompasses less phylogenetic diversity than expected based on its total species number, i.e. the species are more closely related to each other than expected by chance in that given community. There was a strong correlation between the taxonomic and phylogenetic measures of diversity (Appendix S3, species richness vs phylogenetic diversity, $r = 0.89$, $P < 0.001$).

The number of grass species was lower in I+F 3/3-plots (7.2 ± 0.62 species) compared to all other experimental treatments (e.g. 9.6 ± 0.62 in C-plots; Fig. 3a, Table 3). Forb species richness was lower in both I+F 2/3- and I+F 3/3-plots (29.6 ± 1.91 and 26.6 ± 1.91) compared to all other treatments (e.g. 32.3 ± 1.82 in C-plots). I-plots (7.3 ± 0.40) and I+F 2/3-plots (7.0 ± 0.40) had higher species richness of legumes compared to other treatments (Fig. 3a). Forb cover was experimentally increased in F- and all I+F-plots (by 13.9–27.9%) compared to C-plots ($42.1 \pm 7.83\%$), while legume cover increased in I-, I+F 2/3- and I+F 3/3-plots (by 4.2–7.9%) compared to C-plots

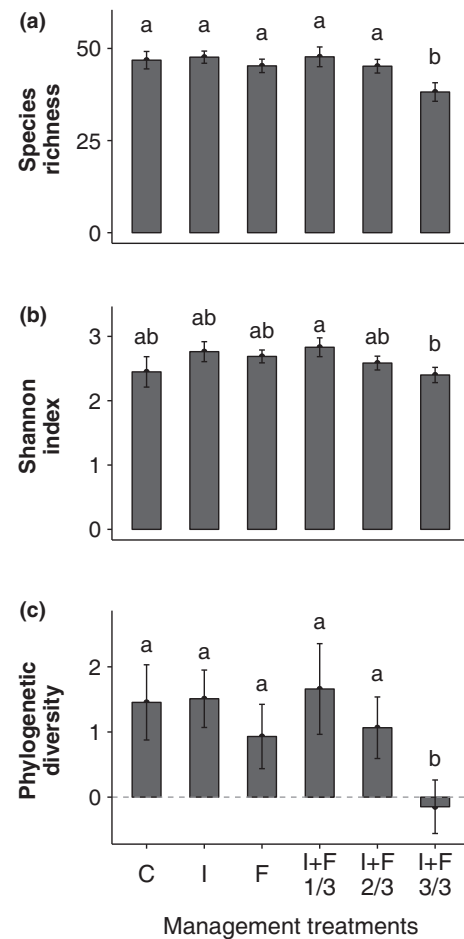


Fig. 2. Effects of management treatment (LMM with site as random factor) on (a) species richness, (b) Shannon index and (c) phylogenetic diversity (measured as standardized effect size of phylogenetic diversity to correct for the correlation with species richness) of the plant communities. The *relevel* function in R, which allows changing the reference level of the fixed effects, was used to carry out comparisons among treatments. For statistical outputs, see Table 3; for treatment abbreviations, see Table 2. Fractions of I+F refer to the relative amount of fertilizer applied in comparison to the input necessary to achieve maximum hay yield locally, the latter corresponding to I+F 3/3 (following Sinaj et al. 2009). Different letters indicate significant differences at an alpha rejection level of 0.05, as based on multiple comparisons. Means \pm SE are given.

($7.1 \pm 2.64\%$; Fig. 3b). Grass cover did not differ among treatments, with an overall average of $51.2 \pm 9.59\%$ (Fig. 3b, Table 3).

Discussion

There is an increasingly urgent need to develop guidelines for regional agriculture policies that efficiently protect the remaining biodiversity of extensively managed hay meadows. This field experiment evaluated the response of montane and sub-alpine grassland plant communities to

Table 3. LMM outputs on effects of management treatment on species richness, Shannon diversity index, phylogenetic diversity (measured as standardized effect size of phylogenetic diversity to correct for the correlation with species richness), species richness and total cover (%) of grasses, forbs and legumes. The *relevel* function in R, which allows changing the reference level (intercept) of the fixed effects (management treatments; C, I, F, I+F 1/3, I+F 2/3 and I+F 3/3; see Table 2 for abbreviations), was used to carry out multiple comparisons among treatments. Study site was set as random factor. Parameter estimate, SE and *P*-value are given for each of the paired treatment comparisons, while significant differences are highlighted in bold.

