Traditional versus sprinkler irrigation of mountain hay meadows in the Valais:

Consequences for biodiversity

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CONTENTS

SUMMARY

Semi-natural grasslands including hay meadows belong to the most species-rich habitats in central Europe and are therefore of high conservation value. The high biodiversity of these grasslands has been maintained for many centuries through the regular disturbance by traditional management practices. Furthermore, the biodiversity of semi-natural grasslands is suggested to be affected by a combination of several other factors including small-scale habitat heterogeneity and the surrounding landscape. In the Valais, an arid mountain region of Switzerland, traditional management of hay meadows includes irrigation by open water channels. In the past decades, however, the traditional irrigation technique was increasingly replaced by more efficient sprinkler-irrigation systems or irrigation was stopped on marginal and poorly accessible areas. Within the scope of this thesis, four studies were conducted to investigate different aspects of these changes in meadow irrigation.

The aim of the first study was to examine whether land-use abandonment resulting from the cessation of irrigation influenced the biodiversity of hay meadows in the Valais. For this purpose, plant and gastropod surveys were conducted in three serial stages of succession (hay meadows, early abandoned meadows and young forests). Meadow abandonment resulted in an increase in gastropod species richness and a loss of plant and gastropod species characteristic for open grassland habitats. Furthermore, functional traits of plants (plant height, the start of seed shedding and the type of reproduction) and gastropods (shell size) were affected by abandonment.

Traditional meadow irrigation is assumed to distribute the water more heterogeneously than sprinkler irrigation, which might affect meadow biodiversity as well as the distribution of plants in a small scale. The aim of the second study was to examine whether the change from traditional to sprinkler irrigation affected the local biodiversity (plants and gastropods) of hay meadows in the Valais. A high plant species richness was found in the hay meadows investigated. The diversity and composition of plant and gastropod species did not differ between traditionally and sprinkler-irrigated meadows. However, the installation of sprinkler systems resulted in an increase in the grass-to-forb ratio and affected the leaf distribution and the start of seed shedding in plants.

The third study aimed to investigate whether the change in irrigation technique affected the small-scale distribution of plants and soil characteristics in these hay meadows. Three sampling plots consisting of 13 subplots of increasing size were installed in traditionally and sprinkler-irrigated meadows to assess plant species richness and soil characteristics within subplots. The type of irrigation technique did not affect the shape of the plant species-area relationship. Furthermore, spatial autocorrelation in the soil characteristics examined was low and their small-scale distributions were mostly not influenced by the irrigation technique.

These findings indicate a pronounced small-scale heterogeneity in the distribution of plant species and soil characteristics in the hay meadows investigated. Therefore, as practiced in our study areas, the distribution of water by sprinklers might be less homogenous than commonly assumed.

The abandonment of traditional management practices of semi-natural grasslands is suggested to result in a reduced landscape heterogeneity, which in turn might contribute to the loss of local plant diversity. The fourth study aimed to investigate whether the change from traditional to sprinkler irrigation resulted in alterations in the surrounding landscape of species-rich hay meadows. Furthermore, we asked if plant diversity of differently irrigated meadows is influenced by landscape composition and the heterogeneity of the surrounding landscape. Landscape composition was more diverse for traditionally than for sprinkler-irrigated meadows, but did not differ prior to the installation of sprinklers. A diverse small-scale landscape composition in the close surroundings of hay meadows had a positive effect on the number of generalists but not on total plant species richness or the number of specialists. Finally, sprinkler-irrigated meadows had an increased number of generalist plant species.

The findings of this thesis suggest that the installation of sprinklers did not affect the local species richness of plants and gastropods in the hay meadows investigated. Nevertheless, the change in irrigation technique influenced functional aspects of plant diversity (plant traits, grass-to-forb ratio and generalist species). Furthermore, the installation of sprinklers was associated with a homogenization of the landscape, which may eventually result in an intensification of land use. For the conservation of the biodiversity of these hay meadows it is recommended to maintain the relatively extensive irrigation and management practices.

GENERAL INTRODUCTION

Biodiversity is threatened worldwide by human-induced changes in the environment including habitat destruction, the increase of atmospheric CO_2-concentration, climate change, biotic introductions, nitrogen deposition and land-use change. Out of these factors, land-use change has been suggested to currently represent the most important driver for biodiversity loss (Vitousek, 1994). Moreover, scenarios for the end of the 21st century identified land-use change as the main factor for the biodiversity loss in global terrestrial ecosystems, particularly in grassland habitats (Sala et al., 2000).

Semi-natural grasslands including hay meadows belong to the most species-rich habitats in Central Europe and are therefore of high conservation value (Poschlod and WallisDeVries, 2002; Baur et al., 2006). As human-made habitats, the persistence of semi-natural grasslands depends on the regular disturbance by traditional management practices such as extensive grazing or mowing, which maintained the high biodiversity of these grasslands for many centuries (Poschlod and WallisDeVries, 2002). Nowadays, semi-natural grasslands are considered as refugia for numerous rare species whose primordial habitats were destroyed (Baur et al., 1996, 2004). However, since the mid 20th century, alterations in socio-economic conditions led to changes in agricultural practices of semi-natural grasslands (Strijker, 2005; Stöcklin et al., 2007; Fischer et al., 2008). Land use was intensified (e.g. more frequent cutting, higher amount of fertilizer; Fischer et al., 2008) on favourable areas or abandoned on less productive and remote areas. As a consequence, the total area of semi-natural grasslands declined throughout Europe (Strijker, 2005) and plant diversity decreased (Tasser and Tappeiner, 2002; Maurer et al., 2006; Niedrist et al., 2009; Jacquemyn et al., 2011; Homburger and Hofer, 2012).

In arid regions, the maintenance of hay meadows and their typical species composition also depends on irrigation. As a consequence, far-reaching irrigation systems have been constructed in several arid mountain regions of Europe (Rodewald, 2008). One of these regions is the Valais (Switzerland) with its south-facing slopes where a long tradition of meadow irrigation exists (Crook and Jones, 1999). The Valais belongs to the driest regions of Switzerland with a total annual precipitation of 500 to 600 mm in its most arid parts (MeteoSwiss, 2008). Moreover, the lowest amount of rainfall is during the vegetation period (MeteoSwiss, 2013), which affects agricultural activities including the production of hay. Hence, in this region, a considerable net of open water channels was constructed from the 11th century onwards to transport glacial melt water from mountain streams to meadows at lower elevations (Crook and Jones, 1999; Leibundgut, 2004). Hay meadows are irrigated by flooding them at regular intervals, the so-called traditional irrigation technique. However, in the 20th century, the modernization and rationalization of agriculture led to two main changes in the irrigation practices of the Valais. Traditional meadow irrigation was replaced by more efficient sprinkler irrigation systems and irrigation was stopped on marginal areas with poor accessibility (Werner, 1995; Crook and Jones, 1999).

Focus of the thesis

The main aim of this thesis was to examine the consequences of these changes in meadow irrigation for the biodiversity of hay meadows in the Valais. To address this question, field surveys were conducted in the upper Valais in the following municipalities: Ausserberg (all Chapters), Birgisch (Chapters I and II), Mund (Chapter II), Erschmatt (Chapters II, III and IV) and Guttet (Chapters II, III and IV). In these study areas, sprinkler irrigation systems were installed 11–28 years before this thesis was conducted (between 1986 and 2003; various farmers, pers. com.). Nowadays, 10% to 30% of the hay meadows are still irrigated in the traditional way leading to a small-scale arrangement of either traditionally or sprinkler-irrigated meadows (K. Liechti, pers. com.).

Numerous studies addressed the consequences of grassland abandonment for the diversity of various organisms (e.g. Balmer and Erhardt, 2000; Tasser and Tappeiner, 2002; Baur et al., 2006; Azcarate and Peco, 2012). However, the effects of abandonment in combination with the cessation of irrigation have to our knowledge not been examined so far. This is of particular importance in the Valais, where irrigation is required to secure hay production (Crook and Jones, 1999). As a consequence of the cessation of irrigation the productivity of hay meadows in this region decreased, leading to the abandonment of mowing or to conversion to pastures (Werner, 1995). **Chapter I** presents the results of a field survey, which aimed to examine the effects of land-use abandonment resulting from the cessation of irrigation for the biodiversity of species-rich hay meadows in the Valais. In this survey, we compared the diversity and composition of plant and gastropod species of three serial stages of succession (hay meadows, early abandoned meadows and young forests). These organisms are considered as ideal diversity indicators in small-scale grassland habitats, owing to their high habitat specificity and low mobility (Boschi and Baur, 2008; Gaujour et al., 2012). Beside these taxonomic indicators for biodiversity, functional traits were considered because they represent another aspect of biodiversity and therefore supplement the results of taxonomy-based analyses.

In addition to irrigation abandonment, the replacement of the traditional irrigation technique by sprinkler irrigation represents another major change in grassland management in the Valais. Traditional and sprinkler irrigation are assumed to differ substantially in their water distribution. In sprinkler irrigation, the water is distributed relatively homogeneously from above, whereas in the traditional irrigation technique the ground is inundated irregularly, depending on the micro-relief (Meurer and Müller, 1987). Owing to this spatially unequal water distribution, traditional meadow irrigation is expected to lead to the coexistence of different microhabitats, which are either more or less moist (Werner, 1995). This mosaic of different microhabitats might increase the floristic and faunistic diversity in traditionally irrigated meadows (Werner, 1995). However, to our knowledge, the effects of different irrigation techniques on the biodiversity of hay meadows have not been examined so far. **Chapter II** presents a field survey, which compared the local biodiversity of traditionally and sprinkler-irrigated hay meadows in the Valais. As in Chapter I, the diversity of vascular plants and terrestrial gastropods was recorded as a proxy for biodiversity as well as functional traits of plants and gastropods.

As a result of the unequal water distribution traditionally irrigated meadows are expected to show a more heterogeneous spatial distribution of plants and soil characteristics than sprinkler-irrigated meadows. **Chapter III** presents a field survey, which investigated the potential influence of the two irrigation techniques on the small-scale distribution of plant species and soil characteristics of hay meadows in the Valais. Three sampling plots consisting of 13 subplots of increasing size were installed in traditionally and sprinkler-irrigated meadows to assess plant species richness and soil characteristics within subplots. Plant species-area relationships, obtained by this sampling procedure, can be used to explore the spatial pattern of plant diversity in grasslands (Connor and McCoy, 1979; Rosenzweig, 1995). Mantel r statistics were used to assess the small-scale distribution of soil characteristics.

Traditional management practices not only maintained a high biodiversity but also a high heterogeneity of landscape elements within and in the surroundings of semi-natural grasslands (Diacon-Bolli et al., 2012). Both, land-use intensification as well as abandonment were shown to result in a homogenization of the agricultural landscape (Benton et al., 2003; Baessler and Klotz, 2006; Kulakowski et al., 2011; Diacon-Bolli et al., 2012). Beside the direct effects of land-use changes, the decrease in landscape heterogeneity may contribute to the loss of plant diversity in semi-natural grasslands (Diacon-Bolli et al., 2012). Moreover, not only landscape heterogeneity but also individual landscape traits can affect the plant diversity of semi-natural grasslands (e.g. Söderström et al., 2001; Reitalu et al., 2012). **Chapter IV** presents the results of a field survey, which aimed to examine the potential influences of the surrounding landscape on the local plant diversity of differently irrigated hay meadows in the Valais.

The final section of this thesis, the **General Discussion**, discusses the most important findings of the four chapters and their implications for sciences as well as for the management of the hay meadows in the Valais.

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Chapter I

Land-use abandonment owing to irrigation cessation affects the biodiversity of hay meadows in an arid mountain region

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Land-use abandonment owing to irrigation cessation affects the biodiversity of hay meadows in an arid mountain region

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ABSTRACT

In arid regions, irrigation is required to secure agricultural production including the production of hay. The Valais, a dry inner alpine valley of Switzerland, has a long tradition of meadow irrigation. However, in the 20th century irrigation was stopped on marginal, poorly accessible areas usually accompanied by the entire abandonment of these meadows. The aim of this study was to examine the consequences of land-use abandonment resulting from the cessation of irrigation for the biodiversity of species-rich hay meadows in the Valais. We compared soil characteristics and species richness and composition, habitat specificity and functional traits of plants and gastropods of three serial stages of succession (each five hay meadows, early abandoned meadows and young forests). Soil moisture was lower in young forests than in the other two stages. Soil nitrogen content decreased following abandonment, which was due to the cessation of fertilization. The three successional stages did not differ in plant species richness but harboured distinct plant communities. Gastropod richness increased with progressive succession and species composition of hay meadows differed from those of the two other stages. The proportion of grassland (plants) and open-land (gastropods) species decreased following abandonment. Furthermore, meadow abandonment led to an increase in the height of non-woody plant species, a later start of seed shedding, a change in the type of plant reproduction and an increase in the shell size of gastropods. In conclusion, this study showed that extensive land-use, which is strongly linked to irrigation, is required for the characteristic species-rich hay meadows of this arid mountain region.

1. Introduction

Semi-natural grasslands including hay meadows are of high conservation value owing to their high species richness (Baur et al., 2006; Poschlod and WallisDeVries, 2002; Riedener et al., 2013). The high biodiversity of these grasslands is a result of traditional management practices, which have been applied for many centuries (Poschlod and WallisDeVries, 2002). Since the mid 20th century, however, alterations in socio-economic conditions led to the intensification of land-use or to the abandonment of semi-natural grasslands throughout Europe (Fischer et al., 2008; Stöcklin et al., 2007; Strijker, 2005). As a result, the total area of semi-natural grasslands declined (Strijker, 2005) and plant species richness was negatively affected (Jacquemyn et al., 2011; Niedrist et al., 2009; Tasser and Tappeiner, 2002; Wesche et al., 2012).

In arid regions, agricultural activity including the production of hay essentially depends on irrigation. As a consequence, far-reaching irrigation systems have been constructed in several arid mountain regions of Europe (Rodewald, 2008). One of these regions is the Valais, Switzerland, where a long tradition of meadow irrigation exists (Crook and Jones, 1999). In the Valais, meadows are traditionally irrigated using open water channels, whereby the water is conducted from the channel to the meadow based on gravity (Crook and Jones, 1999). However, in the 20th century, the modernization and rationalization of agriculture led to two main changes in the irrigation practices of this region. Traditional meadow irrigation was replaced by more efficient sprinkler irrigation systems and irrigation was stopped on marginal areas with poor accessibility (Crook and Jones, 1999; Werner, 1995). As a consequence of the cessation of irrigation, the productivity of these meadows decreased leading to the abandonment of mowing or to conversion to pastures (Werner, 1995).

While numerous papers addressed the effects of mowing or grazing abandonment on biodiversity, the effects of irrigation abandonment has to our knowledge not been examined so far. The aim of this study was to investigate the consequences of land-use abandonment resulting from the cessation of irrigation for the biodiversity of species-rich hay meadows in the Valais. For this, the biodiversity of three serial stages of succession (hay meadows, early abandoned meadows and young forests) was compared.

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The majority of studies on land-use abandonment considered only the effects on plant species, even though other organisms might respond as well (Baur et al., 2006; Cremene et al., 2005). Therefore, the species richness of plants and gastropods were used as a proxy for biodiversity in this study. These organisms are considered as ideal diversity indicators in small-scale habitats owing to their high habitat specificity and low mobility (Boschi and Baur, 2008; Gaujour et al., 2012). Functional traits of these organisms were also considered because they represent another aspect of biodiversity and therefore supplement the taxonomy-based analysis.

This study focused on the following questions: (1) Does land-use abandonment owing to the cessation of irrigation (henceforward: meadow abandonment) lead to a change in soil conditions? (2) Does meadow abandonment affect the species richness and number of threatened species of plants and gastropods? (3) Does meadow abandonment affect the composition and habitat specificity of species? (4) Is there a shift in functional traits with ongoing succession?

2. Methods

The study was conducted in two areas on the south-facing slope of the Rhone valley in the Valais, Switzerland, namely in Ausserberg (AU; 46°19′ N, 7°51′ E) and Birgisch (BM; 46°19′ N, 7°57′ E). The two areas are situated 8 km apart. Both are characterized by a small-scale patchy landscape consisting of different land-use types including hay meadows, woodlands and settlements. Mean annual temperature in this region is 9.4 °C and total annual precipitation is 596 mm with the lowest amount of rainfall during the vegetation period (MeteoSwiss, 2013).

Three different serial stages of succession were considered: extensively managed hay meadows (ME, $n = 5$) belonging to the *Trisetetum* association (Ellenberg, 1986), early abandoned hay meadows (AB, $n = 5$) with naturally growing shrubs, and young, naturally regrown forests (NF, $n = 5$), resulting in a total of 15 study sites (Table 1). Three groups of study sites, each group containing all three successional stages were situated in AU and two groups in BM. Average distances among study sites within a group ranged from 50 m to 1.5 km in AU and from 0.2 to 0.9 km in BM. Detailed information on the land-use of the study sites were obtained by personal interviews with farmers and the age of forest stands was estimated from old maps. The hay meadows investigated are irrigated every 2nd to every 3rd week during the vegetation period using the traditional irrigation technique. In autumn, the hay meadows are grazed for a few days.

Study sites were situated underneath a water channel on an elevation of 1237 ± 4 m a.s.l. (mean ± SE) in AU and 1120 ± 7 m a.s.l. in BM (ANOVA, $F_{1,11} = 310.19$, $p < 0.001$). Sites in AU were south exposed (186 ± 8°) while sites in BM were south-east exposed (140 ± 10°; ANOVA, $F_{1,11} = 11.53$, $p = 0.006$). Inclination averaged 21.7 ± 2.5° (SE) and did not differ among study sites in the two areas (ANOVA, $F_{1,11} = 1.62$, $p = 0.23$). Furthermore, the study sites of the three successional stages did not differ in elevation, exposure and inclination (ANOVA, all $p > 0.10$).

One 10 m × 10 m sampling plot was established in a homogenous part of each study site. Sampling plots were placed at least 2 m from water channels and trails and 3 m from roads to minimize potential edge effects.

2.1. Surveys

Plant species richness and abundances of single species were assessed in a 5 m × 5 m subplot established in a randomly chosen corner of each 10 m × 10 m sampling plot. The cover of each plant species in the herbaceous layer (herbs and woody plants up to 40 cm height) was estimated using the Braun-Blanquet (1964) method. To complete the species list of the entire sampling plot, the other three 5 m × 5 m subplots were searched for 20 min each and all new species were recorded. In addition, we counted the number of shrubs (40 cm to 2 m high) and trees (>2 m) occurring in the 10 m × 10 m plot, excluding dead individuals. Coppiced shrubs and trees were regarded as different individuals. Plant species were identified according to Lauber et al. (2012). Two surveys were carried out between May and September 2011, one in spring and the other in autumn.

Two methods were used to assess the species richness and relative abundance of terrestrial gastropods (Oggier et al., 1998). First, one person visually searched for living snails and empty shells in each 10 m × 10 m plot for 30 min. Second, a soil and litter sample was collected at randomly chosen spots within each sampling plot using a shovel (in total 1 L per plot). Soil samples were put through sieves (smallest mesh size 1 mm) and examined under the binocular microscope. Gastropod shells were sorted out of the samples and identified according to Turner et al. (1998). Gastropod surveys were carried out twice in each plot (first sampling: first week of July 2010 and from 15 June to 7 July 2011; second sampling: September 2010 and from 24 August to 21 September 2011). For the analyses, data of both surveys were pooled. Snails can be detected in any weather due to the presence of empty shells. Slugs were not considered because their activity depends largely on weather conditions.

2.2. Soil characteristics

To assess the soil characteristics of the study sites, four soil samples approximately 50 cm apart were taken to a depth of 5 cm using a soil corer (diameter 5 cm; volume 100 cm^3) at the edge of each of the four subplots in October 2010 and 2011. For the analyses, the mean value of the four samples from a given study site was used. The soil samples were sieved (mesh size 2 mm) and dried for six days at 50 °C. Soil moisture (%) was determined using the fresh weight to dry weight ratio and soil pH was assessed in distilled water (1:2.5 soil:water) (Allen, 1989). Total soil organic matter content (%) was determined as loss-on-ignition of oven-dried soil at 750 °C for 16 h (Allen, 1989). Total soil organic nitrogen content was assessed using the standard method of Kjeldahl (Bremner, 1965) and total carbonate content (%) was measured by the addition of hydrochloric acid and subsequent back titration with sodium hydroxide (Allen, 1989). Finally, total phosphorous content and plant available phosphorous content were assessed using standard methods (Allen, 1989).

2.3. Red List species and trait data

Information on threatened plant and gastropod species was obtained from the Red List of ferns and flowering plants of Switzerland (Moser et al., 2002) and the Red List of Mollusca (gastropods and bivalves) (Rüetschi et al., 2012). Species were considered as threatened if they were classified as critically endangered, endangered, vulnerable or nearly threatened.

Data of nine plant traits (Table 2) were obtained from the databases BIOPOP (Jackel et al., 2006), LEDA (Kleyer et al., 2008), BiolFlor (Klotz et al., 2002) and CloPla3 (Klimesova and de Bello, 2009) and additional information from Lauber et al. (2012), Grime et al. (1988) and personal observations. Species which were found exclusively in a single subplot (5 m × 5 m) were excluded as were 10 species with missing values for some traits, because the method used does not allow for missing values. Since succession implies the increase in woody species, we excluded the eight woody species resulting in a total of 105 plant species in the analysis. For gastropods, data of six traits were obtained from Kerney et al. (1983),

Table 1
Characteristics and land-use features of the 15 study sites located in Ausserberg (AU) and Birgisch (BM).

Successional stage	Study site	Area	Coordinates	Elevation (m a.s.l.)	Exposure	Inclination (°)	Land-use	No. of shrubs/trees (per 100 m²)	Age/time since land-use change (years)
Hay meadow	ME1	AU	N 46° 19′ 4.6″, E 7° 50′ 45.5″	1236	S	28.3	- Fertilized once per year with manure - Mown once per year - Grazed in autumn	–/–	–
	ME2	AU	N 46° 19′ 8.1″, E 7° 52′ 20.3″	1251	S	16.4	- No fertilization - Mown twice per year - Occasionally grazed in autumn	–/–	–
	ME3	AU	N 46° 19′ 6.2″, E 7° 52′ 20.5″	1229	SE-S	12.9	- No fertilization - Mown twice per year - Occasionally grazed in autumn	–/–	–
	ME4	BM	N 46° 19′ 11.2″, E 7° 57′ 48.2″	1135	SE-S	7.7	- Fertilized once per year with manure - Mown twice per year - Grazed in autumn	–/–	–
	ME5	BM	N 46° 19′ 13.0″, E 7° 57′ 51.9″	1142	SE-S	8.6	- Fertilized once per year with manure - Mown twice per year - Grazed in autumn	–/–	–
Early abandoned meadow	AB1	AU	N 46° 19′ 4.2″, E 7° 50′ 47.7″	1221	S	12.3	- Wood clearing once within 20 years	19/–	Abandoned since 20 years
	AB2	AU	N 46° 19′ 15.3″, E 7° 51′ 10.2″	1253	S-SW	26.6	- Mown every 2–4 years - Occasionally grazed	18[a]/12[a]	–
	AB3	AU	N 46° 19′ 12.8″, E 7° 51′ 10.7″	1225	SW	21.9	- Occasionally grazed	–/1	–
	AB4	BM	N 46° 19′ 41.3″, E 7° 58′ 37.1″	1097	E	34.9	- Mown every 2nd year - Occasionally grazed	60/–	–
	AB5	BM	N 46° 19′ 17.5″, E 7° 58′ 3.7″	1103	SE-S	32.0	- na[b]	18/–	na[b]
Young forest	NF1	AU	N 46° 19′ 4.7″, E 7° 50′ 48.3″	1230	S	15.0	–	134/85	20–30
	NF2	AU	N 46° 19′ 14.6″, E 7° 51′ 10.3″	1239	S-SW	22.4	- Wood thinning 5 years ago - Shelter for livestock	55/26	20–30
	NF3	AU	N 46° 19′ 13.7″, E 7° 51′ 3.4″	1249	S	19.2	–	197/141	20–30
	NF4	BM	N 46° 19′ 18.9″, E 7° 58′ 4.9″	1122	SE-S	30.0	–	24/17	15–20
	NF5	BM	N 46° 19′ 17.5″, E 7° 58′ 1.7″	1124	SE	38.0	- Shelter for livestock	65/50	15–20

[a] The shrubs and trees of this plot were growing in two patches.

[b] Land-use data are not available. However, this site showed clear signs of grazing (dung patches) indicating that it was occasionally grazed.

Table 2
Functional traits of plants and gastropods.

Trait	Type	Description
Plants		
Maximal plant height [1]	Categorical	Height < 0.5 m; 0.5 ≤ height < 1 m; 1 m ≤ height < 2 m; height ≥ 2 m
Woodiness [2,3]	Categorical	Semi-woody; herbaceous
Leaf distribution [2,3]	Categorical	Rosette; semi-rosette; leaves distributed regularly; both mentioned: semi-rosette and leaves distributed regularly
Seed bank longevity index [3]	Continuous	From 0 (strictly transient) to 1 (strictly persistent)
Earliest month of seed shedding [3,4]	Categorical	May; June; July; August; September; October
Life span [5]	Categorical	Annual; biennial; perennial
Leaf anatomy [5]	Categorical	Scleromorphic; mesomorphic; hygromorphic; meso- and scleromorphic; meso- and hygromorphic; helo- and hygromorphic
Type of reproduction [5]	Categorical	s, by seed; ssv, mainly by seed; sv, by seed and vegetatively; vvs, mainly vegetatively
Clonal growth organ (CGO) [6]	Categorical	1 = rooting horizontal stems at or above soil surface; 4 = pseudovivipary; 9 = belowground stems (epigeogenous or hypogeogenous); 12 = stem tubers; 14 = root-splitters or adventitious buds on roots; 18 = no clonal growth
Gastropods		
Adult shell size [7,8]	Categorical	Size < 5.0 mm; size ≥ 5.0 mm
Age at sexual maturity [7,8]	Categorical	Age < 1 year; age = 1 year; age > 1 year
Longevity [7,8]	Categorical	Longevity = 1–2 years; longevity > 2 years
Humidity preference [7,8]	Categorical	Wet; moist; dry
Inundation tolerance [7,8]	Categorical	Low; moderate; high
Shell shape [9]	Categorical	Depressed; conical; oblong

Source: [1] Lauber et al. (2012), [2] BIOPOP, [3] LEDA, [4] Grime et al. (1988), [5] BiolFlor, [6] CloPla3, [7] Kerney et al. (1983), [8] Falkner et al. (2001), [9] Bengtsson and Baur (1993).

Falkner et al. (2001) and Bengtsson and Baur (1993) for all 27 species (Table 2).

2.4. Data analyses

All statistical analyses were performed in R, version 2.15.0 (R Development Core Team, 2012). We applied two-way analyses of variance (ANOVA) to test whether soil characteristics differed among successional stages and between study areas. Tukey post hoc tests were used to compare the differences between pairs of successional stages.

To test whether successional stages differed in plant and gastropod species richness and in gastropod abundance we used generalized linear models (GLM) with quasi-Poisson distributed errors and log link function using the MASS package in R. Successional stage and study area were included as factors and three soil parameters as cofactors (plants: pH, plant available phosphorous and nitrogen; gastropods: moisture, carbonate content and nitrogen). Due to intercorrelations the other assessed soil parameters were excluded from the analyses. Spearman rank correlations were used to examine the relationship between species richness and the soil parameters, which had a significant effect on species richness in the GLM. Multiple comparisons (Tukey Contrasts) were applied to compare the differences between pairs of successional stages using the glht function in the multcomp package in R. Data for plant and gastropod species richness consisted of presence/absence data of all species recorded in the entire sampling plot of the 15 study sites. For gastropods, individual-based rarefaction curves were calculated for the three successional stages in the vegan package in R. All models were stepwise reduced as recommended by Crawley (2007).

To assess whether successional stages differed in plant and gastropod species composition non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity measure was applied as recommended by Austin (2013). Plant data consisted of cover values (%) of 123 species. Species occurring only in one subplot (5 m × 5 m) were excluded from the analysis. For gastropods, the abundance of all species recorded in the 15 study sites were used for the ordination. Data were square-root transformed and Wisconsin double standardization was applied. The ordinations were fitted using the metaMDS function with default options on two dimensions in the vegan package in R (Oksanen, 2013). The goodness of fit of this ordination method is indicated by the stress coefficient: stress < 0.05: excellent ordination; stress < 0.1: good ordination; stress < 0.2: usable ordination (Clarke, 1993). In a second step, environmental variables were fitted onto the ordinations of plants and gastropods using the function envfit with 999 permutations in the vegan package in R (Oksanen, 2013). Environmental variables consisted of the seven soil parameters, elevation, exposure and inclination of the 15 study sites as well as information about the stage of succession and study area.

To assess the habitat specificity of plants and gastropods, we assigned each species to one of the following categories: grassland (plants) or open-land (gastropods), generalist and forest species. Information was obtained from Lauber et al. (2012) and Landolt et al. (2010) for plants and from Kerney et al. (1983) and Falkner et al. (2001) for gastropods. To examine whether the proportion of grassland, open-land, generalist and forest species differed among successional stages we applied the same GLM as described above with quasi-binomial errors and logit link function.

Fourth-corner analyses (Dray and Legendre, 2008; Legendre et al., 1997) were applied to examine the relationship between species traits and environmental variables using the ade4 package in R. This approach allowed the simultaneous analysis of three tables: an R table containing the seven soil parameters and the kind of successional stage of each site, an L table containing species abundance data of plants or gastropods, and a Q table containing information on trait values of single species. A combination of permutation models 2 and 4 with 999 permutations was used as proposed by Dray and Legendre (2008) to obtain a correct level of Type I error. Correlation analyses showed that shell size of gastropods and age at sexual maturity were correlated. Consequently, shell size can be considered as a surrogate for the other life-history trait.

3. Results

Meadow abandonment affected both soil moisture and nitrogen content (Table 3). Soil moisture was significantly higher in hay meadows and abandoned meadows than in young forests (Tukey post hoc test, both $p < 0.004$), but did not differ between hay meadows and abandoned meadows (Tukey post hoc test, $p = 0.06$). The significant interaction between successional stage and area (ANOVA, $F_{2,9} = 16.31$, $p = 0.001$) resulted from the opposite reaction of soil moisture in hay meadows and abandoned meadows in the two areas examined. Soil nitrogen content was higher in hay meadows than in abandoned meadows and young forests (Tukey post hoc test, both $p < 0.037$). The other assessed soil characteristics including soil pH,

Table 3
Soil characteristics and aspects of plant and gastropod diversity (mean ± SE) of the three successional stages (ME = hay meadow, AB = abandoned meadow, NF = young forest) located in two study areas.

	Ausserberg (AU)			Birgisch (BM)			Successional stage			Area		
	ME ($n = 3$)	AB ($n = 3$)	NF ($n = 3$)	ME ($n = 2$)	AB ($n = 2$)	NF ($n = 2$)	F	df	p	F	df	p
Soil characteristics												
Soil moisture (%)[a]	35.4 ± 1.5	27.5 ± 0.8	22.2 ± 1.4	22.4 ± 0.4	26.4 ± 1.1	21.2 ± 0.3	25.86	2, 9	**0.0002**	26.34	1, 9	**0.0006**
Nitrogen content (%)[b]	0.64 ± 0.10	0.52 ± 0.04	0.41 ± 0.01	0.73 ± 0.09	0.42 ± 0.04	0.55 ± 0.04	5.82	2, 11	**0.019**	0.52	1, 11	0.49
Plants												
No. of species[c]	63.7 ± 6.7	62.3 ± 7.4	55.3 ± 7.7	49.0 ± 2.0	65.5 ± 14.5	49.0 ± 2.0	1.65	2, 12	0.24	1.45	1, 11	0.26
Gastropods												
No. of species[d]	7.0 ± 0.6	12.3 ± 1.8	14.7 ± 3.0	6.0 ± 0.0	8.5 ± 2.5	14.5 ± 1.5	17.79	2, 12	**0.0005**	2.18	1, 11	0.17
No. of individuals[d]	164.3 ± 32.8	145.0 ± 22.0	330.3 ± 195.0	230.0 ± 94.0	29.0 ± 2.0	170.0 ± 68.0	4.41	2, 12	**0.042**	2.18	1, 11	0.17

Final model: [a] ANOVA with successional stage, study area and the corresponding interaction, [b] ANOVA with successional stage and study area, [c] GLM with successional stage, study area and plant available phosphorous, [d] GLM with successional stage, study area and soil carbonate content.

carbonate, organic matter, total phosphorous and plant available phosphorous content did not differ among successional stages or between areas (ANOVA, all $p > 0.06$; Appendix A).

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.12.023.

3.1. Species richness

A total of 206 plant species were recorded in the 15 study sites (ME: 110, AB: 150, NF: 118; Appendix B). Six of the 206 species (2.9%) are considered as threatened in Switzerland. We found two threatened plant species both in hay meadows and young forests and four threatened species in abandoned meadows. Plant species richness differed neither among successional stages nor between areas (Table 3). However, plant available phosphorous content affected the number of plant species (GLM, $F_{1,10} = 6.94$, $p = 0.025$). Spearman rank correlation showed that plant species richness increased with increasing plant available soil phosphorous content ($r_S = 0.71$, $n = 15$, $p = 0.003$).

