

A balance between productivity and biodiversity conservation in montane and subalpine semi-natural grasslands

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**“Biodiversity is not a threat to agriculture;
it is the key to its sustainability.”**

**– Perrings et al. 2006
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Abstract

Humans are exploiting a large part of the planet to fulfill their needs. The prevention of further biodiversity loss must involve not only protecting the small pristine areas left of this planet, but by changing the way humans exploit ecosystems and resources. One of the greatest threats to biodiversity comes from the activities surrounding food production: agriculture. The negative impacts of agricultural practices on biodiversity have been widely studied and documented over the last few decades. However, agro-ecosystems, where humans produce their food, have a great potential to provide substitute habitats for biodiversity if managed properly. Thanks to a long history of traditional, low intensity management, some of the most biodiversity-rich agro-ecosystems in Europe are semi-natural grasslands situated in mountainous areas. However, this situation is evolving and, over the last few decades, management practices in mountain grasslands have been intensified in the quest for higher forage production, threatening mountain grassland biodiversity. Preserving the natural value of these semi-natural grasslands is a conservation challenge and evidence-based propositions to preserve biodiversity while ensuring modern farming viability are still lacking.

The aim of this thesis was to develop concrete and practical recommendations for a biodiversity conservation-productivity balance in mountain semi-natural grasslands, i.e. a sustainable management that would preserve biodiversity while maintaining acceptable levels of hay production. This aim was addressed by experimentally assessing the effect of six different management treatments applied during five years (2010 to 2015) to existing hay meadows; 1) control receiving no input, 2) irrigation with sprinklers 3) fertilisation with organic slurry, and 3-6) low, medium or high amounts of both irrigation and fertilisation combined. The study took place in eleven species-rich hay meadows in the montane-subalpine belt of the Swiss Alps. The experimental design thus created a four-level intensification gradient, mimicking modern agricultural practices, as well as a 2 x 2 factorial design that allowed disentangling the separate effects of irrigation and fertilisation. To obtain a thorough appraisal of the effects of these management regimes on the mountain semi-natural grassland components, responses of plant diversity (Chapter 1), ground-dwelling arthropod diversity (Chapter 2) and agronomic aspects (Chapter 3) were investigated.

The main outcomes of this thesis are that plant species richness and phylogenetic diversity are highest under traditional, very low intensity management, corresponding to the control, and are lowest under high management intensification. Both ground beetle and spider abundance (as proxy for ground-dwelling arthropod diversity) showed curvilinear relationships with the intensification gradient, with spider populations peaking at moderate intensity while ground beetle abundance was highest under high management intensification. No significant changes were detected for neither taxon's species richness. Phytomass production (a proxy for hay) and nitrogen yield increased with the intensification gradient.

In the light of these results, a low intensity management regime consisting of combined irrigation and fertilisation corresponding to one-third of the amount required to achieve maximum hay yield with two hay harvests per year would represent a good trade-off between grassland diversity conservation and hay production. However, as no single management regime favours all diversity or agronomic components investigated here, I suggest heterogeneous management across the mountain agricultural landscape. Various management regimes, ranging from no inputs with one hay harvest per year, to medium inputs of water and fertiliser with two hay harvests per year would contribute to maintaining biodiversity across semi-natural grasslands in the Alps. These managements regimes could be facilitated by the adoption of agricultural policies to take into account the opportunity costs from the potential hay production losses faced by the farming community, and would contribute to meet the conservation goals required of European farmlands.

General Introduction

TIME FOR CONSERVATION

The science of conservation biology emerged in the early 1980s, recognizing and addressing species depletion and disruption of life-supporting systems by human activities (Soulé 1985). It was described as a multidisciplinary science linking basic and applied research, which has the objective to protect and ensure the continuity of entire communities and ecosystems. It was also described as being a “crisis discipline”, calling for action before knowing all the facts, and where tolerating uncertainty is often necessary. By the late 1980s, concerns regarding the unprecedented global extent of contemporary diversity loss started to appear in the scientific literature and the need for global solutions were recognized (Myers 1989). A scientific call-to-arms was put out to develop strategies to reduce the magnitude and impact of global diversity loss. At the Earth Summit in Rio de Janeiro in 1992, the Convention on Biological Diversity was adopted as an international agreement, with the primary goal of conserving biological diversity (Convention on Biological Diversity 2006). Building on this, considerable conservation efforts have been focused on pristine or relatively untouched habitats in order to save the last remnants of the planet’s wild nature (Mittermeier et al. 2003). However, since population exchanges and community dynamics are occurring among areas affected by different levels of human pressure and/or disturbance, improved preservation of biodiversity outside protected areas must also be considered in conservation targets. In central Europe, truly natural ecosystems are almost absent and most nature reserves or other areas of high nature conservation value are already anthropogenically-influenced and require management (Bignal & McCracken 1996; Gaston et al. 2008). Tscharntke et al. (2005) stated that “Biodiversity conservation will not work without protecting the just 5% remaining pristine habitats, but also not without recognition of the contribution of the ‘rest’.” Whether it is in pristine areas or in the “rest” of the world, the goal of conservation is to provide principles and tools for preserving biological diversity (Soulé et al. 2005). After the first conservation wave for pristine area protection, research and conservation efforts have been focusing on how humans interact with nature in the context of resource exploitation, as well as land-use such as agriculture, and how to render those interactions

less destructive and even beneficial for biodiversity (Naeem 2009; Nelleman & Corcoran 2010; Rands et al. 2010; Lin et al. 2012; Barnosky et al. 2017).

AGRICULTURE SHARE

Extended exploitation and intensification of agricultural practices has been one of the major causes of biodiversity loss and ecosystem degradation during recent decades (Vitousek 1997; Tilman et al. 2001; Foley et al. 2005). The massive biodiversity loss in agricultural intensive areas has alarmed scientists as well as the public (Carson 1962; Vitousek 1997; Krebs et al. 1999). In response, some stakeholders have started to put into place measures in an attempt to prevent further loss of biodiversity (Kleijn & Sutherland 2003; EEA 2004; EU 2005). In many cases, restoration actions must be undertaken since sites are too altered for proper ecosystem function (Walker et al. 2004; Donald & Evans 2006). Kleijn et al. (2011) gave a comprehensible overview of measures taken, such as agri-environmental schemes amongst others, to reverse biodiversity decline on farmland, and discussed their mitigated effects. The initial failure to recognize the wider role of biodiversity in agricultural landscapes means that insufficient attention has been paid to the risks associated with the loss of important ecosystem services that are supported by biodiversity. As described by Daily (1997), ecosystem services are the conditions and processes through which natural ecosystems, and associate species, benefit humans. Biodiversity in agro-ecosystems supports a variety of functions that are perceived as services to humans, such as biological pest control, pollination, nutrient cycling processes and resistance to plant invasion (Matson et al. 1997; Altieri 1999). Agricultural land use affects a large proportion of terrestrial area regionally and globally, so its contribution to biodiversity maintenance is critical for future successful conservation (Tscharntke et al. 2005). Low-intensity agriculture systems may contribute significantly to large-scale conservation programmes (Bignal & McCracken 1996; Tscharntke et al. 2005), especially grasslands (Hopkins & Holz 2006).

GRASSLANDS

Most of natural grasslands are now destroyed in Europe, so the grasslands present today in the landscape are mainly artificially maintained, leading to

qualification by the term “semi-natural” (Svenning 2002; Sutherland 2002). Nowadays, grasslands represent much of human-created reserves and also a major emblematic habitat of traditional farmland in temperate European regions (Prins 1998). Thanks to low-intensity exploitation, such as harvesting hay once a year in a way that mimics large herbivore dynamics, these semi-natural grasslands formed a network of substitute habitat for plants and wildlife associated with open landscapes (Martínez-Abraín & Jiménez 2016).

Low-intensity managed grasslands are among the most species-rich ecosystems in central Europe, especially the ones that are situated in the Alps (Poschlod & Wallis de Vries 2002; Väre et al. 2003; Wilson et al. 2012). For centuries, semi-natural grasslands were maintained below the treeline to support local livestock rearing, and the variety of cultural traditions enhanced landscape diversity and biodiversity within the landscape (Maurer et al. 2006; Fischer et al. 2008). However, these semi-natural grasslands are nowadays threatened by either agricultural intensification or abandonment, both of which lead to a dramatic decline of biodiversity (Tasser & Tappeiner 2002; Strijker 2005; Kleijn et al. 2009). The topology in mountainous regions may render farming more challenging than elsewhere and this is probably why intensification of agricultural land was somewhat delayed in the mountains compared to the lowlands. However, the technical improvement of machinery, allowing farmers to access and exploit steeper areas, means that agricultural intensification is an on-going and even accelerating process in mountain agro-ecosystems, notably in the European Alps (Tasser & Tappeiner 2002; Fischer et al. 2008; Niedrist et al. 2009). Intensification aims at increasing agro-ecosystem’s productivity and it was mainly achieved via two practices in the Alps. First, fertilisation was used to increase soil fertility with regular addition of nutrients (Isselstein et al. 2005), shifting from spreading solid cattle manure to a more recent use of liquid manure (slurry). Second, irrigation became a common practice on dry soils and shifted from open water channels to sprinklers (Crook & Jones 1999; Leibundgut 2004). Both of these practices led to higher yields and hay harvest frequency (Strijker 2005), but also to a dramatic decline of traditionally managed, biodiversity-rich meadows (Tasser & Tappeiner 2002; Poschlod & Wallis de Vries 2002; Fischer et al. 2008; Niedrist et al. 2009). In the Swiss Alps, for example, approximately 95% of the area of dry meadows and pastures were lost between 1900 and 2010 (Lachat et al. 2011). Abandonment is also on-going in the mountains because of the high cost of maintenance or difficulty in accessing machinery in the steepest areas (e.

g. Gellrich et al. 2008; Graf et al. 2014). Semi-natural grassland abandonment results in a process of natural vegetation succession with colonization by trees, eventually leading to forest that constitutes most of the natural climax vegetation (Prins 1998; Svenning 2002). Avoiding intensive agricultural land-use and abandonment is crucial for grassland conservation and its biodiversity (Bignal & McCracken 1996; Pfiffner & Luka 2003; Tschardt et al. 2005). To date, the relationship between grassland biodiversity and management intensity has not been addressed experimentally in mountain grassland systems, which hinders the formulation of clear management recommendations for sustainable farming practices. There is therefore an urgent need to design guidelines for regional mountain agriculture policies that will ensure acceptable levels of hay production in semi-natural grasslands while preserving the biological diversity that depends on this now threatened ecosystem in Europe (Tschardt et al. 2005; Marini et al. 2007; Fischer et al. 2008).

AIMS OF THIS THESIS

Under the umbrella of conservation biology, the goal of this thesis is to identify principles and tools for preserving biological diversity in mountain semi-natural grasslands to ensure the delivery of associated ecosystem services. This thesis aims at identifying which management practices and intensity levels can contribute positively to maintaining the biodiversity value of mountain hay meadows without jeopardizing agricultural revenue. To match the modern farming reality in montane and subalpine areas, practices that are already implemented in the management of semi-natural grasslands were tested and could thus be easily be adopted by the farming community. To simulate the realistic local standards for managed grasslands, a yield-based mowing regime was applied. The following management treatments were tested:

- 1) The first treatment served as a control (no input, referred to as C-plot) and was mown once during the growing season.
- 2) The second treatment involved irrigation with sprinklers (I-plot) once per week from May until mid-September, except when there was heavy rainfall (>20 mm water during the previous week), and these experimental plots were mown twice during the growing season.
- 3) The third treatment involved fertilisation with slurry (F-plot) composed of

dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4) dissolved into water so as to reach the same nutrient (NPK)-water concentration in kg of nutrient per m³ as standard farm slurry (Sinaj et al. 2009). Fertilisation was carried out twice during the growing season, once in the spring and a second time after the first hay harvest, and plots were mown twice during the growing season.

- 4) The fourth treatment involved a combination of fertilisation and irrigation in low amounts (I+F 1/3) and mowing twice during the growing season.
- 5) The fifth treatment involved a combination of fertilisation and irrigation in medium (I+F 2/3) amounts and mowing twice during the growing season.
- 6) The sixth treatment involved a combination of fertilisation and irrigation in high amounts (I+F 3/3), corresponding to the amount required to achieve the maximum local hay yield according to Sinaj et al. (2009), and mowing twice during the growing season.

The experimental design thus created a 2 x 2 factorial design that allowed disentangling the separate effects of irrigation and fertilisation in addition to a 4-level management intensity gradient. The experiment was replicated at eleven sites in the south-western Swiss Alps, among traditionally managed, species-rich montane and subalpine hay meadows. This research project lasted six years. It started in 2010 and was divided in two three-year PhD projects; the short-term effects of the experiment were investigated by a first PhD student (Aline Andrey) and I investigated the mid-term effects for the second half of the project.