	Species Richness			Shannon Index			Phylogenetic Diversity		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Intercept (C)	46.81	2.18	<0.001	2.45	0.15	<0.001	1.42	0.52	<0.001
I vs C	0.82	2.67	0.761	0.31	0.20	0.128	0.10	0.52	0.848
F vs C	-1.55	2.67	0.566	0.24	0.20	0.243	-0.53	0.52	0.321
I+F 1/3 vs C	0.91	2.67	0.735	0.38	0.20	0.065	0.28	0.52	0.599
I+F 2/3 vs C	-1.64	2.67	0.543	0.14	0.20	0.503	-0.35	0.52	0.505
I+F 3/3 vs C	-8.64	2.67	0.002	-0.05	0.20	0.813	-1.60	0.52	0.004
Intercept (I)	47.64	2.18	<0.001	2.76	0.15	<0.001	1.53	0.52	<0.001
F vs I	-2.36	2.67	0.381	-0.07	0.20	0.717	-0.63	0.52	0.238
I+F 1/3 vs I	0.09	2.67	0.973	0.07	0.20	0.737	0.18	0.52	0.738
I+F 2/3 vs I	-2.45	2.67	0.363	-0.18	0.20	0.387	-0.45	0.52	0.392
I+F 3/3 vs I	-9.45	2.67	0.001	-0.36	0.20	0.080	-1.70	0.52	0.002
Intercept (F)	45.27	2.18	<0.001	2.69	0.15	<0.001	0.90	0.52	<0.001
I+F 1/3 vs F	2.45	2.67	0.363	0.14	0.20	0.486	0.80	0.52	0.132
I+F 2/3 vs F	-0.09	2.67	0.973	-0.10	0.20	0.614	0.17	0.52	0.742
I+F 3/3 vs F	-7.09	2.67	0.011	-0.29	0.20	0.162	-1.07	0.52	0.047
Intercept (I+F 1/3)	47.73	2.18	<0.001	2.83	0.15	<0.001	1.70	0.52	<0.001
I+F 2/3 vs I+F 1/3	-2.55	2.67	0.345	-0.25	0.20	0.232	0.63	0.52	0.236
I+F 3/3 vs I+F 1/3	-9.55	2.67	0.001	-0.43	0.20	0.039	-1.87	0.52	0.001
Intercept (I+F 2/3)	45.18	2.18	<0.001	2.58	0.15	<0.001	1.07	0.52	0.05
I+F 3/3 vs I+F 2/3	-7.00	2.67	0.012	-0.19	0.20	0.366	-1.24	0.52	0.022