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For gastropods, a total of 27 species with 2777 individuals were recorded in the 15 sites (ME: 10 species with 953 individuals, AB: 21 species with 493 individuals, NF: 23 species with 1331 individuals; Appendix C). Individual-based rarefaction curves showed that abandoned meadows and young forests harboured more gastropod species than hay meadows, as indicated by the non-overlapping 95% confidence intervals (Fig. 1). Five of the 27 species (18.5%) with 84 individuals (3.0%) are considered as threatened in Switzerland. We found one threatened species (two individuals) in hay meadows, three threatened species (35 individuals) in abandoned meadows and five threatened species (47 individuals) in young forests. The number of gastropod species per plot increased with ongoing succession (Table 3). In addition, more individuals were found in hay meadows and young forests than in abandoned meadows (Table 3; Tukey Contrasts, both $p < 0.009$). Carbonate content affected both the number of gastropod species (GLM, $F_{1,10} = 8.85$, $p = 0.014$) and the number of individuals (GLM, $F_{1,10} = 14.43$, $p = 0.004$). However, only the number of individuals was positively correlated with carbonate content of the soil (Spearman rank correlation, $r_S = 0.52$, $n = 15$, $p = 0.048$).

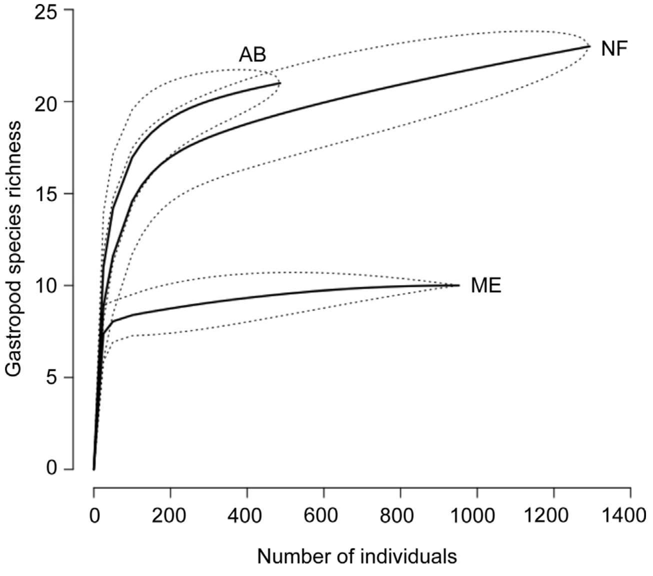

Fig. 1. Individual-based rarefaction curves for gastropods in hay meadows (ME), abandoned meadows (AB) and young forests (NF). Solid lines represent means and dotted lines represent 95% confidence intervals.

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.12.023.

3.2. Species composition

NMDS ordination analyses showed that successional stages differed significantly in the composition of plant species (Fig. 2a; $R^2 = 0.66$, $p = 0.001$). Furthermore, soil moisture and nitrogen content separated species composition along the first NMDS axis (Fig. 2a; soil moisture: $R^2 = 0.47$, $p = 0.028$, nitrogen: $R^2 = 0.43$, $p = 0.029$) and inclination separated species composition along the second axis (Fig. 2a; $R^2 = 0.60$, $p = 0.013$). For gastropods, species composition of hay meadows was clearly separated from that of the other two stages (Fig. 2b; $R^2 = 0.78$, $p = 0.002$). Nitrogen content separated gastropod species composition along the first NMDS axis (Fig. 2b; $R^2 = 0.63$, $p = 0.002$). The two areas did not differ in plant and gastropod species composition (plants: $R^2 = 0.01$, $p = 0.84$, gastropods: $R^2 = 0.01$, $p = 0.88$) and there was no significant effect of any other environmental variable (all $p > 0.07$).

3.3. Habitat specificity

Meadow abandonment affected plants with different habitat specificities in different ways. The proportion of grassland species decreased with progressive succession, while the proportion of forest species increased (Fig. 3a; grassland: GLM, $F_{2,12} = 93.57$, forest: GLM, $F_{2,12} = 54.84$, both $p < 0.0001$). In both groups, differences were significant among all successional stages (Tukey Contrasts, all $p < 0.021$). The proportion of generalist species differed also among successional stages (Fig. 3a; GLM, $F_{2,12} = 34.94$, $p < 0.0001$), being lower in hay meadows than in the other two stages (Tukey Contrast, both $p < 0.0001$, abandoned meadows – forests: $p = 0.50$). In addition, soil nitrogen content negatively affected the proportion of forest species (GLM, $F_{1,10} = 9.01$, $p = 0.013$).

As in plants, meadow abandonment affected gastropods with different habitat specificities in different ways. Successional stages differed in the proportion of open-land, generalist and forest species (Fig. 3b; open-land: GLM, $F_{2,12} = 46.20$, $p < 0.0001$, generalist: GLM, $F_{2,12} = 49.23$, $p < 0.0001$, forest: GLM, $F_{2,12} = 8.88$, $p = 0.006$). There was a higher proportion of open-land species and a lower proportion of generalist species in hay meadows than in the other two stages (Tukey Contrasts, all $p < 0.0001$). Furthermore, there was a negative effect of the carbonate content of the soil on the proportion of generalist species (GLM, $F_{1,10} = 7.44$, $p = 0.021$) and a positive effect of nitrogen content on the proportion of forest species (GLM, $F_{1,10} = 5.88$, $p = 0.036$). The factor study area was retained in all models. The two areas differed in the proportion of forest species (mean ± SE, AU: 0.7 ± 0.3%, BM: 0.2 ± 0.2%; GLM, $F_{1,11} = 8.83$, $p = 0.014$). However, in all other comparisons, the two areas did not differ in terms of habitat specificities of plants and gastropods (GLM, all $p > 0.15$).

3.4. Functional traits

The fourth-corner analysis indicated a significant relationship between plant traits and environmental variables ($S_{\mathrm{RLQ}} = 4.79$, $p = 0.003$). Successional stages differed in the height of non-woody species ($\chi^2 = 1811.03$, $p = 0.027$), in the earliest month of seed shedding ($\chi^2 = 2222.87$, $p = 0.030$) and in the type of reproduction ($\chi^2 = 1881.71$, $p = 0.020$). Hay meadows were associated with small (height < 1 m: 58.2%), early seed shedding species (May to June: 74.3%), mainly reproducing by seeds and vegetatively (70.6%). With ongoing succession plant height of non-woody species increased (height ≥ 1 m: AB 74.1%, NF 35.7%; height ≥ 2 m: AB 6.7%, NF

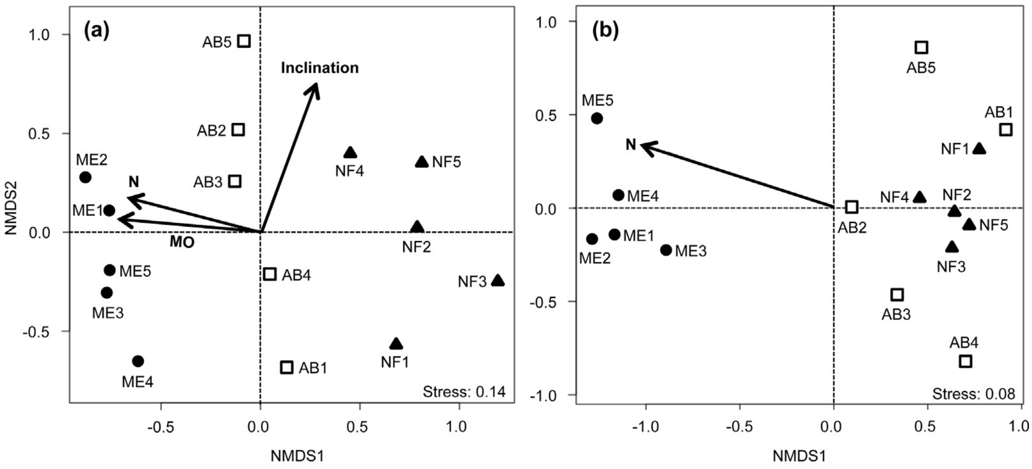

Fig. 2. NMDS ordination diagram based on Bray–Curtis dissimilarities in (a) plant and (b) gastropod species composition of hay meadows (dots), abandoned meadows (squares) and young forests (triangles). Significant environmental variables affecting species composition are shown (MO, soil moisture; N, nitrogen).

34.0%) and seed shedding started later in the year (July to October: AB 68.4%, NF 65.7%). Species on abandoned meadows reproduced mainly by seeds and vegetatively (61.9%), whereas for species in young forests other reproduction types gained in importance (by seeds and vegetatively: 36.3%, by seeds: 30.7% or vegetatively: 33.0%).

Soil moisture and nitrogen content negatively affected non-woody species taller than 2 m (both $p < 0.020$). In addition, soil moisture negatively affected late seed shedding species and the extent of vegetative reproduction, while nitrogen content negatively affected species reproducing by seeds (all $p < 0.042$). Furthermore, soil nitrogen content positively affected early seed shedding species and species reproducing by seeds and vegetatively with belowground stems (all $p < 0.039$).

The fourth-corner analysis indicated a significant relationship between gastropod traits and environmental variables ($S_{RLQ} = 0.65$, $p = 0.001$). Shell size increased with ongoing succession (size ≥ 5 mm: ME 16.0%, AB 51.0%, NF 69.6%; $\chi^2 = 635.26$, $p = 0.042$). In addition, soil moisture and nitrogen content were negatively associated with shell size (all $p < 0.046$). Further details on plant and gastropod traits are presented in Appendix D.

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.12.023.

4. Discussion

The present study showed that land-use abandonment resulting from the cessation of irrigation significantly altered the biodiversity of hay meadows in an arid mountain region. Gastropod richness as well as the species community and functional traits of both taxa were affected by meadow abandonment. We observed a decrease in the moisture content of the upper soil layer of young forests. The observed decline in soil nitrogen content can be explained by the cessation of fertilization with manure. This is in agreement with other studies demonstrating a decrease in soil nitrogen due to the lack of faeces input after grazing abandonment (Farris et al., 2010; Peco et al., 2006).

4.1. Effects of abandonment on species richness

Plant species richness was not affected by abandonment as recorded in several other studies (Baur et al., 2006; Cremene et al., 2005; Öckinger et al., 2006; Peco et al., 2006). This finding contrasts the results of numerous other studies on grassland succession showing that abandonment is usually associated with a decline in plant species richness (Jacquemyn et al., 2011; Maurer et al., 2006; Tasser and Tappeiner, 2002; Vassilev et al., 2011). Our finding could be explained by the small-scale mosaic of the landscape, which facilitates the colonization of species characteristic for other habitats and/or the dry soil conditions. This might lead to a delay in succession (Cremene et al., 2005).

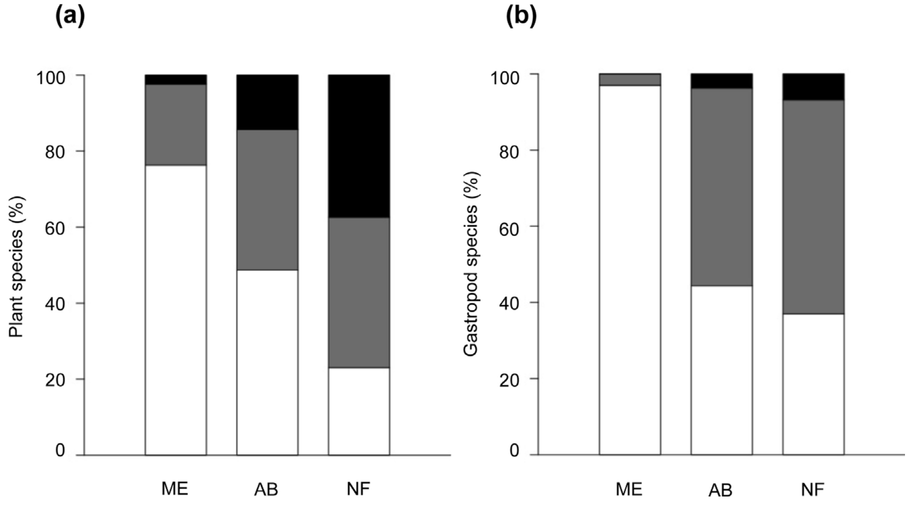

Fig. 3. Habitat specificity of (a) plants and (b) gastropods found in hay meadows (ME), abandoned meadows (AB) and young forests (NF). The white area of the bars represents the proportion of grassland species (plants) or open-land species (gastropods), the grey area that of generalist species and the black area that of forest species. Bars represent mean values of replicates for each stage ($n = 5$).

Gastropod richness increased with progressive succession, being highest in young forests. A very similar pattern was recorded in a successional grassland study in the Transylvanian mountains, Romania (Baur et al., 2006). However, possible effects of grassland abandonment are less well studied in gastropods than in plants and no consensus exists on whether gastropods are positively or negatively affected by land-use abandonment (see Boschi and Baur, 2008; Cremene et al., 2005 for negative effects). The increased gastropod species richness can be explained by the increase of structural heterogeneity (different food sources, refuges, open and shady spots) in the abandoned stages (Azcarate and Peco, 2012; Boschi and Baur, 2007), which allows the coexistence of more species than in homogenous hay meadows.

Plant and gastropod species richness were positively affected by plant available phosphorous and carbonate content of the soil, respectively. These two soil parameters were shown to affect the diversity of plants (Peco et al., 2006) and gastropods (Wäreborn, 1970).

Our results confirmed that different taxa vary in their response to grassland abandonment. For example, particular ant (Azcarate and Peco, 2012) and butterfly species (Balmer and Erhardt, 2000; Baur et al., 2006) as well as grasshopper species (Marini et al., 2009) were favoured by different successional stages. Overall, the number of threatened species was highest in abandoned meadows for plants and increased with progressive succession for gastropods. Other studies showed that the number of threatened plant species was not affected by grassland abandonment (Baur et al., 2006, 2007; Ruprecht et al., 2009), whereas intensive management negatively affected the number of threatened gastropod species (Boschi and Baur, 2007).

4.2. *Effects of abandonment on species composition and habitat specificity*

The compositions of plant and gastropod species changed with progressive succession confirming other studies on grassland abandonment (Baur et al., 2006, 2007; Farris et al., 2010; Peco et al., 2012). The shift in plant species composition was related to the decrease in soil moisture and soil nitrogen content (Fig. 2a). This suggests that both irrigation and fertilization are important in shaping the plant community of these hay meadows. However, the increased abundance of *Brachypodium pinnatum* in early abandoned meadows and young forests (Appendix B), a species associated with the reduction of mowing and abandonment (Bobbink and Willems, 1987, 1991), most notably reflected the decrease in disturbance frequency caused by the cessation of mowing.

The gastropod communities of hay meadows differed in their composition from those of the other two successional stages (Fig. 2b). This change was related to the decrease in soil nitrogen content, indicating that the stop of fertilization was crucial for this shift. Fertilization is known to negatively affect gastropod richness (Boschi and Baur, 2007) and probably also influences species composition, because different species show different responses to grassland fertilization (Boschi and Baur, 2008).

Changes in species composition are mirrored in the habitat specificity of plants and gastropods. The proportion of grassland (plants) and open-land species (gastropods) decreased following abandonment, which is in agreement with other studies (Baur et al., 2006; Cremene et al., 2005). These results confirm the importance of semi-natural grasslands as refuges for open-land species (Baur et al., 2006).

The gastropod community of hay meadows consisted nearly exclusively of species characteristic for dry, open habitats, whereas about 50% of all open-land species were lost already in early abandoned meadows. This could be explained by the increased plant height and shrub cover observed in this stage, which probably led to an increase in above-ground humidity (Boschi and Baur, 2008). These microclimatic conditions are less favourable for open-land species (Boschi and Baur, 2008) such as *Pupilla muscorum*, a species showing a pronounced decrease in abundance following grassland abandonment (Appendix C), but allow the colonization of generalist species.

4.3. *Effects of abandonment on functional traits*

Meadow abandonment led to an increase in the height of non-woody plant species, confirming other studies (Kahmen and Poschlod, 2004; Pavlu et al., 2011; Peco et al., 2005, 2012; Römermann et al., 2009; Vassilev et al., 2011). This can be explained by the lack of disturbance. In abandoned grasslands, tall competitive species expand and together with a dense vegetation layer suppress the growth of slowly growing species (Grime, 2001). Furthermore, seed shedding started later in the two abandoned stages supporting the finding of Römermann et al. (2009) that later seed shedding is positively related to the time since abandonment. Early mowing could suppress late seed shedding species (Smith et al., 1996). Therefore, the absence of early mowing or grazing in the abandoned stages might explain our result. Furthermore, meadow abandonment led to a change in the type of plant reproduction with vegetative reproduction gaining in importance in young forests. An increase in the proportion of vegetative reproduction was also recorded in other abandoned grasslands (Jensen and Schrautzer, 1999; Pakeman and Marriott, 2010). The success of reproduction by seeds depends on the presence of gaps, whereas vegetative reproduction is more successful in habitats with low disturbance (Grime, 2001).

Shell size of gastropods increased with ongoing succession, which could be related to the lack of disturbance in the abandoned stages. Boschi and Baur (2007) recorded that species with small shells were less affected by grazing than species with large shells. The authors suggested that the more compact soil in intensively grazed pastures might restrain large but not small gastropods to take shelter from trampling animals in the soil. Therefore, under these conditions gastropods with large shells are more easily crushed by grazing animals than gastropods with small shells. In our study, heavy mowers, tractors and hay wagons probably led to more compact soils in hay meadows (Soane and van Ouwerkerk, 1994), only allowing relatively small gastropods to take shelter from machineries in the soil and thereby excluding larger animals from these meadows. Another explanation for the increase in shell size with ongoing succession is that structural elements in the abandoned stages (e.g. branches, trunks, stones) represent suitable hiding places for gastropods with large shells.

Soil moisture and soil nitrogen content also affected the functional traits of plants and gastropods, showing the same pattern as the effects of succession. However, the affected plant traits (height, vegetative reproduction) are related to the competitive ability of plants (Grime, 2001) suggesting that the responses of these traits were probably related to the lower level of disturbance owing to the cessation of mowing. In contrast, the negative effect of soil moisture on late seed shedding species could be interpreted as a response to irrigation abandonment. This might be of importance in dry years, because the onset of flowering was shown to be later in the season as an adaptation to water stress (Crimmins et al., 2011), which could also apply for the start of seed shedding.

5. Conclusion

Our study showed that extensive land-use is required to maintain the hay meadows of the Valais and their characteristic plant and gastropod communities. Moreover, the findings suggest that the observed changes in biodiversity were most likely related to the cessation of annual mowing. However, in this dry climatic region, irrigation is important to secure hay production and hence to maintain annual mowing. Therefore, both mowing and irrigation can be regarded as important land-use features in the Valais. Nevertheless, a generalization of our findings to other arid regions should be made with caution, because the geographical region covered was relatively small. Furthermore, our study areas are characterized by a small-scale patchy landscape consisting of small meadows, fallow land, hedgerows, few buildings and roads with adjacent forest. Therefore, our findings should not be extrapolated to land-use abandonment in large, homogenous areas.

The observed high plant diversity of hay meadows and the two following successional stages as well as the high gastropod diversity of both abandoned stages demonstrate that all three stages should be maintained in order to preserve the high biodiversity at the landscape level. In addition, the two successional stages were important for threatened gastropod species. To maintain these stages it is recommended to continue the current management practices (Table 1) with occasional removing of shrubs and trees to prevent the transition into forests. However, despite the high diversity of the two successional stages, further abandonment of hay meadows is not recommended for several reasons. First of all, golden oat meadows (*Trisetetum flavescentis*, Ellenberg, 1986), the typical hay meadows of the Valais, represent a grassland type, which has become increasingly rare in the Swiss Alps in the past decades (Stöcklin et al., 2007). Furthermore, hay meadows are an important landscape feature attracting tourists owing to their high plant diversity. Finally, these meadows represent a permeable matrix for the unique steppe grasslands of the Valais, which are considered to be a primary habitat of national importance (Dipner et al., 2010). The maintenance of the characteristic hay meadows could be achieved by ecological compensation payments for farmers. In the future, however, meadow abandonment might become more severe owing to global warming and the decrease in precipitation and irrigation water in the summer months (Moser, 2013).

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Supplementary material Chapter I

Appendix A. Soil characteristics of hay meadows, early abandoned meadows and young forests located in the two study areas.

Appendix B. List of plant species and their habitat specificity of the hay meadows, early abandoned meadows and young forests investigated.

Appendix C. List of gastropod species and their habitat specificity of the hay meadows, early abandoned meadows and young forests investigated.

Appendix D: Two tables showing the summary of the fourth-corner analyses for plants (Table D.1) and gastropods (Table D.2).

Appendix A

Table A.1

Soil characteristics (mean ± SE) of hay meadows (ME), abandoned meadows (AB) and young forests (NF) located in the two study areas.

	Ausserberg (AU)			Birgisch (BM)			Successional stage			Area			Successional stage * area		
	ME (n=3)	AB (n=3)	NF (n=3)	ME (n=2)	AB (n=2)	NF (n=2)	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*
pH[a]	6.2 ± 0.2	6.7 ± 0.5	6.7 ± 0.5	6.3 ± 0.1	6.1 ± 0.0	6.3 ± 0.3	0.42	2, 11	0.67	0.94	1, 11	0.35	–	–	n.s.
Carbonate content (%)[a]	3.7 ± 0.5	6.7 ± 2.0	6.4 ± 2.0	3.8 ± 0.3	3.4 ± 0.8	4.1 ± 0.5	0.93	2, 11	0.43	2.30	1, 11	0.16	–	–	n.s.
Soil organic matter content, SOM (%)[a]	18.8 ± 2.9	17.7 ± 0.8	15.9 ± 0.9	20.9 ± 2.1	14.5 ± 1.4	18. 0 ± 1.6	1.79	2, 11	0.21	0.04	1, 11	0.84	–	–	n.s.
Total phosphorous (μg PO_{4-} /g)[b]	795.7 ± 109.3	874.0 ± 85.9	780.1 ± 60.1	1130.6 ± 140.9	644.3 ± 28.8	848.0 ± 8.9	1.57	2, 9	0.26	0.60	1, 9	0.46	4.81	2, 9	**0.038**
Plant available phosphorous (μg PO_{4-} /g))[a]	247.5 ± 25.7	179.4 ± 21.1	192.4 ± 16.1	143.5 ± 65.4	189.0 ± 31.0	108.2 ± 42.1	0.99	2, 11	0.40	4.52	1, 11	0.06	–	–	n.s.

Final model: [a] ANOVA with successional stage and study area, [b] ANOVA with successional stage, study area and the corresponding interaction

Appendix B

List of plant species and their habitat specificity showing the average vegetation cover (%) observed in hay meadows (ME), early abandoned meadows (AB) and young forests (NF) located in the two study areas Ausserberg and Birgisch.

		ME		AB		NF	
Species	Habitat specificity	Ausserberg (n=3)	Birgisch (n=2)	Ausserberg (n=3)	Birgisch (n=2)	Ausserberg (n=3)	Birgisch (n=2)
Forbs							
Achillea millefolium aggr.	Grassland	2.935	0.953	1.460	0.005	0	0
*Actaea spicata **	Forest	0	0	0	0	0	0
Agrimonia eupatoria	Grassland	0	0	0	0.318	0	0
Ajuga reptans	Generalist	0.420	0.038	0	0	0.427	0.318
Alchemilla glabra aggr.	Grassland	0.002	0	0	0.638	0.002	0
Alchemilla xanthochlora aggr.	Grassland	0.008	0.033	0	0	0	0
Alliaria petiolata	Forest	0	0	0	0	0	0.625
Allium oleraceum	Generalist	0	0	0.005	0	0	0
Allium sphaerocephalon	Grassland	0	0	0	0	0	0.005
*Amaranthus retroflexus **	Generalist	0	0	0	0	0	0
Angelica sylvestris	Forest	0	0	0	0	2.500	0
Anthriscus sylvestris	Grassland	0	0.315	0.002	0	0	0
Anthyllis vulneraria s.l.	Generalist	0.013	0	0	0	0	0
Arabis hirsuta aggr.	Grassland	0.012	0	0	0	0	0
Arabis turrita	Forest	0.003	0	0	0	0	0
Arctium lappa	Generalist	0	0	0.003	0	1.250	0.003
Artemisia absinthium	Generalist	0	0	0.002	0.003	0	0.633
Artemisia vulgaris	Generalist	0	0	1.668	0	0.002	0
*Botrychium lunaria **	Grassland	0	0	0	0	0	0
Bunium bulbocastanum	Grassland	0	0	0.007	0	0	0
Campanula glomerata s.l.	Grassland	0.860	0.003	0.008	0.003	0	0
Campanula rhomboidalis	Grassland	0.835	0.320	0	0.003	0	0
Campanula scheuchzeri	Grassland	0.012	0	0.010	0	0.003	0
Campanula trachelium	Forest	0	0	0	0.005	0	0.008
Carduus nutans s.l.	Generalist	0	0	0.002	0	0	0
Carlina acaulis ssp. caulescens	Grassland	0.020	0	0	0	0	0
Carum carvi	Grassland	0	1.250	0	0	0	0
*Centaurea jacea s.l. **	Grassland	0	0	0	0	0	0
Centaurea scabiosa s.l.	Grassland	0.208	0	0	0	0	0
Cerastium fontanum s.l.	Grassland	0.003	0	0	0.003	0	0
Chaerophyllum aureum	Grassland	0.002	5.625	0.002	0	0.837	0
Chelidonium majus	Generalist	0	0	0.002	0	0	0
Chenopodium glaucum	Generalist	0	0	0.002	0.003	0	0.003
Cirsium arvense	Generalist	0	0	13.750	3.750	0.002	2.813
Cirsium vulgare	Generalist	0	0	0.002	0	0.003	2.508
Clinopodium vulgare	Generalist	0	0	3.133	0	0.427	0
Colchicum autumnale	Grassland	0.003	0.318	0	0	0	0
*Convolvulus arvensis **	Generalist	0	0	0	0	0	0
Crepis biennis	Grassland	0	0.315	0	0	0	0
Daucus carota	Grassland	0	0	0	0.645	0	0
Dianthus carthusianorum s.l.	Generalist	0.018	0	0	0.003	0	0
Epilobium roseum	Generalist	0	0	0.625	0.003	0.213	0.003
Equisetum palustre	Grassland	0	0.018	0.227	0	0	0
Erigeron acer s.l.	Generalist	0	0	0	0	0	0.003
*Erodium sp. cf **	Generalist	0	0	0	0	0	0
Euphorbia cyparissias	Grassland	0	0	0.212	0.630	0	0
Euphrasia rostkoviana s.l.	Grassland	0.013	0	0	0	0	0
*Fallopia convolvulus **	Generalist	0	0	0	0	0	0
Fragaria vesca	Forest	0	0	0	0.315	0	0
Galeopsis tetrahit	Generalist	0	0	0	1.900	0.217	0.003
Galium aparine	Generalist	0	0	1.668	0.315	0.635	0.955
Galium boreale	Grassland	1.055	2.500	0.217	0.630	0.008	0
Galium mollugo aggr.	Generalist	1.470	0.313	4.170	0.945	0.208	0
*Geranium pusillum **	Generalist	0	0	0	0	0	0
Geranium pyrenaicum	Generalist	0	0	0	0	0.002	0

Geranium robertianum s.l.	Generalist	0	0	5.833	0.315	14.583	2.500
Geranium sylvaticum	Grassland	0	2.500	0	0.625	0	0
Geum urbanum	Generalist	0	0.318	0.635	0.008	0.845	0.643
Gymnadenia conopsea	Grassland	0.002	0	0	0	0	0
Helianthemum nummularium s.l.	Grassland	0.425	0	0.208	0	0	0
Hepatica nobilis	Forest	0	0	0.010	0.003	0.210	0.313
Heracleum sphondylium s.l.	Grassland	2.920	5.015	0.212	0	0.008	0
Hieracium pilosella (Artengruppe)	Grassland	0.427	0	0	0	0	0
Hippocrepis comosa	Grassland	0	0	0.208	0.015	0	0
Hypericum perforatum s.str.	Generalist	0	0	0	0.013	0	0
*Knautia arvensis **	Grassland	0	0	0	0	0	0
Knautia dipsacifolia	Generalist	0.002	0.018	0	0.938	0.212	0
Laserpitium latifolium	Generalist	0	0	0	0	0.003	0
Lathyrus pratensis	Grassland	1.878	0.653	1.275	0.630	0.002	0.318
Leontodon hispidus s.l.	Grassland	16.667	17.188	0.003	0.005	0	0
Leucanthemum vulgare aggr.	Grassland	0.850	0.323	0	0	0	0
Lilium martagon cf	Forest	0	0	0	0	0.012	0
*Listera ovata **	Generalist	0	0	0	0	0	0
Lotus corniculatus aggr.	Grassland	1.678	1.563	0.417	0.323	0	0
Medicago lupulina	Generalist	0.427	0	0	0	0.002	0
*Mentha longifolia **	Grassland	0	0	0	0	0	0
*Mercurialis perennis **	Forest	0	0	0	0	0	0
Mycelis muralis	Generalist	0	0	0	0.318	0.018	0
Myosotis arvensis	Generalist	0	0.330	0	0	0	0
Myosotis sylvatica cf	Generalist	0	0	0.417	0	0.418	0
Ononis repens	Grassland	0.633	0	0	0	0	0
Orchis mascula s.str.	Grassland	0.003	0	0	0	0	0
Orchis ustulata	Grassland	0.002	0	0	0	0	0
Origanum vulgare	Generalist	0	0	0	0	0.010	0
Oxalis acetosella	Forest	0	0	0	0	0.208	0
Peucedanum austriacum s.l. cf	Grassland	0	0	0.002	0	0	0
Peucedanum oreoselinum	Generalist	0.628	0	0	1.250	0	0.003
*Phyteuma orbiculare **	Grassland	0	0	0	0	0	0
Phyteuma spicatum	Forest	0	0	0.843	0.643	0.420	0.630
Picris hieracioides s.l.	Grassland	0.215	0	0.212	0.005	0	0.005
Pimpinella major	Grassland	0.002	0.643	0	0	0.425	0
Pimpinella saxifraga aggr.	Grassland	0.018	0	0.445	0	0.002	0
Plantago lanceolata	Grassland	1.693	2.200	0.012	0.325	0	0
Plantago major s.l.	Generalist	0	0	0.017	0	0	0
Plantago media	Grassland	0	0	0.208	0	0	0
*Platanthera bifolia **	Forest	0	0	0	0	0	0
Polygonatum odoratum	Generalist	0	0	0	0	0.003	0.003
Potentilla erecta	Grassland	0.217	0	0	1.878	0	0
Potentilla pusilla	Grassland	0.427	0	0	0	0	0
Prunella vulgaris	Grassland	0.212	0	0.002	0	0	0
Ranunculus acris s.l.	Grassland	0.838	0.005	0	0	0	0
Ranunculus bulbosus	Grassland	1.668	0	0	0	0	0
Ranunculus nemorosus aggr.	Generalist	0.433	0.020	1.048	0.318	0.225	0
Rhinanthus alectorolophus	Grassland	1.900	2.500	0	0	0	0
Rorippa sylvestris cf	Generalist	0	0	0	0	0	0.003
Rumex acetosa	Grassland	1.670	0.660	0.013	0	0	0
Rumex obtusifolius	Grassland	0	0.630	0.633	0	0.003	0
Salvia pratensis	Grassland	0.428	0	3.335	0.005	0	0
Sanguisorba minor s.l.	Grassland	0	0	0	0.333	0	0
Scabiosa columbaria s.l.	Grassland	0.640	0	0	0	0	0
*Scrophularia nodosa **	Forest	0	0	0	0	0	0
*Sedum album **	Generalist	0	0	0	0	0	0
*Sedum rupestre aggr. **	Grassland	0	0	0	0	0	0
*Sedum telephium s.l. **	Generalist	0	0	0	0	0	0
Silene dioica	Generalist	0	0	0.002	0	0.833	0
Silene flos-cuculi	Grassland	0	0.028	0	0	0	0
Silene nutans s.l.	Grassland	0.002	0	0	0	0.002	0
Silene vulgaris s.l.	Grassland	1.678	1.250	1.050	0.313	0.013	0.630
*Solidago virgaurea s.l. **	Forest	0	0	0	0	0	0
*Stachys recta s.l. **	Grassland	0	0	0	0	0	0