Because not all species respond equally to land use changes in agricultural landscapes, it is essential to address differences in responses among species and/or ecological trait groups to understand the mechanisms driving species loss (Kleijn et al. 2009). Various indicators were thus studied during the experiment. The short term responses of plants as well as plant-associated arthropod abundance and biomass have been assessed after the first year of the experiment (Andrey et al. 2014). From the second year of the experiment onwards, diverse indicators were used to evaluate the impact of intensification on grassland diversity. Leaf and plant-hoppers were chosen during the second year (Andrey et al. 2016), and orthopterans during the third year (Delley 2014). Caterpillars (Dosch 2014), snails (Dani, unpublished), and arbuscular mycorrhizal fungi (Herzog 2016) were also studied during the last two years of the research project.

THESIS OUTLINE

In Chapter 1, I present how agricultural intensification affects species richness and diversity as assessed by the Shannon Index, and favours or excludes particular functional groups and alters the phylogenetic diversity of plant communities in mountain semi-natural grasslands. There has been a recent increased interest in integrating phylogenetic information into biodiversity assessments and for conservation purposes (Mouillot et al. 2011; Rolland et al. 2012; Faith 2013; Diniz-Filho et al. 2013; Buerki et al. 2015). However, there has been little consideration of including phylogenetic diversity in agro-ecosystem management to promote plant diversity (but see Egorov et al. 2014; Rader et al. 2014). This is an unfortunate oversight, as phylogenetic diversity provides insights into ecologically important diversity features such as ecosystem functioning and evolutionary potential, while accounting for the non-independence between species (Purvis & Hector 2000; Cadotte & Davies 2010). Phylogenetic diversity has been proven to be useful as a tool to assess prioritization for land protection (Forest et al. 2007), to estimate ecosystem stability (Cadotte et al. 2012) and to predict which species losses are most likely to alter ecosystem function (Maherali & Klironomos 2007). Preserving phylogenetic diversity is thus a good way to ensure that both genotypic and functional diversity are maximised. Vegetation plays an important role in shaping higher trophic level communities (Hunter & Price 1992). Agricultural inputs directly affect plants, which in turn will affect other trophic levels. I thus present results on the plant community first in the thesis.

In Chapter 2, I explore the impact of management practices on ground-dwelling arthropod communities, focusing on ground beetles and spiders. Ground-dwelling arthropods comprise an essential part of the community in grassland ecosystems because they occupy a variety of functional niches. They thus fulfill important roles influencing features such as soil structure and function, decomposition and nutrient cycling, and are predators of many invertebrates as well as prey for many vertebrates (Work et al. 2002). These roles serve as ecosystem services essential to the good functioning of grasslands. Ground-dwelling arthropods are also suitable as bioindicators of human impacts through activities such as land management, fragmentation or pollution (Pfiffner & Luka 2003; Avgin et al. 2010), because they have a short generation time and respond quickly to ecological changes (Kremen et al. 1993). Generally, their taxonomy and ecology is well known, they are distributed over a broad geographic area, they are

specialized to certain habitat requirements, they are easy and cost-effective to survey, and they have an economic importance as they are natural predators of pest species (Rainio & Niemelä 2003). Agricultural intensification affects ground dwelling arthropods indirectly by altering vegetation, which in turn affects their food sources and micro-habitat conditions (Gibson et al. 1992; Dennis et al. 1998; Woodcock et al. 2007). I thus present results on the ground-dwelling arthropods second in the thesis.

In Chapter 3, I evaluate phytomass and nitrogen yields as well as nutrient content in plants and soil. Forage quantity and quality are considered to be the ecosystem service of main importance to farmers, as well as soil stability and water quality, among others (Lamarque et al. 2011). Some management is required in semi-natural grassland to prevent woody vegetation encroachment leading to succession towards forest, which would cause habitat loss for grassland species (Tasser et al. 2007). As farmers are the ones to manage their own land, they have a major potential role to play in grassland biodiversity conservation. At the same time, the agronomic outputs they gain from their meadows must also be sufficient to guarantee the viability of their farming activities. Without interesting agronomic outputs, there would be less incentives in maintaining the grassland habitat, and meadows may be abandoned and revert to forest. These agronomical aspects of semi-natural mountain grasslands therefore constitute the counter-weight in the biodiversity-productivity equilibrium that I seek to address in this thesis.

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

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ABSTRACT

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

Location: Eleven semi-natural meadows distributed across the canton of Valais, in the inner Alps of south-western Switzerland.

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

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

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

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INTRODUCTION

For centuries, grasslands below the tree line of European mountain ranges have been managed traditionally, creating diverse, biodiversity-rich cultural landscapes (Poschlod & Wallis de Vries 2002). These grasslands result from a long history of human exploitation for hay production, which varied according to local culture and natural context (Fischer & Wipf 2002; Väre et al. 2003; Baur et al. 2006). These semi-natural grasslands were all characterised by low-intensity management involving mostly limited inputs of solid manure obtained from the farmer's own livestock (Maurer et al. 2006). However, in drier mountain regions, such as the inner Rhône and Rhine valleys, grasslands exploited for hay were also irrigated to reduce stress caused by drought, using a network of open water channels which distributed water to the meadows by gravity (Crook & Jones 1999; Leibundgut 2004).

In recent decades, many of these semi-natural mountain hay meadows have been abandoned in difficult terrain that is inaccessible to agricultural machinery, which has led to progressive encroachment by woody plants and eventually, reverting to forest (e.g., Gellrich et al. 2008; Graf et al. 2014). Yet, in more accessible areas, the meadows have been farmed more intensively in the quest for higher forage production (Tasser & Tappeiner 2002). Throughout Europe, these changes have provoked a dramatic decline of traditionally managed, biodiversity-rich meadows (Tasser & Tappeiner 2002; Poschlod & Wallis de Vries 2002; Fischer et al. 2008; Niedrist et al. 2009). In the Swiss Alps, for example, approximately 95% of the area of dry meadows and pastures were lost between 1900 and 2010 (Lachat et al. 2011). Grassland management intensification in Alpine regions involves fertilisation with slurry [compound fertiliser from livestock wastes composed mostly of nitrogen (N), phosphorus (P) and potassium (K)], and irrigation via sprinklers (Crook & Jones 1999). These modern practices alter plant community composition because some species profit from enhanced nutrient and water supply, increasing biomass production (Fischer & Wipf 2002; Bassin et al. 2012), whereas others disappear through competitive exclusion (Grime 1973). This phenomenon is well explained by the hump-shaped model, which posits that plant diversity peaks at intermediate levels of productivity (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015). At low productivity levels, where soil nutrients are deficient, only a few species can tolerate environmental stress,

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whereas at high productivity levels, only a few highly competitive species predominate. To date, the coupling of irrigation and fertilisation along an intensification gradient has not been addressed experimentally in mountain grassland systems, which hinders the formulation of clear management recommendations for sustainable farming practices.

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

Based on the hump-shaped model (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015), our broad hypothesis was that conventional plant biodiversity metrics (species richness and diversity) would show the greatest values at moderate management intensity (typical of traditional, low-intensity management), and the lowest values at maximum management intensity (modern approach to maximize hay production). Although the impact of fertilisation on grasslands has received considerable attention, changes in irrigation techniques (i.e., from traditional irrigation with open gravity channels to the use of sprinklers) are little documented. In two studies, the type of irrigation did not affect plant biodiversity in mountain areas (Riedener et al. 2013; Melliger et al. 2014). Given data scarcity for both the impact of irrigation, and of irrigation combined with fertilisation, we designed an experiment that merged different intensities of fertilisation and irrigation, thereby mimicking different options for modern hay production intensification.

In addition to those traditional biodiversity metrics, we also relied on phylogenetic information, most commonly referred to as phylogenetic diversity. It is a measure of the proportion of evolutionary history (i.e., how species are related to each other measured by the distance between them in a

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phylogenetic tree) represented within a given community (Faith 1992). This approach provides information on the evolutionary trajectory of the species pool, and its evolutionary potential and functional diversity, as most traits are phylogenetically conserved (Purvis & Hector 2000; Cadotte & Davies 2010). Therefore, phylogenetic diversity represents a separate and distinct measure of biodiversity that supplements conventional information derived from mere taxonomy-based analyses. More specifically, we hypothesised that high management intensity reduces phylogenetic diversity, predicting that plant communities in highly productive meadows are composed of closely related species (Grime 1973; Harvey & Pagel 1991).

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

MATERIALS AND METHODS

Study sites

In 2010, eleven traditionally managed hay meadows were selected within the canton of Valais, in the inner Alps of south-western Switzerland (Fig. 1). The region is characterized by a continental climate with cool and wet winters, as well as warm and dry summers. Average monthly ambient temperature (2004-2014) in the valley at 482 m a.s.l. ranged from a minimum of 0.3 °C in January to a maximum of 20.5 °C in July (Federal Office of Meteorology and Climatology 2016). The eleven meadows were situated within the

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montane and subalpine belts, between 880 and 1770 m a.s.l. (Table 1). These meadows have been extensively managed for at least ten years preceding the experiment. The extensive management consisted of no (n = 8 meadows) or low amounts of fertilisation once per year (3 meadows), no (5 meadows) or some irrigation during droughts (6 meadows), as well as one harvest of hay per year in all meadows.

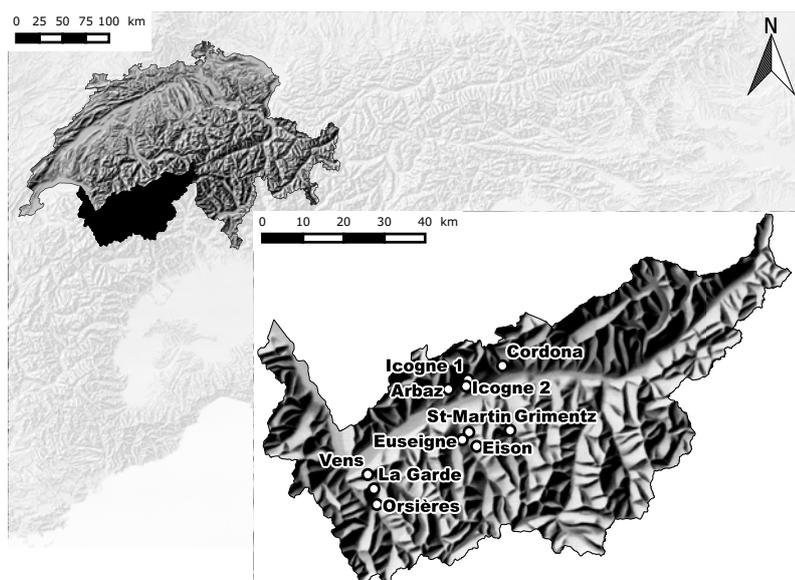


Figure 1. Location of the eleven meadows used as study sites in the canton of Valais (outlined in black on the country map), southwestern Switzerland.

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

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

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Experimental design

Within each of the eleven meadows, six management treatments were randomly assigned to 20 m diameter plots, with at least 5 m separating the boundaries of adjacent plots. The same treatment was applied consistently each year. The first treatment served as a control (no input: C-plot) while the second was irrigated with sprinklers (I-plot) (see Table 2 for irrigation level) weekly from May until mid-September, except when there was heavy rainfall (>20 mm water during the previous week). The third plot was fertilised with slurry twice during the summer, once in the spring and a second time after the first hay cut (F-plot). The three other plots received a combination of fertilisation and irrigation at three levels, which corresponded to 1/3, 2/3 or 3/3 of the amount required to achieve the maximum local hay yield (I+F 1/3-, I+F 2/3-, I+F 3/3-plots, respectively) according to Sinaj et al. (2009). This design allowed us to test the different influences of irrigation and fertilisation along a gradient of management intensification. All plots were mown twice during the growing season, except the C-plots, which were mown once to simulate local standards for extensively managed meadows. The fertiliser consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4) dissolved in water so as to reach the viscosity of standard farm slurry (Sinaj et al. 2009). One m³ of this solution contained 2.4 kg of available nitrogen, 0.87 kg of P and 6.64 kg of K. The amount of slurry applied per plot depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site elevation (see Appendix A in Andrey et al. 2016). Study sites were therefore divided into categories of similar potential productivity (Table 1) (which correlates strongly with elevation), with the amount of added fertiliser adjusted accordingly (Table 2).

Vegetation survey

In each plot, one permanently marked subplot of 2 x 4 m was established randomly, either on the right or left of the centre when facing upslope. Vegetation surveys were conducted during June and July 2014. In each subplot, all individuals were identified to species level and their percent coverage was visually estimated by two observers, and averaged if different. The species were further classified according to functional groups: grasses

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(Poaceae), legumes (Fabaceae) and forbs (other families). Tree and shrub species seedlings were excluded from the analysis.