Species richness of functional groups

	Grasses			Forbs			Legumes		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Intercept (C)	9.54	0.62	<0.001	32.27	1.82	<0.001	5.91	0.41	<0.001
I vs C	0.36	0.85	0.671	-0.91	1.91	0.636	1.36	0.51	0.010
F vs C	0.36	0.85	0.671	-1.55	1.91	0.422	-0.18	0.51	0.723
I+F 1/3 vs C	-0.09	0.85	0.915	0.27	1.91	0.887	0.73	0.51	0.160
I+F 2/3 vs C	-0.09	0.85	0.915	-2.64	1.91	0.174	1.09	0.51	0.037
I+F 3/3 vs C	-2.36	0.85	0.007	-5.72	1.91	0.004	-0.64	0.51	0.218
Intercept (I)	9.91	0.62	<0.001	31.36	1.82	<0.001	7.27	0.41	<0.001
F vs I	0.00	0.85	1.000	-0.63	1.91	0.741	-1.54	0.51	0.004
I+F 1/3 vs I	-0.45	0.85	0.595	1.18	1.91	0.539	-0.63	0.51	0.218
I+F 2/3 vs I	-0.45	0.85	0.595	-1.73	1.91	0.371	-0.27	0.51	0.595
I+F 3/3 vs I	-2.72	0.85	0.002	-4.82	1.91	0.015	-2.00	0.51	<0.001
Intercept (F)	9.91	0.62	<0.001	30.73	1.82	<0.001	5.73	0.41	<0.001
I+F 1/3 vs F	-0.45	0.85	0.595	1.82	1.91	0.346	0.91	0.51	0.080
I+F 2/3 vs F	-0.45	0.85	0.595	-1.09	1.91	0.571	1.27	0.51	0.016
I+F 3/3 vs F	-2.72	0.85	0.002	-4.18	1.91	0.033	-0.45	0.51	0.377
Intercept (I+F 1/3)	9.46	0.62	<0.001	32.55	1.82	<0.001	6.64	0.41	<0.001
I+F 2/3 vs I+F 1/3	0.00	0.85	1.000	-2.91	1.91	0.134	0.36	0.51	0.479
I+F 3/3 vs I+F 1/3	-2.27	0.85	0.010	-6.00	1.91	0.003	-1.36	0.51	0.010
Intercept (I+F 2/3)	9.46	0.62	<0.001	29.63	1.82	<0.001	7.00	0.41	<0.001
I+F 3/3 vs I+F 2/3	-2.27	0.85	0.010	-3.09	1.91	0.112	-1.73	0.51	0.001

Cover of functional groups (log-transformed)

	Grasses			Forbs			Legumes		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Intercept (C)	4.04	0.20	<0.001	3.63	0.14	<0.001	1.75	0.21	<0.001
I vs C	-0.38	0.21	0.081	0.29	0.15	0.058	0.58	0.28	0.042
F vs C	-0.41	0.21	0.056	0.52	0.15	0.001	0.39	0.28	0.171

Table 3. (Continued).

	Cover of functional groups (log-transformed)								
	Grasses			Forbs			Legumes		
I+F 1/3 vs C	-0.37	0.21	0.081	0.31	0.15	0.040	0.50	0.28	0.076
I+F 2/3 vs C	-0.35	0.21	0.101	0.37	0.15	0.015	0.58	0.28	0.043
I+F 3/3 vs C	-0.21	0.21	0.314	0.31	0.15	0.042	0.76	0.28	0.009
Intercept (I)	3.66	0.20	<0.001	3.92	0.14	<0.001	2.33	0.21	<0.001
F vs I	-0.04	0.21	0.864	0.23	0.15	0.122	-0.07	0.28	0.793
I+F 1/3 vs I	0.00	0.21	0.995	0.02	0.15	0.871	-0.19	0.28	0.497
I+F 2/3 vs I	0.02	0.21	0.910	0.08	0.15	0.575	0.18	0.28	0.526
I+F 3/3 vs I	0.16	0.21	0.448	0.02	0.15	0.886	0.00	0.28	0.987
Intercept (F)	3.63	0.20	<0.001	4.15	0.14	<0.001	2.26	0.21	<0.001
I+F 1/3 vs F	0.04	0.21	0.859	-0.21	0.15	0.164	-0.12	0.28	0.676
I+F 2/3 vs F	0.06	0.21	0.776	-0.15	0.15	0.317	0.25	0.28	0.371
I+F 3/3 vs F	0.20	0.21	0.353	-0.21	0.15	0.159	0.08	0.28	0.781
Intercept (I+F 1/3)	3.66	0.20	<0.001	3.94	0.14	<0.001	2.14	0.21	<0.001
I+F 2/3 vs I+F 1/3	0.02	0.21	0.915	0.06	0.15	0.691	0.37	0.28	0.192
I+F 3/3 vs I+F 1/3	0.16	0.21	0.451	0.00	0.15	0.984	0.20	0.28	0.487
Intercept (I+F 2/3)	3.82	0.20	<0.001	4.00	0.14	<0.001	2.51	0.21	<0.001
I+F 3/3 vs I+F 2/3	-0.14	0.21	0.517	-0.06	0.15	0.676	-0.17	0.28	0.537