Stachys sylvatica	Forest	0	0	0	0	0	0.313
Taraxacum officinale aggr.	Generalist	0.220	0.020	0.440	0.003	0.012	0.008
Teucrium chamaedrys	Grassland	0	0	0.002	0	0	0
Thymus serpyllum aggr.	Grassland	2.293	0.638	0.212	0.953	0	0
Torilis japonica	Generalist	0	0	0.210	0.625	0	0
Tragopogon pratensis s.l.	Grassland	0.002	0.010	0.005	0	0	0
*Trifolium aureum **	Grassland	0	0	0	0	0	0
Trifolium montanum	Grassland	0.627	0.013	0.020	0.008	0	0
Trifolium pratense s.l.	Grassland	4.583	2.500	0.417	0.003	0	0
Trifolium repens s.l.	Grassland	0.212	1.250	0.208	0	0	0
Urtica dioica	Generalist	0	0	0.220	3.750	0.625	0
0Valeriana officinalis aggr.	Grassland	0	0	0	0.313	0	0
Veronica arvensis	Generalist	0.850	0.005	0.008	0	0	0
Veronica chamaedrys	Generalist	0.625	0	1.253	1.255	0.627	0.318
*Veronica officinalis **	Generalist	0	0	0	0	0	0
Veronica spicata	Grassland	0.833	0	0	0	0	0
Veronica teucrium	Grassland	0	0	0.002	0	0	0
Vicia cracca s.l.	Generalist	0.850	0.943	0.853	1.250	0	0
Vicia lathyroides	Grassland	0.002	0	0	0	0	0
Vicia sativa s.l.	Generalist	0	0	0	0.008	0	0
Vicia sepium	Generalist	0.017	0	0.002	0	0.003	0.313
Vincetoxicum hirundinaria	Forest	0	0	0	0	0	0.313
Viola reichenbachiana	Forest	0	0	0	0.003	0	0
Grasses							
Agrostis capillaris	Grassland	3.542	1.250	0.627	0.003	0	0.315
Anthoxanthum odoratum aggr.	Grassland	4.583	1.578	0	0.025	0	0
Arrhenatherum elatius	Grassland	0	0	0.220	0.013	0.002	0
Brachypodium pinnatum aggr.	Generalist	0.233	0	43.750	36.875	4.792	8.128
Brachypodium sylvaticum	Forest	0	0	0	0	1.250	0.313
Briza media	Grassland	1.892	0.315	0	0	0	0
Bromus benekenii	Forest	0	0	0	0	0.002	0
Bromus erectus s.l.	Grassland	27.927	0.005	4.380	12.188	0.208	11.563
Bromus sterilis	Generalist	0	0	0	0	0	0.640
Calamagrostis epigejos	Forest	0	0	1.458	0	0	0
Carex caryophyllea	Grassland	0	1.250	0	0.005	0	0
Carex flacca	Generalist	0	0.010	0.008	0	0	0
Carex liparocarpos	Grassland	0	0.313	0	0	0	0
Carex muricata aggr.	Generalist	0	0	1.042	0	0	0
Carex pallescens	Grassland	0.012	0	0.210	0.005	0.002	0
Carex sp.	–	0.220	0	0	0	0.422	0
Cynosurus cristatus	Grassland	0.833	0.018	0	0	0	0
Dactylis glomerata	Generalist	4.388	1.900	3.335	5.943	2.717	0.320
Danthonia decumbens	Generalist	0	0	0	0.003	0	0
Echinochloa crus-galli	Generalist	0	0.340	0	0	0	0
Elymus caninus	Forest	0	0	0	3.750	1.668	0
Elymus hispidus	Generalist	0	0	0	0	6.667	0
Festuca gigantea	Forest	0	0	0	2.513	0	0
Festuca pratensis s.l.	Grassland	1.877	1.255	0	0.003	0	0
Festuca rubra aggr.	Generalist	14.375	13.438	0.215	0.965	1.668	0.313
Festuca valesiaca	Grassland	0	0	0.003	0	0	0
Helictotrichon pubescens	Grassland	0.652	0.953	0.430	0	0	0
Holcus lanatus	Grassland	0.225	25.315	3.750	0.003	0.010	0
Juncus articulatus	Grassland	0	0.003	0	0	0	0
Lolium perenne	Grassland	0.425	0.003	0.417	0	0	0
Luzula campestris	Grassland	0.245	0.040	0	0.008	0	0
Melica nutans	Forest	0	0	0	0	2.708	0.005
Phleum pratense aggr.	Grassland	0	1.250	1.458	0	0	0
Poa alpina	Grassland	0.002	0	0.002	0	0	0
Poa nemoralis	Forest	0	0	0	0	0.842	7.193
Poa pratensis aggr.	Grassland	0	1.250	0.643	0.003	0.833	1.875
Poa variegata	Generalist	0.230	0	0	0	0	0
Trisetum flavescens	Grassland	7.720	2.500	0.628	0.003	0	0
Woody plants							
*Acer pseudoplatanus **	Forest	0	0	0	0	0	0
Alnus incana	Forest	0	0	0.002	0.313	4.197	0.028
Berberis vulgaris	Forest	0	0	0	0	0.208	0
Betula pubescens	Forest	0	0	0	0.005	0	0

Clematis vitalba	Forest	0	0	1.467	4.688	0.843	0.315
Cornus sanguinea	Forest	0	0	0	0	3.547	0.003
Fraxinus excelsior	Forest	0	0	0.228	1.885	19.375	7.188
Juniperus communis s.l.	Forest	0	0	0	0	0.002	0
Larix decidua *	Forest	0	0	0	0	0	0
Lonicera periclymenum *	Forest	0	0	0	0	0	0
Lonicera xylosteum	Forest	0	0	0	0	0.220	0
Populus tremula	Forest	0	0	0	0	0.627	0
Populus sp.	Forest	0	0	0.003	0.940	0	0
Prunus avium	Forest	0	0	0	0	0.005	0
Prunus mahaleb	Forest	0	0	0	0	0.003	0.003
Prunus spinosa	Forest	0	0	0	0	0.002	0
Quercus petraea	Forest	0	0	0	0.003	0.002	0
Rosa sp.	–	0	0	0.002	0	0.212	0.003
Rubus fruticosus aggr.	Forest	0	0	7.502	0	21.877	20.325
Rubus idaeus	Forest	0	0	1.250	4.063	1.462	0.325
Salix caprea *	Forest	0	0	0	0	0	0
Sambucus nigra	Forest	0	0	0	0	2.502	0.003
Sorbus aria	Forest	0	0	0	0	0.003	0
Sorbus aucuparia	Forest	0	0	0.002	0	0	0
Viburnum lantana	Forest	0	0	0	0	0.002	0

* Species marked with an asterisk only occurred in the remaining area of a sampling plot (i.e. not observed with Braun-Blanquet method) and therefore no cover values were obtained.

Appendix C

List of gastropod species and their habitat specificity showing the sum of gastropod individuals observed in hay meadows, early abandoned meadows and young forests located in the two study areas Ausserberg and Birgisch.

			Hay meadow		Early abandoned meadow		Young forest	
Family	Species	Habitat specificity	Ausserberg (n=3)	Birgisch (n=2)	Ausserberg (n=3)	Birgisch (n=2)	Ausserberg (n=3)	Birgisch (n=2)
Lymnaeidae	*Galba truncatula*	Generalist	0	0	4	0	1	0
Succineidae	*Succinella oblonga*	Open-land	0	105	0	0	0	0
Cochlicopidae	*Cochlicopa sp.*	Open-land	14	29	74	3	204	88
Vertiginidae	*Columella edentula*	Generalist	0	0	3	2	3	1
	Truncatellina cylindrica	Open-land	99	5	87	1	20	4
	Vertigo pusilla	Generalist	0	0	0	0	0	1
	Vertigo pygmaea	Open-land	17	35	1	1	0	0
Pupillidae	*Pupilla muscorum*	Open-land	87	143	0	0	1	0
Valloniidae	*Acanthinula aculeata*	Forest	0	0	6	0	39	0
	Vallonia costata	Open-land	92	64	22	0	13	4
	Vallonia excentrica	Open-land	138	2	0	0	0	0
	Vallonia pulchella	Open-land	41	77	0	0	0	0
Enidae	*Jaminia quadridens*	Open-land	0	0	1	0	1	0
	Merdigera obscura	Forest	0	0	1	0	22	2
	Zebrina detrita	Open-land	0	0	0	0	1	0
Vitrinidae	*Vitrina pellucida*	Open-land	2	0	17	2	195	21
Zonitidae	*Perpolita hammonis*	Generalist	0	0	8	6	13	6
	Aegopinella minor	Generalist	0	0	51	4	163	97
	Vitrea contracta	Open-land	0	0	32	8	85	40
Euconulidae	*Euconulus fulvus*	Generalist	0	0	7	2	10	8
Hygromiidae	*Euomphalia strigella*	Generalist	2	0	5	2	18	18
	Helicella itala	Open-land	0	0	27	0	8	0
	Trichia sericea	Generalist	0	0	11	1	15	8
Helicidae	*Arianta arbustorum*	Generalist	0	0	23	1	9	7
	Cepaea nemoralis	Generalist	0	0	0	17	0	2
	Helix pomatia	Generalist	0	0	4	0	10	10
Punctidae	*Punctum pygmaeum*	Generalist	0	0	45	7	136	9
-	unknown	–	1	0	6	1	24	14

Appendix D

Table D.1

Summary of the fourth-corner analysis for plants. For the combination of plant traits and successional stage (qualitative variable) test statistics (χ^2 or *F*) and *p*-values are shown. Significant combinations are presented in bold. For each significant ($p < 0.05$) combination of plant traits and soil parameters (quantitative variables) Pearsons *r* is shown. SOM = soil organic matter content

	Successional stage	Soil moisture	Nitrogen content	Carbonate content	pH	SOM	Total phosphorous	Plant available phosphorous
Plant height	**$\chi^2 = 1811.0$, $p = 0.027$**							
height < 0.5 m		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
0.5 ≤ height < 1 m		n.s.	n.s.	n.s.	n.s.	0.21	n.s.	n.s.
1 m ≤ height < 2 m		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
height ≥ 2 m		– 0.27	– 0.25	n.s.	n.s.	n.s.	n.s.	n.s.
Woodiness	$\chi^2 = 793.6$, $p = 0.11$							
Semi-woody		n.s.	– 0.21	n.s.	n.s.	n.s.	n.s.	n.s.
Herbaceous		n.s.	0.21	n.s.	n.s.	n.s.	n.s.	n.s.
Leaf distribution	$\chi^2 = 1323.2$, $p = 0.20$							
Rosette		n.s.	0.32	n.s.	n.s.	0.29	0.25	n.s.
Semi-rosette		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Leaves distributed regularly		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Semi-rosette and leaves distributed regularly		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Seed bank longevity index	$F = 42.3$, $p = 0.83$	n.s.	n.s.	– 0.24	n.s.	n.s.	n.s.	n.s.
Earliest month of seed shedding	**$\chi^2 = 2222.9$, $p = 0.030$**							
May		n.s.	0.29	n.s.	n.s.	0.26	0.22	0.20
June		n.s.	n.s.	– 0.26	– 0.25	n.s.	n.s.	n.s.
July		n.s.	n.s.	n.s.	0.26	n.s.	n.s.	n.s.
August		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
September		– 0.27	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
October		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Life span	$\chi^2 = 375.8$, $p = 0.36$							
Annual		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Biennial		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Perennial		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Leaf anatomy	$\chi^2 = 864.7$, $p = 0.62$							
Mesomorphic		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Meso- and hygromorphic		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	– 0.28
Scleromorphic		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Meso- and scleromorphic		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hygromorphic		n.s.	– 0.19	n.s.	n.s.	n.s.	n.s.	n.s.

Helo- and hygromorphic		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Type of reproduction	**χ^2 = 1881.7, p = 0.020**							
By seed (s)		n.s.	– 0.25	n.s.	n.s.	– 0.20	– 0.19	n.s.
Mainly by seed (ssv)		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
By seed and vegetatively (sv)		n.s.	0.25	n.s.	n.s.	n.s.	n.s.	n.s.
Mainly vegetatively (vvs)		– 0.28	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Clonal growth organ	χ^2 = 1016.8, p = 0.52							
Rooting horizontal stems (1)		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Pseudovivipary (4)		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Belowground stems (9 or 10)		n.s.	0.31	n.s.	n.s.	0.23	n.s.	n.s.
Stem tubers (12)		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Root-splitters or adventitious buds (14 or 15)		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
No clonal growth (18)		n.s.	– 0.25	n.s.	n.s.	– 0.20	– 0.19	n.s.

Table D.2

Summary of the fourth-corner analysis for gastropods. For the combination of gastropod traits and successional stage (qualitative variable) test statistics (χ^2) and *p*-values are shown. Significant combinations are presented in bold. For each significant ($p < 0.05$) combination of gastropod traits and soil parameters (quantitative variables) Pearsons *r* is shown. SOM = soil organic matter content

	Successional stage	Soil moisture	Nitrogen content	Carbonate content	pH	SOM	Total phosphorous	Plant available phosphorous
Adult shell size	**χ^2 = 635.3 p = 0.042**							
size < 5.0 mm		0.40	0.35	n.s.	n.s.	n.s.	n.s.	n.s.
size ≥ 5.0 mm		– 0.40	– 0.35	n.s.	n.s.	n.s.	n.s.	n.s.
Age at sexual maturity	**χ^2 = 962.8, p = 0.033**							
< 1 year		0.46	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
1 year		– 0.50	– 0.45	0.38	n.s.	n.s.	n.s.	n.s.
> 1 year		n.s.	n.s.	n.s.	– 0.22	n.s.	n.s.	n.s.
Longevity	χ^2 = 87.0, p = 0.54							
1-2 years		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
> 2 years		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Humidity preference	χ^2 = 362.2, p = 0.29							
Wet		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Moist		– 0.39	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dry		0.39	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Inundation tolerance	χ^2 = 349.4, p = 0.39							
Low		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Moderate		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
High		n.s.	0.38	n.s.	n.s.	n.s.	0.37	n.s.
Shell shape	χ^2 = 375.5, p = 0.35							
Depressed		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Conical		n.s.	– 0.33	n.s.	n.s.	– 0.24	n.s.	n.s.
Oblong		n.s.	n.s.	n.s.	n.s.	0.26	0.29	n.s.

Chapter II

Effects of different irrigation systems on the biodiversity of species-rich hay meadows

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Effects of different irrigation systems on the biodiversity of species-rich hay meadows

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ABSTRACT

The maintenance of traditional management practices is essential for the conservation of the biodiversity of semi-natural grasslands including species-rich hay meadows. In the canton Valais (Switzerland), hay meadows are traditionally irrigated using open water channels. However, since the 1980s, this labour intensive irrigation technique has been increasingly replaced by sprinkler irrigation. This study examined whether the different irrigation techniques (traditional vs. sprinkler) influence the local biodiversity of species-rich hay meadows. In particular, the diversity and composition of plant and gastropod species of eight traditionally irrigated meadows were compared with those of eight sprinkler-irrigated meadows. It was also assessed whether the species of either meadow type differed in functional traits. A high plant species richness was found in the meadows investigated. The study showed that the diversity and composition of plant and gastropod species of hay meadows were not affected by the change in irrigation technique 8–18 years ago. However, a lower grass/forb-ratio was observed in traditionally than in sprinkler-irrigated meadows. Furthermore, irrigation technique affected the leaf distribution and the onset of seed shedding in plants. Thus, the change in the irrigation technique altered only some aspects of biodiversity. Therefore, irrigation system alone does not represent the major factor affecting the biodiversity of hay meadows investigated.

1. Introduction

Semi-natural grasslands including hay meadows belong to the most species-rich habitats in Central Europe and therefore are of high conservation value (Baur et al., 2006; Poschlod and WallisDeVries, 2002). The high biodiversity of these grasslands is a result of traditional management practices such as grazing and mowing, which have been applied since many centuries and allow the coexistence of several species through regular disturbance (Poschlod and WallisDeVries, 2002). Nowadays, these grasslands are considered as refugia for numerous rare species whose primordial habitats were destroyed (Baur et al., 1996). Above all relative changes in costs for labour and fertilizers led to changes in agricultural practices beginning in the mid 20th century (Strijker, 2005). As a consequence, semi-natural grasslands are either used more intensively or were abandoned, resulting both in a decline in the area of these habitats throughout Europe (Strijker, 2005) and a decrease in plant species richness (Homburger and Hofer, 2012; Maurer et al., 2006; Niedrist et al., 2009).

The maintenance of hay meadows and their typical species composition also depends on irrigation, especially in arid regions where meadows are traditionally irrigated using open water channels (Leibundgut, 2004). These water channels are found in several parts of Europe, amongst others on the south-facing slopes of the Valais, Switzerland, where their first occurrence dates back to the 11th century (Leibundgut, 2004). Since the mid 20th century, however, the modernization and rationalization of agricultural practices in the Valais have led increasingly to the replacement of the traditional irrigation technique by sprinkler irrigation systems (Crook and Jones, 1999; Meurer and Müller, 1987).

Traditional and sprinkler irrigation differ substantially in their distribution of the water used, which may have potential effects on the biodiversity of the meadows. In traditional irrigation, the ground is inundated irregularly, depending on the micro-relief, whereas a sprinkler distributes the water over the meadow more homogeneously from above (Meurer and Müller, 1987). Traditional meadow irrigation therefore leads to the coexistence of different microhabitats and hence to a high floristic and faunistic diversity (Werner, 1995). Previous surveys focused on the plant species composition of meadows with either traditional or sprinkler irrigation (Volkart and Godat, 2007; Werner, 1995). However, to the best of our knowledge, no study compared the effects of different irrigation systems on the biodiversity of meadows.

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In the present study, we examined whether changes in irrigation technique influence the local biodiversity of species-rich hay meadows in the Valais. As a proxy for the local biodiversity, the species richness and abundance of vascular plants and terrestrial gastropods were recorded. Owing to the high habitat specificity and low mobility, these organisms are considered as ideal diversity indicators in small-scale grassland habitats (Boschi and Baur, 2008; Gaujour et al., 2012). Beside these taxonomic indicators for biodiversity, functional traits are of interest because they represent another aspect of biodiversity and therefore supplement the results of taxonomy-based analyses. In the analyses of functional traits, species are grouped according to their attributes, which are assumed to respond similarly to an environmental factor such as irrigation technique (Lavorel and Garnier, 2002). The aim of the present study was to identify traits of plants and gastropods responding to the different irrigation techniques.

In particular, the following questions were addressed: (1) Do traditionally and sprinkler-irrigated meadows differ in their diversity and composition of plants and gastropods after 8–18 years since the change in irrigation technique took place? (2) Do different irrigation techniques result in an alteration in the functional traits of vascular plants and gastropods?

2. Methods

Field surveys were conducted in three areas located on the south-facing slope of the Rhone valley in the canton Valais (Switzerland), namely in Ausserberg (46°19′N, 7°51′E; hereafter referred to as AU), Birgisch-Mund (46°19′N, 7°57′E; BM) and Guttet-Erschmatt (46°19′N, 7°40′E; GE; Table 1). The distances among these areas ranged from 8 to 22 km. Mean annual temperature in this region is 8.6 °C and total annual precipitation is 599 mm (MeteoSwiss, 2012).

The vegetation types of hay meadows investigated belonged to the *Trisetetum* association (Ellenberg, 1986). On these meadows, traditional irrigation technique was replaced by sprinkler irrigation 8–18 years ago (various farmers, pers. com.; Table 1). Nowadays, 10–30% of the hay meadows in the study areas are still irrigated in the traditional way leading to a small-scale arrangement of either traditionally or sprinkler-irrigated meadows (K. Liechti, pers. com.). Furthermore, the meadows investigated were mown, fertilized and served as pastures in autumn for 1–30 d (various farmers, pers. com; Table 1). Data regarding the amount of fertilizer, stocking rate and forage yield were obtained by personal interviews with farmers. The amount of water applied per irrigation event was calculated based on the duration of a single irrigation event (various farmers, pers. com.) and the specific water need of the areas (2 l/s ha for traditional and 0.7 l/s ha for sprinkler irrigation; Dienststelle für Bodenverbesserung Oberwallis, 1991).

To investigate the effects of the two irrigation techniques on the biodiversity of hay meadows, eight pairs consisting of a traditionally and a sprinkler-irrigated meadow were chosen in the study areas. Two pairs were located in AU and three pairs each in BM and GE. Distances between the meadows of a given pair ranged from 50 to 100 m. The distances among pairs within an area ranged from 0.2 to 2 km in AU and BM and from 0.2 to 1 km in GE. One 10 m × 10 m sampling plot was set up in a homogenous part of each meadow. The sampling plots were installed at a minimum distance of 2 m from the water channels and trails and 3 m from the roads to minimize potential edge effects. Elevation, exposure and inclination were assessed for each of the 16 study plots distributed over the three study areas.

2.1. Plant and gastropod surveys

Plant species richness and abundances of single species were assessed in a 5 m × 5 m subplot established in a randomly chosen

Table 1

Characteristics and land use features of the eight traditionally irrigated (T) and eight sprinkler-irrigated (S) meadows investigated.

Study area[a]	Irrigation type, plot number	Time since change (year)	Elevation (m a.s.l.)	Exposure	Inclination (°)	Irrigation interval (weeks)	Water amount per irrigation (l/ha)	Fertilizing frequency (per year)[b]	Amount of fertilizer (m^3/ha y)	Mowings (per year)	Forage yield (kg/ha)	Grazing regime	Stocking rate (no. of animals/ha d)[e]
AU	S1	15	1192	S	17	3	5040	None	0	2	na	No grazing	0
AU	T1	–	1236	S	26	2	3600	Once	8.6	1	na	Autumn (cattle)	na
AU	S2	18	1212	SE-S	19	2–3	10080	Every 2nd y	8.6 [c]	2	6500	Autumn (sheep)	0.8 (8, 30)
AU	T2	–	1237	SE-S	21	3	16200	Every 2nd y	4.3 [c]	2	8250	Autumn (cattle)	6.2 (10, 7)
BM	S3	9	1148	SE	11	3	25200	Once	10.1	2	5403	Autumn (cattle)	291.6 (34, 1)
BM	T3	–	1142	SE-S	9	2	14400	Once	33.3	2	na	Autumn (cattle)	1166.7 (35, 2)
BM	S4	8	1128	SE	20	2	12600	Once	6.3	2	3281	Autumn (cattle)	56.3 (12, 1)
BM	T4	–	1135	SE-S	8	3	18000	Once	10.1	2	5057	Autumn (cattle)	258.6 (34, 1)
BM	S5	10	1279	SE	16	3	25200	Once	24.0	2	11000	Spring and autumn (goats) [d]	685.7 (15, 2)
BM	T5	–	1275	SE	16	3	14400	Once	36.0	2	18000	Spring and autumn (goats) [d]	685.7 (15, 2)
GE	S6	8	1317	SE	6	3	30240	Once	33.3	2	23810	Occasionally in autumn (cattle)	190.5 (35, 2)
GE	T6	–	1313	SE-S	13	3	39600	None	0	2	na	Autumn (cattle)	80.0 (35, 2)
GE	S7	8	1373	SE	22	3	30240	Once	33.3	2	5952	Occasionally in autumn (cattle)	95.2 (35, 2)
GE	T7	–	1396	E	16	3	39600	Once	33.3	2	20833	Occasionally in autumn (cattle)	166.7 (35, 2)
GE	S8	8	1310	S-SW	19	3	10080	Every 2nd y	6.0 [c]	2	64000	Autumn (horses)	10.0 (10, 10)
GE	T8	–	1291	W	16	3	25200	Every 2nd y	5.8 [c]	2	3750	Autumn (horses)	na

na: data were not available.

[a] AU: Ausserberg; BM: Birgisch-Mund; GE: Guttet-Erschmatt.

[b] Manure in all meadows.

[c] Values are per year.

[d] Grazing in spring was applied in 2010 and 2011 only. In the years before, meadows served as a pasture in autumn.

[e] The number of animals and the duration of grazing (in d) are given in brackets.

corner of each 10 m × 10 m sampling plot. The cover of each plant species was estimated using the Braun-Blanquet (1964) method. To complete the species list of the entire sampling plot, the other three 5 m × 5 m subplots were searched for 20 min each and all new species were recorded. Plant species were identified following Lauber and Wagner (2007). Plant surveys were carried out between May and September 2011, once in spring and once in autumn.

Two methods were used to assess the species richness and relative abundance of terrestrial gastropods (Oggier et al., 1998). First, one person visually searched for living snails and empty shells in each 10 m × 10 m plot for 30 min. Second, a soil sample including dead plant material was collected at randomly chosen spots on bare ground within each plot using a shovel (in total 1 l per plot). Soil samples were put through sieves (smallest mesh size 1 mm) and examined under the binocular microscope. Gastropod shells were sorted out of the samples and identified according to Turner et al. (1998). Gastropod surveys were carried out twice in each plot (first sampling: first week of July 2010 and from 21 June to 8 July 2011; second sampling: September 2010 and from 16 August to 9 September 2011). For the analyses data of both surveys were pooled. Slugs were not considered because their activity depends largely on weather conditions. Snails can be detected in any weather due to the presence of empty shells. Thus, slugs could not be surveyed using this standard method.

2.2. Soil characteristics

To assess soil characteristics of the meadows, four soil samples approximately 50 cm apart were taken to a depth of 5 cm using a soil corer (diameter 5 cm; volume 100 cm^3) at the edge of each of the four subplots in October 2010 and 2011. These four samples were pooled and mixed giving a total of 64 soil samples from 16 meadows, i.e. four samples from each meadow. This allowed accounting for the spatial heterogeneity of soil parameters within a meadow. For the analyses, the mean value of the four samples from a given meadow was used. The soil samples were sieved (mesh size 2 mm) and dried for 6 d at 50 °C. Soil moisture (MO, %) was determined using the fresh weight to dry weight ratio and soil pH was assessed in distilled water (1:2.5 soil: water) (Allen, 1989). Total soil organic matter content (SOM, %) was determined as loss-on-ignition of oven-dried soil at 750 °C for 16 h (Allen, 1989). Total soil organic nitrogen content (N) was assessed using the standard method of Kjeldahl (Bremner, 1965) and total carbonate content (CC, %) was measured by the addition of hydrochloric acid and subsequent back titration with sodium hydroxide (Allen, 1989). Finally, total phosphorous content (PT) and plant available phosphorous content (PP) were assessed using standard methods (Allen, 1989).

2.3. Trait data

Data of 12 plant traits were obtained from the databases BIOPOP (Jackel et al., 2006), LEDA (Kleyer et al., 2008), BiolFlor (Klötz et al., 2002) and CloPla3 (Klimesova and de Bello, 2009) and additional information from Lauber and Wagner (2007), Grime et al. (1988) and personal observations. The following traits were considered (Table A.1): minimum and maximum canopy height, woodiness, leaf distribution, specific leaf area (SLA), seed bank longevity index, earliest month of seed shedding, legume, life span, leaf anatomy, the type of reproduction and the type of clonal growth organ (CGO). When databases provided more than one entry for a particular trait per species, the most frequent or the more logical entry was chosen. Species which occurred only in one subplot (5 m × 5 m) and further 11 species with missing values for some traits were excluded, because the method used did not allow missing values. Thus, 79 plant species were used in the analysis.

For gastropod species, data of eight traits were obtained from Kerney et al. (1983), Falkner et al. (2001), Bengtsson and Baur (1993) and B. Baur (unpublished data). The following traits were considered (Table A.1): shell size, habitat preference, inundation tolerance, humidity preference, longevity, age at sexual maturity, clutch size and egg size.

2.4. Data analyses

Statistical analyses were performed using the software R (R Development Core Team, 2012, version 2.15.0). To examine whether exposure, inclination, elevation, the amount of water, the amount of fertilizer, forage yield, stocking rate and the assessed soil parameters differed between the two meadow types (traditional vs. sprinkler) and among the study areas, two-way analyses of variance (ANOVA) were used with the factors study area and irrigation technique or a Kruskal–Wallis test in the case of non-normally distributed residuals. A Kruskal–Wallis test was also used to examine whether the time since change in irrigation technique differed among study areas. Preliminary analyses revealed intercorrelations among soil variables and correlations between soil variables and time. Therefore, total phosphorous and either total nitrogen content or SOM were excluded from the subsequent analyses.

Generalized linear mixed models (GLMM) were applied to examine the effects of irrigation technique on plant species richness, grass/forb-ratio and legume/forb-ratio. The models were structured as nested randomised block designs, with irrigation technique, study area and the corresponding interaction as fixed factors and meadow pairs (block) nested in study area as random factor. Time since change in irrigation technique, soil pH, carbonate content, plant available phosphorous and total nitrogen content were used as cofactors. For plant species richness, a GLMM with Poisson errors and penalized quasi-likelihood (PQL) for parameter estimation was conducted using the MASS package in R. As the grass/forb-ratio and the legume/forb-ratio represented proportions, a GLMM with binomial errors and PQL was used in both cases. Since the results of plant species weighted by their abundances were similar to those of the presence/absence data, only the results of the presence/absence data for plant species richness were presented. Shannon diversity index for plants was calculated using the package vegan in R, followed by a two-way ANOVA to test for differences between irrigation technique and among study areas.

The same GLMM was used to examine the effects of irrigation technique on the number of gastropod species and the number of gastropod individuals (pooled data of both sampling periods). Individual-based rarefaction curves were calculated for traditionally and sprinkler-irrigated meadows using the package vegan (R Development Core Team, 2012, version 2.15.0). All models were stepwise reduced as recommended by Crawley (2007).

Canonical correspondence analysis (CCA) was applied to examine plant and gastropod communities in relation to environmental variation using CANOCO version 4.5 (ter Braak and Smilauer, 2002). Environmental data consisted of the seven soil parameters. For plants, those species were excluded which occurred only in one subplot (5 m × 5 m) giving a total of 90 species. For gastropods all species were used in the CCA with bi-plot scaling. Monte-Carlo permutations (499 permutations) were conducted to evaluate the significance of the environmental variables. To test whether the composition of plant and gastropod species differed between traditionally and sprinkler-irrigated meadows, a two-sample *t*-test was applied on the sample scores of the first three axes obtained by the CCA. Finally, Spearman-rank correlations were used to examine whether the distances between pairs of meadows were related to time since change in irrigation. For this, the distances between the meadows of a given pair were calculated using the geographical coordinates. Because preliminary analyses of both taxa showed similar results for presence/absence and abundance data, only the results of presence/absence data were presented.

Fourth-corner analysis (Dray and Legendre, 2008; Legendre et al., 1997) was applied to examine the relationship between species traits and environmental variables using the ade4 package in R. This approach allowed the simultaneous analysis of three tables: an R table containing the seven soil parameters and the type of irrigation technique of each meadow, an L table containing species data (presence/absence), and a Q table containing the trait values of single species, 12 traits for plants (Table A.1) and six traits for gastropods (Table A.1; clutch and egg size were excluded due to missing values). A combination of permutation model 2 and 4 with 999 permutations was used as proposed by Dray and Legendre (2008) to obtain a correct level of Type I error.

Correlation analyses showed that shell size, age at sexual maturity, clutch and egg size, habitat preference and longevity as well as inundation tolerance and humidity preference were intercorrelated (Spearman rank correlation, all $p < 0.048$). Shell size was therefore used as surrogate for the other life-history traits. Contingency table tests were applied to evaluate the differences in the proportion of gastropod species and individuals of different size, habitat preference and inundation tolerance between traditionally and sprinkler-irrigated meadows.

3. Results

Traditionally and sprinkler-irrigated meadows did not differ in exposure (Kruskal–Wallis, $p = 0.40$), inclination and elevation (ANOVA, both $p > 0.76$). Plots in the three study areas did not differ in inclination (ANOVA, $p = 0.12$) and exposure (Kruskal–Wallis, $p = 0.13$), but were situated at different elevations (mean ± se, AU: 1219 ± 11 m a.s.l., BM: 1185 ± 29 m a.s.l., GE: 1333 ± 17 m a.s.l.; ANOVA, $p = 0.001$; Table 1). Furthermore, the two meadow types did not differ in the amount of water applied per irrigation, the amount of fertilizer, stocking rate (ANOVA, all $p > 0.28$) and forage yield (Kruskal–Wallis, $p = 0.81$). Meadows in the three study areas did also not differ in the amount of fertilizer (ANOVA, $p = 0.24$) and forage yield (Kruskal–Wallis, $p = 0.42$), but in the amount of water used for irrigation (ANOVA, $p = 0.008$; Table 1) and in stocking rate (ANOVA, $p = 0.031$; Table 1). None of the soil parameters examined differed between traditionally and sprinkler-irrigated meadows (Table 2). However, soil moisture, pH and the content of total phosphorous differed among the three study areas (Table 2). Time since change in irrigation technique differed also among the study areas (Kruskal–Wallis, $p = 0.002$; Table 1) and was marginally positively correlated with plant available phosphorous (Spearman rank correlation, $r_s = 0.49$, $n = 16$, $p = 0.057$).

3.1. Species diversity

A total of 125 vascular plant species was recorded in the differently irrigated meadows; 105 species (84.0%) were found in traditionally and 112 species (89.6%) in sprinkler-irrigated meadows. Plant species richness of a meadow was not affected by the irrigation technique and did not differ among study areas (Table 3). This finding was confirmed by the Shannon diversity index (Table 3). However, the grass/forb-ratio was higher in sprinkler than in traditionally irrigated meadows and differed among study areas (Table 3). This was mainly a result of the higher grass/forb-ratio in the area BM (0.40 ± 0.03) than in the other two areas (AU: 0.26 ± 0.02, GE: 0.28 ± 0.02, Table 3). However, the legume/forb-ratio was not influenced by the irrigation technique and did not differ among study areas (Table 3). Finally, time since change of irrigation technique affected the grass/forb-ratio (GLMM,

Table 2
Soil characteristics (mean ± SE) of traditionally and sprinkler-irrigated meadows in the three study areas. p-Values from a Kruskal–Wallis test (total and plant available phosphorous) and from a two-way ANOVA (all other variables) with the factors irrigation type and study area are shown.