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

Treatment	No. of cut per year	Slurry fertilisation (kg ha ⁻¹ year ⁻¹)									Sprinkler irrigation (mm week ⁻¹)
		Category A			Category B			Category C			
		N	P	K	N	P	K	N	P	K	
C	1	0	0	0	0	0	0	0	0	0	0
I	2	0	0	0	0	0	0	0	0	0	20
F	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	0
I+F 1/3	2	13.3	4.8	36.9	20	7.3	55.4	26.7	9.7	73.8	10
I+F 2/3	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	20
I+F 3/3	2	40.0	14.5	110.6	60	21.8	166.0	80	29.1	221.4	30

Phylogenetic reconstruction

Phylogenetic relationships between all the plant species found in the study meadows (Appendix S1) were retrieved from a well resolved and dated phylogeny of 4685 European species (Durka & Michalski 2012). This phylogeny was constructed by manually combining subtrees from recent molecular studies of recognized family relationships, dated with the most recent fossil records (Durka & Michalski 2012). An ultrametric phylogenetic tree was calculated so that distances from the root to every branch tip (current species) were equal. We pruned this phylogeny to match the species pool found in all our sites using the R-package *ape* (Paradis et al. 2004).

Statistical analysis

The effects of irrigation, fertilisation and the gradient of irrigation and fertilisation combined (C, I, F, I+F 1/3, I+F 2/3 and I+F 3/3) on biodiversity metrics (species richness and diversity, phylogenetic diversity and functional group species richness and coverage) were tested with linear mixed effects

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models (LMMs) using the R-package *lme4* (Bates et al. 2015). Species richness was defined as the total number of vascular plant species recorded in each subplot. The Shannon-Wiener index of diversity (Spellerberg & Fedor 2003), hereafter referred to as the Shannon index, was computed using the diversity function from the R-package *vegan* (Oksanen et al. 2013). Phylogenetic diversity was calculated from the phylogenetic tree described in the Phylogenetic reconstruction section associated with the evolutionary distance matrix built from our plant community data. As phylogenetic diversity is positively correlated with species richness (Kembel 2009), we used the standardized effect size of phylogenetic diversity. We applied the function *ses.pd* from the R-library *picante* (Kembel et al. 2010), which compares the observed phylogenetic diversity to that expected from a null model that would consist of sampling the same number of species at random. By doing so, it is possible to identify communities with phylogenetic diversity higher or lower than expected given the number of species in the community (Mouillot et al. 2011). Phylogenetic diversity is measured in units of standard deviations. The relationship between species richness and phylogenetic diversity was measured using Pearson correlation, with the *cor.test* function. The coverage of functional groups was log-transformed to respect normality assumptions in the model residual's distribution. All models included the management treatments as fixed effects (i.e., a six-level categorical variable; C, I, F, I+F 1/3, I+F 2/3 and I+F 3/3) and study sites as random effects. The *relevel* function in R, which allows changing the reference level of the fixed effects, was used to carry out comparisons among treatments when performing the LMMs. All analyses were conducted using R statistical software, version 3.1.2 (R Development Core Team 2015). SE indicates standard error of the mean.

RESULTS

A total of 197 vascular plant species belonging to 34 families were recorded (Appendix S2). Species richness per subplot (8 m²) ranged from a minimum of 25 in the most intensive (I+F 3/3) treatment in Euseigne at 1028 m a.s.l. to a maximum of 66 in the low intensive (I+F 1/3) treatment in Grimentz at 1738 m a.s.l. (mean ± SE: 46.8 ± 2.18 in C-plots). Overall, only the I+F 3/3-treatment (38.2 species ± 2.67) harboured significantly fewer species than the other treatments (Fig. 2a; Table 3). Species diversity (Shannon index)

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was significantly lower in I+F 3/3-plots (2.4 ± 0.15) than in I+F 1/3-plots (2.8 ± 0.15) while there was no difference between the other treatments (Fig. 2b; Table 3). As for species richness, phylogenetic diversity was significantly lower in I+F 3/3-plots (-0.2 ± 0.52) than in C-plots (1.4 ± 0.52), with no other differences between treatments (Fig. 2c; Table 3). A negative value indicates that the plant community encompasses less phylogenetic diversity than expected based on its total species number, i.e. the species are more closely related to each other than expected by chance in that given community. There was a strong correlation between the taxonomic and phylogenetic measures of diversity (Appendix S3, species richness versus phylogenetic diversity, $r = 0.89$, $P < 0.001$).

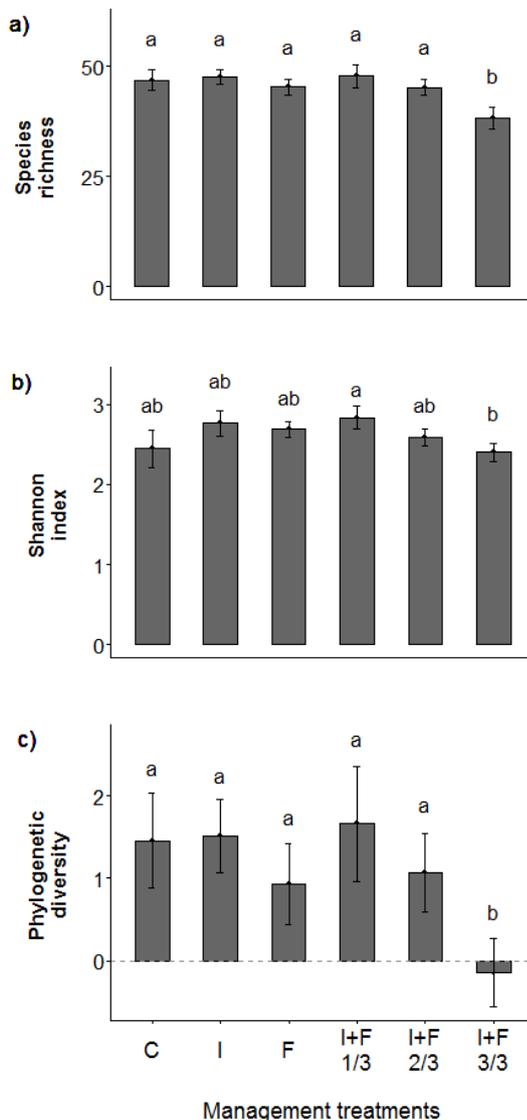


Figure 2. Effects of management treatment (linear mixed-effect model with site as a random factor) on a) species richness, b) Shannon index and c) phylogenetic diversity (measured as standardized effect size of phylogenetic diversity to correct for the correlation with species richness) of the plant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

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

	Species richness			Shannon index			Phylogenetic diversity		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Intercept (C)	46.81	2.18	< 0.001	2.45	0.15	< 0.001	1.42	0.52	< 0.001
I vs C	0.82	2.67	0.761	0.31	0.20	0.128	0.10	0.52	0.848
F vs C	-1.55	2.67	0.566	0.24	0.20	0.243	-0.53	0.52	0.321
I+F 1/3 vs C	0.91	2.67	0.735	0.38	0.20	0.065	0.28	0.52	0.599
I+F 2/3 vs C	-1.64	2.67	0.543	0.14	0.20	0.503	-0.35	0.52	0.505
I+F 3/3 vs C	-8.64	2.67	0.002	-0.05	0.20	0.813	-1.60	0.52	0.004
Intercept (I)	47.64	2.18	< 0.001	2.76	0.15	< 0.001	1.53	0.52	< 0.001
F vs I	-2.36	2.67	0.381	-0.07	0.20	0.717	-0.63	0.52	0.238
I+F 1/3 vs I	0.09	2.67	0.973	0.07	0.20	0.737	0.18	0.52	0.738
I+F 2/3 vs I	-2.45	2.67	0.363	-0.18	0.20	0.387	-0.45	0.52	0.392
I+F 3/3 vs I	-9.45	2.67	0.001	-0.36	0.20	0.080	-1.70	0.52	0.002
Intercept (F)	45.27	2.18	< 0.001	2.69	0.15	< 0.001	0.90	0.52	< 0.001
I+F 1/3 vs F	2.45	2.67	0.363	0.14	0.20	0.486	0.80	0.52	0.132
I+F 2/3 vs F	-0.09	2.67	0.973	-0.10	0.20	0.614	0.17	0.52	0.742
I+F 3/3 vs F	-7.09	2.67	0.011	-0.29	0.20	0.162	-1.07	0.52	0.047
Intercept (I+F 1/3)	47.73	2.18	< 0.001	2.83	0.15	< 0.001	1.70	0.52	< 0.001
I+F 2/3 vs I+F 1/3	-2.55	2.67	0.345	-0.25	0.20	0.232	0.63	0.52	0.236
I+F 3/3 vs I+F 1/3	-9.55	2.67	0.001	-0.43	0.20	0.039	-1.87	0.52	0.001
Intercept (I+F 2/3)	45.18	2.18	< 0.001	2.58	0.15	< 0.001	1.07	0.52	0.05
I+F 3/3 vs I+F 2/3	-7.00	2.67	0.012	-0.19	0.20	0.366	-1.24	0.52	0.022
Species richness of functional groups									
	Grasses			Forbs			Legumes		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Intercept (C)	9.54	0.62	< 0.001	32.27	1.82	< 0.001	5.91	0.41	< 0.001
I vs C	0.36	0.85	0.671	-0.91	1.91	0.636	1.36	0.51	0.010
F vs C	0.36	0.85	0.671	-1.55	1.91	0.422	-0.18	0.51	0.723
I+F 1/3 vs C	-0.09	0.85	0.915	0.27	1.91	0.887	0.73	0.51	0.160
I+F 2/3 vs C	-0.09	0.85	0.915	-2.64	1.91	0.174	1.09	0.51	0.037
I+F 3/3 vs C	-2.36	0.85	0.007	-5.72	1.91	0.004	-0.64	0.51	0.218
Intercept (I)	9.91	0.62	< 0.001	31.36	1.82	< 0.001	7.27	0.41	< 0.001
F vs I	0.00	0.85	1.000	-0.63	1.91	0.741	-1.54	0.51	0.004

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Table 3. (continued)

		Grasses			Forbs			Legumes	
I+F 1/3 vs I	-0.45	0.85	0.595	1.18	1.91	0.539	-0.63	0.51	0.218
I+F 2/3 vs I	-0.45	0.85	0.595	-1.73	1.91	0.371	-0.273	0.51	0.595
I+F 3/3 vs I	-2.72	0.85	0.002	-4.82	1.91	0.015	-2.00	0.51	<0.001
Intercept (F)	9.91	0.62	<0.001	30.73	1.82	<0.001	5.73	0.41	<0.001
I+F 1/3 vs F	-0.45	0.85	0.595	1.82	1.91	0.346	0.91	0.51	0.080
I+F 2/3 vs F	-0.45	0.85	0.595	-1.09	1.91	0.571	1.27	0.51	0.016
I+F 3/3 vs F	-2.72	0.85	0.002	-4.18	1.91	0.033	-0.45	0.51	0.377
Intercept (I+F 1/3)	9.46	0.62	<0.001	32.55	1.82	<0.001	6.64	0.41	<0.001
I+F 2/3 vs I+F 1/3	0.00	0.85	1.000	-2.91	1.91	0.134	0.36	0.51	0.479
I+F 3/3 vs I+F 1/3	-2.27	0.85	0.010	-6.00	1.91	0.003	-1.36	0.51	0.010
Intercept (I+F 2/3)	9.46	0.62	<0.001	29.63	1.82	<0.001	7.00	0.41	<0.001
I+F 3/3 vs I+F 2/3	-2.27	0.85	0.010	-3.09	1.91	0.112	-1.73	0.51	0.001
Cover of functional groups (log transformed)									
		Grasses			Forbs			Legumes	
Intercept (C)	4.04	0.20	<0.001	3.63	0.14	<0.001	1.75	0.21	<0.001
I vs C	-0.38	0.21	0.081	0.29	0.15	0.058	0.58	0.28	0.042
F vs C	-0.41	0.21	0.056	0.52	0.15	0.001	0.39	0.28	0.171
I+F 1/3 vs C	-0.37	0.21	0.081	0.31	0.15	0.040	0.50	0.28	0.076
I+F 2/3 vs C	-0.35	0.21	0.101	0.37	0.15	0.015	0.58	0.28	0.043
I+F 3/3 vs C	-0.21	0.21	0.314	0.31	0.15	0.042	0.76	0.28	0.009
Intercept (I)	3.66	0.20	<0.001	3.92	0.14	<0.001	2.33	0.21	<0.001
F vs I	-0.04	0.21	0.864	0.23	0.15	0.122	-0.07	0.28	0.793
I+F 1/3 vs I	0.00	0.21	0.995	0.02	0.15	0.871	-0.19	0.28	0.497
I+F 2/3 vs I	0.02	0.21	0.910	0.08	0.15	0.575	0.18	0.28	0.526
I+F 3/3 vs I	0.16	0.21	0.448	0.02	0.15	0.886	0.00	0.28	0.987
Intercept (F)	3.63	0.20	<0.001	4.15	0.14	<0.001	2.26	0.21	<0.001
I+F 1/3 vs F	0.04	0.21	0.859	-0.21	0.15	0.164	-0.12	0.28	0.676
I+F 2/3 vs F	0.06	0.21	0.776	-0.15	0.15	0.317	0.25	0.28	0.371
I+F 3/3 vs F	0.20	0.21	0.353	-0.21	0.15	0.159	0.08	0.28	0.781
Intercept (I+F 1/3)	3.66	0.20	<0.001	3.94	0.14	<0.001	2.14	0.21	<0.001
I+F 2/3 vs I+F 1/3	0.02	0.21	0.915	0.06	0.15	0.691	0.37	0.28	0.192
I+F 3/3 vs I+F 1/3	0.16	0.21	0.451	0.00	0.15	0.984	0.20	0.28	0.487
Intercept (I+F 2/3)	3.82	0.20	<0.001	4.00	0.14	<0.001	2.51	0.21	<0.001
I+F 3/3 vs I+F 2/3	-0.14	0.21	0.517	-0.06	0.15	0.676	-0.17	0.28	0.537

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The number of grass species was lower in I+F 3/3-plots ($7.2 \text{ species} \pm 0.62$) compared to all other experimental treatments (e.g. 9.6 ± 0.62 in C-plots) (Fig. 3a; Table 3). Forb species richness was lower in both I+F 2/3- and I+F 3/3-plots (29.6 ± 1.91 and 26.6 ± 1.91) compared to all other treatments (e.g., 32.3 ± 1.82 in C-plots). I-plots (7.3 ± 0.40) and I+F 2/3-plots (7.0 ± 0.40) had higher species richness of legumes compared to other treatments (Fig. 3a). Forb cover was experimentally increased in F- and all I+F-plots (by 13.9–27.9%) compared to C-plots ($42.1\% \pm 7.83$), while legume cover increased in I-, I+F 2/3- and I+F 3/3-plots (by 4.2–7.9%) compared to C-plots ($7.1\% \pm 2.64$) (Fig. 3b). Grass cover did not differ among treatments, with an overall average of $51.2\% \pm 9.59$ (Fig. 3b; Table 3).