different management intensities applied 4 yr in a row. Our study reveals that low to medium inputs of fertilizer (slurry) and water via aerial irrigation with sprinklers did not negatively impact species richness and diversity, or phylogenetic diversity, while high levels of water and fertilizer application did. A moderate level of management intensity did, however, already have a negative effect on the functional diversity of forbs. All previous studies on the impact of grassland management intensification on biodiversity have largely focused on comparing high input of fertilizer vs no input at all (Hejman et al. 2007; Dickson & Foster 2011; Rose et al. 2012). Furthermore, they mostly investigated the effects of N addition alone (Humbert et al. 2016). The importance of the present study resides in the complex range of management practices tested. It paves the way for identifying threshold values for biodiversity-friendly management of mountain hay meadows.

Our study shows that after 4 yr of experimental manipulation, plant species richness was reduced by 18% in the most intensive treatment (I+F 3/3-plots), in line with earlier observational (Maurer et al. 2006; Niedrist et al. 2009; Müller et al. 2016) and experimental (Rajaniemi 2002; Niu et al. 2008) findings of similar agricultural practices. This pattern was driven by the loss of some forb (-13%) and grass (-5%) species, perhaps due to exacerbated above- and below-ground competition for access to light and minerals, respectively (Grime 1973). Notably, the communities in the most intensive treatment were often dominated by highly competitive species such as *Arrhenatherum elatius*, *Heracleum sphondylium* and *Geranium sylvaticum*, which formed a thick canopy obstructing light for the lower ground vegetation. Short-stature species such as

Linum catharticum and *Polygala vulgaris* were thus likely to be shaded out in these conditions (Grime 1973; Hautier et al. 2009), occurring only in the control or irrigated-only plots. Forb species richness also fell under medium intensity management (I+F 2/3) while, in the same plots, the number of legume species increased relative to the controls (no input; C-plots), illustrating a shift in community composition. In summary, overall species richness and diversity were maintained relatively high under the low (I+F 1/3) management treatment and, to a somewhat lesser extent, medium (I+F 2/3) management intensity. This pattern matches the prediction of the hump-shaped model of species richness (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015).

Species diversity (Shannon index) was higher in the low-intensity treatment (I+F 1/3) compared to the most intensive treatment (I+F 3/3), but did not differ from other treatments. Low management intensity in our study was characterized by limited water and nutrient inputs, which slightly enhanced forb and legume cover, without leading to a decrease in species richness. Low-intensity management thus enhanced diversity. In a meta-analysis of the effects of N fertilization on grassland biodiversity, Humbert et al. (2016) reached similar conclusions to our study.

The observed plant community shifts were mirrored by the trends in relative cover of the three functional groups, with typical species-specific responses. For example, among the grasses, there was a considerable decline in cover of *Bromus erectus* with increasing management intensity, and an increase in cover of more competitive species such as *A. elatius* and *Dactylis glomerata* (Peter et al. 2008). Previous studies have shown that grass cover and/or