	Ausserberg (AU)		Birgisch-Mund (BM)		Guttet-Erschmatt (GE)		p	
	Traditional ($n = 8$)	Sprinkler ($n = 8$)	Traditional ($n = 12$)	Sprinkler ($n = 12$)	Traditional ($n = 12$)	Sprinkler ($n = 12$)	Irrigation	Study area
Soil moisture (%)	34.3 ± 3.7	28.5 ± 7.3	20.7 ± 1.7	23.1 ± 1.8	26.2 ± 2.7	23.0 ± 1.4	0.476	**0.028**
pH	6.8 ± 0.2	6.5 ± 0.1	6.3 ± 0.1	6.2 ± 0.04	6.9 ± 0.1	7.0 ± 0.1	0.330	**<0.001**
SOM (%)	20.4 ± 3.4	16.3 ± 1.4	19.8 ± 1.6	18.5 ± 2.3	19.9 ± 0.5	18.2 ± 2.0	0.166	0.905
Total organic nitrogen (%)	0.65 ± 0.13	0.49 ± 0.04	0.68 ± 0.07	0.59 ± 0.06	0.67 ± 0.02	0.61 ± 0.09	0.107	0.586
Carbonate (%)	4.2 ± 0.4	3.5 ± 0.6	4.0 ± 0.3	4.4 ± 0.03	4.0 ± 0.1	4.1 ± 0.3	0.939	0.520
Total phosphorous (μg PO_{4-}/g)	958.4 ± 46.3	809.3 ± 180.0	1202.8 ± 108.8	1204.5 ± 104.0	1193.3 ± 99.9	1153.4 ± 109.7	0.674	**0.038**
Plant available phosphorous (μg PO_{4-}/g)	268.8 ± 0.6	104.0 ± 9.7	122.8 ± 43.1	161.0 ± 22.4	105.1 ± 29.7	106.5 ± 19.6	0.916	0.217

Table 3
Aspects of plant and gastropod diversity (mean ± SE) in traditionally and sprinkler-irrigated meadows in the three study areas (AU, BM and GE) located in the Valais.

	Ausserberg (AU)		Birgisch-Mund (BM)		Guttet-Erschmatt (GE)		Irrigation			Study area		
	Traditional ($n = 2$)	Sprinkler ($n = 2$)	Traditional ($n = 3$)	Sprinkler ($n = 3$)	Traditional ($n = 3$)	Sprinkler ($n = 3$)	F	df	p	F	df	p
Plants												
Number of species[a]	54.0 ± 8.0	53.0 ± 8.0	47.7 ± 1.8	49.3 ± 2.3	59.7 ± 3.9	59.3 ± 3.8	0.03	1, 7	0.869	2.50	2, 5	0.177
Shannon index[b]	2.93 ± 0.02	2.58 ± 0.12	2.47 ± 0.08	2.61 ± 0.12	2.82 ± 0.16	2.69 ± 0.08	0.65	1, 12	0.436	2.11	2, 12	0.164
Grass/forb-ratio[c]	0.24 ± 0.03	0.29 ± 0.04	0.36 ± 0.03	0.43 ± 0.06	0.26 ± 0.02	0.30 ± 0.02	13.12	1, 7	**0.009**	16.27	2, 4	**0.012**
Legume/forb-ratio[a]	0.25 ± 0.02	0.25 ± 0.04	0.22 ± 0.01	0.20 ± 0.03	0.23 ± 0.02	0.20 ± 0.01	3.43	1, 7	0.106	1.07	2, 5	0.410
Gastropods												
Number of species[d]	7.5 ± 1.5	11.5 ± 2.5	6.7 ± 0.7	7.7 ± 0.3	7.7 ± 0.7	6.7 ± 0.3	1.86	1, 6	0.222	4.11	2, 5	0.088
Number of individuals[e]	119.0 ± 74.0	258.5 ± 153.5	195.3 ± 64.4	236.0 ± 69.1	82.3 ± 27.7	39.3 ± 10.4	2.15	1, 4	0.216	4.28	2, 5	0.083
Shannon index[b]	1.66 ± 0.02	1.85 ± 0.04	1.47 ± 0.05	1.61 ± 0.02	1.70 ± 0.06	1.65 ± 0.08	2.54	1, 12	0.137	5.73	2, 12	**0.018**

Models used:

[a] GLMM.

[b] ANOVA.

[c] GLMM with time as cofactor.

[d] GLMM with carbonate content as cofactor ($p = 0.09$).

[e] GLMM with pH, soil moisture and carbonate content as cofactors.

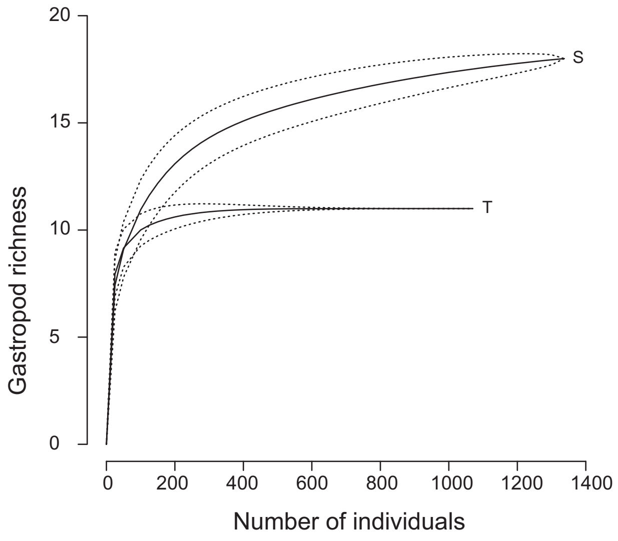

Fig. 1. Individual-based rarefaction curve for gastropods in traditionally (T) and sprinkler-irrigated meadows (S). Solid lines represent means and dotted lines are corresponding standard errors.

$F_{1,4} = 10.93$, $p = 0.030$), but was not significant in the models of the other parameters of plant species diversity and therefore excluded from the analyses.

A total of 18 gastropod species with 2407 individuals was recorded in the 16 meadows. 11 species (61.1%) and 1070 individuals (44.5%) were found in traditionally irrigated meadows, 18 species (100%) and 1337 individuals (55.5%) in sprinkler-irrigated meadows. The rarefaction curves based on the entire data set showed that sprinkler-irrigated meadows harboured more gastropod species than traditionally irrigated meadows (Fig. 1). At the meadow level, however, neither the number of gastropod species nor the number of individuals was affected by the irrigation technique (Table 3). Study areas differed marginally in the number of gastropod species and in the number of individuals (Table 3). Similarly, Shannon diversity index for gastropods was not influenced by the irrigation technique (Table 3) but differed among study areas (AU: S = 1.75 ± 0.06; BM: S = 1.54 ± 0.04; GE: S = 1.67 ± 0.05; Table 3). Furthermore, soil pH, soil moisture and carbonate content affected the number of individuals (GLMM, pH: $F_{1,4} = 9.37$, $p = 0.038$; soil moisture: $F_{1,4} = 11.08$, $p = 0.029$; carbonate content: $F_{1,4} = 7.88$, $p = 0.049$). Finally, time since change in irrigation did neither affect the number of gastropod species and individuals nor the Shannon diversity index and was therefore excluded from the analyses.

3.2. Species composition

For plants, the first three axes of the CCA explained 34.9% of the species variation and 67.6% of the species-environment relation. There was no significant difference in plant species composition between traditionally and sprinkler-irrigated meadows (axis 1–3: two sample t-test, all $p > 0.16$, Fig. 2a). Furthermore, time since irrigation change did not affect the distances between the meadows of a given pair (Spearman rank correlation, $r_s = 0.19$, $n = 8$, $p = 0.65$). However, the CCA revealed that soil pH ($F = 1.95$, $p = 0.008$) and the content of total phosphorous ($F = 1.60$, $p = 0.040$; Fig. 2a) significantly affected plant species composition. All other soil parameters did not influence plant species composition (all $p > 0.23$; Fig. 2a).

For gastropods, the first three axes of the CCA explained 52.6% of the species variation and 86.0% of the species-environment relation. The multivariate analyses did not reveal any differences in

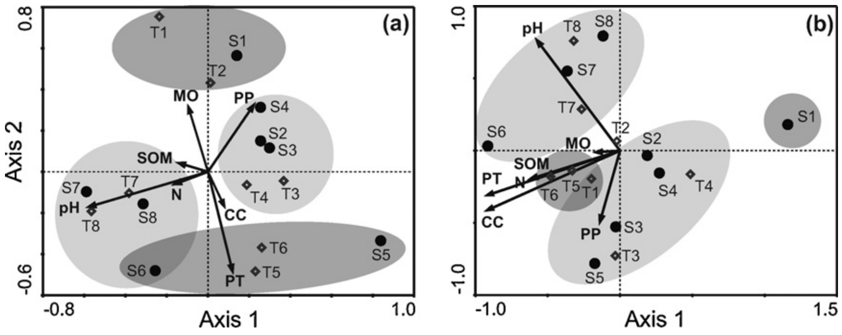

Fig. 2. Ordination diagrams based on canonical correspondence analysis (CCA) of (a) plants and (b) gastropod species in traditionally (T) and sprinkler-irrigated (S) meadows of the three study areas (AU: 1–2, BM: 3–5, GE: 6–8) in relation to the seven soil parameters (for abbreviations see Section 2.2).

gastropod species composition between the two meadow types (axis 1–3: two sample *t*-test, all $p > 0.18$; Fig. 2b). Distances between pairs of meadows were not correlated with time since irrigation change (Spearman rank correlation, $r_s = 0.33$, $n = 8$, $p = 0.43$). As for plant species, the CCA showed a separation of gastropod species composition in meadows differing in soil pH ($F = 3.60$, $p = 0.002$; Fig. 2b). Furthermore, carbonate content of soil affected species composition ($F = 3.38$, $p = 0.002$; Fig. 2b). The other soil parameters did not influence gastropod species composition (all $p > 0.15$).

3.3. Functional traits

The fourth-corner analysis of plant species indicated a significant relationship between the plant trait matrix and environmental variables ($S_{RLQ} = 0.23$, $p = 0.004$). Furthermore, the fourth-corner analysis revealed significant effects of the irrigation technique on the leaf distribution ($\chi^2 = 2.85$, $p = 0.039$). Traditionally irrigated meadows were associated with a larger proportion of plant species with leaves distributed regularly along the stem (traditional: 24.1%, sprinkler: 19.4%), whereas sprinkler-irrigated meadows harboured more semi-rosettes (traditional: 31.3%, sprinkler: 36.1%). In traditionally irrigated meadows, a larger relative amount of species started seed shedding later in the year than in sprinkler-irrigated meadows (July to September: traditional: 35.0%, sprinkler: 27.5%; $\chi^2 = 4.41$, $p = 0.036$). Finally, a marginal effect of irrigation technique on seed bank longevity was found ($F = 1.42$, $p = 0.066$), with a tendency to a higher ratio of longer-lived seeds in sprinkler, than in traditionally irrigated meadows.

The fourth-corner analysis revealed significant effects of soil parameters on plant traits. Seed bank longevity was negatively correlated with nitrogen ($r = -0.05$, $p = 0.038$) and soil organic matter content ($r = -0.05$, $p = 0.041$). SLA and the type of clonal growth organ were both affected by soil pH (SLA: $r = -0.10$, $p = 0.008$; type of clonal growth organ: $F = 2.16$, $p = 0.007$). Finally, the type of reproduction was influenced by the content of total phosphorous ($F = 2.16$, $p = 0.010$). Sexual reproduction was positively correlated ($r = 0.04$) and mostly vegetative reproduction was negatively correlated ($r = -0.08$) with phosphorous content.

The fourth-corner analysis did not show any effects of irrigation technique on the traits of gastropod species (Appendix D). However, single-trait analyses revealed that the proportion of gastropod individuals with different habitat specificity differed between irrigation techniques (ubiquitous gastropod individuals: 0.7% in traditionally irrigated meadows and 2.3% in sprinkler-irrigated meadows; $\chi^2 = 10.60$, df = 1, $p = 0.001$). Furthermore, the percentage of small-sized individuals was lower in traditionally (80.8%) than in sprinkler-irrigated meadows (90.8%; $\chi^2 = 50.09$, df = 1, $p < 0.0001$).

4. Discussion

4.1. Species diversity and composition

A high plant richness was found in the meadows examined (54 species per 100 m^2) compared to other *Trisetetum*-meadows (31–34 species per 100 m^2) on similar elevations in the Swiss Alps (Homburger and Hofer, 2012). This emphasizes the high conservation value of the investigated meadows. In contrast, gastropod species diversity was low compared to other grassland studies with similar soil pH (Boschi and Baur, 2008).

We assumed that traditional irrigation results in temporarily and spatially irregular inundation of the ground causing a higher microhabitat diversity and therefore a higher local biodiversity in this meadow type. Surprisingly, no differences were found in the diversity and composition of plant and gastropod species between the differently irrigated meadows after 8–18 years since the change in irrigation had took place. This time period should have been long enough to detect changes in the groups of organisms examined. Other studies reported significant effects of management changes or abandonment on plant diversity and composition after 4–11 years (Jacquemyn et al., 2003, 2011). On the other hand, irrigation technique might only play a role in combination with other management factors affecting biodiversity (Gaujour et al., 2012) such as stocking rate and grazing seasonality, mowing regime and the type, frequency and the amount of fertilizer applied. These factors, however, did not differ between the two meadow types (Table 1). Furthermore, no differences were observed in irrigation frequency and the amount of water applied per irrigation event. Obviously, the change in irrigation technique was not accompanied by an intensification in land use. This is surprising, since a yield increase through increased application of fertilizer or irrigation would have been necessary to charge off the high installation costs of sprinkler systems (Meurer and Müller, 1987).

Other factors might confound the effect of irrigation technique such as the surrounding landscape, which was shown to be important for both plant species diversity and composition (Aavik and Liira, 2010; Gaujour et al., 2012; Weibull and Ostman, 2003). Furthermore, species composition in the present study was affected by soil pH (both taxonomic groups), the content of total phosphorous (plants) and carbonate content (gastropods). These soil parameters were reported to influence the species distribution and composition of plants (Grime et al., 1988) and gastropods (Boschi and Baur, 2007).

Overall, gastropod species richness and the proportion of ubiquitous and small-sized individuals were higher in sprinkler-irrigated meadows. This was mainly a result of a single sprinkler-irrigated meadow in the area AU (S1), which harboured 15 species. Five of these species (three ubiquitous species) were unique to this meadow but occurred in very low individual numbers. This meadow was the only with an adjacent belt of forest (50 m) situated uphill.

4.2. *Grass/forb-ratio and functional traits*

A higher proportion of grass species was observed in sprinkler- than in traditionally irrigated meadows. In addition, the grass/forb-ratio was increased in the study area BM compared to the other two areas (Table 3). Willems and van Nieuwstadt (1996) related a higher grass/forb-ratio to fertilization, i.e. to higher nutrient conditions and to the composition of fertilizer. The increased grass/forb-ratio in the area BM could be a consequence of the higher total phosphorous content compared to the other two areas, since phosphorus fertilization was shown to affect plant species composition (Hejcman et al., 2007). In this area, an elevated stocking rate was observed, which may also have contributed to the observed result. Furthermore, this was the only area where goats were grazing in one of the meadow pairs, which might be of importance since livestock species could affect plant species diversity (Gaujour et al., 2012) and hence the grass/forb-ratio.

On the other hand, the amount of fertilizer did not differ between the two differently irrigated meadow types, which were all fertilized with manure (Table 1). Furthermore, the two meadow types did not differ in forage yield, stocking rate and soil characteristics ruling out the suggestion that differences in nutrient conditions could have caused the differences in the grass/forb-ratio. Therefore, the higher proportion of grass species in sprinkler-irrigated meadows might potentially be related to differences underlying the two irrigation techniques, especially since the amount and frequency of irrigation did not differ between the two irrigation techniques.

Similarly, traditionally and sprinkler-irrigated meadows differed in leaf distribution and the onset of seed shedding. In particular, a higher proportion of semi-rosette species was observed in sprinkler-irrigated meadows. Plants with more basal leaves such as rosettes (Diaz et al., 2007; Jacquemyn et al., 2011; Römermann et al., 2009) and semi-rosettes (Drobnik et al., 2011) were shown to be promoted by disturbances such as grazing or mowing. Furthermore, a higher proportion of plant species started seed shedding later in the year in traditionally than in sprinkler-irrigated meadows. Early mowing and other kinds of disturbances exclude species that shed their seeds later in the year (Römermann et al., 2009; Smith et al., 1996). However, because pairs of differently irrigated meadows were mown approximately at the same time, the timing of the first mowing might not be of importance. Therefore, the mentioned differences in plant traits and in the grass/forb-ratio suggest that sprinkler irrigation might represent a kind of a disturbance for plants, which influences plant traits and the grass/forb-ratio in addition to other management practices. Such a disturbance for instance could be the high water pressure of the sprinkler combined with the long irrigation duration (2–12 h).

The higher proportions of ubiquitous and small-sized gastropod individuals over all sprinkler-irrigated meadows indicate that gastropod traits might also be affected by the type of irrigation system. The higher proportion of small-sized individuals was probably a response to the disturbance by sprinkler systems, as large-sized individuals were found to be negatively influenced by grazing intensity (Boschi and Baur, 2007).

5. Conclusion

In conclusion, this study showed that a change in the irrigation technique of species-rich hay meadows altered only some aspects of biodiversity after 8–18 years. The high plant diversity of the meadows investigated probably resulted from the extensive management. This management should be maintained in order to preserve the high biodiversity in the study areas. Traditional meadow irrigation had several positive effects for landscape heterogeneity. The passive irrigation of shrubs and trees growing along water channels positively affected their growth. Thus, the abandonment of open water channels could lead to a loss of these hedges representing an important feature of landscape heterogeneity. These positive effects may justify the maintenance of open water channels in areas where the channels still exits. On the other hand, water availability might become an issue in the Valais in the future when the shortage of snow during winter months or the melting of glaciers becomes more severe.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2012.09.020.

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Supplementary material Chapter II

Table A.1. Table providing the description of studied functional traits of plant and gastropod species.

Appendix A. List of plant species observed in the traditionally and sprinkler-irrigated hay meadows investigated.

Appendix B. List of gastropod species observed in the traditionally and sprinkler-irrigated hay meadows investigated.

Appendix C. Fourth-corner statistics for plant species.

Appendix D. Fourth-corner statistics for gastropod species.

Table A.1

Functional traits of plant and gastropod species.

Trait	Type	Description of classes
Plants		
Canopy height, minimum (Hmin) [1]	Continuous	Minimum canopy height in m
Canopy height, maximum (Hmax) [1]	Continuous	Maximum canopy height in m
Woodiness (W) [2, 3]	Categorical	1 = woody, 2 = semi-woody, 3 = not woody (herbaceous)
Leaf distribution (LD) [3, (2)]	Categorical	1 = rosette, 2 = semi-rosette, 3 = leaves distributed regularly along stem, 4 = species with 2 and 3 mentioned
Specific leaf area (SLA) [3, (2)]	Continuous	in mm^2mg^{-1}
Seed bank longevity index (SB) [3]	Continuous	Index ranging from 0 (strictly transient) to 1 (strictly persistent)
Earliest month of seed shedding (SEED) [3, (4)]	Categorical	Month in which seed shedding starts; 5 = May to 9 = September
Legume (LEG) [1]	Binominal	1 = yes, 2 = no
Life span (LS) [5]	Categorical	1 = annual, 2 = biennial, 3 = perennial
Leaf anatomy (LA) [5]	Categorical	1 = mesomorph, 2 = meso- and hydromorphic, 3 = scleromorph, 4 = sclero- and mesomorph
Type of reproduction (REPR) [5]	Categorical	1 = seed, 2 = mostly seed and rarely vegetative, 3 = seed and vegetative, 4 = mostly vegetative and rarely seed
Clonal growth organ (CGO) [6]	Categorical	1 = horizontal aboveground stem, 4 = pseudovivipary, 5 = plant fragment of stem origin, 9 = belowground stem (epigeogenous or hypogeogenous), 12 = stem tuber, 14 = root-splitter or root with adventitious buds, 16 = root tuber, 18 = not clonal
Gastropods		
Shell size [7, 8]	Categorical	1 = adult size < 5.0 mm, 2 = adult size ≥ 5.0 mm
Habitat preference [7, 8]	Categorical	1 = open-land, 2 = ubiquitous
Inundation tolerance [7, 8]	Categorical	1 = low, 2 = moderate, 3 = high
Humidity preference [7, 8]	Categorical	1 = wet, 2 = moist, 3 = dry
Longevity [7, 8]	Categorical	1 = < 1 year, 2 = 1-2 years, 3 = > 2 years
Age at sexual maturity [7, 8]	Categorical	1 = < 1 year, 2 = 1 year, 3 = > 1 years
Clutch size [9, 10]	Continuous	number of eggs
Egg size [9, 10]	Continuous	in mm

Source: [1] Lauber and Wagner (2007), [2] BIOPOP, [3] LEDA, [4] Grime *et al.* 1988, [5] BiolFlor, [6] CloPla3, [7] Kerney *et al.* (1983), [8] Falkner *et al.* (2001), [9] Bengtsson and Baur (1993), [10] B. Baur (unpublished).

Appendix A

List of plant species showing the average vegetation cover (%) of traditionally and sprinkler-irrigated meadows located in the three study areas AU, BM and GE. Species in bold were only observed in the remaining three 5 m x 5 m subplots of a given sampling plot, not applying the Braun-Blanquet method. Therefore, no cover values were obtained.

	Ausserberg (AU)		Birgisch-Mund (BM)		Guttet-Erschmatt (GE)	
Species	Traditional (n = 2)	Sprinkler (n = 2)	Traditional (n = 3)	Sprinkler (n = 3)	Traditional (n = 3)	Sprinkler (n = 3)
Forbs						
Achillea millefolium agg.	4.063	2.190	0.635	0.837	3.975	1.050
Acinos arvensis	0	0	0	0	2.708	1.675
Ajuga genevensis	**0**	**0**	**0**	**0**	**0**	**0**
Ajuga reptans	0	0.020	0.650	0.650	0.020	0.002
Alchemilla vulgaris agg.	0	0	0.032	0.003	0	0
Anthriscus sylvestris	5.938	0	0.843	0.837	0	0
Anthyllis vulneraria s.l.	0.003	4.375	0	0	0.002	6.875
Arabis hirsuta agg.	0	0.003	0	0	0.005	0.007
Arabis turrita	**0**	**0**	**0**	**0**	**0**	**0**
Astrantia major	0	0	0	0	0.002	0
Botrychium lunaria	0	0.005	0	0	0	0
Campanula glomerata s.l.	0.353	0.003	0.002	0.002	0.020	0.212
Campanula rhomboidalis	0.343	1.250	0.433	0.022	0.880	0.030
Campanula scheuchzeri	0	0	0	0	0.007	0.020
Carlina acaulis ssp. caulescens	0.025	0	0	0	0.002	0.003
Carum carvi	0	0	1.667	0.625	0.627	0
Centaurea scabiosa s.l.	0.313	0	0	0.002	15.833	5.005
Cerastium fontanum s.l.	0	0.003	0	0.218	0	0.228
Chaerophyllum aureum	0.313	1.875	3.958	6.667	13.142	1.252
Clinopodium vulgare	2.813	0.950	0	0	0	0
Colchicum autumnale	0	0	0.638	0.033	0.440	0.022
Crepis biennis	0	0	0.213	0.008	0	0
Crepis pyrenaica	0	0	0	0	1.677	0.018
Dianthus carthusianorum s.l.	0.028	0.340	0	0	0	0.210
Equisetum palustre	0	0	0.012	0	0	0
Euphorbia cyparissias	**0**	**0**	**0**	**0**	**0**	**0**
Euphrasia rostkoviana	0	0.318	0	0	0	0.027
Galium boreale	2.500	0.315	1.667	0.835	1.878	2.302
Galium mollugo agg.	1.250	0.328	0.208	0	0.642	0
Galium pumilum	0.325	0	0	0	0	0
Geranium pusillum	**0**	**0**	**0**	**0**	**0**	**0**
Geranium sylvaticum	4.375	0	2.500	6.667	8.550	0.208
Geum urbanum	0	0.003	0.212	0	0	0
Gymnadenia conopsea	0.003	0	0	0	0.003	0
Helianthemum nummularium s.l.	0.638	1.250	0	0	0	0.417
Heracleum sphondylium s.l.	0.950	2.840	4.177	17.085	6.253	4.793

Hieracium pilosella (Artengruppe)	0.003	0.940	0	0	0	0
Hippocrepis comosa	0	0.940	0	0	0	0.008
Knautia arvensis	0	0	0	0	0.008	0
Knautia dipsacifolia	0.005	0	0.445	1.045	1.055	1.252
Laserpitium latifolium	0	0	0	0	0	5.833
Lathyrus pratensis	3.125	0.018	1.068	1.262	0.852	0.007
Leontodon hispidus s.l.	17.500	10.000	12.292	18.542	11.667	4.792
Leucanthemum vulgare agg.	0.630	1.270	0.227	1.270	0.435	0.652
Lotus corniculatus agg.	1.875	3.440	1.042	0.873	2.500	2.708
Medicago lupulina	0	0	0	0	0.843	0.630
Myosotis arvensis	0	0.003	0.223	0.212	0	0
Myosotis ramosissima	0.025	0	0.003	0	0.833	1.262
Odontites sp.	0	0	0	0	0.217	0.002
Onobrychis viciifolia	0	0	0	0	3.542	5.418
Ononis repens	0.938	0	0	0	0.208	0
Orchis mascula	0	0.005	0	0	0	0
Peucedanum oreoselinum	0	0.950	0	0	0	0.002
Phyteuma orbiculare	0	0.003	0	0.003	0.642	0.002
Picris hieracioides s.l.	0.315	4.693	0.833	1.272	0.652	0.432
Pimpinella major	1.250	0	0.862	0.840	0.010	0
Pimpinella saxifraga agg.	0.005	0.020	0	0	0	0
Plantago lanceolata	4.063	4.395	2.100	1.893	1.887	1.478
Plantago media	0	0	0	0	0.007	0.630
Platanthera chlorantha	0	0.003	0	0	0	0
Polygala comosa	**0**	**0**	**0**	**0**	**0**	**0**
Populus nigra s.l.	0	0	0	0	0	0.002
Potentilla erecta	0.325	0	0	0	0	0
Potentilla pusilla	0	0.318	0	0	0	0.208
Primula veris s.l.	0	0	0	0	0	0.002
Prunella vulgaris	0	0	0	0.002	0	0
Pulmonaria obscura	**0**	**0**	**0**	**0**	**0**	**0**
Quercus petraea	0	0.003	0	0	0	0
Ranunculus acris s.l.	1.875	0.960	0.017	1.085	0.850	0.242
Ranunculus bulbosus	0.003	0.953	0.002	0.010	0.015	0.233
Ranunculus nemorosus agg.	0.650	1.250	0.027	0.430	0	0
Rhinanthus alectorolophus	0.950	1.250	1.880	0.215	1.680	1.480
Rosa sp.	0	0.003	0	0	0	0
Rumex acetosa	1.258	1.260	0.860	0.867	0.260	0.442
Rumex obtusifolius	0	0	0.420	0	0	0
Salvia pratensis	4.378	1.568	0	0.215	4.797	2.712
Sanguisorba minor s.l.	0	0.010	0	0	0	0
Scabiosa columbaria	0	0.315	0	0	0.005	0.002
Silene dioica	0	0	0.417	0	0	0
Silene flos-cuculi	0	0	0.018	0	0	0
Silene nutans s.l.	0.003	0	0	0	0	0.002
Silene vulgaris s.l.	3.130	1.278	1.667	4.377	7.500	7.302

Stachys recta s.l.	0	0	0	0	0	1.252
Taraxacum officinale agg.	0.008	0.010	0.640	0.652	0.003	0.843
Teucrium chamaedrys	**0**	**0**	**0**	**0**	**0**	**0**
Thalictrum aquilegiifolium	**0**	**0**	**0**	**0**	**0**	**0**
Thymus serpyllum agg.	1.265	1.565	0.435	0.002	0.643	1.267
Tragopogon pratensis s.l.	0.003	0.005	0.007	0.007	0.012	0.010
Trifolium montanum	0.943	0.643	0.008	0	0.837	0.638
Trifolium pratense s.l.	5.325	10.313	12.292	3.542	2.093	1.700
Trifolium repens	0.340	0.325	0.835	0.847	0.008	0.835
Trollius europaeus	**0**	**0**	**0**	**0**	**0**	**0**
Veronica chamaedrys	1.565	0.318	0.217	0.003	0.013	0
Veronica teucrium	0	0	0	0	0	0.417
Vicia cracca s.l.	4.063	1.568	1.045	1.053	1.055	0.455
Vicia sepium	0.328	1.250	0.002	0.008	0	0
Viola tricolor agg.	**0**	**0**	**0**	**0**	**0**	**0**
Grasses						
Agrostis capillaris	2.813	1.250	0.833	2.300	0	0
Anthoxanthum odoratum	1.250	1.250	1.053	1.680	1.087	0.853
Arrhenatherum elatius	4.375	0.350	0	0	0	0
Briza media	1.250	1.250	0.210	1.675	0.013	0.418
Bromus erectus s.l.	10.000	25.628	0.003	4.375	0.418	12.293
Bromus inermis	2.813	5.938	1.470	0.218	1.673	1.055
Carex caryophyllea	0	0	0.833	0.002	0.005	0.007
Carex flacca	0	0	0.007	0	0	0
Carex liparocarpos	0	0	0.208	0	0	0
Carex sylvatica	0	0.015	0.625	0.013	0.220	0.228
Cynosurus cristatus	0	0.020	0.012	0.210	0.012	0.235
Dactylis glomerata	5.015	1.255	7.100	5.425	2.935	7.500
Danthonia decumbens	0	0.938	0	0	0	0
Echinochloa crus-galli	0	0	0.227	0	0	0
Elymus repens	0.020	0.950	0	0	0	0
Festuca rubra agg.	20.625	19.690	16.667	21.667	18.333	22.292
Festuca ovina agg.	0	0	0	0	0.003	0.633
Helictotrichon pubescens	0.640	0	0.635	3.753	0.445	0.837
Holcus lanatus	0.333	0.648	17.303	4.377	0	0
Juncus articulatus	0	0	0.002	0	0	0
Koeleria pyramidata agg.	0	0	0	0	0	0.625
Lolium perenne	0	0.003	0.002	0.002	0.005	0.015
Luzula campestris	0.003	0.020	0.027	0.233	0	0
Phleum pratense agg.	0	0	0.833	0.010	0	4.167
Poa alpina	0	0	0	0	0.838	0.838
Poa trivialis s.l.	0	0	1.043	1.057	0.002	0.008
Poa variegata	0.340	0.008	0	0.210	0.630	0.833
Trisetum flavescens	13.125	5.965	2.500	4.383	5.625	8.960

Appendix B

List of gastropod species showing the sum of gastropod individuals observed in traditionally and sprinkler-irrigated meadows located in the three study areas AU, BM and GE.