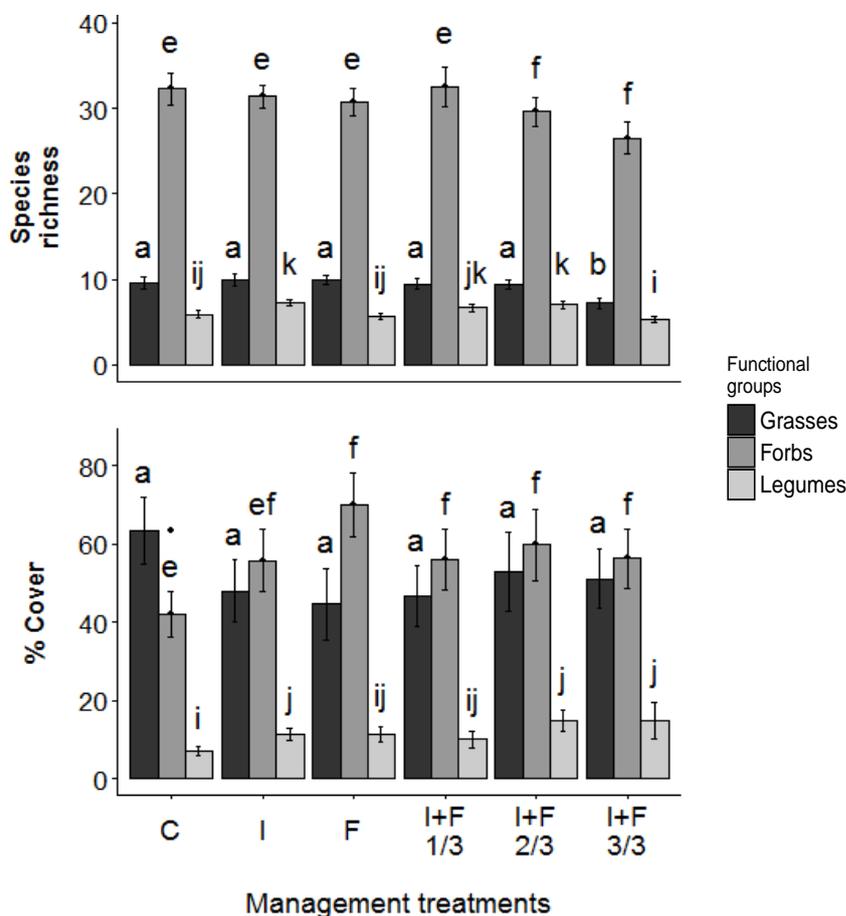


Figure 3. Effects of management treatment (linear mixed-effect model with site as a random factor) on a) plant species richness and b) mean percentage cover of functional groups (i.e., grasses, forbs and legumes). The relevel function in R, which allows changing the reference level of the fixed effects,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

DISCUSSION

There is an increasingly urgent need to develop guidelines for regional agriculture policies that efficiently protect the remaining biodiversity of extensively managed hay meadows. This field experiment evaluated the response of montane and subalpine grassland plant communities to different management intensities applied four years in a row. Our study reveals that low to medium inputs of fertiliser (slurry) and water via aerial irrigation with sprinklers did not negatively impact species richness and diversity, or phylogenetic diversity, whilst high levels water and fertiliser application did. A moderate level of management intensity did, however, already had a negative effect on the functional diversity of forbs. All previous studies on the impact of grassland management intensification on biodiversity have largely focused on comparing high input of fertiliser versus no input at all (Hejerman et al. 2007; Dickson & Foster 2011; Rose et al. 2012). Furthermore, they mostly investigated the effects of N-addition alone (Humbert et al. 2016). The importance of the present study resides in the complex range of management practices tested. It paves the way for identifying threshold values for biodiversity-friendly management of mountain hay meadows.

Our study shows that after four years of experimental manipulation, plant species richness was reduced by 18% in the most intensive treatment (I+F 3/3-plots), in line with earlier observational (Maurer et al. 2006; Niedrist et al. 2009; Müller et al. 2016) and experimental findings (Rajaniemi 2002; Niu et al. 2008) of similar agricultural practices. This pattern was driven by the loss of some species of forbs (-13%) and grasses (-5%), perhaps due to exacerbated above- and below-ground competition for access to light and minerals, respectively (Grime 1973). Notably, the communities in the most intensive treatment were often dominated by highly competitive species such as *Arrhenatherum elatius*, *Heracleum sphondylium* and *Geranium sylvaticum*, which formed a thick canopy obstructing light for the lower ground vegetation. Short-stature species such as *Linum catharticum* and *Polygala vulgaris* were thus likely shaded out in these conditions (Grime 1973; Hautier et al. 2009), occurring only in the control or irrigated only plots. Forb species richness also diminished under medium intensity management (I+F 2/3) while, in the same plots, the number of legume species increased relative to the controls (no input; C-plots), illustrating a shift in community

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composition. In summary, overall species richness and diversity were maintained relatively high under the low (I+F 1/3) management treatment and, to a somewhat lesser extent, medium (I+F 2/3) management intensity. This pattern matches the prediction of the hump-shaped model of species richness (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015).

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

The observed plant community shifts were mirrored by the trends in relative cover of the three functional groups, with typical species-specific responses. For example, among the grasses, there was a considerable decline in cover of *Bromus erectus* with increasing management intensity, and an increase in cover of more competitive species such as *Arrhenatherum elatius* and *Dactylis glomerata* (Peter et al. 2008). Previous studies have shown that grass cover and/or biomass are enhanced by the addition of water and nutrients (e.g., Mountford, Lakhani & Kirkham 1993; Jeangros & Troxler 2008; Leto et al. 2008). Yet, we must stress here that when plant communities are partially composed of grasses, an increase of *Gramineae* biomass will translate into taller grasses without modifying coverage, contrary to what is observed with forbs and legumes, which grow both broader and taller. This bias may have affected our grass cover estimates, thus blurring any existing pattern.

All treatments involving fertilisation increased forb coverage. Nutrients are a key limiting factor for some forbs which, in presence of additional fertilisation, allocate more resources to aboveground growth (Mamolos et al. 2005). Tall, nitrophilous, competitive flower species such as *Geranium sylvaticum* and *Heracleum sphondylium* (Grime 1973; Peter et al. 2008) were noticeably much larger and abundant under increased management intensity, generating greater overall cover despite the general decrease observed in the number of forb species. The cover of legumes, generally the most valuable functional group for livestock forage (Frame 2005), was

enhanced by irrigation and/or fertilisation (Fig. 3b). The slurry we applied was composed of a mix of nitrogen, potassium and phosphate. The addition of nutrients other than nitrogen may have further promoted this competitive functional group since legumes have the capacity to fix the nitrogen naturally present in the soil (Mountford et al. 1993; Onipchenko et al. 2012).

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

Effects of irrigation vs fertilisation

The traditional irrigation system of semi-natural meadows in the dry inner Alps consisted of a network of open channels distributing water kilometres away from the main streams. Modern irrigation with sprinklers is progressively replacing traditional irrigation via open channels in the mountain regions (Crook & Jones 1999). In order to render our management recommendations readily implementable for modern practice, we experimentally tested the effects of sprinkler irrigation on grassland biodiversity. As found in previous mid- and long-term studies in the Alps (Riedener et al. 2013; Melliger et al. 2014), irrigation alone (I-treatment) did not appear to have any noticeable negative impact on biodiversity, even promoting legume species richness and

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abundance. Within the same experimental set up as used in our study, Andrey et al. (2014) found a similar pattern for legume and grass abundance, but a negative effect on forb abundance. They also found that irrigation had an even stronger positive effect than fertilisation on total plant species richness. However, that study was very short term (surveys in the year following the onset of the experimental manipulation) and furthermore carried out during a rather dry year when water supply might have been the main limiting factor for vegetation growth. Water is used by plants both directly as a resource for growth and indirectly by affecting nutrient availability (Mamolos et al. 2005). These processes can be achieved irrespective of the way water is delivered to the meadow (Riedener et al. 2013; Müller et al. 2016). Over time, irrigation could probably modify floristic composition because of reduced physiological stress during drought episodes. When comparing wet and dry meadow sites, Mamolos et al. (2005) found that tissue nutrient concentration varied between functional groups according to soil water content. Legumes had higher concentrations of N and P in wet sites, which allowed them to invest more in biomass, hence increasing their percentage cover with increased water availability. Our results are in line with these findings.

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

slurry dilution ratio (Mountford et al. 1993; Mamolos et al. 2005).

Conclusion and management recommendations

We suggest that low to medium inputs of water and slurry, as well as a medium level of irrigation with sprinklers in the absence of fertilisation, can sustain a rich flora in mountain hay meadows. More specifically, we propose two main recommendations for sustainable hay meadow management, depending on land-use context: 1) where meadows are still managed and when flora preservation is of concern, inputs of water and nutrients must be limited to 1/3–2/3 of what would be necessary to achieve the maximum hay yield possible locally; 2) where traditional management (roughly equivalent to our control and irrigated-only plots) is progressively given up, moderate management (1/3-2/3) with modern farming techniques (slurry spraying and aerial irrigation) is preferable to land abandonment that leads to encroachment by woody vegetation, i.e. a loss of the rich biodiversity typical of open habitats (Tasser & Tappeiner 2002).

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Biodiversity-friendly meadow management

Appendix S2. List of plant species recorded in each meadow.