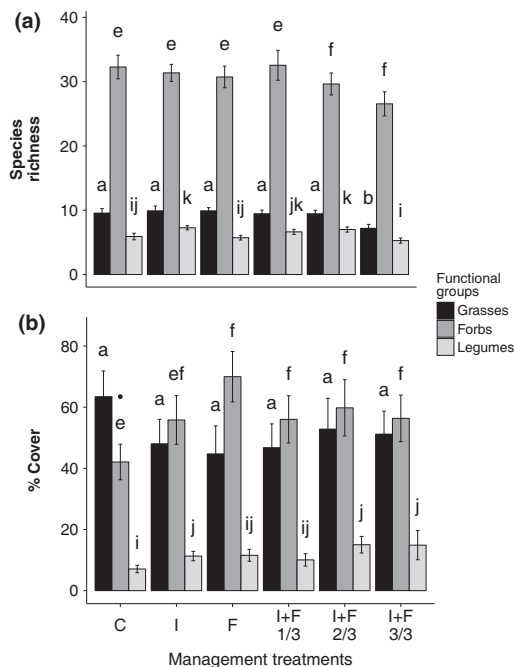


Fig. 3. Effects of management treatment (LMM with site as random factor) on (a) plant species richness and (b) mean percentage cover of functional groups (i.e. grasses, forbs and legumes). The *relevel* function in R, which allows changing the reference level of the fixed effects, was used to carry out comparisons among treatments. Total cover within a given treatment can exceed 100% because plant functional group canopies sometimes overlap. For abbreviations, see Table 2. Means \pm SE are given while statistical significant differences are depicted for each functional group.

biomass are enhanced by the addition of water and nutrients (e.g. Mountford et al. 1993; Jeangros & Troxler 2008; Leto et al. 2008). Yet, we must stress here that when plant communities are partially composed of grasses, an increase of Gramineae biomass will translate into taller grasses without modifying cover, contrary to what is observed with forbs and legumes, which grow both broader and taller. This bias might have affected our grass cover estimates, thus blurring any existing pattern.

All treatments involving fertilization increased forb coverage. Nutrients are a key limiting factor for some forbs, which, in the presence of additional fertilization, allocate more resources to above-ground growth (Mamollos et al. 2005). Tall, nitrophilous, competitive flower species such as *G. sylvaticum* and *H. sphondylium* (Grime 1973; Peter et al. 2008) were noticeably much larger and more abundant under increased management intensity, generating higher overall cover despite the general decrease observed in the number of forb species. The cover of legumes, generally the most valuable functional group for livestock forage (Frame 2005), was enhanced by irrigation and/or fertilization (Fig. 3b). The slurry we applied was composed of a

mix of N, K and P. The addition of nutrients other than N may have further promoted this competitive functional group since legumes have the capacity to fix the N naturally present in the soil (Mountford et al. 1993; Onipchenko et al. 2012).

The patterns for phylogenetic diversity echoed those of species richness; only the most intensive management treatment had a clear negative impact. First, this means that fewer species constituted the plant communities typical for high-intensity management. Second, these species were more clustered in the phylogenetic tree, i.e. more closely related than would have been expected under a random pattern of species association from the original pool. There are a growing number of studies integrating a phylogenetic perspective into both biodiversity assessments and practical conservation advice (e.g. Forest et al. 2007; Mouillot et al. 2011; Buerki et al. 2015; Cisneros et al. 2015; Costion et al. 2015), although research on the effects of agricultural intensification of hay grasslands on phylogenetic diversity remains scarce (but see Egorov et al. 2014; Rader et al. 2014). Our results on phylogenetic diversity suggest that species loss is not random, raising the possibility that a set of traits, such as perennial life cycle, short height, rosette growth form or high standing flowering shoots, might disappear from the community at high management intensity (Klimesova et al. 2008). Losing such functional traits would irrevocably alter the natural functioning and evolutionary potential of the system (Purvis & Hector 2000; Cadotte & Davies 2010).

Effects of irrigation vs fertilization

The traditional irrigation system of semi-natural meadows in the dry inner Alps consisted of a network of open channels distributing water kilometres away from the main streams. Modern irrigation with sprinklers is progressively replacing traditional irrigation via open channels in the mountain regions (Crook & Jones 1999). In order to render our management recommendations readily implementable for modern practice, we experimentally tested the effects of sprinkler irrigation on grassland biodiversity. As found in previous mid- and long-term studies in the Alps (Riedener et al. 2013; Melliger et al. 2014), irrigation alone (I-treatment) did not appear to have any noticeable negative impact on biodiversity, even promoting legume species richness and abundance. Within the same experimental set up as used in our study, Andrey et al. (2014) found a similar pattern for legume and grass abundance, but a negative effect on forb abundance. They also found that irrigation had an even stronger positive effect than fertilization on total plant species richness. However, that study was very short term (surveys in the year following the onset of the experimental manipulation) and