	Ausserberg (AU)		Birgisch-Mund (BM)		Guttet-Erschmatt (GE)	
Species	Traditional (n = 2)	Sprinkler (n = 2)	Traditional (n = 3)	Sprinkler (n = 3)	Traditional (n = 3)	Sprinkler (n = 3)
Succinella oblonga	0	0	105	13	0	0
Cochlicopa sp.	6	9	39	55	11	10
Columella edentula	0	11	0	0	0	0
Truncatellina cylindrica	57	57	6	39	67	6
Vertigo pygmaea	1	14	36	36	4	2
Pupilla muscorum	33	72	162	162	34	5
Vallonia costata	50	163	109	147	75	28
Vallonia excentrica	67	98	2	19	15	11
Vallonia pulchella	22	75	115	234	10	23
Vitrina pellucida	0	3	0	0	0	0
Perpolita hammonis	0	8	0	1	0	0
Aegopinella minor	0	2	0	0	0	0
Vitrea contracta	0	2	0	0	0	0
Candidula unifasciata	0	0	11	0	17	11
Helicella itala	1	0	0	0	8	12
Trichia sericea	1	1	1	0	5	6
Helix pomatia	0	1	0	0	0	0
Punctum pygmaeum	0	1	0	0	0	0
Unknown	0	0	0	2	1	4

Appendix C

Fourth-corner statistics for plant species (presence/absence data) showing the combination of each environmental variable (irrigation technique = trt, soil parameters) and each plant trait. For abbreviations of soil parameters see text, for abbreviations of plant traits see Table A.1.

```
Var. R   Var. Q Stat. Value        p
 trt   / Hmin   F     0.5379       0.369
 trt   / Hmax   F     0.48247      0.296
 trt   / W      Chi2  0.0352722    0.768
 trt   / LD     Chi2  2.84714      0.039 *
 trt   / SLA    F     0.195764     0.713
 trt   / SB     F     1.4161       0.066 .
 trt   / SEED   Chi2  4.40718      0.036 *
 trt   / LEG    Chi2  0.30735      0.330
 trt   / LS     Chi2  0.2673       0.872
 trt   / LA     Chi2  0.301112     0.953
 trt   / REPR   Chi2  0.144565     0.929
 trt   / CGO    Chi2  2.55191      0.830
  MO   / Hmin   r     -0.0464732   0.071 .
  MO   / Hmax   r     -0.0384434   0.083 .
  MO   / W      F     0.758327     0.173
  MO   / LD     F     0.564076     0.238
  MO   / SLA    r     0.000574143  0.480
  MO   / SB     r     -0.0169118   0.288
  MO   / SEED   F     0.663295     0.184
  MO   / LEG    F     1.345        0.081 .
  MO   / LS     F     1.02983      0.314
  MO   / LA     F     1.38484      0.259
  MO   / REPR   F     1.0445       0.136
  MO   / CGO    F     0.621667     0.514
   N   / Hmin   r     -0.0193198   0.273
   N   / Hmax   r     -0.00772345  0.384
   N   / W      F     0.10816      0.608
   N   / LD     F     0.518918     0.202
   N   / SLA    r     -0.0132009   0.419
   N   / SB     r     -0.046928    0.038 *
   N   / SEED   F     0.573436     0.236
   N   / LEG    F     0.0311225    0.755
   N   / LS     F     0.231997     0.756
   N   / LA     F     1.25712      0.282
   N   / REPR   F     0.299473     0.681
   N   / CGO    F     0.463953     0.702
  CC   / Hmin   r     0.0113024    0.325
  CC   / Hmax   r     0.00268934   0.426
  CC   / W      F     0.172539     0.530
  CC   / LD     F     0.201509     0.599
  CC   / SLA    r     0.0346937    0.199
  CC   / SB     r     -0.00733577  0.396
  CC   / SEED   F     0.662042     0.173
  CC   / LEG    F     0.158148     0.443
  CC   / LS     F     0.223628     0.805
  CC   / LA     F     0.358061     0.735
  CC   / REPR   F     0.652871     0.365
  CC   / CGO    F     0.0947041    0.997
  pH   / Hmin   r     -0.0284074   0.175
  pH   / Hmax   r     -0.0298366   0.168
  pH   / W      F     0.0284989    0.826
  pH   / LD     F     0.519218     0.425
```

```
 pH   / SLA    r     -0.100887    0.008 **
 pH   / SB     r     -0.0152524   0.312
 pH   / SEED   F     1.29275      0.099 .
 pH   / LEG    F     1.11658      0.174
 pH   / LS     F     2.43899      0.059 .
 pH   / LA     F     1.47781      0.227
 pH   / REPR   F     0.391934     0.605
 pH   / CGO    F     2.16422      0.007 **
SOM   / Hmin   r     -0.021644    0.231
SOM   / Hmax   r     -0.00990169  0.354
SOM   / W      F     0.160895     0.541
SOM   / LD     F     0.468074     0.244
SOM   / SLA    r     -0.00307721  0.510
SOM   / SB     r     -0.0475529   0.041 *
SOM   / SEED   F     0.53953      0.264
SOM   / LEG    F     0.127769     0.526
SOM   / LS     F     0.339192     0.659
SOM   / LA     F     1.24006      0.291
SOM   / REPR   F     0.141021     0.873
SOM   / CGO    F     0.549433     0.604
 PT   / Hmin   r     0.0274981    0.196
 PT   / Hmax   r     0.0257579    0.171
 PT   / W      F     1.03916      0.138
 PT   / LD     F     0.379432     0.521
 PT   / SLA    r     0.0370937    0.204
 PT   / SB     r     -0.0135722   0.324
 PT   / SEED   F     0.807327     0.187
 PT   / LEG    F     0.455306     0.341
 PT   / LS     F     1.06047      0.289
 PT   / LA     F     0.712924     0.505
 PT   / REPR   F     2.16345      0.010 **
 PT   / CGO    F     0.465702     0.707
 PP   / Hmin   r     0.000198134  0.494
 PP   / Hmax   r     -0.000600866 0.493
 PP   / W      F     0.860449     0.147
 PP   / LD     F     0.530417     0.244
 PP   / SLA    r     0.0380471    0.201
 PP   / SB     r     -0.0136801   0.327
 PP   / SEED   F     0.159758     0.834
 PP   / LEG    F     0.0135257    0.857
 PP   / LS     F     0.768736     0.419
 PP   / LA     F     0.72387      0.490
 PP   / REPR   F     0.518464     0.480
 PP   / CGO    F     0.776878     0.369
```

Appendix D

Fourth-corner statistics for gastropod species (presence/absence data) showing the combination of each environmental variable (irrigation technique = trt, soil parameters) and each gastropod trait. For abbreviations of soil parameters see text. Abbreviations of gastropod traits: ShellC = shell size, Habit = habitat preference, Matur = sexual maturity, Long = longevity, Humid = humidity preference, Inund = inundation tolerance.

```
Var. R    Var. Q Stat. Value      p
 trt   / ShellC Chi2  0.0744262  0.636
 trt   / Habit  Chi2  1.84392    0.525
 trt   / Matur  Chi2  0.0772807  0.894
 trt   / Long   Chi2  0.111787   0.650
 trt   / Humid  Chi2  2.55416    0.145
 trt   / Inund  Chi2  0.954365   0.393
  MO   / ShellC F     0.00194291 0.945
  MO   / Habit  F     0.141164   0.805
  MO   / Matur  F     0.0400954  0.850
  MO   / Long   F     0.115123   0.498
  MO   / Humid  F     0.817681   0.433
  MO   / Inund  F     0.133309   0.781
   N   / ShellC F     0.321095   0.291
   N   / Habit  F     3.23751    0.211
   N   / Matur  F     0.244951   0.419
   N   / Long   F     0.251041   0.341
   N   / Humid  F     1.24836    0.326
   N   / Inund  F     0.147384   0.719
  CC   / ShellC F     0.0978033  0.656
  CC   / Habit  F     7.39245    0.040 *
  CC   / Matur  F     0.287694   0.571
  CC   / Long   F     0.935753   0.176
  CC   / Humid  F     1.65909    0.248
  CC   / Inund  F     0.427976   0.438
  pH   / ShellC F     1.11344    0.281
  pH   / Habit  F     0.715792   0.657
  pH   / Matur  F     0.23571    0.818
  pH   / Long   F     0.0106207  0.932
  pH   / Humid  F     4.87208    0.025 *
  pH   / Inund  F     3.19908    0.041 *
 SOM   / ShellC F     0.569745   0.143
 SOM   / Habit  F     2.41235    0.296
 SOM   / Matur  F     0.27639    0.362
 SOM   / Long   F     0.305625   0.269
 SOM   / Humid  F     1.18209    0.338
 SOM   / Inund  F     0.069325   0.865
  PT   / ShellC F     0.014168   0.852
  PT   / Habit  F     7.04582    0.036 *
  PT   / Matur  F     0.132187   0.748
  PT   / Long   F     0.743751   0.214
  PT   / Humid  F     1.60802    0.260
  PT   / Inund  F     0.606937   0.354
  PP   / ShellC F     0.261627   0.428
  PP   / Habit  F     0.580985   0.650
  PP   / Matur  F     0.216115   0.598
  PP   / Long   F     0.00629235 0.905
  PP   / Humid  F     0.190445   0.714
  PP   / Inund  F     0.930041   0.118
```

Chapter III

Do different irrigation techniques affect the small-scale patterns of plant diversity and soil characteristics in mountain hay meadows?

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Do different irrigation techniques affect the small-scale patterns of plant diversity and soil characteristics in mountain hay meadows?

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Abstract Traditional management practices are suggested to maintain species-rich grasslands. In the Valais, an arid region of Switzerland, hay meadows are traditionally irrigated using open water channels. However, in the past decades this irrigation technique has been increasingly replaced by sprinkler irrigation, which is assumed to result in a more homogeneous water distribution than open water channels. This study examined whether the change in irrigation technique affected the small-scale distribution of plants and soil characteristics in hay meadows in the Valais. Three plots consisting of 13 subplots of increasing size (0.1 × 0.1 to 6.4 × 6.4 m) were installed in six traditionally and six sprinkler-irrigated meadows. In all subplots, plant species richness and soil characteristics [moisture, pH, total organic nitrogen, organic matter content (SOM), total and plant available phosphorus] were recorded. The type of irrigation technique did not affect the shape of the plant species–area relationship. In none of the meadows did the species area–curves reach the asymptote within the range of plot sizes examined. Mantel *r* statistics showed that spatial autocorrelation in the soil characteristics examined was low and their small-scale distributions were not influenced by the irrigation technique except for soil pH and SOM. Our results indicate a pronounced small-scale heterogeneity in the distribution of plant species and soil characteristics for both types of irrigation technique. This can partly be explained by the fact that sprinklers distribute the water less homogeneously than commonly assumed. As applied in the Valais, sprinkler irrigation does not reduce the spatial heterogeneity and hence biodiversity of hay meadows.

Keywords Semi-natural grassland · Water management · Land use change · Species–area relationship · Spatial autocorrelation · Valais (Switzerland)

Introduction

Semi-natural grasslands including hay meadows are habitats, which were formed by traditional management practices. These habitats harbour numerous species whose primordial habitats have been vastly destroyed (Baur et al. 1997, 2004), and therefore, they are of high conservation value (Poschlod and

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WallisDeVries 2002; Baur et al. 2006). Since the mid twentieth century, changes in land use including intensification and abandonment resulted both in a decline in the area of semi-natural grasslands (Strijker 2005) and in a decrease in plant species richness, especially in grassland specialists (Poschlod and WallisDeVries 2002; Tasser and Tappeiner 2002; Homburger and Hofer 2012; Riedener et al. 2014).

The maintenance of hay meadows and their typical species composition also depends on irrigation, particularly in arid regions such as the south-facing slopes of the Valais in the Swiss Alps. In this region, a dense net of open water channels was constructed from the eleventh century onwards to transport glacial melt water from mountain streams to meadows at lower elevations (Leibundgut 2004). With this water, the hay meadows are flooded at regular intervals. The farmers put a temporary dam across the water channel causing an overflow with a resulting flooding of the downslope parts of the meadow (Crook and Jones 1999). This traditional irrigation technique is very labour intensive (Meurer and Müller 1987). Therefore, the modernization and rationalization of agricultural practices in the Valais have increasingly led to the replacement of the traditional irrigation technique by sprinkler irrigation systems in the past decades (Meurer and Müller 1987; Crook and Jones 1999).

Various elements of meadow spatial heterogeneity affect plant species richness at different scales (Weiher and Howe 2003; Olofsson et al. 2008; Giladi et al. 2011). At the landscape level, different types of land use lead to a mosaic of different habitats, which may impact plant species richness and dispersal of organisms (Gaujour et al. 2012). At the level of a few square metres, microhabitat conditions including the distribution of soil nutrients and water become more important for the spatial arrangement of co-existing plant species and hence plant species richness (Shmida and Wilson 1985; Zhou et al. 2008; Shi et al. 2010). In hay meadows, different management practices including the type of irrigation technique may influence meadow spatial heterogeneity and thus plant species richness. In the present study, we focused on the potential impact of different irrigation techniques on the small-scale heterogeneity of plant diversity and soil characteristics.

Traditional and sprinkler irrigation are assumed to differ in their kind of small-scale water distribution. Sprinklers may distribute the water homogeneously from above over the meadow, whereas in traditional irrigation different parts of the ground are inundated irregularly, depending on the microrelief of the meadows (Meurer and Müller 1987). This spatially unequal water distribution can increase the small-scale variation in both soil moisture and nutrients and may, therefore, lead to a mosaic of different microhabitats and hence to an increased floristic and faunistic diversity (Rosenzweig 1995; Werner 1995; Diacon-Bolli et al. 2012).

The shapes of species–area relationships have been used to explore spatial patterns of plant diversity in grasslands (Connor and McCoy 1979; Rosenzweig 1995). Meadows with a homogeneous plant distribution reach the maximum species richness (asymptote of the curve) at a smaller area and show a steeper increase in the cumulative species number than meadows with a heterogeneous plant distribution. The recorded spatial small-scale distribution of plant species and thus the shape of the species–area relationship of a meadow can be influenced by different factors including meadow spatial heterogeneity (Kallimanis et al. 2008; Shen et al. 2009; Kolasa et al. 2012), competitive interactions (Tilman 1982), shape and size of sampling plots (Condit et al. 1996), shape of the habitats (Harte et al. 1999), grain size of the vegetation (He and Legendre 2002; Braschler et al. 2004; Hortal et al. 2006), and the length of time taken to conduct sampling (Preston 1960; White 2004). Meadow spatial heterogeneity is assumed to increase with increasing sampling area and may, therefore, be an important descriptor of the species–area relationship (Rosenzweig 1995; Proença and Pereira 2013).

In the present study, we examined the potential influence of the two irrigation techniques on the small-scale distribution of plant species and soil characteristics of extensively managed hay meadows in the Valais. A previous study conducted in the same region showed that traditionally and sprinkler-irrigated hay meadows did not differ in plant diversity and species composition on the basis of 100 m^2 plots (Riedener et al. 2013). However, effects of different irrigation techniques on the small-scale spatial patterns ranging from 0.01 to 40 m^2 have not been investigated so far.

As a result of unequal water distribution by traditional irrigation, we expect that traditionally irrigated meadows show a higher variation in the pattern of plant distribution than sprinkler-irrigated meadows. Therefore, the shape of the species–area curves should differ between the two types of irrigation. In sprinkler-irrigated meadows, the slope of the species–area curve should be steeper and reach the asymptote at a smaller spatial scale than in traditionally irrigated meadows. Spatial autocorrelation can be used as an indicator for spatial heterogeneity of different soil characteristics. High positive values of autocorrelation indicate a high spatial dependency of soil characteristics. The spatial dependency may change in different comparisons of various soil properties. Furthermore, we assume that soil characteristics show a more heterogeneous spatial distribution in traditionally irrigated meadows than in sprinkler-irrigated meadows. In particular, we addressed the following questions: (1) Do traditionally and sprinkler-irrigated meadows differ in the shape of their plant species–area relationships and in the small-scale spatial pattern of soil characteristics? and (2) Are soil characteristics spatially autocorrelated and if yes, at which spatial scale?

Methods

Study area and survey design

The study was conducted in two areas located on the south-facing slope of the Rhone valley in the canton Valais (Switzerland), namely in Ausserberg (46°19′N, 7°51′E, elevation: 1,191–1,255 m a.s.l.; hereafter referred to as AU) and Guttet–Erschmatt (46°19′N, 7°40′E, elevation: 1,281–1,400 m a.s.l.; GE). The two areas are 15 km apart. Mean annual air temperature in this region is 9.4 °C and annual precipitation is 596 mm (MeteoSwiss 2013).

The vegetation types of the hay meadows investigated belonged to the *Trisetetum* association (Ellenberg 1986). Information on management was obtained by personal interviews with farmers. On most of these meadows, the traditional irrigation technique was replaced by sprinkler irrigation 8–25 years ago. Nowadays, only 10–30 % of the meadows of this region are still irrigated in the traditional way resulting in a mosaic of traditionally and sprinkler-irrigated meadows (K. Liechti, pers. com.). The majority of sprinklers were installed at permanent positions, but on two meadows there were also mobile sprinklers. Management intensity of the investigated meadows is relatively low (see Table S1 for details). The meadows investigated were mown once or twice a year and grazed for a few days in autumn by sheep or cattle. Fertilizer (manure; mean ± SE, $10.8 \pm 3.2\ \text{m}^3\ \text{ha}^{-1}\ \text{y}^{-1}$) was applied every year or every second year in autumn, except for two meadows in AU, which were not fertilized at all. Irrigation occurred every 2nd or 3rd week during the vegetation period (from May to the end of September in both irrigation techniques). Irrigation frequency and the amount of water applied per irrigation event did not differ between the two irrigation techniques (amount of water: ANOVA, $F_{1,9} = 1.51$, $p = 0.25$). Moreover, traditionally and sprinkler-irrigated meadows did not differ in the amount of fertilizer or grazing intensity (ANOVA, both $p > 0.32$). Neither did meadows in the two study areas differ in the amount of water received or grazing intensity (ANOVA, both $p > 0.10$). However, the amount of fertilizer was marginally higher in GE than in AU (ANOVA, $F_{1,9} = 4.62$, $p = 0.06$).

Six pairs of hay meadows were chosen in the two study areas, each pair consisting of a traditionally and a sprinkler-irrigated meadow. Four pairs of meadows were located in AU and two pairs in GE. The distance between pairs of meadows was 1 km in GE and ranged from 50 m to 2 km in AU (see Table S1 for distances between meadow pairs).

Traditionally and sprinkler-irrigated meadows did not differ in size, elevation, exposure and inclination (ANOVA, all $p > 0.19$). Neither did meadows in the two study areas differ in exposure or inclination (ANOVA, both $p > 0.29$). Average exposure was SSE (157 ± 10°) and average inclination was 18 ± 1°. However, mean elevation of the hay meadows was 1,222 ± 7 m a.s.l. (±SE) in AU and 1,339 ± 26 m a.s.l. in GE (ANOVA, $F_{1,9} = 33.54$, $p < 0.001$). Furthermore, meadows were smaller in AU than in GE (AU: $3{,}049 \pm 623\ \text{m}^2$, GE: $6{,}198 \pm 1{,}507\ \text{m}^2$; ANOVA, $F_{1,9} = 5.44$, $p = 0.045$).

Vegetation surveys

In each meadow, three starting points (lower left corner of a plot) were randomly chosen to install three plots of increasing size using a nested design (Fig. 1). Each plot was built up an initial area of 0.1 × 0.1 m (subplot 1). This area was duplicated twelve times to reach a size of 6.4 × 6.4 m (subplot 13). The plots had a minimum distance of 2 m to water channels and trails and of 3 m to roads to minimize potential edge effects. The distances among the three starting points

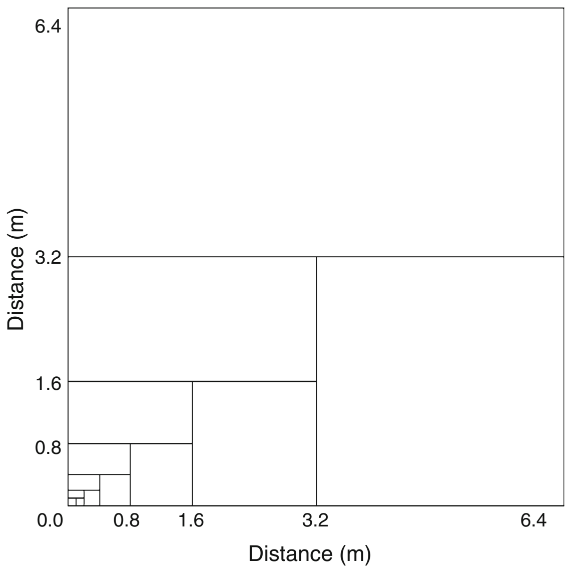

Fig. 1 Nested plot design consisting of 13 subplots of increasing size. The area of the first subplot (0.1 × 0.1 m) is doubled 12 times to reach a total area of 6.4 × 6.4 m

within a meadow ranged from 8 to 40 m. All vascular plant species present in subplot 1 were recorded. In subplot 2 and the succeeding subplots only additional species were recorded. Plant surveys were conducted by R. L. M. and E. R. between May and June 2012. Pseudoturnover, i.e. the turnover accounting for two sampling persons, ranged from 5.3 to 9.8 % (Nilsson and Nilsson 1985).

Soil characteristics

To analyse the spatial variation in soil characteristics, soil samples were collected in the most central plot of the three plots in each meadow. Beginning in subplot 1, three soil samples were taken close to its centre to a depth of 5 cm using a soil corer (diameter 5 cm, volume 100 cm^3) in October 2012. This procedure was repeated in subplot 2 and in the following subplots. The three samples of a subplot were mixed and pooled resulting in 13 soil samples per plot. In this way, 156 soil samples were obtained in the six traditionally irrigated and six sprinkler-irrigated meadows. The soil samples were sieved (mesh size 2 mm) and dried for 96 h at 50 °C. Soil pH was assessed in distilled water (1:2.5 soil:water) (Allen 1989). Total soil organic matter content (SOM, %) was determined as loss-on-ignition of oven-dried soil at 750 °C for 16 h (Allen 1989) and total soil organic nitrogen content (OrgN, %) was assessed using the standard method of Kjeldahl (Bremner 1965). Finally, total phosphorus content (PT, µg PO_{4^-}/g) and plant available phosphorus content (PP, µg PO_{4^-}/g) were extracted using hydrochloric acid (PT) and ammonium acetate (PP) and determined by photometric analyses (Allen 1989).

Soil moisture (%) was measured on the same spots as soil samples were taken on the same day in October 2013 using a soil moisture sensor (FOM/mts). This resulted in three measurements per subplot. The mean of the three measurements in a subplot was used in the data analysis. Average air temperature in the 2 weeks before soil moisture measurements was 16.8 °C and mean precipitation was 1.1 mm, with the last rain occurring three (GE) and 4 days (AU) prior to sampling dates (Weather Underground 2014).

Data analyses

Statistical analyses were performed using the software R (R Development Core Team 2012, version 2.15.2). We examined the potential influence of the two irrigation techniques on the species–area relationship at two levels. At the plot level, we calculated the intercepts and slopes (both log-transformed) of each of the 36 species–area relationships. To test whether the two types of irrigation affected the intercepts and slopes of species–area relationships, nested analyses of variance (ANOVA) were used with the factor irrigation type nested in study area. To minimize local variation in environmental factors (exposition, inclination, soil type), we considered differences in the cumulative species curves between pairs consisting of a traditionally irrigated and its nearest situated sprinkler-irrigated meadow (hereafter meadow-pair level). For this purpose, we calculated mean species richness for each subplot size (ranging from 0.01 to 40.96 m^2) for each meadow and determined the intercept and slope of the resulting species–area relationship of this meadow. Paired *t* tests were applied to examine whether pairs of differently irrigated meadows ($n = 6$) differed in the intercepts and slopes of their species–area relationships.

We constructed two types of distance matrices to analyse differences in the spatial pattern of the soil characteristics between traditionally and sprinkler-irrigated meadows. The first distance matrix considered the geographical coordinates of the 13 sampling points (midpoint of each subplot) to calculate Euclidean distances among all sampling points using the *ecodist* package (Goslee and Urban 2007). The pairwise distances among the 13 sampling points within a plot ranged from 10 to 570 cm ($n = 78$) and were the same for all plots and for all soil characteristics investigated. The second distance matrix had exactly the same structure, but considered a particular soil characteristic instead of geographical coordinates. The distance matrices were calculated separately for all plots for the following characteristics: soil moisture, soil pH, SOM, total soil organic nitrogen content (OrgN), total phosphorus content (PT) and plant available phosphorus content (PP) resulting in a total of 12 distance matrices. Due to a missing value in the sprinkler-irrigated meadow GE2 only 11 distance matrices were obtained for PT. We performed Mantel tests with 999 permutations for each distance matrix of the soil characteristics and calculated Mantel correlograms using the *mantel* and *mgram* functions of the *ecodist* package (Goslee and Urban 2007). To examine whether the Mantel coefficients (r_M) of the soil characteristics differed between irrigation techniques, we created reference bands for equality derived from the standard errors of the difference between r_M at each lag distance (Bowman and Young 1996) using the *sm.ancova* function of the *sm* package with a smoothing parameter $h = 20$ (Bowman and Azzalini 2013). At scales at which the plotted means of r_M exceeded this reference band, irrigation technique had a significant influence on the spatial pattern of the soil characteristic investigated (Bowman and Young 1996).

Finally, to assess the spatial scale of positive autocorrelation of soil characteristics, we determined the largest lag distance with a significant positive r_M value for each soil characteristic and for each Mantel correlogram for both irrigation techniques separately. If there was no positive autocorrelation within a Mantel correlogram, we took 0 as lag distance. In the results section, we present the mean lag distance for each irrigation type and soil characteristic.

Results

A total of 149 vascular plant species were recorded in the two types of meadows, 122 species (81.9 %) in traditionally irrigated meadows and 133 species (89.3 %) in sprinkler-irrigated meadows. Considering single meadows, the cumulative number of species ranged from 57 to 82 species (mean ± SE 68.8 ± 4.0) in traditionally irrigated meadows and from 63 to 78 species (70.0 ± 2.8) in sprinkler-irrigated meadows.

Species–area relationship

At the plot level (40.96 m^2), plant species richness ranged from 39 to 70 species (mean ± SE 53.1 ± 2.1) in traditionally irrigated meadows and from 47 to 64 species (53.9 ± 1.1) in sprinkler-irrigated meadows. The relationship between cumulative species richness and area was significant in all 36 plots (all $p < 0.0001$). However, in none of the species–area curves an asymptote was reached (Fig. 2). Neither the intercepts nor the slopes of the species–area curves were influenced by the type of irrigation (ANOVA, intercept: $F_{1,32} = 0.019$, $p = 0.89$; slope: $F_{1,32} = 0.17$, $p = 0.68$). However, the interaction between study area and irrigation technique had a significant effect on the intercepts ($F_{2,32} = 3.60, p = 0.039$), but not on the slopes of the species–area curves ($F_{2,32} = 1.23$, $p = 0.31$). Intercepts were higher in the study area GE (mean ± SE 3.34 ± 0.04) than in AU (3.23 ± 0.03).

At the meadow-pair level, neither the intercepts (paired t test, $t = -0.01$, d.f. = 5, $p = 0.99$) nor the slopes ($t = -0.80$, d.f. = 5, $p = 0.46$) of the mean species–area curves differed between meadows with either irrigation technique.

Spatial variation in soil characteristics

In general, the mean values of the Mantel coefficients (r_M) of the assessed soil characteristics decreased with increasing distance between the sampling points except for total soil organic matter content (SOM) and total soil organic nitrogen content (OrgN), which both increased with increasing distance in the sprinkler-irrigated meadows (Fig. 3).

The type of irrigation did not affect the spatial variation in soil moisture, OrgN, total phosphorus content (PT) and plant available phosphorus content (PP) (non-parametric ANCOVA, test of equality, soil moisture: $p = 0.93$; OrgN: $p = 0.52$; PT: $p = 0.90$; PP: $p = 0.99$; Fig. 3a, d–f). In contrast, irrigation technique affected the spatial pattern of soil pH and

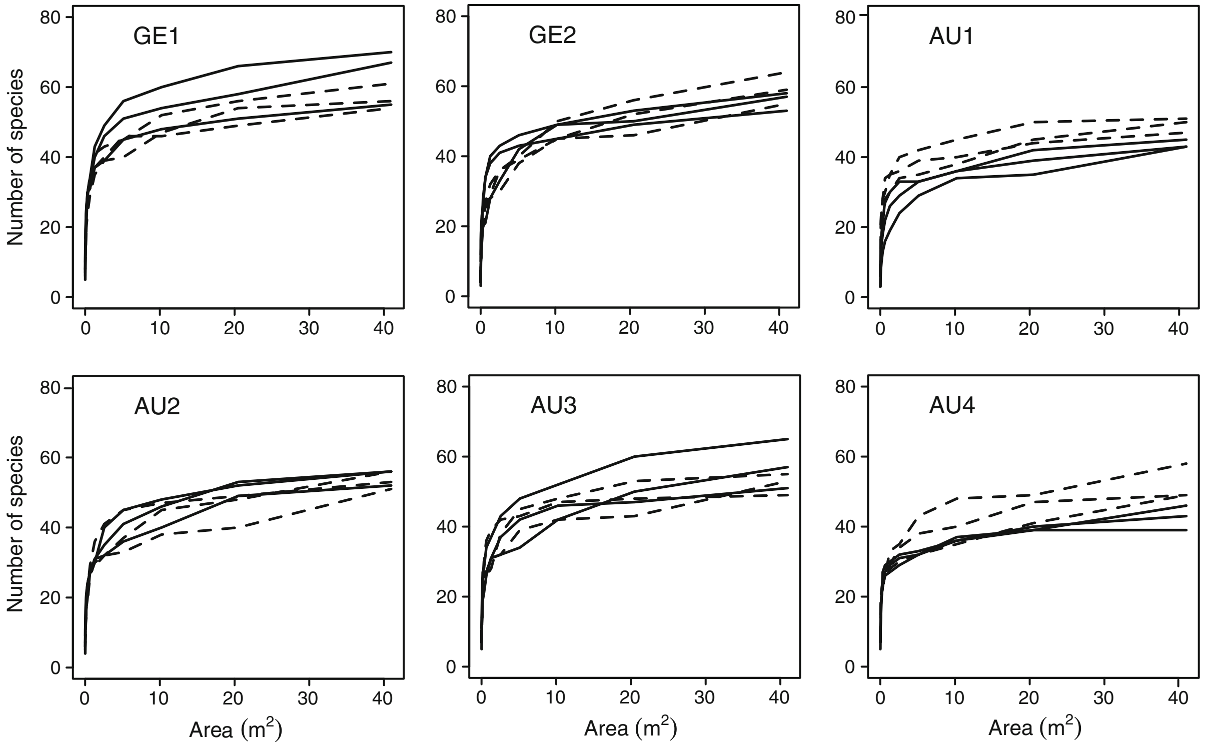

Fig. 2 Species–area curves of six pairs of traditionally and sprinkler-irrigated meadows, two in Guttet–Erschmatt (GE) and four in Ausserberg (AU). In each meadow pair, three plots were examined in a traditionally irrigated meadow (*dashed lines*) and three in a sprinkler-irrigated meadow (*solid lines*)

SOM (pH: $p = 0.011$; SOM: $p = 0.019$; Fig. 3b, c). For both soil characteristics the means of r_M exceeded the reference band at sampling distances between 440 and 520 cm. However, none of the means within this range showed a positive autocorrelation (Fig. 3b, c). In contrast, the mean r_M values of pH between 40 and 120 cm were significantly positively autocorrelated in the sprinkler-irrigated meadows, whereas no similar autocorrelation was found in the traditionally irrigated meadows (Fig. 3b).

The pattern of autocorrelation of soil characteristics did not differ between the two irrigation techniques. In most soil characteristics, no positive spatial autocorrelation among samples was found. Only in a few cases, average spatial autocorrelation ranged from a few to 60 cm (Appendix; Fig. S2).

Discussion

The present study showed that traditionally and sprinkler-irrigated hay meadows did not differ in the shape of the plant species–area relationships and in the small-scale patterns of soil characteristics (exceptions being the spatial distribution of soil pH and SOM).

Plant species richness of hay meadows

Based on a total plot area of 122.88 m^2, we recorded on average 69.4 plant species per meadow. In a previous study conducted in the same region (eight of the 16 meadows were also considered in the present study), an average of 54 species was found per meadow in a single plot of 100 m^2 (Riedener et al. 2013). This difference can be explained by a smaller sampling area, different arrangements of sampling plots (one 10 × 10 m plot versus three 6.4 × 6.4 m plots randomly distributed across a meadow), and the slightly but not significantly lower plant diversity in meadows located in Birgisch–Mund not considered in the present study.

Plant species richness recorded in the plots of the present study (39–70 species per 40.96 m^2) was relatively high compared to plots in other *Trisetetum*-

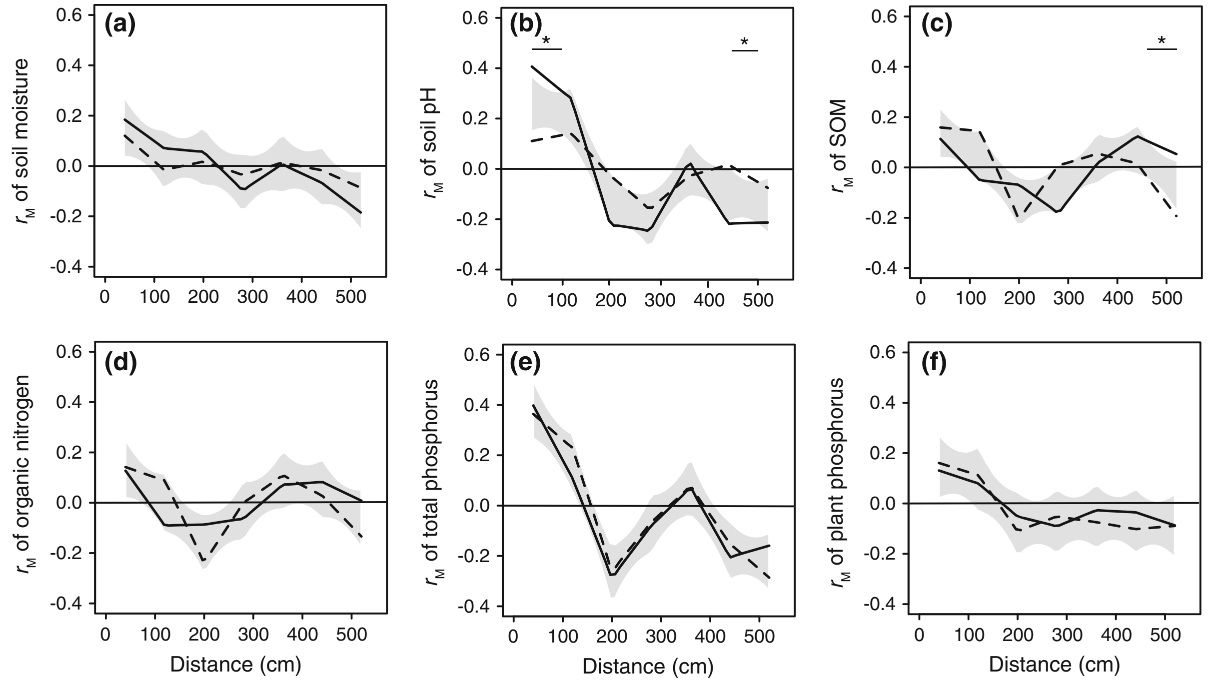

Fig. 3 Non-parametric curves for the mean Mantel coefficients (r_M) of the six soil characteristics in traditionally (*dashed lines*) and sprinkler-irrigated (*solid lines*) meadows. Reference bands for equality of r_M in the two differently irrigated meadows are presented. At distances where the means of r_M exceeded the reference band, the two curves differ significantly from each other, as indicated by the *asterisk*. Smoothing parameter $h = 20$. *SOM* soil organic matter content

meadows situated on similar elevations in the Swiss Alps (31–34 species per 100 m^2, Homburger and Hofer 2012 and 23–43 species per 25 m^2, Volkart and Godat 2007). However, none of the species–area curves reached the asymptote within the range of the plot sizes examined in the present study. This was also true when the data from the three plots of a meadow were combined (total area: 122.88 m^2; data not shown). This indicates a high plant diversity, as well as a pronounced variation in the spatial distribution of single plant species within a meadow compared to vegetation surveys in other *Trisetetum* meadows (Marschall 1947; Ellenberg 1986; Lüth et al. 2011). The pronounced variation in the spatial distribution of single plant species can be explained by various factors including clonal reproduction, uneven distribution of soil nutrients, variation in soil depth and seed distribution.