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Achillea millefolium</i> L.		+	+	+		+	+	+	+	+	+
<i>Acinos alpinus</i> (L.) Moench		+	+		+	+		+			+
<i>Agrimonia eupatoria</i> L.							+				
<i>Agrostis capillaris</i> L.						+			+		
<i>Agrostis stolonifera</i> L.			+							+	+
<i>Ajuga pyramidalis</i> L.					+					+	
<i>Ajuga reptans</i> L.		+		+		+			+	+	
<i>Alchemilla vulgaris</i> aggr.		+	+	+	+	+			+	+	+
<i>Allium oleraceum</i> L.			+				+				+
<i>Anthericum ramosum</i> L.	+										
<i>Anthoxanthum odoratum</i> L.	+	+	+	+	+	+		+	+	+	+
<i>Anthriscus sylvestris</i> (L.) Hoffm.						+			+		
<i>Anthyllis vulneraria</i> L.	+	+	+		+			+	+		
<i>Arabis ciliata</i> Clairv.	+	+				+	+	+	+		
<i>Arabis hirsuta</i> (L.) Scop.		+	+		+	+	+	+		+	+
<i>Arenaria serpyllifolia</i> L.	+	+				+	+	+	+		
<i>Arrhenatherum elatius</i> (L.) J. & C. Presl	+	+		+	+	+	+	+	+		+
<i>Asperula cynanchica</i> L.	+							+			
<i>Biscutella laevigata</i> L.			+		+						
<i>Bistorta officinalis</i> Delarbre									+		
<i>Bistorta vivipara</i> (L.) Delarbre			+		+					+	
<i>Botrychium lunaria</i> (L.) Sw.			+								
<i>Brachypodium pinnatum</i> (L.) P. Beauv.	+			+			+	+	+		
<i>Briza media</i> L.	+		+	+	+		+	+	+	+	
<i>Bromus erectus</i> Huds.	+	+	+	+	+	+	+	+	+	+	+
<i>Bromus sterilis</i> L.							+				
<i>Campanula barbata</i> L.					+						
<i>Campanula glomerata</i> L.	+					+	+	+	+		
<i>Campanula rhomboidalis</i> L.			+	+	+					+	+
<i>Campanula rotundifolia</i> L.	+	+	+	+	+	+	+	+			+
<i>Capsella bursa-pastoris</i> (L.) Medik.		+									
<i>Carex caryophyllea</i> Latourr.	+	+	+	+			+	+	+	+	
<i>Carex flacca</i> Schreb.									+	+	
<i>Carex ornithopoda</i> Willd.			+	+	+						
<i>Carex pallescens</i> L.										+	
<i>Carex sempervirens</i> Vill.	+		+		+						
<i>Carum carvi</i> L.		+	+		+	+	+		+	+	+
<i>Centaurea jacea</i> L.	+	+				+	+		+		

Chapter 1

Appendix S2 *continued.*

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Centaurea scabiosa</i> L.	+	+	+	+	+	+	+	+	+	+	
<i>Cerastium arvense</i> L.								+			+
<i>Cerastium fontanum</i> Baumg.							+		+	+	+
<i>Chaerophyllum aureum</i> L.		+									
<i>Chaerophyllum hirsutum</i> L.										+	
<i>Chaerophyllum villarsii</i> W. D. J. Koch					+						
<i>Cirsium acaule</i> Scop.			+		+					+	
<i>Cirsium palustre</i> (L.) Scop.	+							+	+	+	
<i>Cirsium vulgare</i> (Savi) Ten.	+										
<i>Clinopodium vulgare</i> L.		+				+	+	+			
<i>Coeloglossum viride</i> (L.) Hartm.						+					
<i>Colchicum autumnale</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Cornus sanguinea</i> L.				+				+			
<i>Crepis biennis</i> L.						+			+		
<i>Crepis conyzifolia</i> (Gouan) A. Kern.					+						
<i>Crepis pyrenaica</i> (L.) Greuter										+	+
<i>Crocus albiflorus</i> Kit.			+		+					+	
<i>Cynosurus cristatus</i> L.						+	+				+
<i>Dactylis glomerata</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Daucus carota</i> L.		+		+				+	+	+	
<i>Dianthus carthusianorum</i> L.	+										
<i>Elymus repens</i> (L.) Gould.							+				
<i>Erucastrum nasturtiifolium</i> (Poir.) O. E. Schulz									+		
<i>Euphorbia cyparissias</i> L.	+	+	+				+	+			
<i>Euphorbia verrucosa</i> L.						+					
<i>Euphrasia minima</i> Schleich.					+						
<i>Festuca arundinacea</i> Schreb.							+		+		
<i>Festuca ovina</i> L.			+					+			
<i>Festuca pratensis</i> Huds.		+		+		+	+		+	+	+
<i>Festuca rubra</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Filipendula ulmaria</i> (L.) Maxim.									+		
<i>Filipendula vulgaris</i> Moench	+	+				+			+		
<i>Fragaria vesca</i> L.		+									
<i>Galium boreale</i> L.	+	+		+	+	+			+	+	
<i>Galium mollugo</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Galium pumilum</i> Murray				+					+		
<i>Galium pusillum</i> L.				+							
<i>Galium verum</i> L.	+			+	+	+	+	+	+		+

Biodiversity-friendly meadow management

Appendix S2 continued.

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Gentiana acaulis</i> L.					+						
<i>Gentiana campestris</i> L.			+							+	
<i>Gentiana lutea</i> L.	+										
<i>Gentiana verna</i> L.			+					+			
<i>Geranium pyrenaicum</i> Burm. f.							+				
<i>Geranium sanguineum</i> L.	+	+				+					
<i>Geranium sylvaticum</i> L.		+	+	+	+	+	+		+	+	+
<i>Geum rivale</i> L.					+						
<i>Globularia bisnagarica</i> L.	+										
<i>Gymnadenia conopsea</i> (L.) R. Br.	+		+		+			+			
<i>Helianthemum nummularium</i> (L.) Mill.	+	+	+		+	+	+	+	+	+	+
<i>Helictotrichon pubescens</i> (Huds.) Pilg.	+	+	+	+	+	+	+	+	+	+	+
<i>Hepatica nobilis</i> Schreb.				+	+						
<i>Heracleum sphondylium</i> L.		+	+	+	+	+	+		+	+	+
<i>Hieracium lactucella</i> Wallr.								+			
<i>Hippocrepis comosa</i> L.	+	+	+		+			+		+	
<i>Holcus lanatus</i> L.									+		
<i>Hypericum perforatum</i> L.		+							+		
<i>Hypochoeris maculata</i> L.	+		+		+						
<i>Knautia arvensis</i> (L.) Coult.	+	+	+	+	+	+	+	+	+	+	+
<i>Koeleria pyramidata</i> (Lam.) P. Beauv.	+		+					+			
<i>Laserpitium latifolium</i> L.	+		+		+	+					
<i>Laserpitium siler</i> L.	+										
<i>Lathyrus pratensis</i> L.		+	+	+	+	+		+	+	+	+
<i>Leontodon hispidus</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Leucanthemum vulgare</i> Lam.	+	+	+	+	+	+	+	+	+	+	+
<i>Linaria vulgaris</i> Mill.								+			
<i>Linum catharticum</i> L.	+				+			+	+	+	
<i>Listera ovata</i> (L.) R. Br.			+	+	+				+	+	
<i>Lolium multiflorum</i> Lam.				+							
<i>Lolium perenne</i> L.							+		+		
<i>Lotus corniculatus</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Luzula campestris</i> (L.) DC.											+
<i>Luzula multiflora</i> (Ehrh.) Lej.			+		+					+	
<i>Maianthemum bifolium</i> (L.) F. W. Schmidt										+	
<i>Medicago lupulina</i> L.	+	+	+	+		+	+	+	+	+	+
<i>Medicago sativa</i> L.									+		
<i>Muscari comosum</i> (L.) Mill.								+			

Chapter 1

Appendix S2 *continued.*

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Muscari racemosum</i> (L.) Mill.								+			
<i>Myosotis arvensis</i> Hill	+	+		+	+	+	+	+	+	+	+
<i>Myosotis scorpioides</i> L.			+							+	
<i>Onobrychis viciifolia</i> Scop.	+	+	+	+		+	+	+	+	+	+
<i>Ononis repens</i> L.	+	+					+	+	+		
<i>Orchis militaris</i> L.									+		
<i>Orchis ustulata</i> L.										+	
<i>Paradisea liliastrum</i> (L.) Bertol.			+								
<i>Peucedanum oreoselinum</i> (L.) Moench	+										
<i>Phleum alpinum</i> aggr.										+	
<i>Phleum pratense</i> L.					+				+	+	
<i>Phleum rhaeticum</i> (Humphries) Rauschert					+					+	
<i>Phyteuma orbiculare</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Phyteuma spicatum</i> L.		+			+						
<i>Picris hieracioides</i> L.		+			+		+	+	+	+	
<i>Pimpinella nigra</i> Mill.	+										
<i>Pimpinella saxifraga</i> L.	+	+		+		+	+	+	+		+
<i>Plantago alpina</i> L.										+	
<i>Plantago lanceolata</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Plantago media</i> L.	+	+	+	+	+		+	+	+	+	+
<i>Platanthera chlorantha</i> (Custer) Rchb.	+										
<i>Poa alpina</i> L.			+							+	
<i>Poa bulbosa</i> L.								+			
<i>Poa pratensis</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Poa trivialis</i> L.			+	+			+		+		+
<i>Polygala chamaebuxus</i> L.					+			+			
<i>Polygala vulgaris</i> L.	+		+		+			+		+	
<i>Polygonatum multiflorum</i> (L.) All.	+			+							
<i>Potentilla aurea</i> L.					+					+	
<i>Potentilla erecta</i> (L.) Raeusch.				+	+				+	+	
<i>Potentilla recta</i> L.				+			+				
<i>Potentilla rupestris</i> L.					+						
<i>Potentilla tabernaemontani</i> Asch.	+	+	+		+		+	+			+
<i>Primula veris</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Primula vulgaris</i> Huds.		+									
<i>Prunella vulgaris</i> L.	+		+	+	+		+	+		+	
<i>Pulmonaria australis</i> (Murr) W. Sauer										+	
<i>Pulsatilla alpina</i> (L.) Delarbre					+						

Biodiversity-friendly meadow management

Appendix S2 continued.

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Ranunculus acris</i> L.	+	+	+	+	+	+			+	+	+
<i>Ranunculus bulbosus</i> L.	+		+			+	+	+	+		+
<i>Rhinanthus alectorolophus</i> (Scop.) Pollich	+	+	+		+	+	+	+	+	+	+
<i>Rhinanthus minor</i> L.									+		
<i>Rubus caesius</i> L.				+							
<i>Rumex acetosa</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Salvia pratensis</i> L.	+	+	+	+		+	+	+	+	+	+
<i>Sanguisorba minor</i> Scop.	+						+	+			+
<i>Sanguisorba officinalis</i> L.	+	+				+			+		
<i>Scabiosa columbaria</i> L.		+						+			+
<i>Securigera varia</i> (L.) Lassen								+			
<i>Silene nutans</i> L.	+	+			+			+			
<i>Silene vulgaris</i> (Moench) Garcke	+	+	+	+	+	+	+	+	+	+	+
<i>Soldanella alpina</i> L.			+		+						
<i>Stachys recta</i> L.								+			
<i>Stellaria graminea</i> L.											+
<i>Taraxacum officinale</i> Weber	+	+	+	+	+	+	+	+	+	+	+
<i>Tetragonolobus maritimus</i> (L.) Roth									+		
<i>Teucrium chamaedrys</i> L.								+			
<i>Thalictrum minus</i> L.			+								
<i>Thesium alpinum</i> L.					+						
<i>Thesium pyrenaicum</i> Pourr.		+						+	+		
<i>Thlaspi perfoliatum</i> L.		+							+		
<i>Thymus pulegioides</i> L.	+	+	+	+	+	+		+			
<i>Thymus serpyllum</i> aggr.					+						
<i>Tragopogon pratensis</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Trifolium badium</i> Schreb.					+						
<i>Trifolium dubium</i> Sibth.						+					
<i>Trifolium montanum</i> L.	+	+	+	+	+			+	+	+	+
<i>Trifolium pratense</i> L.	+	+	+	+	+	+	+	+	+	+	+
<i>Trifolium repens</i> L.	+	+		+	+	+	+	+	+	+	+
<i>Trisetum flavescens</i> (L.) P. Beauv.	+	+	+	+	+	+	+	+	+	+	+
<i>Trollius europaeus</i> L.			+	+	+				+	+	
<i>Urtica dioica</i> L.										+	
<i>Vaccinium myrtillus</i> L.					+						
<i>Veronica arvensis</i> L.	+	+	+		+	+	+	+	+	+	+
<i>Veronica chamaedrys</i> L.		+			+	+	+	+	+	+	+
<i>Veronica persica</i> Poir.							+				
<i>Veronica teucrium</i> L.	+	+				+		+			
<i>Vicia cracca</i> L.		+	+	+	+	+	+	+	+	+	

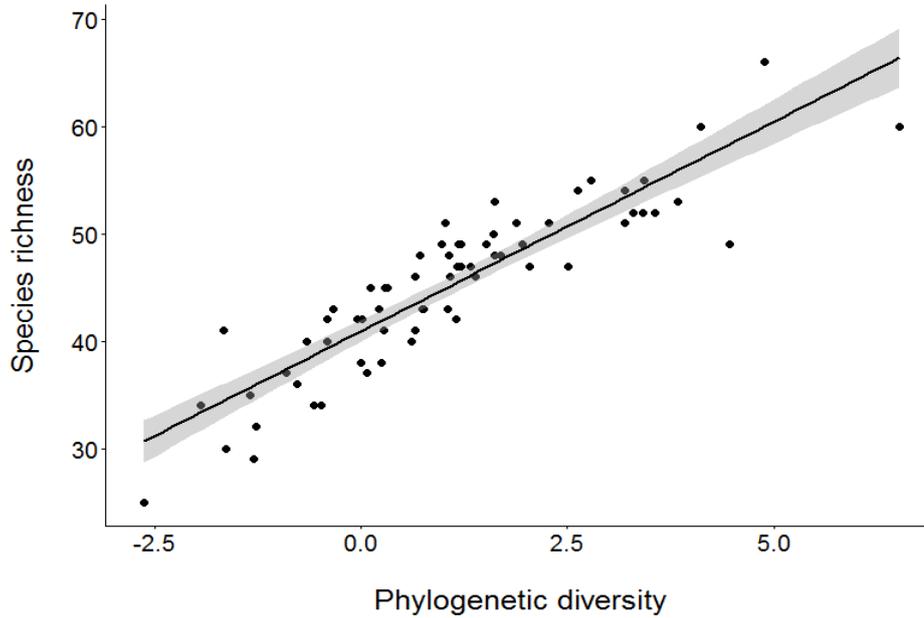
Chapter 1

Appendix S2 *continued.*

	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne1	Icogne2	LaGarde	Orsieres	StMartin	Vens
<i>Vicia sativa</i> L.							+				
<i>Vicia sepium</i> L.		+		+	+					+	+
<i>Viola collina</i> Besser		+	+		+			+		+	+
<i>Viola rupestris</i> F. W. Schmidt								+			
<i>Viola tricolor</i> L.		+									+

Biodiversity-friendly meadow management

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





Moderate irrigation and fertilisation of mountain hay meadows promotes predatory ground-dwelling arthropod communities

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ABSTRACT

Agricultural intensification is one of the major threats to the biodiversity of montane and subalpine grasslands. This calls for regional agriculture policies that efficiently protect their flora and fauna without jeopardizing agricultural viability. We experimentally sought a sustainable trade-off between hay yield and biodiversity, testing the effects of fertilisation (slurry) and aerial irrigation – separately and in combination (at different levels of intensity) – on the arthropod communities occurring in extensively-managed montane and subalpine meadows in the SW Swiss Alps. Four years after the start of our intensification experiment, we measured the abundance, species richness, community composition and variability (β -diversity) of ground-dwelling beetles and spiders. The abundance of both taxa showed a curvilinear relationship with management intensity. Spider abundance peaked at a moderate level of intensification while ground beetle abundance appeared to be more resilient to intensification, peaking at a high level of intensification. These responses were mainly driven by fertilisation, while irrigation played a lesser role. For both taxa, we found no impact of irrigation or fertilisation, either when applied separately or jointly on species richness. Community composition was altered by management intensification in both taxa, but community variability was not. Given these taxon-specific patterns for abundance, irrigation and fertilisation at levels corresponding to two-thirds of the quantity necessary to achieve local maximum hay yield appear to provide a good compromise between hay yield and predatory arthropod diversity in semi-natural mountain meadows.