furthermore carried out during a rather dry year when water supply might have been the main limiting factor for vegetation growth. Water is used by plants both directly as a resource for growth and indirectly by affecting nutrient availability (Mamolos et al. 2005). These processes can be achieved irrespective of the way water is delivered to the meadow (Riedener et al. 2013; Müller et al. 2016). Over time, irrigation could probably modify floristic composition because of reduced physiological stress during drought episodes. When comparing wet and dry meadow sites, Mamolos et al. (2005) found that tissue nutrient concentration varied between functional groups according to soil water content. Legumes had higher concentrations of N and P in wet sites, which allowed them to invest more in biomass, hence increasing their percentage cover with increased water availability. Our results are in line with these findings.

Surprisingly, fertilization alone did not appear to have any significant impact on biodiversity, although there was a noticeable drop in species richness and phylogenetic diversity. One year after the onset of our experiment, plant species richness had already increased with fertilization alone (Andrey et al. 2014), but this positive effect was expected to remain true only in the short term, progressively reversing to a negative trend over time (Gough et al. 2000; Crawley et al. 2005; Yang et al. 2011). Indeed, in I+F 2/3-plots (where the same amount of fertilizer as in F-plots was applied, in addition to irrigation) and in I+F 3/3-plots, forb species richness decreased significantly, indicating an interaction between nutrient uptake and water input. As a corollary, we speculate that under a humid climate and/or rainy weather, the effects of fertilization alone may become more acute than under dry circumstances. In line with this, we predict that species richness and phylogenetic diversity would further decrease under high-intensity management in the long term. Management involving a medium amount of fertilizer addition without irrigation might therefore become detrimental to plant diversity over time. A shift from fertilization with manure to slurry, as observed during the past decades, is thus likely to affect plant community differently according to the slurry dilution ratio (Mountford et al. 1993; Mamolos et al. 2005).

Conclusion and management recommendations

We suggest that low to medium inputs of water and slurry, as well as a medium level of irrigation with sprinklers in the absence of fertilization, can sustain a rich flora in mountain hay meadows. More specifically, we propose two main recommendations for sustainable hay meadow management, depending on land-use context: (1) where meadows are still managed and when flora preservation is of concern, inputs of water and nutrients must be limited

to 1/3–2/3 of what would be necessary to achieve the maximum hay yield possible locally; (2) where traditional management (roughly equivalent to our control and irrigated-only plots) is progressively given up, moderate management (1/3–2/3) with modern farming techniques (slurry spraying and aerial irrigation) is preferable to land abandonment that leads to encroachment by woody vegetation, i.e. a loss of the rich biodiversity typical of open habitats (Tasser & Tappeiner 2002).

Acknowledgements

We thank our colleagues at the Division of Conservation Biology and members of the accompanying group for their valuable inputs. We thank the farmers for their collaboration, Stéphane Mettaz for field assistance and Bärbel Koch for help with vegetation surveys. We are grateful to Pierri Buri for providing the map of the study sites, to Alexis Lupien-Meilleur for figure editing, T. Jonathan Davies for fruitful discussions on the phylogenetic analysis, Peter Convey and Roel van Klink for providing useful comments on earlier versions of the manuscript. This work was supported by the Swiss National Science Foundation (grant 31003A_149656/1 to Raphaël Arlettaz), the Swiss Federal Offices for Agriculture and the Environment, and the cantons of Graubünden and Valais. RA originally formulated the idea and raised the research funds, RA and JYH developed field design and methodology, MLT conducted fieldwork and performed statistical analyses and MLT, JYH and RA wrote the manuscript.