Effect of irrigation technique on species–area curves

We assumed that traditionally irrigated meadows have an uneven distribution of water, which results in a higher variation in the spatial distribution of plant species than in sprinkler-irrigated meadows. As a consequence, the slopes of the species–area relationships should differ between meadows irrigated by different techniques. However, this was not the case in our study. A possible explanation for the discrepancy is that the water distribution of sprinklers is more heterogeneous than commonly assumed (Meurer and Müller 1987). In fact, sprinkler irrigation systems in the study areas obtain their water from channels, and hence only rely on natural water pressure gradients from the sloping land (Crook 1997). Seasonal variation in water supply can, therefore, influence the reach of a sprinkler and thus the distribution of water. Furthermore, spray water can be misdirected by wind (Meurer and Müller 1987) and additional water can be supplied by uphill-situated meadows irrigated in the traditional way (R. L. M., pers. obs.). Moreover, the spatial arrangement of sprinklers at permanent positions and the seasonal relocation of mobile sprinklers may lead to a mosaic of partly overlapping circular areas with increased water supply and gaps that are tenuously irrigated. Hence, as practiced in our study areas, the distribution of water by sprinklers might be as heterogeneous as in the traditional irrigation technique. As a consequence, the two differently irrigated meadow types show a similar spatial distribution of plant species.

However, differences in the intercept of the species–area relationship were recorded between the two study areas. Irrespective of plot size, plant diversity was higher in Guttet–Erschmatt (GE) than in Ausserberg (AU; Fig. 2). This might be a result of site-specific differences in elevation (Kreft et al. 2008), different grazing animals (GE: horses and occasionally cattle, AU: cattle and sheep), amount of fertilizer, or meadow size (Gaujour et al. 2012).

Effect of irrigation technique on the spatial pattern of soil characteristics

Mantel correlograms revealed that traditionally and sprinkler-irrigated meadows did not differ in the spatial patterns of the soil characteristics examined, except in soil pH (see below). This result is in agreement with the findings of the plant species–area relationship.

Mantel correlograms also provide insight into the occurrence and spatial scale of autocorrelations (Borcard and Legendre 2012). In general, r_M decreased with increasing distances between sampling points, indicating a decreasing dependency the longer the distances between the sampling points were. Average positive autocorrelations were only found over distances ranging from 7 to 60 cm (Appendix). This suggests a high heterogeneity in soil characteristics even at a very small spatial scale. Thus, the heterogeneity in soil nutrients and soil moisture observed in this study could have led to the spatial heterogeneity in plant species and the high plant species richness, thereby supporting the view that heterogeneity in soil characteristics is positively linked to plant species richness (Harner and Harper 1976; Davies et al. 2005; Zhou et al. 2008).

For soil pH, a positive autocorrelation was recorded in sprinkler-irrigated meadows over a distance of 40–120 cm (Appendix). In contrast, no autocorrelation was found in traditionally irrigated meadows. As suggested by Meurer and Müller (1987), these differences might be explained by differences in the sediment content of the water used for irrigation. In sprinkler irrigation, melt water passes a settlement tank prior to entering the tubes, which substantially reduces sediments and organic materials and thus prevents the clogging of nozzles. In the traditional irrigation technique, unfiltered melt water is used. Through this sediment input irrigation additionally contributes to soil development (Meurer and Müller 1987). These differences in the sediment input and differences in the spatial distribution of water could have affected the pattern observed for soil pH. In contrast, small-scale differences in soil characteristics were hardly influenced by differences in the bedrock type, because in the present study, soil characteristics including soil pH were measured in the upper most 5 cm of the soil layer.

Irrigation technique affected the spatial pattern of soil pH and SOM at sampling distances of 400 and 520 cm. However, in both cases, r_M values were not significantly different from zero indicating that there was no autocorrelation at this distance.

Conclusion

The present study demonstrated a pronounced small-scale heterogeneity in the spatial distribution of both plants and soil characteristics in the hay meadows investigated. However, this variation was not influenced by the irrigation technique used. As it is applied on the slopes of these study areas, sprinkler irrigation does not appear to alter the spatial pattern of plant diversity compared with the traditional irrigation technique. Furthermore, our study areas are characterised by a patchy landscape consisting of small meadows, pastures, fallow land, hedgerows, few buildings and roads with adjacent forest. Therefore, the lack of any influence of irrigation technique on the spatial pattern of plant diversity and soil characteristics should not be extrapolated to large, homogeneous grassland areas that are more intensively irrigated.

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Appendix

See Appendix Table 1.

Table 1 Positive spatial autocorrelation obtained from individual Mantel correlograms for the six soil characteristics in (a) traditionally and (b) sprinkler-irrigated meadows

Plot	Soil moisture	Soil pH	SOM	Nitrogen	Total phosphorus	Plant available phosphorus
(a) Traditional irrigation						
GE1	0.00	0.00	0.00	0.00	119.99	0.00
GE2	0.00	0.00	0.00	0.00	40.00	40.00
AU1	40.00	0.00	0.00	40.00	40.00	0.00
AU2	0.00	0.00	0.00	0.00	0.00	119.99
AU3	0.00	0.00	0.00	119.99	119.99	0.00
AU4	0.00	0.00	0.00	0.00	40.00	0.00
Mean	6.67	0.00	0.00	26.67	60.00	26.67
Median	0.00	0.00	0.00	0.00	40.00	0.00
(b) Sprinkler irrigation						
GE1	0.00	119.99	0.00	0.00	40.00	0.00
GE2	40.00	119.99	0.00	0.00	NA	0.00
AU1	0.00	40.00	0.00	0.00	40.00	0.00
AU2	0.00	40.00	0.00	0.00	0.00	0.00
AU3	0.00	0.00	0.00	0.00	119.99	0.00
AU4	0.00	40.00	0.00	40.00	40.00	0.00
Mean	6.67	60.00	0.00	6.67	48.00	0.00
Median	0.00	40.00	0.00	0.00	40.00	0.00

The table shows the maximal distance (cm) for positive autocorrelation among the samples of a given soil characteristic within a plot, as well as mean and median for each soil characteristic. No positive autocorrelation indicates a high variability among samples

SOM soil organic matter content

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Supplementary material Chapter III

Table S1. Table showing the characteristics and management of the six traditionally and six sprinkler-irrigated hay meadows investigated.

Fig. S1. Mantel correlograms for the six soil characteristics examined assessed in the investigated hay meadows.

Table S1 Characteristics and management of the six traditionally and six sprinkler-irrigated hay meadows investigated, which are located in Ausserberg (AU) and Guttet-Erschmatt (GE).

Meadow pair	Irrigation technique	Irrigation interval (weeks)	Water amount per irrigation (l/ha)	Fertilizing frequency (per year) [a]	Amount of fertilizer (m^3/ha*year)	Mowings (per year)	Grazing regime	Stocking rate (no. of animals/ha*day) [c]	Distance between meadows of a pair (m)
GE1	Sprinkler	3	30240	Once	33.3	2	Occasionally in autumn (cattle)	95.2 (35, 2)	90
GE1	Traditional	3	39600	Once	33.3	2	Occasionally in autumn (cattle)	166.7 (35, 2)	
GE2	Sprinkler	3	10080	Every 2nd year	6.0 [b]	2	Autumn (horses)	10.0 (10, 10)	90
GE2	Traditional	3	25200	Every 2nd year	5.8 [b]	2	Autumn (horses)	na	
AU1	Sprinkler	2-3	10080	Every 2nd year	8.6 [b]	2	Autumn (sheep)	0.8 (8, 30)	315
AU1	Traditional	2	3600	Once	8.6	1	Autumn (cattle)	na	
AU2	Sprinkler	3	5040	None	0	2	No grazing	0	140
AU2	Traditional	3	50400	None	0	2	Autumn (calves)	na	
AU3	Sprinkler	3	12600	Every 2nd year	8.0 [b]	2	Autumn (sheep)	2.7 (25, 21)	225
AU3	Traditional	3	16200	Every 2nd year	4.3 [b]	2	Autumn (cattle)	6.2 (10, 7)	
AU4	Sprinkler	2	10080	Once	13.5	2	Autumn (sheep)	67.4 (30, 2)	485
AU4	Traditional	2	3600	Once	8.6	1	Autumn (cattle)	na	

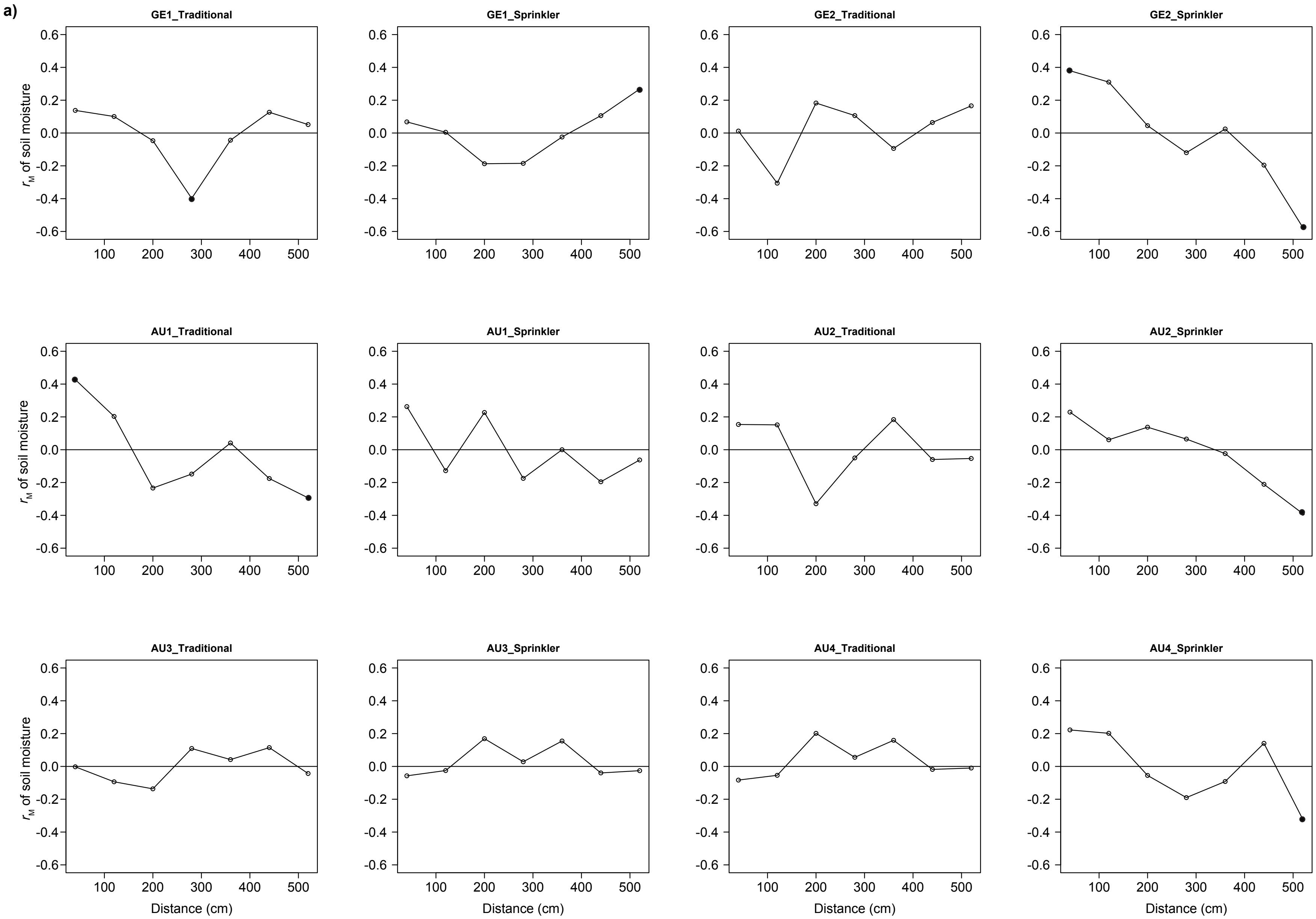
na = data were not available

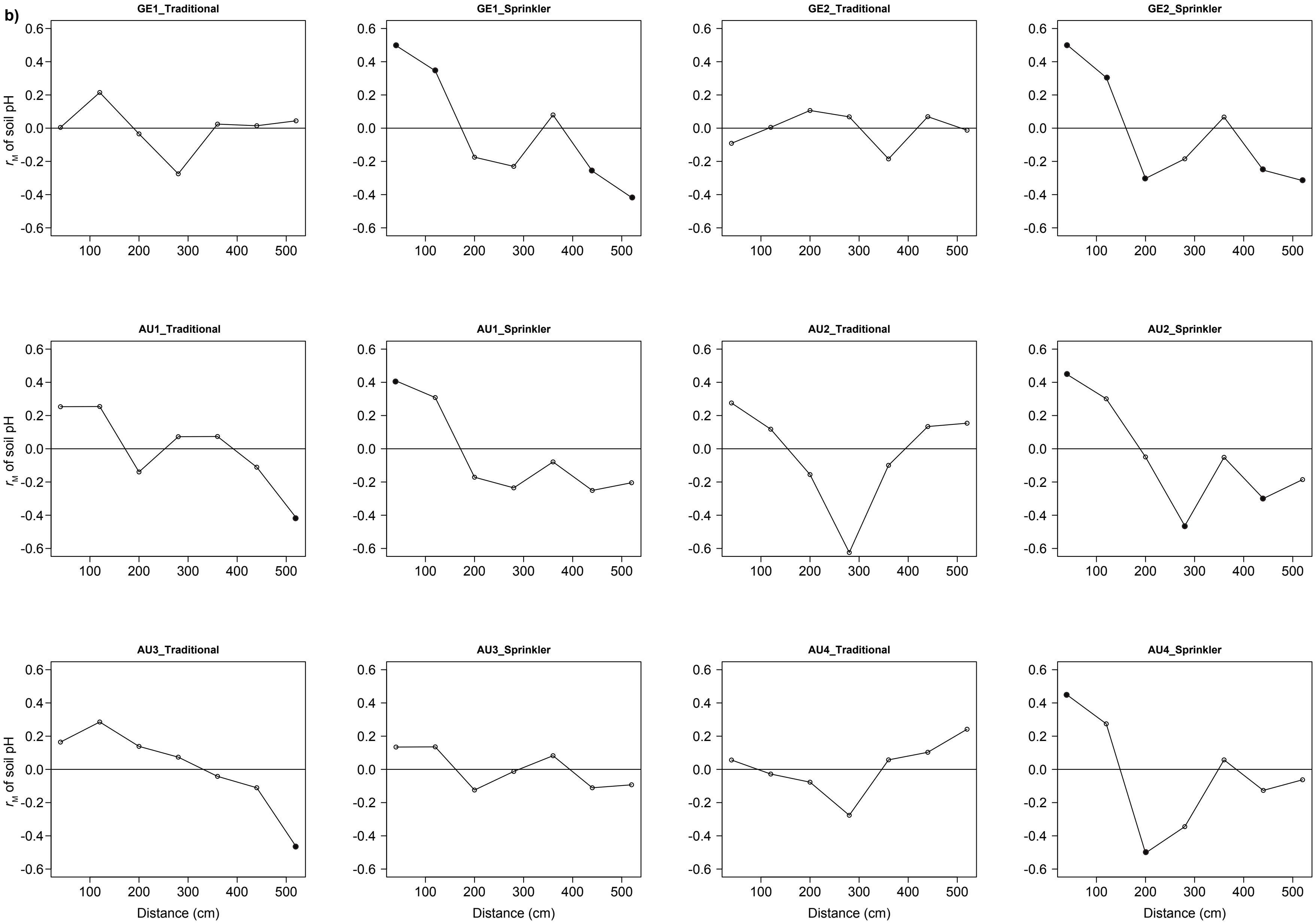
[a] Manure in all meadows

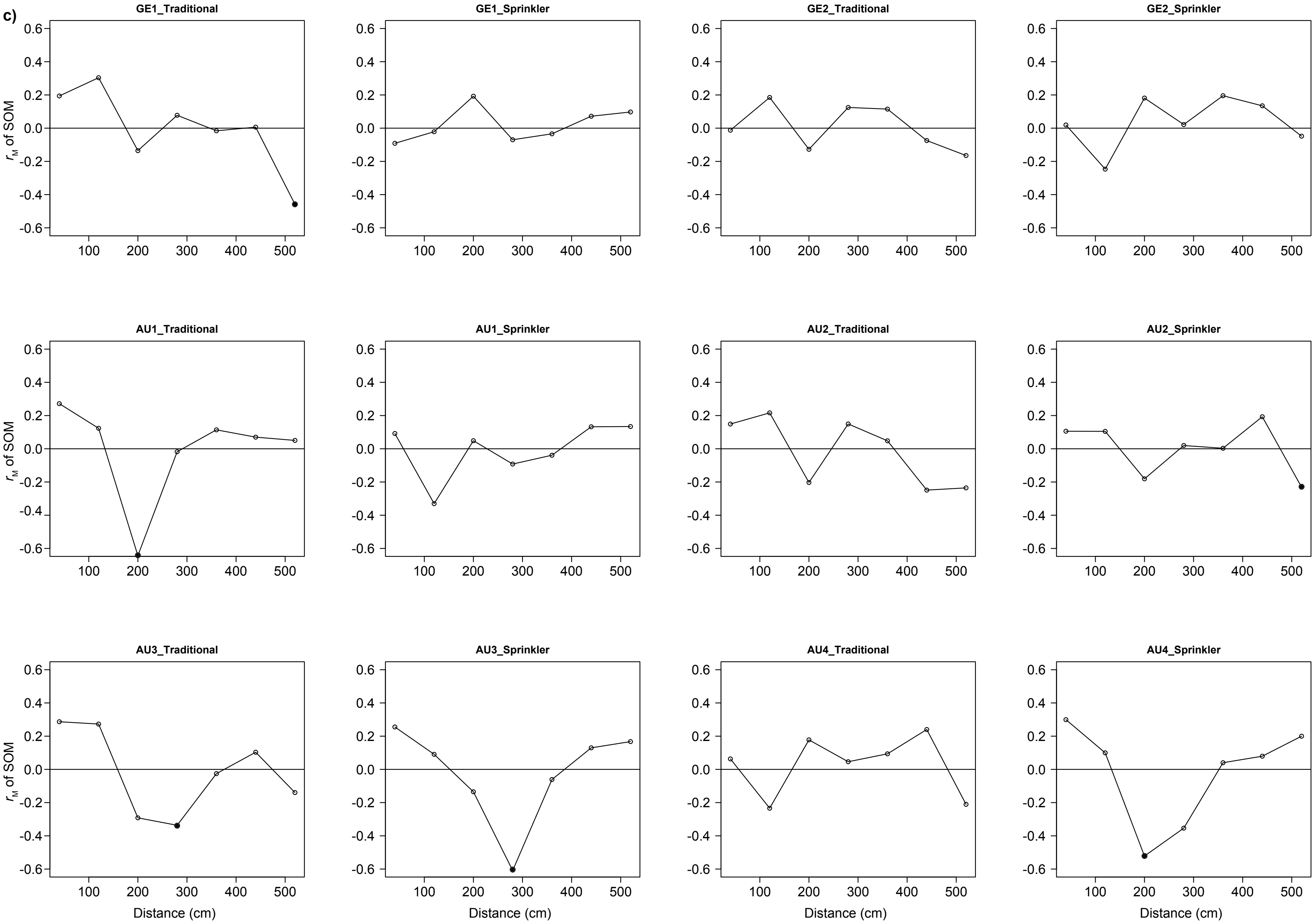
[b] Values are per year

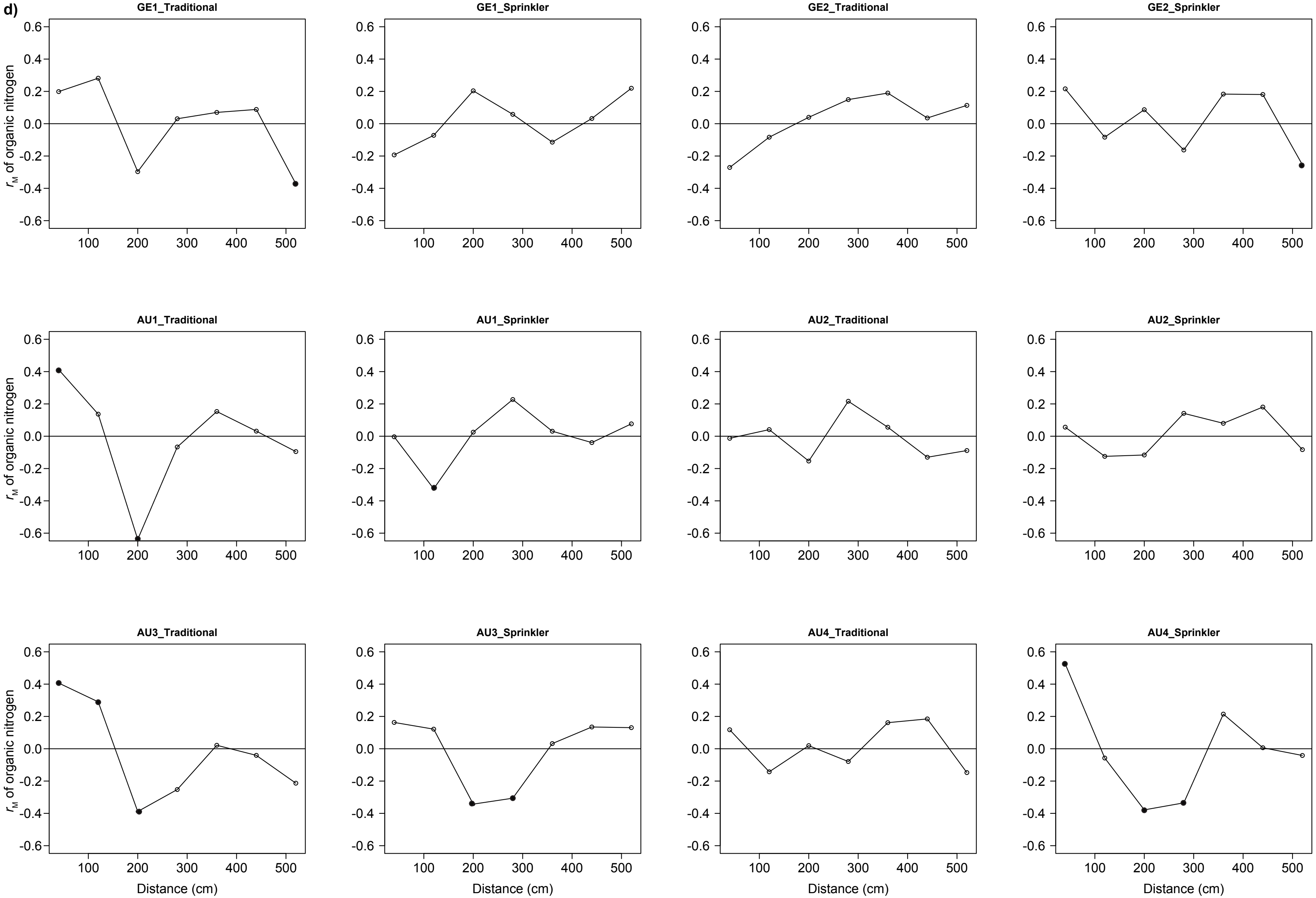
[c] The number of animals and the duration of grazing (in days) are given in brackets.

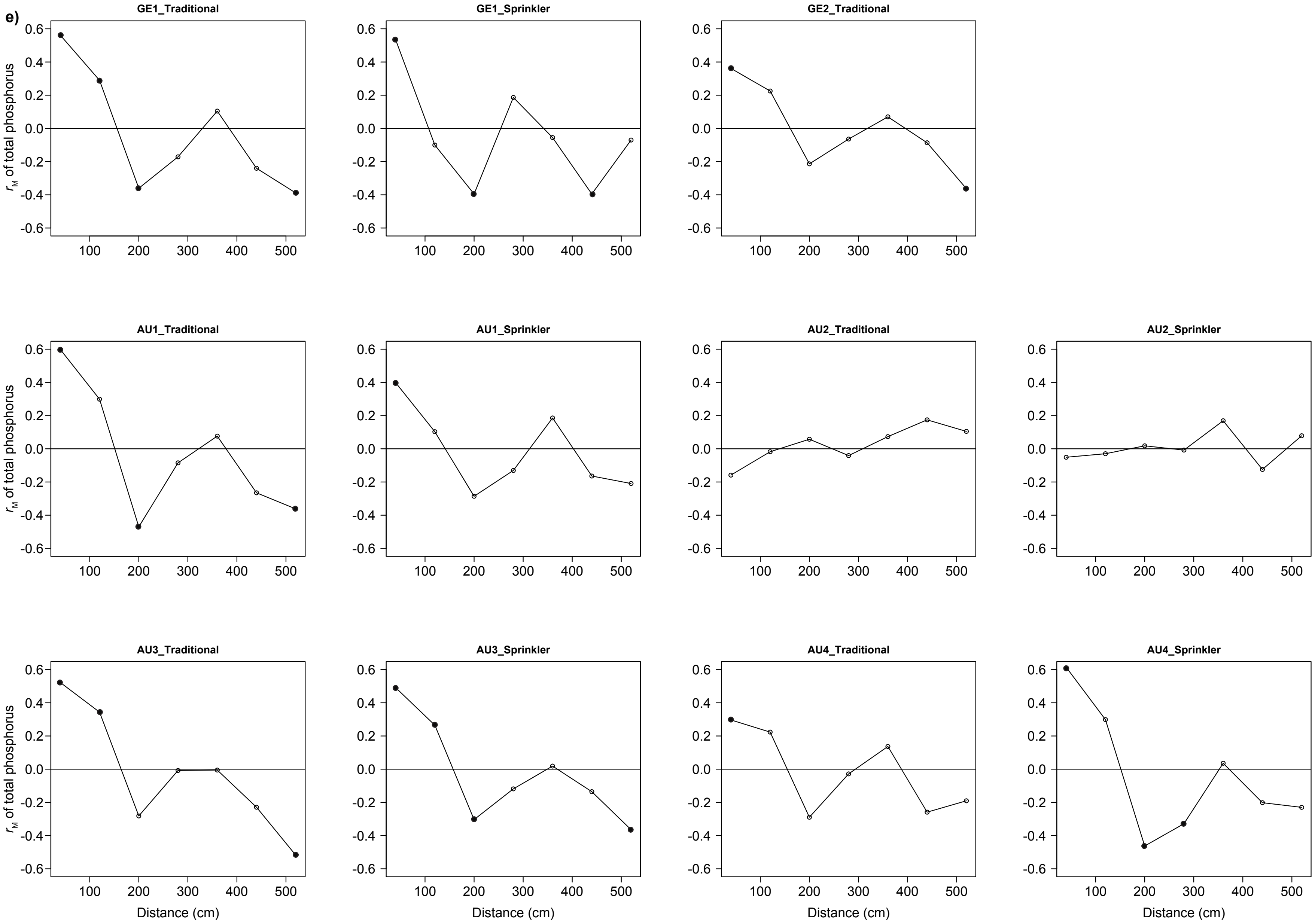
Fig. S1 Mantel correlograms for (a) soil moisture, (b) soil pH, (c) soil organic matter content (SOM), (d) soil organic nitrogen content, (e) total phosphorus content and (f) plant available phosphorus content assessed in the 12 plots located in the two study areas GE (Guttet-Erschmatt) and AU (Ausserberg). This resulted in 12 Mantel correlograms for each soil characteristic. An exception being total phosphorus content, for which only 11 Mantel correlograms were obtained due to a missing value in plot GE2_Sprinkler. Black symbols: rM significantly different from zero ($p < 0.05$), open symbols: rM not significantly different from zero.

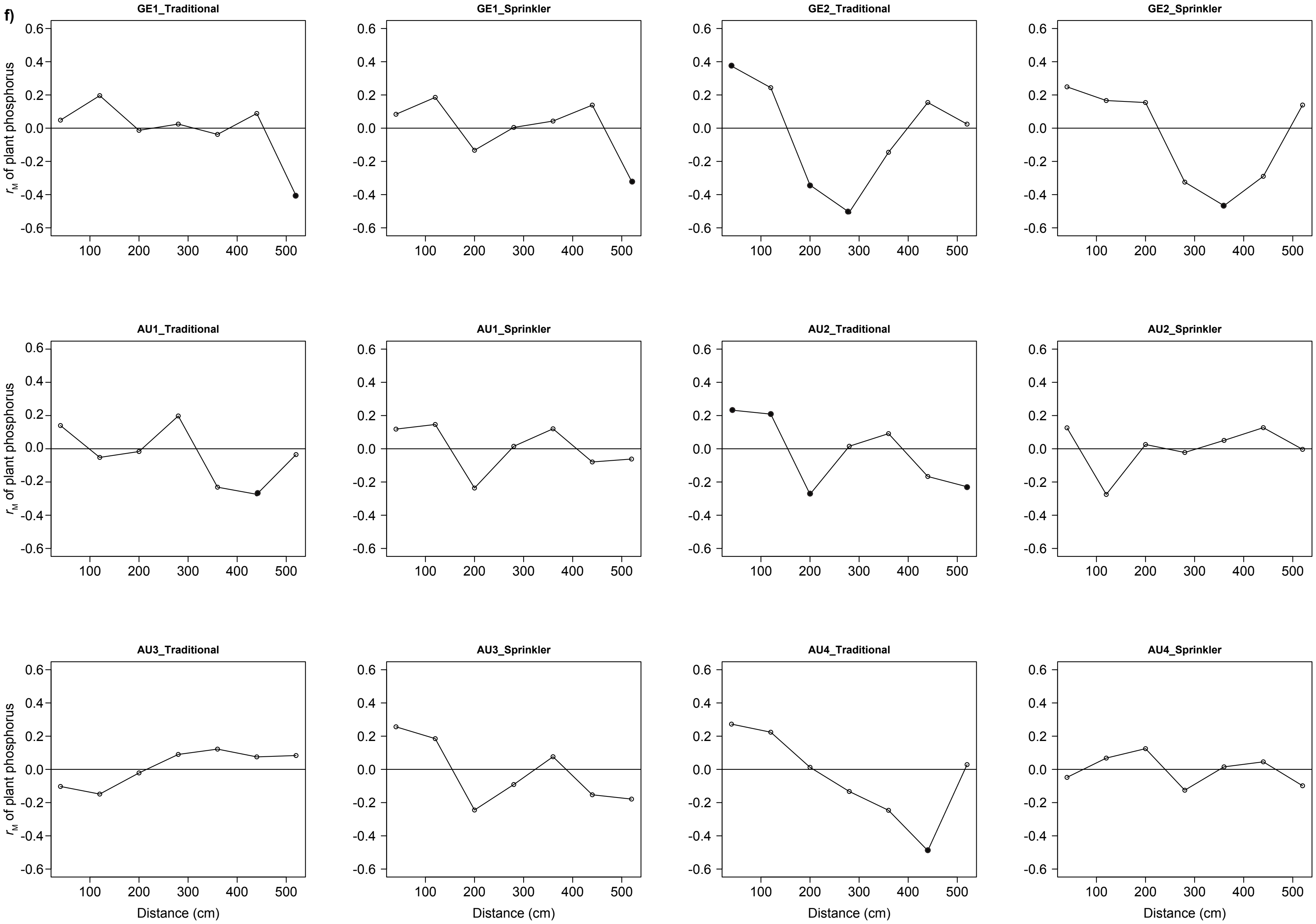

a)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
GE2_Sprinkler
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of soil moisture
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)


b)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
GE2_Sprinkler
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of soil pH
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)


c)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
GE2_Sprinkler
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of SOM
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)


d)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
GE2_Sprinkler
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of organic nitrogen
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)


e)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of total phosphorus
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)


f)
GE1_Traditional
GE1_Sprinkler
GE2_Traditional
GE2_Sprinkler
AU1_Traditional
AU1_Sprinkler
AU2_Traditional
AU2_Sprinkler
AU3_Traditional
AU3_Sprinkler
AU4_Traditional
AU4_Sprinkler
r_M of plant phosphorus
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
100
200
300
400
500
Distance (cm)

Chapter IV

Changes in landscape composition of differently irrigated hay meadows in an arid mountain region

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Changes in landscape composition of differently irrigated hay meadows in an arid mountain region

Eliane Riedener, Ramona L. Melliger, Hans-Peter Rusterholz & Bruno Baur

Keywords
Generalists; Grassland specialists; Landscape traits; Land-use change; Semi-natural grassland; Small-scale landscape; Valais (Switzerland); Water management

Abbreviations
GLM = generalized linear models; NMDS = non-metric multidimensional scaling.

Nomenclature
Lauber et al. (2012)

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Abstract

Questions: Does the recent change from traditional to sprinkler irrigation result in alterations in the surrounding landscape of species-rich hay meadows in an arid Swiss mountain region? Are landscape composition and landscape heterogeneity important determinants of plant diversity in these meadows?

Location: Southwestern Switzerland.