Chapter 2

INTRODUCTION

Marked shifts in grassland farming practices have occurred in recent decades, resulting in a dramatic loss of their wild flora (Hopkins and Holz, 2006; Wesche et al., 2012) and fauna diversity (Attwood et al., 2008; Dahms et al., 2010; Haddad et al., 2000). Among mountain grasslands, these shifts operate in two ways: first, land abandonment, which leads to shrub encroachment and progressive return to forest (Gellrich et al., 2008; Graf et al., 2014); and second, intensification of management practices in the quest for higher forage production (Fischer et al., 2008; Niedrist et al., 2009; Poschlod and Wallis de Vries, 2002). Not surprisingly, in a recent global assessment, grasslands were classified as the terrestrial biome that is the most affected by land use pressure and its impact on biodiversity, with special concerns raised for mountain grasslands that thus deserve particular attention (Newbold et al., 2016).

Under the drier conditions of the large inner valleys of the European Alps, as typically encountered in the Rhone, Rhine and Danube catchments, grassland intensification involves irrigation via sprinklers (Crook and Jones, 1999) and the application of fertiliser, typically in the form of slurry from livestock wastes. These practices alter plant diversity because some species profit from enhanced nutrient and water supply by increasing phytomass production (Bassin et al., 2012; Fischer and Wipf, 2002) while others disappear through competitive exclusion (Grime, 1973), resulting in an homogenisation of plant community composition (Wesche et al., 2012). It is well established that grassland intensification is detrimental to plant diversity in mountain grasslands (Fischer et al., 2008; Humbert et al., 2016; Maurer et al., 2006; Niedrist et al., 2009; Peter et al., 2008). However, the response of invertebrates is much less clear as it seems to depend on the group targeted (Andrey et al., 2016; Grandchamp et al., 2005; Perner et al., 2005).

Arthropod predators are essential community components in grassland ecosystems because they occupy a variety of functional niches and thus fulfil important roles, for instance in the development of soil structure, in litter decomposition and nutrient cycling, as natural pest control agents, and finally as prey species for many insectivorous vertebrates (Altieri, 1999; Bianchi et al., 2006; Cole et al., 2006; Seastedt, 1984; Vickery et al., 2001; Vickery and Arlettaz, 2012). Thus, they are essential for the proper functioning of grasslands, and a decline in arthropod diversity could have serious implications for primary production (Attwood et al., 2008; Perner et al., 2005), notably because of top-down control from predators to herbivorous species and therefore primary producers (Hunter and Price, 1992). Not surprisingly,

Meadow management influence on arthropods

arthropod predators have been described as suitable bioindicators to assess the impact of land management (Kremen et al., 1993; Perner and Malt, 2003; Pfiffner and Luka, 2003; Rainio and Niemelä, 2003). They dependent on microhabitat structure and feed on a wide variety of prey (Dennis et al., 1998; Gibson et al., 1992; Perner et al., 2005; Woodcock et al., 2007).

Previous studies addressing the impact of management intensification, and in particular fertilisation, in different types of grasslands have shown variable and contradictory effects, notably on predatory arthropods. If fertilisation was generally found to have a negative effect on their taxonomic richness (Birkhofer et al., 2015), abundance was affected either positively (Grandchamp et al., 2005; Siemann, 1998) or negatively (Dittrich and Helden, 2012). This calls for further controlled experimental approaches disentangling the specific impacts of irrigation and fertilisation on the biodiversity of mountain grasslands. We investigated the response of arthropod predators, with a focus on ground beetles (Carabidae) and spiders (Araneae), to experimental intensification, via increased irrigation and fertilisation, of farming practices among montane and subalpine hay meadows. Our main objective was to identify the management intensity that represents a viable trade-off for maintaining rich arthropod diversity while ensuring agricultural revenue. Experimental irrigation was achieved with sprinklers and fertilisation through slurry application, mimicking the modern agricultural practices typically encountered in semi-natural meadows dedicated to hay production in the European Alps. After five years of manipulation, we quantified ground beetle and spider species richness and abundance, as well as changes in community composition and variability (a measure of β -diversity) under the different experimental treatments.

Our experimental intensification gradient mimics the actual practices which aim to increase plant phytomass production for agricultural purposes. Different scenarios for the response of predatory arthropods to this intensification gradient might be expected, based upon the hump-shaped diversity-productivity hypothesis (Grime, 1973). Regarding arthropod abundance, our first hypothesis was that it would generally increase, potentially in response to a higher density of their herbivorous prey, that in turn has been increased by a greater phytomass availability (Andrey et al., 2014; Raworth et al., 2004; Siemann, 1998).

Our second, more specific, hypothesis was that predator arthropod abundance drops above a certain threshold of farming intensity. This might be expected as a result of progressively emerging detrimental changes in microclimate or microhabitat structure, generated by a dense sward that

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reduces overall habitat quality (Baker and Dunning, 1975; Honek, 1997; Samu et al., 1999). The identification of such a threshold is particularly important for management to maximise ecological functionality within hay meadows. Regarding species richness, we predicted that it would decrease along the intensification gradient because of a progressive homogenisation (decrease in β -diversity) of the arthropod assemblage (Attwood et al., 2008; Benton et al., 2003; Di Giulio et al., 2001; Gossner et al., 2016).

Regarding the two main drivers of intensification, we hypothesised that fertilisation has a stronger effect than irrigation, as watering usually results in an increased uptake of nutrients by the vegetation (Mamolos et al., 2005). However, it has also been reported that moisture positively influences ground beetle and spider assemblages (Blake et al., 1996; Entling et al., 2007; Eyre et al., 1990).

MATERIALS AND METHODS

Study sites

In 2010, eleven traditionally managed hay meadows were selected within the canton of Valais, in the inner Alps of SW Switzerland (Fig. A.1). The region is characterized by a continental climate with cool and wet winters, as well as warm and dry summers. Average monthly ambient air temperature (2004-2014) in Sion, at valley bottom (482 m a.s.l.), ranged from a 0.3 °C in January to 20.5 °C in July (Federal Office of Meteorology and Climatology, 2016). The eleven meadows were situated within the montane and subalpine belts, between 880 and 1770 m a.s.l. (Table A.1); all had been extensively managed for at least the ten years preceding the experiment.

Experimental design

Replicated across the eleven meadows, six different experimental management treatments were randomly assigned to six 20-m diameter plots per meadow, with one treatment per plot, and a distance of at least 5 m between the boundaries of adjacent plots. The same treatment was applied consistently each year and our measurements took place in 2014.

The experiment consisted of a gradient of management intensity including the control (C) and three plots that received a combination of aerial irrigation (I) via sprinklers and fertilisation (F) with slurry (i.e. liquid manure), with amounts varying in tandem with 1/3, 2/3 or 3/3 of the quantity theoretically needed to achieve maximum hay yield, under a mowing regime

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consisting of two cuts a year and according to site productivity potential (Sinaj et al., 2009). This created a 4-level management intensity gradient: C (no input); I+F 1/3 (low input), I+F 2/3 (medium input); and I+F 3/3 (high input). The experiment also included a 2 x 2 factorial design that allowed disentangling the effects of irrigation (I) and fertilisation (F) (both treatments applied separately at 2/3 of the maximal amount), by comparing controls (C, no input) to both irrigation and fertilisation combined (I+F 2/3). These I 2/3 and F 2/3 treatments are hereafter referred to as I and F, where appropriate.

The fertiliser consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4) dissolved into water so as to reach the same NPK nutrient-water concentration as of standard farm slurry (Sinaj et al., 2009). The amount of slurry applied per plot depended on the theoretical local hay production potential, calculated from site elevation and pre-experimental hay yield (see Appendix A in Andrey et al. 2016; Sinaj et al. 2009), which allowed the study sites to be categorized according to their potential productivity (Table A.2).

Arthropod sampling

In each plot, ground-dwelling arthropods were sampled using three pitfall traps which consisted of plastic cups of 90 mm in diameter with a capacity of 500 ml that were buried flush with the ground surface. The three traps were arranged in a way that they formed a triangle, with triangle top situated 5 m above plot centre upslope, triangle lower tip located 5 m below the center and side top situated 5 m left or right of centre (Fig. A.2). Traps were filled with 0.25 l of propylene glycol (Weeks and McIntyre, 1997) diluted with water (ratio of 2:1) and a drop of detergent to reduce surface tension (Topping and Luff, 1995). Transparent covers measuring 20 x 20 cm were installed 5 cm above the traps, with three nails (at two extremities and in opposite edge centre) planted into to the soil, to prevent rain flooding. The traps were operated for two weeks, being emptied twice, once each week. Sampling was conducted before the first hay harvest, from May to July 2014 depending on elevation, starting from meadows situated at lower elevation and proceeding towards higher elevation. In each plot, we also measured mean vegetation height and visually estimated bare ground cover, two key habitat features that subsequently served as explanatory variables (Bell et al., 2001). Taxonomic nomenclature follows (Freude et al., 2004) for ground beetles and (Nentwig et al., 2016) for spiders.

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Statistical analyses

Species abundance and richness

Statistical analyses were performed on the content of the three traps per plot pooled together. The effects of management treatment, vegetation height and bare ground cover on ground beetle and spider abundance and species richness were tested with generalized linear mixed effect models (GLMM), with a Poisson error distribution, using the R-package *lme4* (Bates et al., 2015). Analyses were conducted separately for the 2 x 2 factorial design and 4-level management intensity gradient. In the factorial design models, we fitted an interaction term between irrigation and fertilisation, which was retained only if significant. In our intensification gradient analysis, the four levels were treated as a single continuous variable: control with no input = 0; I+F 1/3 = 1; I+F 2/3 = 2; and I+F 3/3 = 3. In this analysis, we compared linear and quadratic regression models based on the Akaike information criterion (AIC, Akaike, 1987): the model with the lowest AIC value was retained. Study site (n = 11) was a random effect in all models. Concerning abundance data, we had to account for overdispersion by including an observation-level random effect in relevant models (Harrison, 2014). All analyses were conducted using R statistical software, version 3.1.2 (R Core Team, 2015).

Community analyses

We first used non-metric multidimensional scaling (NMDS) ordination (Shepard, 1962) relying on Bray-Curtis distances, with the function *metaMDS* implemented in the *vegan* library in R (Oksanen et al., 2015), to graphically represent community clustering with respect to experimental treatment. As geographic location is very likely to be a determinant of the observed community composition (Hendrickx et al., 2009), we included sampling site as a grouping criterion. In the NMDS analysis, we set the number of dimensions (k) to 3 where stress was < 0.2 to ensure a reliable interpretation of graphical projections (Oksanen et al., 2015).