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Supporting Information

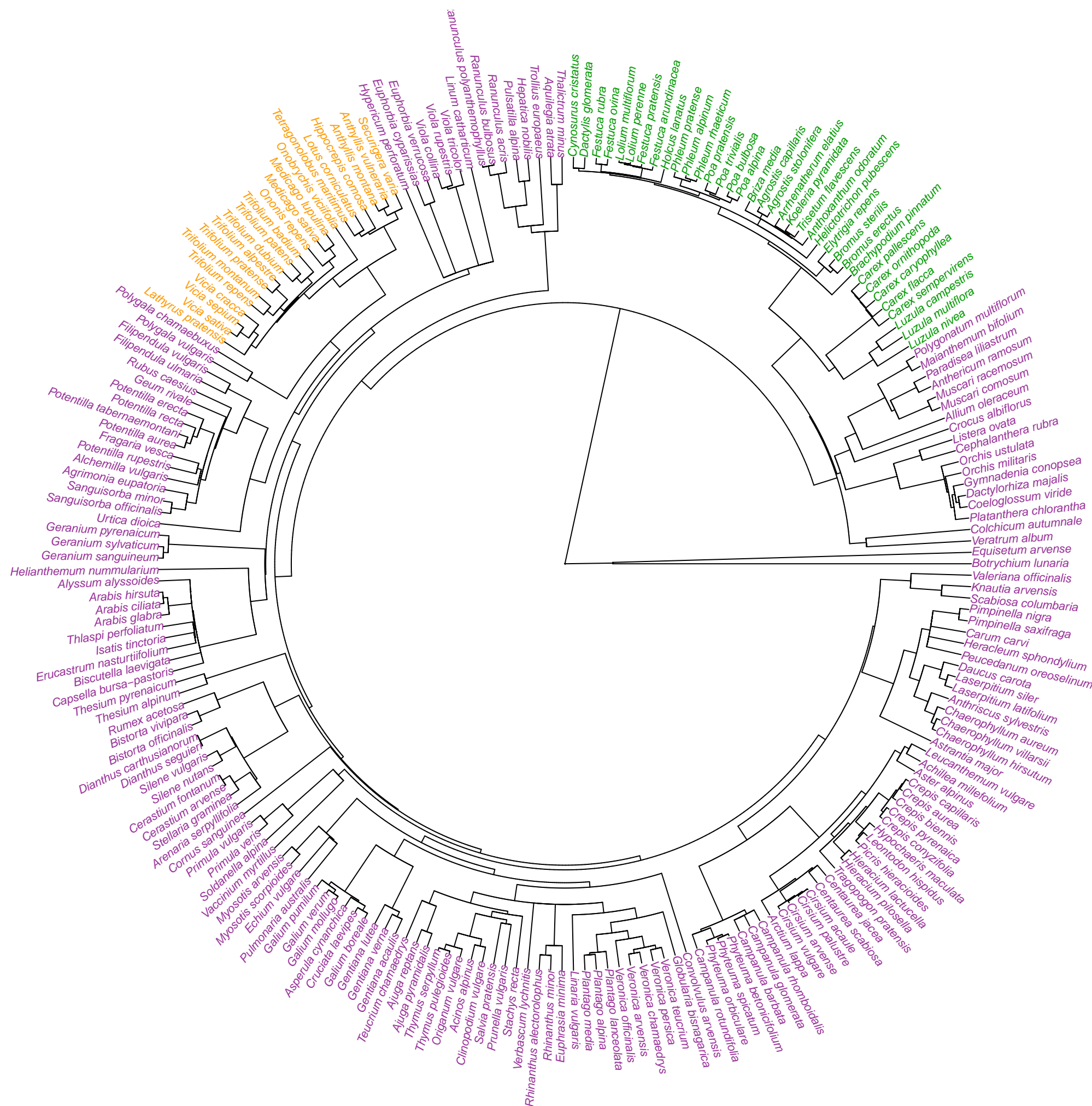
Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogenetic relationships of the species pool from all meadows.

Appendix S2. List of plant species recorded.

Appendix S3. Correlation between species richness and phylogenetic diversity.

	Forbs
	Grasses
	Legumes



Supporting information to the paper

Lessard-Therrien, M., Humbert, JY., Arlettaz, R. Experiment-based recommendations for biodiversity-friendly management of mountain hay meadows. *Applied Vegetation Science*.

Appendix S3. Relationship between species richness and phylogenetic diversity estimated with Pearson product-moment correlation, $r = 0.89$, $P < 0.001$. Shaded area represents SE.