Methods: We surveyed vascular plant species in six traditionally and six sprinkler-irrigated hay meadows. Plant species were divided into grassland specialists and generalists. Individual landscape traits were assessed in circular areas with radii of 50 and 100 m around each meadow in a field survey. Aerial photographs were used to measure the percentage area covered by different habitat types in the present and prior to the installation of sprinklers at the same spatial scale as in the field surveys. The potential effects of irrigation technique and present-day landscape features on the plant diversity and species composition of hay meadows were examined with GLM and NMDS.

Results: Landscape composition was more diverse for traditionally than for sprinkler-irrigated meadows, but did not differ prior to the installation of sprinklers. Total plant species richness and the number of specialists were negatively affected by the distance to the closest haystack. Generalists were positively influenced by a variety of different small-scale landscape traits in the surroundings, whereas the percentage area covered by woodland had a negative effect. Finally, hay meadows irrigated with sprinklers had an increased number of generalist plant species.

Conclusions: This study showed that the small-scale surroundings, and to some extent the type of irrigation, are important for the conservation of plant diversity of these meadows. Furthermore, the study suggests that the installation of sprinklers was associated with a homogenization of the landscape, which facilitates land use. Extensive management should be promoted by compensation payments for farmers to prevent intensification.

Introduction

Semi-natural grasslands including hay meadows belong to the most species-rich habitats in Central Europe and are therefore of high conservation value (Poschlod & WallisDeVries 2002; Baur et al. 2006). The high biodiversity of semi-natural grasslands has been maintained for many centuries through the regular disturbance by traditional management practices such as grazing or mowing (Poschlod & WallisDeVries 2002; Valko et al. 2012). In the 20th century, however, both the intensification of land use as well as abandonment have resulted in a decline in the total area of semi-natural grasslands throughout Europe (Strijker 2005), which has led to a loss of plant diversity (Tasser & Tappeiner 2002; Niedrist et al. 2009; Jacquemyn et al. 2011).

These land-use changes also affect the surrounding landscape of semi-natural grasslands. Traditional management practices not only maintained a high plant diversity but also a high heterogeneity of landscape elements within and in the surroundings of semi-natural grasslands (Diacon-Bolli et al. 2012). The intensification of land use, however, led to a homogenization of the agricultural landscape, mainly by the enlargement of farms and fields and

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by the reduction of adjacent habitat structures (Benton et al. 2003; Baessler & Klotz 2006; Diacon-Bolli et al. 2012). Moreover, land-use abandonment led to an increase in forest area (e.g. Kulakowski et al. 2011) and hence to a reduction in landscape heterogeneity. Beside the direct effects of land-use changes, the decrease in landscape heterogeneity may contribute to the loss of plant species richness in semi-natural grasslands (Diacon-Bolli et al. 2012).

Plant species richness and composition of semi-natural grasslands are generally affected by a combination of several factors, including land use, the local abiotic environment (Dauber et al. 2003; Marini et al. 2008a; Gusmeroli et al. 2012), historical development, competitive interactions (Tilman 1982) and the surrounding landscape. In fact, the potential influence of the surrounding landscape is attracting increasing attention, with contrasting findings. Some studies have shown that individual landscape traits (Söderström et al. 2001; Reitalu et al. 2009; Aavik & Liira 2010; Öckinger et al. 2012) and landscape heterogeneity (Baessler & Klotz 2006; Reitalu et al. 2012) could affect the plant diversity and composition of semi-natural grasslands. Other studies have shown no effect of present-day landscape features on plant species richness (Dauber et al. 2003; Krauss et al. 2004; Marini et al. 2008b), or have identified other factors as being more important than the surrounding landscape (Marini et al. 2008a; Gusmeroli et al. 2012). Furthermore, the effects of the surrounding landscape might differ when considering grassland specialists and generalists separately. However, this question has only been addressed in a few studies, which provided inconsistent results (Krauss et al. 2004; Reitalu et al. 2012).

While most of the above-mentioned studies investigated the effects of the surrounding landscape in radii ranging from 200 m to 5 km, potential influences of the immediate surroundings (radius ≤ 100 m) are less well studied (but see: Dauber et al. 2003; Aavik & Liira 2010). However, small-scale effects might be of importance, especially in fragmented landscapes. In this study, we examined the effects of the surrounding landscape on plant species richness, including the number of grassland specialists and generalists of hay meadows in the Valais, an arid mountain region in Switzerland. The landscape is characterized by a small-scale mosaic of hay meadows, pastures, fallow land, hedgerows and a few buildings and roads embedded in forest. The hay meadows are small (0.04–1.00 ha) and managed in a relatively extensive way. Because of the dry climatic conditions, irrigation is required to secure hay production and hence to maintain the characteristic biodiversity of these meadows (Riedener et al. 2014). In fact, the Valais has a long tradition of meadow irrigation using open water channels. These water channels transport glacial melt water from mountain streams to meadows at lower elevations (Crook & Jones 1999), where the water is used for irrigation. In traditional meadow irrigation, farmers put a temporary dam across the water channel causing an overflow with resulting flooding of the down-slope parts of the meadow (Crook & Jones 1999; App. S1). However, in the last decades, the modernization and rationalization of agriculture has increasingly led to the replacement of this traditional irrigation technique by sprinkler irrigation systems (Crook & Jones 1999). Traditional and sprinkler irrigation are assumed to differ in their distribution of the water used, which may have potential influences on biodiversity. In traditional irrigation, the ground is inundated irregularly, depending on the micro-relief, whereas a sprinkler may distribute the water more homogeneously from above (Meurer & Müller 1987). However, while this change in irrigation technique does not appear to directly influence the local meadow biodiversity (Riedener et al. 2013), it is not known whether the type of irrigation affects the immediate surroundings of hay meadows, which in turn might indirectly affect their biodiversity.

The aim of this study was to examine the potential influences of the surrounding landscape on the local plant diversity of differently irrigated hay meadows in the Valais. Until the 1980s, all hay meadows were irrigated in a traditional way, nowadays most meadows are irrigated by sprinklers; we therefore compared the surrounding landscapes of hay meadows in the present-day situation with those prior to the installation of sprinklers. The landscape elements within radii of 50 and 100 m around the focal meadows were considered. For this, we differentiated between landscape composition and the heterogeneity of the surrounding landscape. Landscape composition was defined as the variety of different habitat types or landscape traits within a given area ($r = 50$ m or 100 m) and therefore also includes the investigated meadows. In contrast, landscape heterogeneity only considers the surroundings of the focal meadows.

In particular, we addressed the following questions: (i) are changes in the surrounding landscape of hay meadows associated with the installation of sprinkler systems; (ii) are plant species richness and species composition of differently irrigated hay meadows affected by landscape composition and the heterogeneity of the surrounding landscape; and (iii) are the number of specialist and generalist species differently influenced by these factors?

Methods

Study area and study sites

The study was conducted in two areas located on the south-facing slope of the Rhone valley in the Valais,

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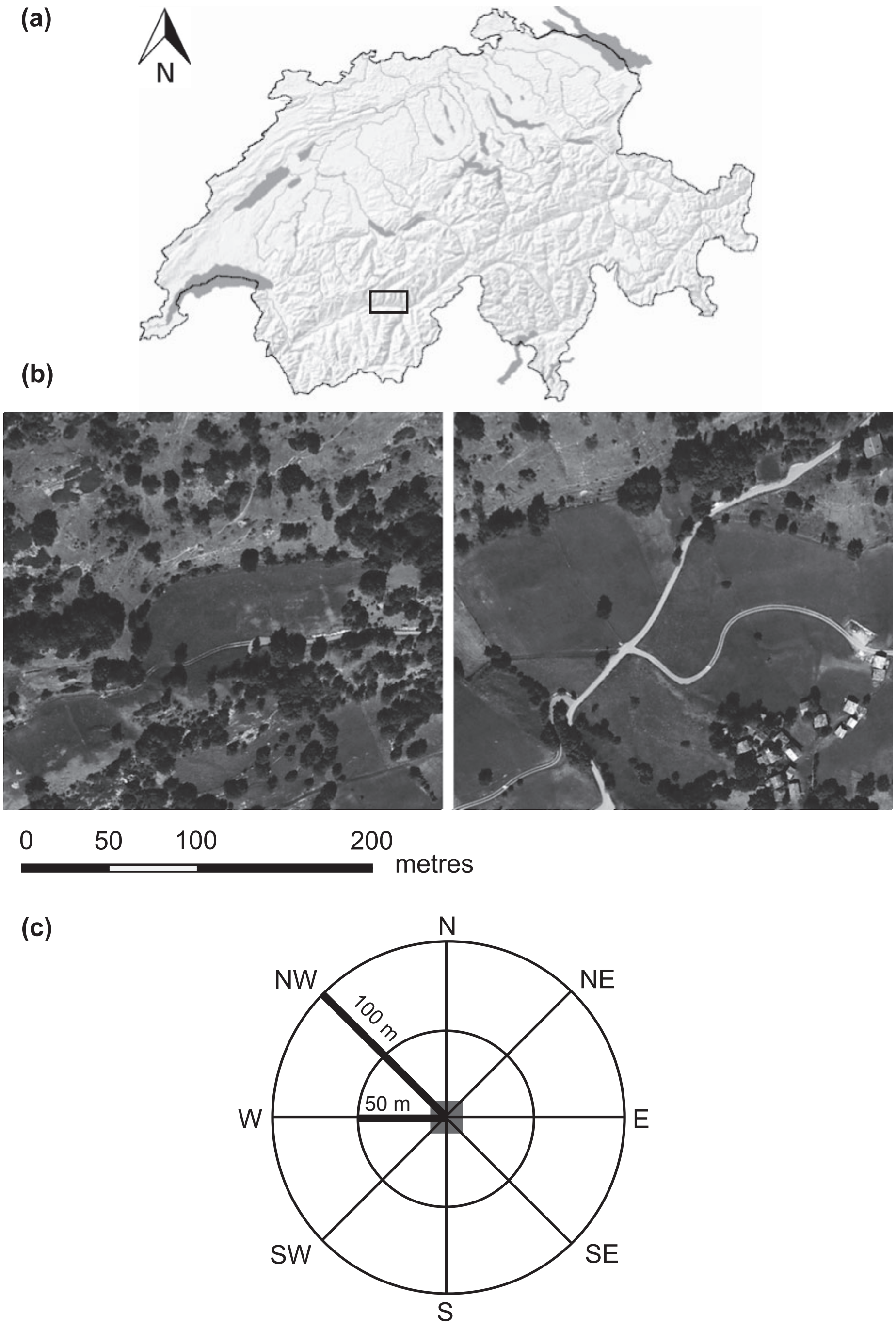

Fig. 1. (**a**) Location of the study region in southwestern Switzerland. (**b**) Aerial photographs showing a traditionally (left) and a sprinkler-irrigated hay meadow (right; situated in the centre of the photograph between the two roads) including their immediate surroundings considered in this study. (**c**) Schematic illustration of the field assessment of landscape traits in the surroundings of hay meadows. Circular areas with radii of 50 and 100 m divided into eight sectors were installed around the sampling plot (grey square) of each hay meadow. The presence of individual landscape traits was recorded in each sector for both radii. © Google-Earth.

Switzerland (Fig. 1a), namely in Ausserberg (46°19′ N, 7°51′ E; hereafter AU) and Guttet-Erschmatt (46°19′ N, 7°40′ E; hereafter GE). The two areas are located 14 km apart. Mean annual temperature in this region is 9.4°C and total annual precipitation is 596 mm (MeteoSwiss 2013; http://www.meteoschweiz.admin.ch/web/en/climate/swiss_climate/climate_diagrams_from_swiss_measuring_stations.html).

The study areas are characterized by a patchy arrangement of small, traditionally irrigated (10% in GE and 30% in AU) and sprinkler-irrigated (70% in AU and 90% in GE) hay meadows belonging to the *Trisetetum* association (Ellenberg 1986). Detailed information on the land use of these meadows was obtained through personal interviews with farmers. On most of these meadows, sprinkler irrigation systems were installed about 11–28 yr before the study was conducted (between 1986 and 2003). The sprinkler systems obtain their water from water channels and therefore rely on the same infrastructure as the traditional irrigation technique. Moreover, irrigation frequency and amount of water applied per irrigation event do not differ between the two irrigation techniques (Riedener et al. 2013). Management of hay meadows is relatively extensive, including irrigation every second to third week during the vegetation period (irrespective of irrigation technique). Furthermore, meadows are mown once or twice a year and grazed for a few days in autumn. Fertilizer (manure) is applied every second year in autumn, except for two meadows in AU, which are not fertilized at all.

We selected 12 hay meadows in the two study areas, six traditionally and six sprinkler-irrigated meadows ranging in size from 374 m^2 to 9616 m^2. Four meadows of each irrigation technique were located in AU and two meadows of each irrigation technique in GE. Distances among the differently irrigated meadows ranged from 150 m to 2.1 km in AU and from 90 m to 900 m in GE. Traditionally and sprinkler-irrigated meadows did not differ in size, elevation, exposure and inclination (ANOVA, all $P > 0.19$). Neither did meadows in the two study areas differ in exposure or inclination (ANOVA, both $P > 0.29$). Average exposure was SSE (157 ± 10°) and average inclination was 18 ± 1°. However, mean elevation of the hay meadows was 1222 ± 7 m a.s.l. (± SE) in AU and 1339 ± 26 m a.s.l in GE (ANOVA, $F_{1,9} = 33.54$, $P < 0.001$). Furthermore, meadows were smaller in AU than in GE (AU: 3049 ± 623 m^2, GE: 6198 ± 1507 m^2; ANOVA, $F_{1,9} = 6.68$, $P = 0.030$).

Vegetation surveys

On each meadow, one sampling plot measuring 6.4 m × 6.4 m was installed to record the presence (i.e. presence–absence data) of vascular plant species. Species–area curves showed that this plot size is appropriate to estimate local plant species richness of these meadows (Melliger et al. 2014). To minimize potential edge effects, the distance between the sampling plot and a water channel or trail was always >2 m, and that between a plot and a road >3 m. Vegetation surveys were carried out by R. L. M. and E. R. between May and June 2012. Pseudo-turnover, i.e. the turnover accounting for two sampling persons, ranged from 5.3 to 9.8% (Nilsson & Nilsson 1985).

Assessment of landscape traits and habitat types

Two methods were applied to assess the composition of the landscape in which the investigated hay meadows were embedded (Fig. 1b). First, we recorded ten different landscape traits (App. S2) in circular areas with radii of either 50 or 100 m around each sampling plot in the field (Fig. 1c). Because of the small-scale patchy landscape of the study region, these spatial scales were chosen to capture the immediate surroundings of hay meadows. For both spatial scales, circular areas were subdivided into eight sectors (directed towards N, NE, E, SE, S, SW, W and NW) and in each sector the occurring landscape traits were recorded. This method allowed the assessment of small-scale landscape traits, which cannot be obtained from maps or aerial photographs. Field surveys were carried out from late August to early September 2012.

Second, aerial photographs were used to measure the percentage area covered by four habitat types including hay meadows, open land, woodland and settlements in the present-day situation (Google-Earth, date: 10 Apr 2013), and prior to the installation of sprinklers (Swiss Federal Office of Topography, date: 4 Jul 1972). These analyses were conducted at the same spatial scales and starting from the same centroid as for the assessment of landscape traits in the field (App. S2). The percentage area covered by different habitat types was determined by counting the number of pixels of the single habitat types using Adobe Photoshop CS3.

As a proxy for the present heterogeneity of the surrounding landscape, the percentage area covered by the same four habitat types described above was assessed using Google-Earth images. In this analysis, we excluded the area of the focal meadow and considered only the percentage area covered by other traditionally (mean ± SE; $r = 50$ m: 6.5 ± 2.8%, $r = 100$ m: 9.6 ± 2.6%) and sprinkler-irrigated ($r = 50$ m: 20.1 ± 6.0%, $r = 100$ m: 25.9 ± 6.9%) hay meadows in the surroundings.

In addition, the shortest distances from sampling plots to the closest woodland, haystack and road were measured for the present-day situation on Google-Earth maps (App. S2). Old maps were used to determine the year in which the main access roads were built in the two study areas.

We used the concept of livestock units per hectare grassland (LU) to examine changes in grazing pressure by livestock in our study areas between 1975 and 2012. LU are defined according to the Swiss ordinance on agricultural terms and types of farming (Swiss Federal Office for Agriculture 2004): steers >2 yr old = 0.6; horses = 1.0;

sheep = 0.15; goats = 0.15. Data on LU were obtained for the years 1975, 1990 and 2008–2012 for Ausserberg and Guttet. No similar data were available for Erschmatt.

Data analyses

All statistical analyses were performed in R v 2.15.0 (R Foundation for Statistical Computing, Vienna, AT) and were carried out separately for the two spatial scales. Wilcoxon rank sum tests were used to assess whether the sampling plots in traditionally and sprinkler-irrigated meadows differed in the distances to the closest woodland, haystack or road.

For each landscape trait recorded, its occurrence in the eight sectors was assessed within the 50- and 100-m radii, resulting in values ranging from zero to eight for each radius. Based on these values of the different traits, a single measure of landscape composition was calculated for both radii using the Shannon diversity index (hereafter 'frequency-based landscape composition') with the vegan package in R. Shannon diversity indices were also calculated from the percentages area covered by the four habitat types, including the sampled meadows from aerial photographs for the present-day situation and prior to the installation of sprinklers (hereafter 'area-based landscape composition'). Finally, Shannon diversity indices were calculated from the percentage area covered by the four habitat types excluding the sampled meadows for the present-day situation (hereafter 'heterogeneity of the surrounding landscape'). Wilcoxon rank sum tests were used to assess whether traditionally and sprinkler-irrigated meadows differed in frequency- and area-based landscape composition and in the heterogeneity of the surrounding landscape.

To examine whether plant species richness was influenced by the type of irrigation technique used and present-day landscape features, we applied generalized linear models (GLM) with quasi-Poisson distributed errors and log link function using the MASS package in R. Three models were tested to evaluate the effects of frequency- and area-based landscape composition, and of the heterogeneity of the surrounding landscape. Spearman rank correlations were applied to test for inter-correlations among variables and only non-correlated variables ($r_S < 0.56$, $P > 0.06$; App. S3) were used in a given model. The percentage area covered by other traditionally irrigated meadows within a 50-m radius was excluded from the model with landscape heterogeneity because of the low occurrence of this habitat type. In a preliminary analysis, the effect of time elapsed since the change from traditional to sprinkler irrigation was tested for the subset of sprinkler-irrigated meadows. However, because time had no significant effect on the variables examined, this factor was omitted in the main analyses. The models tested included the following explanatory variables: irrigation technique as factor, meadow area, the percentages area covered by different habitat types (see Table 2 for details), the distances to the closest road and haystack, as well as either frequency-based landscape composition, area-based landscape composition or the heterogeneity of the surrounding landscape as co-factors. Non-significant variables were step-wise reduced as recommended by Crawley (2007), except for the factor irrigation technique, which was retained in all models.

To assess the habitat specificity of plants, we assigned each species to one of the following categories: grassland specialist, generalist or forest species. Information was obtained from Lauber et al. (2012) and Landolt et al. (2010). Since the number of forest species was very low, species of this category were omitted. Spearman rank correlations were used to test whether the number of plant species was correlated with the number of specialists and generalists. To examine whether the number of specialist and generalist species was influenced by the type of irrigation technique and present-day landscape features, we applied the same GLM models as described above. Furthermore, we assessed whether these variables affected the ratio of generalists to specialists using the same GLM with quasi-binomial errors and logit link function.

To evaluate whether the type of irrigation and present-day landscape features influenced plant species composition, non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measure was applied as recommended by Austin (2013). Vegetation data consisted of the presence/absence data of all observed plant species. The ordination was fitted using the metaMDS function on two dimensions in the vegan package in R. The goodness of fit of this ordination method is indicated by the stress coefficient: stress <0.05: excellent ordination; stress <0.1: good ordination; stress <0.2: usable ordination (Clarke 1993). In a second step, the same variables as used in the GLM and information about the application of fertilizer (fertilized, not fertilized) were fitted onto the vegetation ordination using the function envfit with 999 permutations in the vegan package. However, because the three models revealed very similar results, only the results of the model including landscape heterogeneity are presented.

Results

The surrounding landscape of differently irrigated hay meadows

The construction of main access roads occurred decades before sprinkler irrigation systems were installed on the hay meadows investigated (AU: in 1935, GE: in 1969; App. S4). Plots in traditionally irrigated meadows were located further away from roads than those in sprinkler-irrigated

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meadows (mean ± SE, traditional: 41.7 ± 10.5 m, sprinkler: 13.3 ± 2.8 m; Wilcoxon rank sum test, $n = 12$, $P = 0.028$). The distance to the closest woodland (28.3 ± 4.0 m) or haystack (113.2 ± 16.1 m) did not differ between the sampling plots of differently irrigated meadows (both $P > 0.68$). Grazing pressure by livestock decreased in both study areas between 1975 and 2012 (App. S5).

Considering the present frequency-based landscape composition, traditionally irrigated meadows showed a marginally higher diversity of landscape traits within 50 m than sprinkler-irrigated meadows (Table 1). This was mainly due to the more frequent occurrence of pastures and functioning water channels and the less frequent occurrence of roads in the surroundings of traditionally irrigated meadows (App. S6). Within a radius of 100 m, no difference in frequency-based landscape composition was found (Table 1).

Considering the present area-based landscape composition, traditionally irrigated meadows showed a higher diversity of habitat types than sprinkler-irrigated meadows at the scale of 100-m radius (Table 1). This was mainly a result of the higher percentage of open-land and lower percentage of hay meadows in the surroundings of traditionally irrigated meadows (App. S6). In contrast, area-based landscape composition did not differ between the investigated meadows in the year 1972 (prior to installation of sprinklers; Table 1, App. S6). Similarly, there were no differences between traditionally and sprinkler-irrigated meadows when considering the present heterogeneity of the surrounding landscape (Wilcoxon rank sum test, $n = 12$, $r = 50$ m: $P = 0.82$; $r = 100$ m: $P = 0.18$).

Species richness, number of specialist and generalist species

A total of 125 plant species was recorded in the 12 investigated hay meadows; 103 species (82.4%) were found in traditionally and 108 species (86.4%) in sprinkler-irrigated meadows (App. S7). The average species richness per 6.4 m × 6.4 m plot did not differ between traditionally (mean ± SE, 53.3 ± 4.4) and sprinkler-irrigated meadows (55.8 ± 1.7; Table 2a–c). In all three GLM models, the number of plant species per plot was negatively influenced by the distance to the closest haystack (Table 2a–c). An exception is the model including the heterogeneity of the surrounding landscape, in which the percentage area covered by woodland within a 100-m radius had a marginally negative effect (Table 2c).

The number of specialist species did not differ between the meadows of the two irrigation techniques (traditional: 43.0 ± 3.9 per plot, sprinkler: 42.0 ± 1.5; Table 2a–c, App. S7), but was positively correlated with the total number of plant species per plot (Spearman rank correlation, $r_s = 0.87$, $n = 12$, $P = 0.0003$). Therefore, the GLM results for the number of specialist species were similar to those of the total number of plant species per plot, being negatively affected by the distance to the closest haystack (Table 2a–c).

A lower number of generalist species was observed in traditionally (10.0 ± 0.8 per plot) than in sprinkler-irrigated meadows (12.8 ± 0.9; Table 2a–c, App. S7). The number of generalist species was correlated with the total number of species per plot, however less strongly than the number of specialists (see above; Spearman rank correlation, $r_s = 0.61$, $n = 12$, $P = 0.036$). In the model with frequency-based landscape composition, the number of generalist species was negatively affected by the percentage of woodland area and positively by landscape composition within 100 m (Table 2a). However, within a 50-m radius, and within both radii in the other two models, the percentage of woodland area had only a marginally negative effect (Table 2b–c). The ratio of generalists to specialists was significantly lower in traditionally than in sprinkler-irrigated meadows (traditional: 0.24 ± 0.02, sprinkler: 0.31 ± 0.02; GLM, $F_{1,10} = 5.68$, $P = 0.038$, in all three models). However, this ratio was not affected by any landscape feature in the surroundings.

Table 1. Mean ± SE of landscape composition in the immediate surroundings (r = 50 and 100 m) of traditionally and sprinkler-irrigated hay meadows in 2012–2013 and prior to the installation of sprinklers in 1972. Results of Wilcoxon rank sum tests (n = 12) are shown to indicate differences in landscape composition between the two meadow types. Significant differences are highlighted in bold.

	r = 50 m		P	r = 100 m		P
	Traditional	Sprinkler		Traditional	Sprinkler	
Frequency-Based Landscape Composition [1]						
Situation in 2012	1.88 ± 0.06	1.69 ± 0.07	0.065	2.08 ± 0.03	2.01 ± 0.04	0.38
Area-Based Landscape Composition [2]						
Situation in 2013	0.89 ± 0.13	0.72 ± 0.10	0.49	1.09 ± 0.05	0.93 ± 0.04	**0.045**
Situation in 1972	0.80 ± 0.09	0.82 ± 0.09	0.93	0.96 ± 0.07	0.94 ± 0.08	0.59

[1] Expressed by the Shannon diversity index and calculated from the frequency of occurrence of ten different landscape traits assessed in the field in 2012.

[2] Expressed by the Shannon diversity index and calculated from the percentage area covered by different habitat types obtained from aerial photographs made in 2013 and 1972.

Table 2. Deviance tables for the GLM analyses showing the effects of irrigation technique, the area of hay meadows investigated, habitat types and (a) frequency-based landscape composition, (b) area-based landscape composition, or (c) landscape heterogeneity recorded in the immediate surroundings of hay meadows ($r = 50$ and 100 m) on the total number of plant species and both the number of specialist and generalist species per plot. Only present-day landscape features are considered in these analyses. Variables that were removed from the models are designated by '–'. Empty cells represent variables not included in a given model. (+) and (–) indicate positive and negative effects of significant variables, respectively.

	Total Number of Species						Number of Specialist Species						Number of Generalist Species					
	$r = 50$ m			$r = 100$ m			$r = 50$ m			$r = 100$ m			$r = 50$ m			$r = 100$ m		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
(a)																		
Irrigation	0.47	1, 10	0.51	0.44	1, 10	0.51	0.11	1, 10	0.75	0.11	1, 10	0.75	7.15	1, 10	0.026	15.51	1, 10	0.004
Meadow Area	1.66	1, 9	0.23	1.66	1, 9	0.23	2.65	1, 9	0.14	2.65	1, 9	0.14	–	–	–	–	–	–
Open land[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Woodland[2]				–	–	–				–	–	–	4.13	1, 9	0.07 (–)	8.58	1, 9	0.020 (–)
Settlement[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Road[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Haystack[1]	6.93	1, 8	0.030 (–)	6.93	1, 8	0.030 (–)	8.25	1, 8	0.020 (–)	8.25	1, 8	0.020 (–)	–	–	–	–	–	–
Landscape Composition (Frequency-Based)[3]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.41	1, 8	0.010 (+)
(b)																		
Irrigation	0.46	1, 10	0.52	0.46	1, 10	0.52	0.11	1, 10	0.75	0.11	1, 10	0.75	7.15	1, 10	0.026	7.01	1, 10	0.027
Meadow Area	1.45	1, 9	0.26	1.45	1, 9	0.26	2.30	1, 9	0.17	2.30	1, 9	0.17	–	–	–	–	–	–
Woodland[2]				–	–	–				–	–	–	4.13	1, 9	0.07 (–)	3.88	1, 9	0.08 (–)
Settlement[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Road[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Haystack[1]	6.93	1, 8	0.030 (–)	6.93	1, 8	0.030 (–)	8.25	1, 8	0.020 (–)	8.25	1, 8	0.020 (–)	–	–	–	–	–	–
Landscape Composition (Area-based)[3]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(c)																		
Irrigation	0.46	1, 10	0.52	0.37	1, 10	0.56	0.11	1, 10	0.75	0.11	1, 10	0.75	7.15	1, 10	0.026	6.99	1, 10	0.028
Meadow Area	1.45	1, 9	0.26	–	–	–	2.30	1, 9	0.17	2.30	1, 9	0.17	–	–	–	–	–	–
Other Meadow Sprinkler[1]	–	–	–				–	–	–				–	–	–			
Open land[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Woodland[2]	–	–	–	4.23	1, 9	0.07 (–)	–	–	–	–	–	–	4.11	1, 9	0.07 (–)	3.91	1, 9	0.07 (–)
Settlement[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Road[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Distance to Haystack[1]	6.93	1, 8	0.030 (–)	–	–	–	8.25	1, 8	0.020 (–)	8.25	1, 8	0.020 (–)	–	–	–	–	–	–
Landscape Heterogeneity[3]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[1] Square root-transformed in $r = 50$ and 100 m.

[2] Square root-transformed in $r = 50$ m and log-transformed in $r = 100$ m.

[3] Landscape composition and landscape heterogeneity are expressed as Shannon diversity indices.

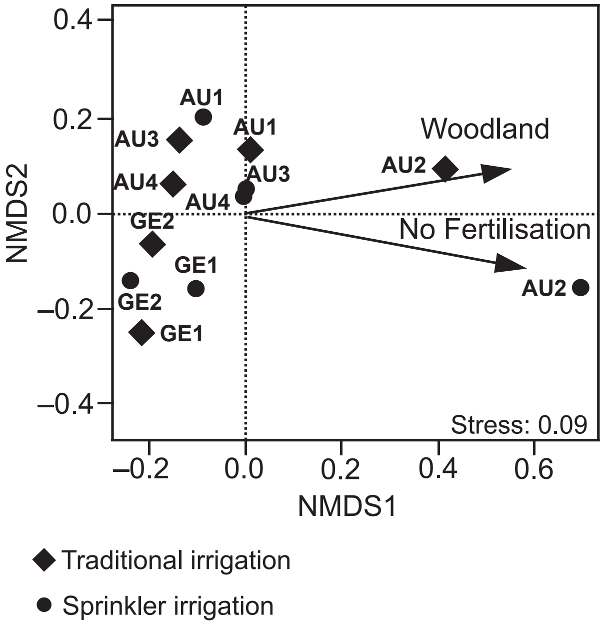

Fig. 2. NMDS ordination diagram based on Bray–Curtis dissimilarities in plant species composition of traditionally and sprinkler-irrigated hay meadows. The percentage of woodland area within a radius of 50 m and the application of fertilizer significantly affected plant species composition of these meadows. Very similar results were obtained for the 100-m radius (not shown).

Species composition

Meadows of either irrigation type did not differ in plant species composition ($P = 0.72$ for $r = 50$ m; Fig. 2; data within $r = 100$ m revealed very similar results). However, plant species composition was influenced by the percentage of woodland ($R^2 = 0.62$, $P = 0.016$) and the application of fertilizer ($R^2 = 0.87$, $P = 0.001$). There was no significant effect of any other landscape feature included in the NMDS analyses (all $P > 0.11$).

Discussion

The surrounding landscape of differently irrigated hay meadows

Our study showed that sprinkler-irrigated meadows were located closer to roads than meadows irrigated by the more labour-intensive traditional irrigation technique. However, the main access roads in these arid mountain areas were constructed decades prior to the installation of sprinklers on the hay meadows examined. Therefore, the change in irrigation technique was not associated with the construction of roads.

This study further showed that still traditionally irrigated meadows were associated with a more diverse small-scale landscape composition with respect to different habitat types than sprinkler-irrigated meadows. In contrast, landscape composition did not differ prior to the installation of sprinklers (in 1972). This suggests that the homogenization of the landscape at the spatial scale considered is associated with the installation of sprinklers, most probably with the goal of facilitating grassland management. The homogenization was most apparent in the higher percentage of hay meadow area within 100 m of sprinkler-irrigated meadows (about 60% vs 45% in the surroundings of traditionally irrigated meadows). Our finding is in agreement with other studies showing that the replacement of traditional management practices by more intensive land-use types often results in a homogenization of the landscape (Benton et al. 2003; Baessler & Klotz 2006; Diacon-Bolli et al. 2012). However, grazing pressure by livestock per hectare grassland decreased in our study areas, suggesting that the installation of sprinklers reduced labour but did not lead to an intensification of land use.

Effects on plant diversity

Our study demonstrates that the immediate surroundings (50 and 100 m) of hay meadows in this small-scale patchy landscape, and to some extent the type of irrigation technique, are important for local plant diversity. Total plant species richness and the number of specialist species were influenced by similar factors and differed from the response of generalist species. This can be explained by the fact that the majority of the recorded plant species (75–80%) were grassland specialists.

The distance to the closest haystacks negatively affected total plant species richness and the number of specialist species. These haystacks may have a function as seed source for the dispersal of characteristic grassland species and thus may positively influence plant species richness and grassland specialists in their surroundings.

We found a positive effect of frequency-based landscape composition within a 100-m radius on the number of generalist species recorded in these meadows. This suggests that small-scale landscape features, rather than habitat types, are of importance for generalists at this spatial scale. In general, a heterogeneous landscape is expected to increase plant diversity by providing a variety of different environmental conditions for many species (Rosenzweig 1995), which in turn may colonize the target habitat. The surrounding landscape in our study areas contained landscape elements that may be suitable for generalists, such as hedgerows, stone walls and road verges (App. S6). This can explain the positive effect of frequency-based landscape composition on generalist species. In contrast, neither total plant species richness nor the number of specialist species was influenced by landscape composition or the heterogeneity of the surrounding landscape. This suggests that plant species richness and the number of specialists of the hay meadows examined rather depend on other suitable grasslands in the surroundings and hence on a large species pool and on connectivity (Adriaens et al. 2006; Reitalu et al. 2009, 2012).