To test for the magnitude of changes in arthropod communities between experimental treatments and study sites we used the function *adonis* in *vegan* R-library, which performs a multivariate analysis of variance using simple distance matrices (Anderson, 2001). A p-value was obtained by permuting the least absolute deviation residuals (Anderson et al., 2006a). Three measures of inter-community distance were then used (Bray-Curtis, Chao, and Morisita-Horn) to assess changes in community composition between treatments and sites. We used three dissimilarity indices to cover the whole range of possible

community variation from emphasising species composition to abundance changes in communities (Anderson et al., 2006b). First, the widely used Bray-Curtis dissimilarity index (Bray and Curtis, 1957) is a version of the Sørensen index (see Magurran, 2004), modified to include abundance. Based on absolute differences in species proportions, it captures variation in community structure (Anderson et al., 2006b). The second metric, Chao's dissimilarity index (Chao et al., 2005), is a probabilistic abundance-based measure that controls for species undetected during sampling. In effect, it is unlikely to census an entire arthropod community during only two weeks of pitfall trapping at only three locations per plot. It is based on the probability that two individuals randomly drawn from two distinct samples belong to any of the species shared by these two samples, but not to the very same shared species, contrary to other dissimilarity indices (Chao et al., 2005). This index is therefore particularly appropriate for species-rich communities that include a large fraction of rare species. The third index, the Morisita-Horn index (Horn, 1966) is another abundance-based dissimilarity metric for measuring spatial variation in diversity, which is fairly sensitive to species richness and sample size (Barwell et al., 2015; Chao et al., 2006; Magurran, 2004)

Tests of community variability (i.e. β -diversity) were performed with the three dissimilarity indices using multivariate homogeneity of group dispersions (Anderson, 2006a) with the function `betadisper`, again in the `vegan` R-library. This approach compares a null hypothesis (no difference between treatments) with an alternative hypothesis stating that community variability decreases along the intensification gradient, which would indicate an homogenisation of the community (Di Giulio et al., 2001; Ekroos et al., 2010). The overall community differences between treatments and sites were tested with ANOVA with post hoc tests of pairwise differences (Tukey Honest Significant Differences test, `TukeyHSD`).

RESULTS

Abundance and species richness

A total of 3840 ground beetles belonging to 50 species were captured (Table B.1). The two most abundant species were *Poecilus versicolor* and *Bembidion lampros*, contributing 47.3% and 15.6%, respectively, to the total of individuals (all other species each accounted for less than 10% of the total). We sampled 9620 spiders in total. All individuals were considered for abundance data. However, for the analysis of species richness, due to logistic constraints, we

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randomly selected two traps out of the three sampled per plot (for a total of 4668 individuals of 94 species; Table B.2). The most abundant species were *Alopecosa trabalis* and *Pardosa palustris* accounting for 49.1% and 12.8% of the individuals, respectively. All other species again contributed <10% each to the total catch.

Ground beetle abundance increased along the intensification gradient involving coupled irrigation and fertilisation inputs, but levelled off at the highest intensification level (Fig. 1 and Table 1). The quadratic model had a slightly lower AIC value than the linear model, and was therefore retained (Table 1) although the linear model also had some good support (Burnham and Anderson, 2004). Spider abundance peaked somewhere at low–medium

Table 1. Effect of management intensity on ground beetle and spider abundance and species richness (generalized linear mixed-effects model). Study site was a random effect in all models. In abundance models, we had observation level as a random effect; it gives a unique level to each data point so as to cope with overdispersed data. The table refers to figures 1 and 2. All estimates are on the log-scale, SE stands for standard error. Significant effects are highlighted in bold.

	Estimate	SE	z	P
Ground beetles				
Abundance				
Intercept	3.002	0.242	12.381	< 0.001
Management intensity	0.794	0.260	-1.870	0.002
Management intensity ²	-0.153	0.082	-1.870	0.061
Species richness				
Intercept	1.741	0.138	12.610	< 0.001
Management intensity	0.051	0.053	0.960	0.337
Spiders				
Abundance				
Intercept	4.665	0.109	42.650	< 0.001
Management intensity	0.555	0.169	3.280	0.001
Management intensity ²	-0.189	0.054	-3.490	< 0.001
Species richness				
Intercept	2.319	0.095	24.396	< 0.001
Management intensity	-0.043	0.043	-0.998	0.318

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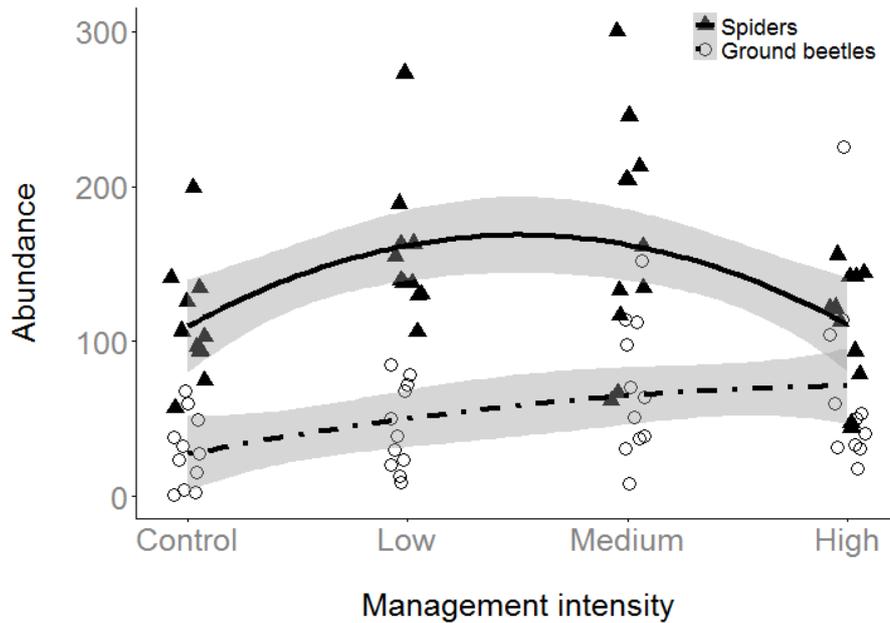


Fig. 1. Effects of combined irrigation and fertilisation on ground-dwelling predatory arthropod abundance with respect to management intensity. The 4-level management intensity gradient consists of control (no input), low, medium and high input levels, i.e. fertilisation and irrigation at, respectively, 1/3, 2/3 or 3/3 of the dose that would be necessary to achieve the local maximum theoretical hay yield.

2

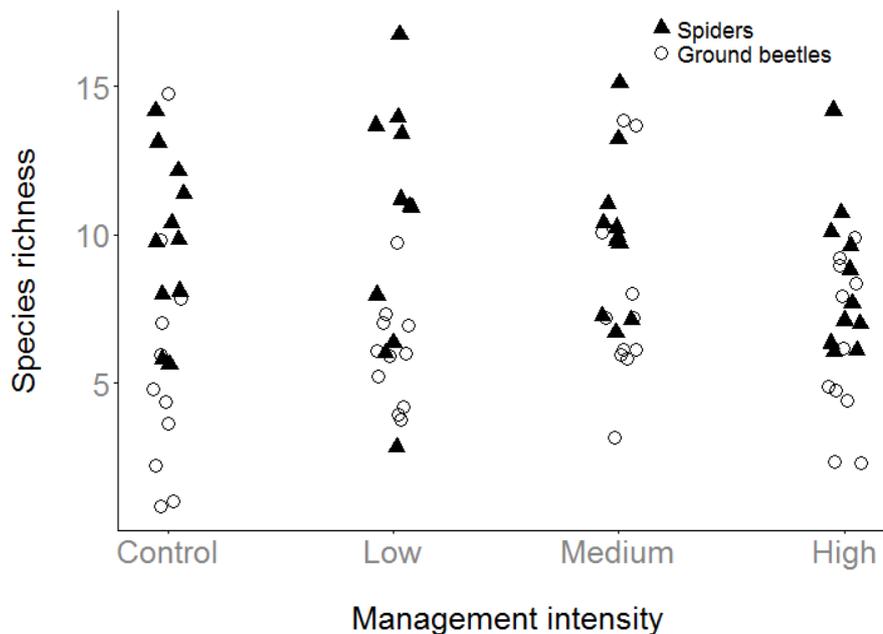


Fig. 2. Absence of effects of management intensity on ground beetle and spider species richness. For more details, see legend of Fig. 1. For statistical analyses see Table 1.

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intensity levels, as expressed by a better fit of the quadratic model (Fig. 1 and Table 1).

Species richness for both taxa remained constant all along the intensification gradient (mean = $6.5 \pm \text{SD} = 3.2$ species of ground beetles and 9.7 ± 3.0 species of spiders; Fig. 2 and Table 1). Neither vegetation height nor bare ground cover significantly explained arthropod diversity patterns; they were thus removed from the models.

Table 2. Outputs of the generalized linear mixed-models of the 2 x 2 factorial design to disentangle the effect of fertilisation and irrigation on ground beetle and spider abundance and species richness. Study site was a random effect in all models. In abundance models, we had observation level as a random effect; it gives a unique level to each data point so as to cope with overdispersed data. All estimates are on the log-scale, SE stands for standard error. Significant effects are highlighted in bold.

	Estimate	SE	z	P
Ground beetles				
Abundance				
Intercept	3.016	0.258	11.673	< 0.001
Irrigation	0.847	0.236	3.586	< 0.001
Fertilisation	0.997	0.236	4.231	< 0.001
Irrigation: Fertilisation	-0.822	0.328	-2.509	0.012
Species richness				
Intercept	1.700	0.158	10.770	< 0.001
Irrigation	0.092	0.114	0.805	0.421
Fertilisation	0.223	0.114	1.951	0.051
Spiders				
Abundance				
Intercept	4.740	0.113	41.810	< 0.001
Irrigation	0.077	0.125	0.620	0.537
Fertilisation	0.279	0.125	2.230	0.026
Species richness				
Intercept	2.224	0.095	23.470	< 0.001
Irrigation	-0.053	0.098	-0.540	0.589
Fertilisation	0.072	0.098	0.737	0.461

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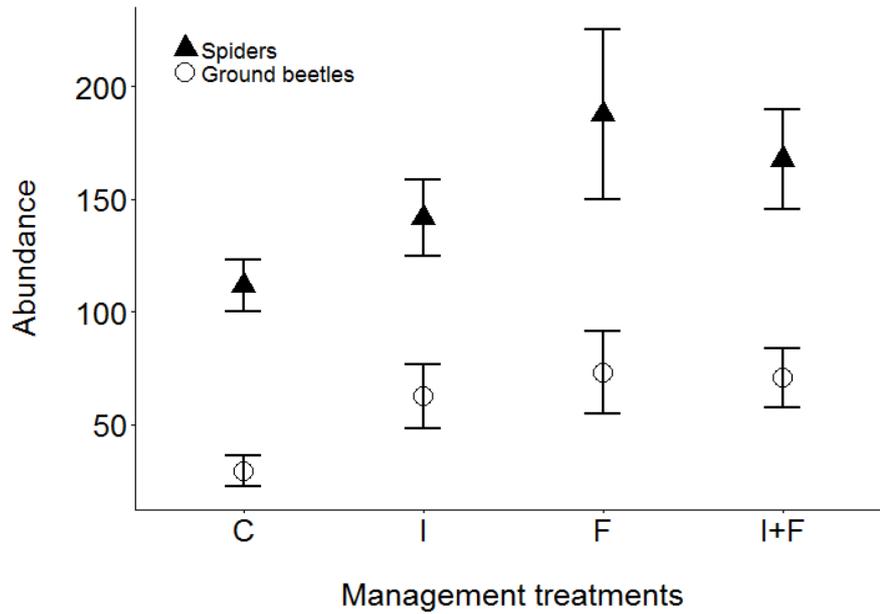


Fig. 3. Separate effects of irrigation and fertilisation tested by the 2 x 2 factorial design on ground beetle and spider abundance. C = control (no input); I = irrigation, F = fertilisation, I+F = irrigation + fertilisation. Mean values \pm SE are shown. See Table 2 for statistical analyses.

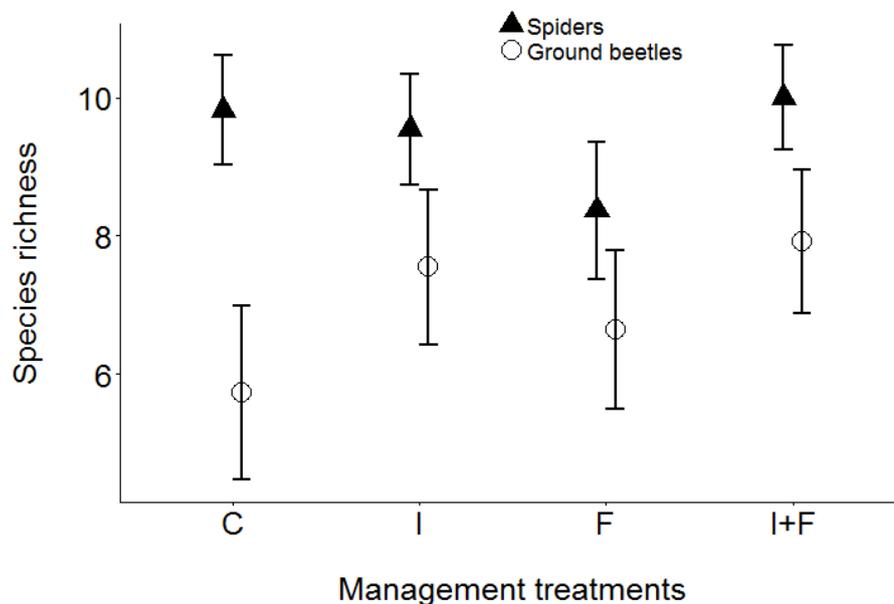


Fig. 4. Absence of separate effects of irrigation and fertilisation tested by the 2 x 2 factorial design on ground beetle and spider species richness. For management treatment description, see legend of Fig. 3. Mean values \pm SE are shown. See Table 2 for statistical analyses.