The percentage area covered by woodland within a 100-m radius negatively influenced the number of generalist species (Table 2a). However, this negative effect was only marginally significant in the other models (Table 2a–c). This indicates that small woodland fragments, as present in our study areas, may act as barriers for the dispersal of generalist species. Furthermore, the percentage of woodland area was the only factor significantly influencing species composition. The two meadows associated with a high proportion of woodland in the surroundings showed a distinct species composition compared to the other meadows investigated. This finding can also be explained by the fact that these meadows were the only two that are not fertilized (Fig. 2).

Finally, we recorded a higher number of generalist plant species in sprinkler-irrigated meadows than in traditionally irrigated meadows. This could be explained by the closer location of sprinkler-irrigated meadows to roads. Aavik & Liira (2010) found a high number of agro-tolerant species in road verges, suggesting that roads can act as a dispersal corridor for generalists. In our study, however, the distance to the closest road did not influence the number of generalists.

Conclusions

Our study showed that the small-scale surroundings and to some extent the type of irrigation are important features for the conservation of plant diversity of the investigated hay meadows in the Valais. While grassland specialists, and hence total plant species richness, were positively affected by potential seed sources for grassland specialists such as haystacks, generalists benefited from various landscape features and irrigation by sprinklers. Furthermore, the installation of sprinklers was associated with a homogenization of the landscape, which could lead to more intensive management of these meadows. For the conservation of these species-rich hay meadows it is recommended to provide suitable habitat for grassland specialists, which can act as a seed source for these meadows. Moreover, ecological compensation payments for farmers could be used to prevent more intensive management.

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Supporting Information

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

Appendix S1. Photos showing the traditional irrigation technique and sprinkler irrigation system.

Appendix S2. Definition of landscape traits assessed in the field and habitat types extracted from aerial photographs.

Appendix S3. Correlation matrices for the assessed landscape variables.

Appendix S4. Table comparing the years of main access road construction and the installation of sprinkler irrigation systems.

Appendix S5. Total livestock units per hectare grassland in the two study areas between 1975 and 2012.

Appendix S6. Mean ± SE of landscape traits and habitat types in the surrounding of the investigated hay meadows.

Appendix S7. List of plant species and their habitat specificity of the investigated hay meadows.

Supplementary material Chapter IV

Appendix S1. Photos showing the traditional irrigation technique and a sprinkler irrigation system.

Appendix S2. Definition of landscape traits assessed in the field and habitat types extracted from aerial photographs.

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Appendix S4. Table showing the years of main access road construction and the installation of sprinklers for each meadow examined.

Appendix S5. Total livestock units per hectare grassland in the two study areas between 1975 and 2012.

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Appendix S7. List of plant species and their habitat specificity of the hay meadows investigated.

Appendix S1.

Photographs showing (a, b) the traditional irrigation technique, and (c) sprinkler irrigation in the Valais. For both irrigation techniques, irrigation water is obtained from water channels (a). In the traditional irrigation technique, farmers put a temporary dam across the water channel causing an overflow with a resulting flooding of the down-slope parts of the meadow. For sprinkler irrigation, hoses are used for water transport.

a) b)

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c)

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Appendix S2.

Definition of **(a)** landscape traits assessed in the field and **(b)** habitat types extracted from aerial photographs. Landscape variables were recorded in circular areas (r = 50 and 100 m) around each sampling plot. In the field assessment, the circular areas were subdivided into eight sectors and the landscape traits were recorded separately for each sector.

Variable	Unit	Definition	Assessment in the field
a) Landscape traits			
Hay meadow	Number of occurrence (in 0–8 sectors)	Mown and irrigated and might serve as pasture in spring and/or autumn	Recorded as present if meadows encompassed a continuous area of more than 10 m^2 in the sector considered
Pasture	Number of occurrence (in 0–8 sectors)	Grassland, which is mainly grazed (not necessarily during the entire vegetation period)	Recorded as present if pastures encompassed a continuous area of more than 10 m^2 in the sector considered
Fallow land	Number of occurrence (in 0–8 sectors)	Abandoned grasslands with high vegetation and first shrubs (first successional stage)	Recorded as present if fallow land encompassed a continuous area of more than 10 m^2 in the sector considered
Hedgerow/single tree	Number of occurrence (in 0–8 sectors)	Single tree or group of trees/shrubs; group extending up to a width of 3 m	Recorded as present if one or more single tree/shrub and/or hedgerow occurred
Forest	Number of occurrence (in 0–8 sectors)	Continuous wooded area or forest fragments > 0.25 ha	Recorded as present if the forest encompassed a continuous area of more than 10 m^2 in the sector considered
Water channel in use	Number of occurrence (in 0–8 sectors)	Maintained water channel which is permanently or temporarily water-bearing	Recorded as present if the section of a water channel was longer than 2 m in the sector considered (also for abandoned water channels)
Water channel abandoned	Number of occurrence (in 0–8 sectors)	Water channel which is not maintained anymore (e.g. more or less overgrown by vegetation, filled with litter or other natural material, broken)	
Settlement and infrastructure	Number of occurrence (in 0–8 sectors)	Houses and stables (mainly of wood with a stone roof), gardens and infrastructure (mainly water pipes, in two occasions a water tank)	Recorded as present if one or more of these elements occurred. If a single element was located in two adjacent sectors, it was only recorded in one sector.
Road	Number of occurrence (in 0–8 sectors)	Road covered with gravel or concrete (including parking areas)	Recorded as present if the section of a road was longer than 2 m in the sector considered
Stonewall, pile of pieces of stone, bare rock (abbr.: stonewall)	Number of occurrence (in 0–8 sectors)	- Stone wall: regularly arranged pile of natural stones originating from the surroundings; joints are not sealed - Pile of stones: similar to stone wall but stones are not regularly arranged and single stones might also vary more in size - Bare rock: vertical cliff or horizontal rock on the ground, larger than 1 m in height	Recorded as present if one or more of these elements occurred. If a single element was located in two adjacent sectors, it was only recorded in one sector

b) Habitat types			
Hay meadow	%	The percentage of area covered by hay meadows within a given radius	-
Open-land	%	The percentage of area covered by open-land within a given radius including pastures, fallow land, arable fields and rocky area	-
Woodland	%	The percentage of area covered by woodland within a given radius including single trees, hedgerows and forests	-
Settlement	%	The percentage of area covered by settlements within a given radius including houses, stables and roads	-
Distance to woodland	m	Shortest distance from the sampling plot to the closest woodland (hedgerows or forests, excluding single trees)	-
Distance to haystack	m	Shortest distance from the sampling plot to the closest haystack	-
Distance to road	m	Shortest distance from the sampling plot to the closest road	-

Appendix S3.

Correlation matrices based on Spearman rank correlations for the assessed landscape variables considering **a)** landscape composition (including the meadows investigated) and **b)** the heterogeneity of the surrounding landscape. Only significant correlations ($r_S > 0.56$, $P < 0.06$) are shown.

a)	Meadow area	Meadow	Open-land	Woodland	Settlement	Landscape composition (area-based)	Landscape composition (frequency-based)	Distance to road	Distance to building	Distance to woodland
r = 50 m										
Meadow area										
Meadow										
Open-land [1]		-0.79								
Woodland [1]		-0.80								
Settlement [1]										
Landscape composition (area-based)		-0.96	0.82	0.67						
Landscape composition (frequency-based)		-0.64		0.56		0.58				
Distance to road [1]										
Distance to haystack [1]										
Distance to woodland [1]		0.63		-0.78						
r = 100 m										
Meadow area										
Meadow										
Open-land [1]		-0.74								
Woodland [2]		-0.61								
Settlement [1]		0.58								
Landscape composition (area-based)		-0.73	0.82							
Landscape composition (frequency-based)						0.71				
Distance to road [1]										
Distance to haystack [1]										
Distance to woodland [1]				-0.72						

b)	Meadow area	Meadow traditional	Meadow sprinkler	Open-land	Woodland	Settlement	Landscape heterogeneity (area-based)	Distance to road	Distance to building	Distance to woodland
r = 50 m										
Meadow area										
Meadow traditional [1]										
Meadow sprinkler [1]										
Open-land [1]										
Woodland [1]										
Settlement [1]										
Landscape heterogeneity (area-based)										
Distance to road [1]										
Distance to haystack										
Distance to woodland [1]					-0.78					
Meadow area										
Meadow traditional										
Meadow sprinkler		-0.67								
Open-land [1]			-0.62							
Woodland [2]										
Settlement [1]		-0.70	0.83							
Landscape heterogeneity (area-based)		0.66								
Distance to road [1]										
Distance to haystack [1]										
Distance to woodland [1]					-0.72					

[1] sqrt- transformed

[2] log-transformed

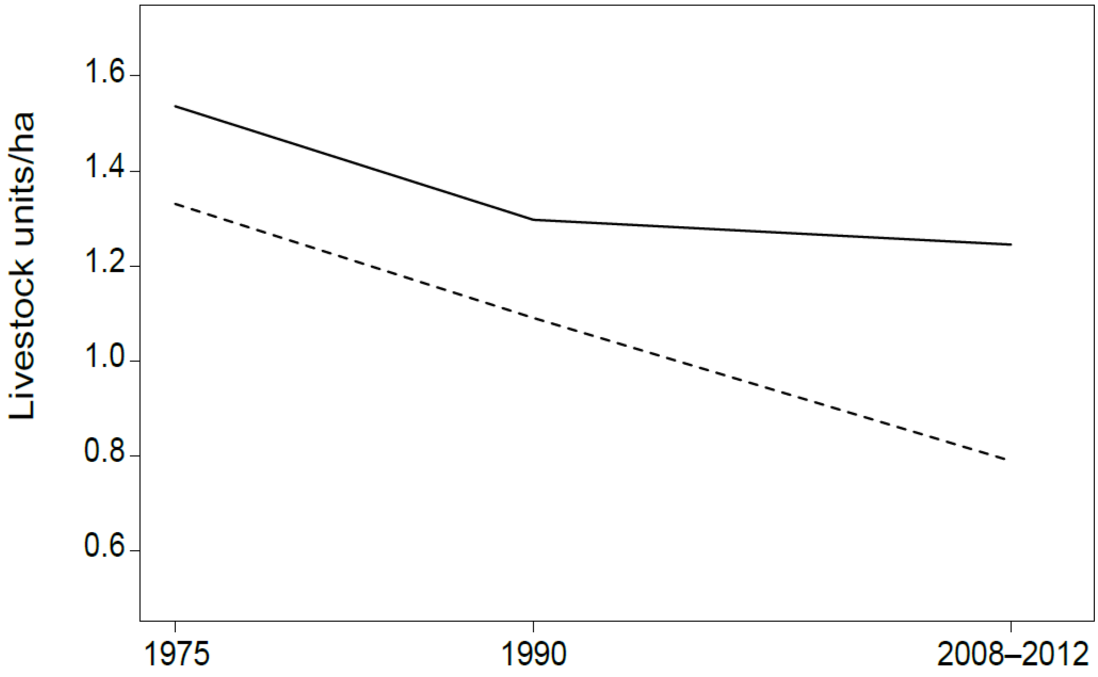
Appendix S4.

Time of change in irrigation technique and the year of road construction in the surroundings of each meadow examined. Main access roads and the usually smaller secondary roads lead to the meadows.

Hay meadow investigated	Present irrigation technique	Installation of sprinklers (year)	Construction of main access roads (year)	Construction of further access roads (year)
GE1_t	traditional	–	1969	–
GE1_s	sprinkler	2003	1969	–
GE2_t	traditional	–	1969	1986
GE2_s	sprinkler	2003	1969	–
AU1_t	traditional	–	1935	1993
AU1_s	sprinkler	1993	1935	1993
AU2_t	traditional	–	1935	–
AU2_s	sprinkler	1996	1935	1987
AU3_t	traditional	–	1935	–
AU3_s	sprinkler	1986	1935	1993
AU4_t	traditional	–	1935	1993
AU4_s	sprinkler	1986	1935	1993

Appendix S5.

Total livestock units (LU) per hectare grasslands in the two villages Ausserberg (solid line) and Guttet (dashed line). Data were available for the years 1975, 1990 and 2008–2012 (average shown).



Appendix S6.

Mean ± SE of landscape traits and habitat types used to assess landscape composition in the close surroundings (r = 50 and 100 m) of traditionally and sprinkler-irrigated hay meadows. Landscape traits were assessed in the field in 2012 (unit: frequency of occurrence). Habitat types and un 2012 and 1972 (prior to the installation of the sprinkler) were obtained from aerial photographs.

	r = 50 m		r = 100 m	
	Traditional	Sprinkler	Traditional	Sprinkler
Landscape traits				
Situation in 2012				
Hay meadow	8.0 ± 0.0	8.0 ± 0.0	8.0 ± 0.0	8.0 ± 0.0
Pasture	3.7 ± 0.9	0.7 ± 0.7	5.5 ± 1.2	2.7 ± 0.9
Fallow land	0.2 ± 0.2	1.0 ± 0.7	1.3 ± 0.5	1.7 ± 1.0
Hedgerow/single tree	6.0 ± 0.7	5.3 ± 0.7	7.7 ± 0.3	7.3 ± 0.7
Forest	1.2 ± 0.5	1.2 ± 1.2	2.8 ± 1.1	1.7 ± 1.3
Water channel in use	4.2 ± 0.4	1.2 ± 1.0	5.8 ± 0.6	3.3 ± 1.1
Water channel abandoned	2.0 ± 0.7	2.5 ± 0.8	3.3 ± 1.2	4.7 ± 1.1
Settlement/infrastructure	1.2 ± 0.4	1.3 ± 0.7	2.5 ± 0.4	2.7 ± 0.5
Road	2.0 ± 0.7	4.7 ± 0.7	4.2 ± 0.7	6.0 ± 0.5
Stonewall	3.5 ± 0.7	2.5 ± 0.7	5.8 ± 0.9	6.0 ± 0.8
Habitat types				
Situation in 2013				
Hay meadow (%)	61.0 ± 7.1	70.3 ± 10.4	43.2 ± 5.9	58.8 ± 9.5
Open-land (%)	19.7 ± 5.8	5.8 ± 4.4	27.2 ± 5.6	12.0 ± 4.2
Woodland (%)	17.0 ± 3.7	16.3 ± 6.9	26.5 ± 4.8	23.3 ± 7.8
Settlement (%)	2.3 ± 1.2	7.5 ± 1.1	3.1 ± 1.1	5.8 ± 1.4
Situation in 1972				
Hay meadow (%)	83.7 ± 2.0	72.7 ±12.0	72.3 ± 7.5	70.2 ± 11.7
Open-land (%)	6.2 ± 2.9	8.5 ± 6.3	13.3 ± 8.1	9.0 ± 4.8
Woodland (%)	8.2 ± 2.3	11.5 ± 7.6	10.3 ± 2.0	14.8 ± 8.2
Settlement (%)	2.0 ± 1.0	7.3 ± 2.7	4.0 ± 1.2	6.0 ± 1.3

Appendix S7. List of plant species and their habitat specificity showing the presence-absence data of traditionally (t) and sprinkler-irrigated (s) hay meadows located in the two study areas Ausserberg (AU) and Guttet-Erschmatt (GE).

Species	**Habitat specificity**	**GE1_t**	**GE1_s**	**GE2_t**	**GE2_s**	**AU1_t**	**AU1_s**	**AU2_t**	**AU2_s**	**AU3_t**	**AU3_s**	**AU4_t**	**AU4_s**
Forbes													
Acer pseudoplatanus	Forest	0	0	0	0	0	0	0	1	0	0	0	0
Achillea millefolium aggr.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Acinos arvensis	Grassland	1	1	0	0	0	0	0	0	0	0	0	0
Ajuga reptans	Generalist	1	1	0	0	0	1	1	0	0	1	1	1
Alchemilla glabra aggr.	Grassland	0	0	0	0	0	0	0	0	0	1	0	1
Alchemilla xanthochlora aggr.	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Allium sphaerocephalon	Grassland	0	0	0	0	0	0	0	0	1	0	0	0
Anthriscus sylvestris	Grassland	1	0	0	1	0	1	0	0	1	0	0	1
Anthyllis vulnerarian s.l.	Generalist	0	1	1	1	0	0	1	1	0	0	0	1
Arabis hirsuta aggr.	Grassland	1	0	0	1	0	0	1	1	1	1	0	0
Arenaria serpyllifolia aggr.	Generalist	0	1	0	1	0	0	0	0	0	0	0	1
Astrantia major	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Biscutella laevigata	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Botrychium lunaria	Grassland	1	0	0	0	0	0	1	1	0	0	0	0
Campanula glomerata s.l.	Grassland	0	1	1	1	1	0	1	1	1	1	1	1
Campanula rhomboidalis	Grassland	1	1	1	1	1	1	0	0	1	1	1	1
Campanula scheuchzeri	Grassland	1	1	0	1	0	0	1	0	0	0	0	0
Carlina acaulis ssp. caulescens	Grassland	0	0	0	0	0	0	1	0	1	0	0	0
Carum carvi	Grassland	1	1	1	0	0	0	0	0	0	0	0	0
Centaurea jacea s.l.	Grassland	0	0	0	0	0	0	0	0	0	1	0	1
Centaurea scabiosa s.l.	Grassland	1	1	1	1	0	0	0	0	0	0	1	0
Cerastium fontanum s.l.	Grassland	0	1	0	0	0	1	1	0	0	1	0	1
Chaerophyllum aureum	Grassland	1	1	1	1	0	0	0	0	0	1	0	1
Chaerophyllum hirsutum aggr.	Grassland	1	1	0	0	0	0	0	0	0	0	0	0
Clinopodium vulgare	Generalist	0	0	0	0	0	1	0	0	1	0	0	1
Colchicum autumnale	Grassland	1	1	1	1	0	0	0	0	0	0	0	0
Crepis biennis	Grassland	0	0	1	1	0	0	0	0	0	0	0	0
Crepis pyrenaica	Grassland	0	1	1	1	0	0	0	0	0	0	0	0

Dianthus carthusianorum s.l.	Generalist	0	0	0	0	0	0	0	1	0	0	0	0
Echium vulgare	Generalist	0	0	0	1	0	0	0	0	0	0	0	0
Euphorbia cyparissias	Grassland	0	0	0	1	0	0	0	1	0	0	0	0
Euphrasia rostkoviana s.l.	Grassland	0	0	0	0	0	0	1	0	0	0	0	0
Galium aparine	Generalist	0	0	0	0	0	0	0	0	1	0	0	0
Galium boreale	Grassland	1	1	1	1	1	1	1	0	1	1	1	0
Galium mollugo aggr.	Generalist	1	0	1	0	1	1	1	1	1	1	0	1
Geranium pusillum	Generalist	0	0	0	0	0	0	0	1	0	0	0	0
Geranium sylvaticum	Grassland	1	1	1	1	0	1	0	0	1	1	1	1
Gymnadenia conopsea	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Helianthemum nummularium s.l.	Grassland	1	0	0	0	0	0	1	1	0	0	0	0
Heracleum sphondylium s.l.	Grassland	1	1	1	1	1	1	1	0	1	1	1	1
Hieracium lactucella	Grassland	0	0	0	0	0	0	0	1	0	0	0	0
Hieracium pilosella	Grassland	0	0	0	0	0	0	1	1	0	0	0	0
Hieracium sp.	NA	0	0	0	0	0	0	0	1	0	0	0	0
Hippocrepis comosa	Grassland	0	0	0	0	0	0	1	1	0	0	0	0
Knautia dipsacifolia s.l.	Generalist	1	1	1	1	0	1	0	0	1	1	0	1
Laserpitium latifolium	Generalist	1	0	0	1	0	0	0	0	0	0	0	0
Lathyrus pratensis	Grassland	1	1	1	1	1	1	0	0	1	1	1	1
Leontodon hispidus s.l.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Leucanthemum vulgare aggr.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Lotus corniculatus aggr.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Medicago lupulina	Generalist	1	1	1	1	0	0	1	0	1	0	0	1
Myosotis arvensis	Generalist	1	1	1	1	1	0	0	1	0	1	0	1
Onobrychis viciifolia	Grassland	1	1	1	1	0	0	0	0	1	0	0	1
Ononis repens	Grassland	0	0	0	0	1	0	1	0	0	0	0	1
Ophioglossum vulgatum	Grassland	0	0	0	0	0	0	1	1	0	0	0	0
Orchis ustulata	Grassland	0	0	0	0	0	0	1	1	0	1	0	0
Peucedanum oreoselinum	Generalist	0	1	0	0	1	0	1	1	0	0	0	0
Picris hieracioides s.str.	Grassland	1	1	1	1	1	1	1	1	0	1	1	1
Pimpinella major	Grassland	1	1	1	1	1	1	0	0	1	0	1	0
Pimpinella saxifraga aggr.	Grassland	0	0	0	0	1	1	1	0	0	0	0	0
Phyteuma orbiculare	Grassland	1	0	1	1	0	0	0	0	1	0	0	0

Plantago lanceolata	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Plantago media	Grassland	1	1	0	0	0	0	0	0	1	0	0	0
Polygala vulgaris s.l.	Grassland	0	0	0	0	0	0	0	1	0	0	0	0
Potentilla erecta	Grassland	0	0	0	0	0	0	1	0	0	0	0	0
Potentilla pusilla	Grassland	0	0	0	0	0	0	1	1	0	0	0	0
Primula veris s.l.	Grassland	1	0	1	1	0	0	0	0	0	0	0	0
Prunella vulgaris	Grassland	0	0	0	0	0	0	1	0	1	1	0	1
Prunus spinosa	Forest	0	0	0	1	0	1	0	0	0	0	0	0
Pseudolysimachion spicatum	Grassland	0	0	0	0	0	0	1	0	0	0	0	0
Ranunculus acris s.l.	Grassland	1	1	1	0	1	1	1	0	1	1	1	1
Ranunculus bulbosus	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Ranunculus nemorosus aggr.	Generalist	0	0	0	0	0	1	0	0	0	0	0	0
Rhinanthus alectorolophus	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Rumex acetosa	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Salvia pratensis	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Sambucus nigra	Forest	0	0	0	0	0	0	0	0	1	1	0	1
Sanguisorba minor s.l.	Grassland	0	0	0	0	0	0	0	1	0	0	0	0
Scabiosa columbaria s.l.	Grassland	0	1	0	0	0	0	1	0	0	0	0	0
Silene nutans s.l.	Grassland	1	0	0	1	0	0	0	1	0	0	0	0
Silene vulgaris s.l.	Grassland	1	1	1	1	1	1	1	0	1	1	1	1
Stellaria graminea	Grassland	0	1	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale aggr.	Generalist	1	1	1	1	0	1	0	0	0	1	1	1
Teucrium chamaedrys	Grassland	0	0	0	0	0	0	0	1	0	0	0	0
Thalictrum minus s.l.	Generalist	0	0	0	0	0	0	0	0	0	0	0	1
Thesium alpinum	Grassland	1	1	0	0	0	0	0	0	0	0	0	0
Thymus serpyllum aggr.	Grassland	1	1	0	0	0	1	1	1	1	1	0	1
Tragopogon pratensis s.l.	Grassland	1	1	1	1	1	0	1	0	1	1	1	1
Trifolium montanum	Grassland	1	0	1	1	1	1	0	1	1	1	1	0
Trifolium pratense s.l.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Trifolium repens s.l.	Grassland	1	1	1	1	1	1	0	1	1	1	1	1
Trollius europaeus	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Veronica arvensis	Generalist	0	1	1	1	1	1	0	0	1	1	1	1
Veronica chamaedrys	Generalist	1	1	1	1	1	1	0	0	1	1	1	1

Veronica serpyllifolia s.l.	Generalist	0	0	0	0	0	1	0	0	0	0	0	0
Veronica teucrium	Grassland	1	0	1	0	0	0	0	0	1	0	0	0
Viola tricolor aggr.	Grassland	1	0	0	0	0	0	0	0	0	0	0	0
Vicia cracca s.l.	Generalist	1	1	1	1	1	1	1	1	1	1	1	1
Vicia hirsuta	Generalist	0	0	0	0	0	0	0	0	1	0	0	0
Vicia sativa s.l.	Generalist	0	0	0	0	0	0	0	0	1	0	0	0
Vicia sepium	Generalist	0	1	0	0	1	1	0	0	1	1	1	1
Grasses													
Agrostis capillaris	Grassland	0	0	0	0	1	0	1	1	0	1	1	1
Anthoxanthum odoratum aggr.	Grassland	1	1	1	1	1	1	1	1	1	1	1	1
Arrhenatherum elatius	Grassland	1	0	1	1	0	1	0	0	1	1	0	1
Briza media	Grassland	1	1	0	1	1	1	1	1	1	0	0	1
Bromus erectus s.l.	Grassland	1	0	1	1	1	0	1	1	1	1	1	1
Bromus hordeaceus	Grassland	0	0	0	0	0	1	0	0	0	0	0	0
Carex caryophyllea	Grassland	0	1	0	0	1	0	1	1	1	1	0	1
Carex sp.	NA	1	0	0	0	0	0	0	0	0	0	0	0
Cynosurus cristatus	Grassland	0	0	1	0	0	1	1	1	0	1	0	0
Dactylis glomerata	Generalist	1	1	1	1	1	1	1	1	1	1	1	1
Danthonia decumbens	Generalist	0	0	0	0	0	0	0	1	0	0	0	0
Festuca pratensis s.l.	Grassland	1	1	1	1	1	1	0	0	1	1	1	1
Festuca rubra aggr.	Generalist	1	1	1	1	1	1	1	1	1	1	1	1
Festuca valesiaca aggr.	Grassland	1	0	0	0	0	0	0	1	0	0	0	0
Helictotrichon pubescens	Grassland	1	1	1	1	1	1	1	0	1	1	1	1
Holcus lanatus	Grassland	0	0	0	0	1	1	1	0	1	1	0	1
Koeleria pyramidata aggr.	Grassland	0	0	0	0	0	0	1	0	0	0	0	0
Lolium perenne	Grassland	0	1	0	1	1	1	0	0	0	1	0	0
Luzula campestris	Grassland	1	0	0	0	1	1	1	1	1	1	0	1
Phleum phleoides	Grassland	0	0	0	0	0	0	0	1	0	0	0	0
Phleum pratense aggr.	Grassland	0	1	0	0	0	0	0	0	0	0	0	0
Poa alpina	Grassland	1	1	1	1	0	0	0	0	0	0	0	0
Poa pratensis aggr.	Grassland	1	1	1	1	1	1	1	0	1	1	1	1
Trisetum flavescens	Grassland	1	1	1	1	1	1	1	1	1	1	1	1

GENERAL DISCUSSION

This thesis examines the consequences of two main changes in the irrigation practices of hay meadows in the Valais during the past decades – the abandonment of irrigation and the replacement of the traditional irrigation technique by sprinkler irrigation. Owing to the dry climatic conditions irrigation is required to secure hay production in this region (Crook and Jones, 1999). Furthermore, traditional meadow irrigation and sprinkler irrigation are assumed to differ in the way the water is distributed over a meadow. Hence, both changes in irrigation practices were expected to significantly influence the local biodiversity of hay meadows.

In the study presented in **Chapter I,** we investigated whether land-use abandonment resulting from the cessation of irrigation influenced the biodiversity of species-rich hay meadows in the Valais. We found that meadow abandonment led to a decrease in the proportion of plant and gastropod species characteristic for open grassland habitats. This finding confirms the importance of extensively managed semi-natural grasslands as refuges for species characteristic for open grassland habitats (Baur et al., 2006). Furthermore, gastropod species richness increased with progressive succession, which was mainly due to the colonization by generalist gastropod species. Generalists were probably favoured by the increased above-ground humidity (as a result of the increased plant height and shrub cover) and by structural heterogeneity in early abandoned meadows and young forests (Boschi and Baur, 2007, 2008). Surprisingly, plant species richness did not decline following abandonment. However, the three successional stages harboured distinct plant communities. Moreover, several functional traits of plants were affected by abandonment. In particular, meadow abandonment led to a later start of seed shedding, to an increase in the height of non-woody plant species and to a change in the type of plant reproduction, with vegetative reproduction gaining in importance in young forests. All these changes can be related to the lack of disturbance in the abandoned stages resulting from the cessation of mowing (e.g. Grime, 2001; Römermann et al., 2009). However, the negative effect of soil moisture on late seed shedding species suggests that this trait also responded to the cessation of irrigation. These findings emphasize the importance of including functional traits in biodiversity studies, since they may help to identify the processes behind changes in biodiversity.

Traditional irrigation was assumed to result in a spatially irregular inundation of the ground as compared to sprinkler irrigation, causing a higher microhabitat diversity and therefore a higher local biodiversity and a more heterogeneous small-scale distribution of plants. However, as shown in **Chapter II** and **Chapter IV** (only plants), the recent change from traditional to sprinkler irrigation neither affected the diversity and composition of plant and gastropod species, nor functional traits of gastropods. This suggests that other management factors might be more important for the local biodiversity of hay meadows. In fact, mowing frequency, the amount and type of fertilizer used and the stocking rate in late autumn did not differ between traditionally and sprinkler-irrigated meadows. Furthermore, the two meadow types did not differ in irrigation frequency and the amount of water applied per irrigation event. Therefore, the similar, relatively extensive management of the investigated meadows might have prevented the loss of biodiversity following the installation of sprinklers.

In contrast to the above stated expectations, **Chapter III** showed that traditionally and sprinkler-irrigated meadows did not differ in the small-scale spatial patterns of plant diversity, as indicated by the almost identical shapes of the plant species-area relationships (Connor and McCoy, 1979; Rosenzweig, 1995). Moreover, no differences were found in the small-scale distributions of soil characteristics examined (exceptions being the spatial distribution of soil pH and SOM). These findings can be explained by the way sprinkler irrigation is applied in the study areas. Sprinklers obtain their water from channels and hence only rely on natural water pressure gradients from the sloping land (Crook, 1997). Seasonal variation in water supply can, therefore, influence the reach of a sprinkler and thus the distribution of water. Furthermore, spray water can be misdirected by wind (Meurer and Müller, 1987) and additional water can be supplied by uphill-situated meadows irrigated in the traditional way (R. L. Melliger, pers. obs.). Therefore, as practiced in theses study areas, the distribution of water by sprinklers might be less homogeneous than commonly assumed (Meurer and Müller, 1987). This could be a further explanation for the similarity in the diversity and composition of plant and gastropod species in traditionally and sprinkler-irrigated meadows.

The change in irrigation technique affected functional aspects of plant diversity. In particular, the installation of sprinklers resulted in an increase in the grass-to-forb ratio as well as in a higher proportion of semi-rosette species and a lower proportion of late seed shedding species (**Chapter II**). Furthermore, sprinkler irrigation was associated with an increased number of generalist but not specialist plant species in the hay meadows investigated (**Chapter IV**). Both, an increased grass-to-forb ratio as well as a higher number of generalist species, are associated with nutrient-rich conditions (Willems and van Nieuwstadt, 1996; Fajmonová et al., 2013), suggesting that the installation of sprinklers may be related to management intensification. In contrast, traditionally and sprinkler-irrigated meadows did not differ in soil nutrients and in forage yield (based on estimates by farmers; see above). However, direct measures of management intensification such as biomass data would be required to conclusively verify this assumption.

Finally, plant diversity of semi-natural grasslands might not only be influenced by management but by a combination of several factors including also the surrounding landscape (Gaujour et al., 2012). The abandonment of traditional management practices of semi-natural grasslands is suggested to result in a reduced landscape heterogeneity, which in turn might contribute to the loss of local plant diversity (Diacon-Bolli et al., 2012). In agreement with this, traditionally irrigated meadows were associated with a more diverse small-scale landscape composition than sprinkler-irrigated meadows. However, landscape composition did not differ among meadows prior to the installation of sprinklers (in 1972). This suggests that the installation of sprinklers was associated with a homogenization of the landscape (**Chapter IV)**, which facilitates land use. Furthermore, **Chapter IV** showed a positive effect of small-scale landscape composition on the number of generalists but not on total plant species richness or the number of specialists. One explanation for this finding is that the surrounding landscape in these study areas contained landscape elements suitable for generalist species, such as hedgerows and road verges. Total plant species richness and specialists on the contrary rather depend on suitable grassland habitats in the surroundings.

Implications and Outlook

This thesis provides new aspects of the abandonment of traditional management of hay meadows in an arid mountain region and its consequences for the local biodiversity by giving insights into species richness, species composition and functional traits of plants and the less well-studied gastropods. However, the small-scale patchy landscape of the study region does not allow extrapolating the findings of this thesis to large homogeneous grasslands. Hence, further studies would be required to verify these findings in other regions. Moreover, the processes responsible for the differences in functional aspects of plant diversity between traditionally and sprinkler-irrigated meadows are not yet fully understood and should be addressed in further investigations.

The findings of this thesis have several implications for the management of hay meadows in this region. This thesis showed that moderate irrigation and extensive land use are required to maintain the species-rich hay meadows of the Valais and their characteristic plant and gastropod communities. Traditionally and sprinkler-irrigated meadows did not differ in the local diversity of plant and gastropod species. This suggests that the type of irrigation is not of primary importance for the local biodiversity of these hay meadows, at least in the way sprinkler irrigation is practiced in these study areas. However, the installation of sprinklers affected functional aspects of plant diversity and resulted in a homogenization of the surrounding landscape, which could eventually lead to a more intensive management of hay meadows. This change in irrigation technique was relatively recent. Consequently, negative effects of sprinklers could be more pronounced in the future. Therefore, it is recommended to maintain the traditional irrigation technique at least on meadows where it is still applied today. These management recommendations could be implemented by compensation payments for farmers and/or by assigning the traditional irrigation technique as a cultural heritage.

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