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The 2 x 2 factorial analysis revealed that fertilisation had a positive effect on both ground beetle and spider abundance (Fig. 3 and Table 2), but no effect on species richness for either taxonomic group (Fig. 4 and Table 2). Irrigation had a positive effect on ground beetle abundance (Table 2) while it had no effect on spider abundance. Species richness of neither taxon was affected by irrigation. A significant interactive effect between fertilisation and irrigation was revealed only for ground beetle abundance (Table 2), indicating that the effects of the two factors were not additive (Fig. 3 and Table 2).

Arthropod community composition

The multivariate analysis of variance performed on the distance matrices using the Bray-Curtis index showed that the ground beetle community was not altered by the experimental treatments (Table 3 and Fig. C.1), but differed significantly between study sites (Table 3 and Fig. C.2). However, the Chao and Morisita-Horn indices indicated that the ground beetle community was significantly influenced by both treatment and site, although the amount of variation explained by the experimental treatment was much lower than by site, based on R² values (Table 3).

Table 3. Effects of experimental management treatment and study site on arthropod community composition computed with permutational multivariate analysis of variance using distance matrices based on the Bray-Curtis, Chao and Morisita-Horn indices. All parameters have been computed from 999 permutations. Significant effects are highlighted in bold.

Dissimilarity index	Communities in	Df	F-value	R ²	P
Ground beetles					
Bray-Curtis	Treatment	5	1.317	0.061	0.103
Bray-Curtis	Study site	10	5.183	0.478	0.001
Chao	Treatment	5	2.571	0.057	0.002
Chao	Study site	10	16.240	0.721	0.001
Morisita-Horn	Treatment	5	2.250	0.069	0.008
Morisita-Horn	Study site	10	10.267	0.626	0.001
Spiders					
Bray-Curtis	Treatment	5	4.082	0.244	0.001
Bray-Curtis	Study site	10	1.323	0.158	0.059
Chao	Treatment	5	7.801	0.383	0.001
Chao	Study site	10	1.281	0.126	0.204
Morisita-Horn	Treatment	5	6.461	0.327	0.001
Morisita-Horn	Study site	10	1.640	0.166	0.043

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The spider community changed significantly under the experimental treatments when applying both the Bray-Curtis and Chao indices (Table 3 and Fig. C.1), but study site had no effect (Table 3 and Fig. C.2). When considering the Morisita-Horn index, the spider community was significantly influenced by both treatment and study site (Table 3). The taxon-specific differences due to study site are clearly visible on the NMDS graphical projections (Fig. C.2): the polygons representing the various ground beetle communities are more distant from one another compared to those of spider communities that overlap a lot.

Table 4. Within group variability in arthropod community composition, computed with multivariate homogeneity of groups dispersions using the Bray-Curtis, Chao and Morisita-Horn indices, separated by treatment and study site as a measure of β -diversity. Significant differences are highlighted in bold.

Dissimilarity index	Communities in	Df	F-value	<i>P</i>
Ground beetles				
Bray-Curtis	Treatment	5	0.451	0.811
Bray-Curtis	Study site	10	1.068	0.402
Chao	Treatment	5	1.081	0.380
Chao	Study site	10	3.042	0.004
Morisita-Horn	Treatment	5	0.716	0.614
Morisita-Horn	Study site	10	2.477	0.016
Spiders				
Bray-Curtis	Treatment	5	1.364	0.251
Bray-Curtis	Study site	10	1.690	0.107
Chao	Treatment	5	0.992	0.431
Chao	Study site	10	0.910	0.530
Morisita-Horn	Treatment	5	2.622	0.033
Morisita-Horn	Study site	10	1.048	0.417

Finally, the analysis of multivariate homogeneity of group dispersions (β -diversity) revealed that there was no significant effect of management treatment or site on the variability of ground beetle communities when using the Bray-Curtis index (Table 4). There was also no difference in community variability with respect to treatment when applying both the Chao and Morisita-Horn indices, but significant differences due to study sites. Significant changes in the community variability of spiders with respect to treatment were only detected when applying the Morisita-Horn index (Table 4).

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DISCUSSION

This study constitutes the first attempt to experimentally quantify the response of key predatory arthropod grassland communities to modern irrigation and fertilisation, applied either separately or in combination, within mountain hay meadows. Both ground beetle and spider abundance showed curvilinear relationships with the intensification gradient, but spider populations peaked at moderate intensity while ground beetle abundance was greatest at a high level of intensification. In contrast, we found no evidence for any effects of experimental treatment upon species richness. Although we observed some change in arthropod community composition with intensification, community variability remained largely unaltered by the experimental treatments in both taxonomic groups. The observed changes were driven by both irrigation and fertilisation for ground beetles, but only by fertilisation for spiders. Applying organic fertiliser and water therefore appears to be compatible with the maintenance of rich ground-dwelling arthropod communities in mountain grasslands, providing that inputs are moderate. This latter point will serve to frame management recommendations in the conclusion section.

Abundance and species richness

In agreement with our first and second hypotheses, arthropod abundance increased with grassland management intensification up to a given threshold (significant quadratic effects for the two taxa). These results establish, to the best of our knowledge for the first time, the existence of a hump-shaped relationship between predatory invertebrate abundance and management intensity. Such a curvilinear relationship was already evidenced for plant species richness along a phytomass productivity gradient (Chalcraft et al., 2009; Fraser et al., 2015; Kelemen et al., 2013). A similar hump-shaped relationship is also commonly found between species richness and disturbance (e.g. sessile organisms Connell, 1978; plants Grime, 1973; Huston, 1979; Wilson and Tilman, 2002; invertebrates Pöyry et al., 2009; Uchida and Ushimaru, 2014). Both the hump-shaped diversity-productivity and intermediate disturbance hypotheses may thus be at play in the present case (Connell, 1978; Grime 1973).

Organic fertilisation was the main underlying driver, apparently playing a more important role than irrigation. Fertilisation generally boosts phytomass production, providing more abundant food resources for herbivorous arthropods (Andrey et al., 2014, 2016; Perner et al., 2005; Prestidge, 1982), soil micro-organisms and mesofauna (Pfiffner and Luka, 2003; Purvis and

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Curry, 1984). Intensification thus leads to an increase in prey density, with positive cascading bottom-up effects along the food chain (Hunter and Price, 1992). Additionally, a thicker canopy layer resulting from a denser plant cover also better protects ground-dwelling arthropods from vertebrate predators such as insectivorous birds (Atkinson et al., 2005), potentially reducing top-down control on their populations (Hunter and Price, 1992).

Yet, there is some notable discrepancy in the responses of our two taxonomic groups to grassland intensification. While spider abundance peaked at low–medium farming intensity, the curvilinear pattern evidenced for ground beetles is hardly visible on the graphical projection (Fig. 1). This indicates that spider populations are more affected by intensification than those of ground beetles. Biotic and abiotic conditions seem to start to degrade beyond a given threshold of intensity, which leads to a drop (spiders) or a levelling off (ground beetles) in abundance. For spiders, the ecological conditions prevailing beyond that threshold might have significantly decreased habitat suitability. Indeed, changes in microhabitat such as an homogenisation of the vegetation three-dimensional structure are especially detrimental to some web-building spider families (Samu et al., 1999; Sunderland and Samu, 2000). The levelling off in ground beetle abundance might be linked with prey density dynamics. In effect, in the same experimental set up as ours, Andrey et al., (2016) have showed that the abundance of leaf- and planthopper (Auchenorrhyncha), a typical prey of ground beetles (Thiele, 1977), start levelling off from low intensity onwards. These findings are in line with the results by Britschgi et al., (2006) who show that hay meadow intensification leads to a progressive impoverishment of the arthropod community, i.e. of the prey supply for insectivorous birds.

The lack of effect on species richness along the intensification gradient contradicted our third hypothesis. This result was surprising as greater richness is usually found in least intensive agricultural systems (Attwood et al., 2008; Uchida and Ushimaru, 2014). As our experimental plots were embedded in an extensively managed grassland matrix, immigration into the plots by these mobile arthropods might have blurred the pattern and consequently reduced the power to detect any drop in species richness. If so, then our results would be fairly conservative, meaning that all the significant patterns observed might in reality be more marked than found in this study. It might also be that the short duration of our experiment (4 years) was not sufficient to provoke strong community changes in terms of species richness, which could occur over longer time periods (Birkhofer et al., 2015; Cole et al., 2005; Dauber et al., 2005).

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Community response

The overall shift in community composition observed for both taxonomic groups was in line with our hypothesis that species composition of ground beetle and spider communities would change with the altered biotic and abiotic conditions created by our experimental gradient of intensification. Clearly, the main compositional differences were underlain by changes in relative species-specific abundances within these communities rather than changes in number of species per se, as this variable did not vary across treatments. The change in ground beetle communities might have been driven mainly by changes in habitat suitability as described above for changes in spider abundance. In effect, previous work has showed that vegetation architectural complexity is a significant driver of assemblage structuring for both taxa, and that it even matters more than prey density for spider diversity (Greenstone, 1984; Luff and Rushton, 1989; Woodcock et al., 2007). Further analyses of changes in species-specific functional traits along the intensification gradient would be needed to investigate the ecological mechanisms underlying the observed shifts in community composition.

Although significant community composition changes were observed, they were apparently too small to significantly affect arthropod community variability, except for spider communities when analysed with the Morisita-Horn dissimilarity index. However, it must be stressed that this index is strongly influenced by the presence of abundant species, which could lead to overestimation of the dissimilarity between communities (Chao et al., 2006). Such an index, being biased towards abundant species, might be more appropriate for ecosystem service assessments, where the abundance of a few common species matters more than species diversity to provide the related service (Winfrey et al., 2015).

Ground beetle community composition differed significantly between study sites. In contrast, however, spiders hardly showed any changes in species composition between study sites (there was only a weak significant effect on the Morisita-Horn index mentioned above). This is well depicted in the multivariate cluster projections (Fig. C.2). The semi-natural grasslands that we used for our experiments were 2-45 km apart, and differed in elevation, soil type, exposition and productivity (Table 1), which provided fairly contrasting environmental conditions. The reason for these diverging taxon-specific patterns may lie in the different dispersal capacities of these two groups of predatory invertebrates (Hendrickx et al., 2009). Small-sized and young spiders are highly mobile, relying mostly on aerial ballooning for dispersal (Bell et al., 2005). This mobility gives spiders the flexibility to

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vacate a locally disturbed or no longer suitable area, and to colonise a habitat patch that becomes suitable again, as typically encountered in hay meadows (Curry, 1994). This contrasts with the lower mobility of ground beetles, which are largely limited to ground level movement (Samu et al., 1999).

Conclusions and management recommendations

Our results indicate that mountain meadowland ground beetle and spider populations were boosted in the mid-term (4 years) under low and medium levels of management intensity, whereas species richness was not affected. Previous work using the same experimental setup has shown that Auchenorrhyncha abundance, biomass and species richness were likely maximized under a moderate management intensity (Andrey et al., 2016) while plant species richness and phylogenetic diversity were detrimentally affected under the highest management intensity (Lessard-Therrien et al., in press). Hence, by combining the outcomes of these controlled experimental investigations, we can already formulate recommendations for the management of biodiversity-rich montane and subalpine hay meadows submitted to a double yearly mowing regime. Applying fertiliser and water inputs at 1/3–2/3 of the quantity that would be necessary to achieve the maximum hay yield that is possible locally, appears to be a strategy that is highly preferable to both meadowland abandonment and to high intensification.

It must be stressed, however, that the high management intensity described here for mountain grasslands corresponds to a low management intensity in productive lowland grasslands. For example, the experimental addition of N in the form of slurry ranged 40–80 kg ha⁻¹ year⁻¹ in our high intensity management plots, which represents a low input compared to the 150–180 kg ha⁻¹ year⁻¹ typically applied in lowland intensive grasslands that are considered detrimental to farmland arthropods in general (Attwood et al., 2008; Batáry et al., 2012; Di Giulio et al., 2001; Fenner and Palmer, 1998). We thus agree with other authors that low-input farming practices are key contributors to the preservation of farmland arthropod diversity (Bell et al., 2001; Dahms et al., 2010; Hole et al., 2005; Piffner and Luka, 2003; Pimentel et al., 1992). Future research has still to show the implications of moderate management intensity from an agronomic point of view. The quantification of hay yield and fodder quality will provide insights into the implications of keeping management at a moderate level of intensity for agricultural revenue. This missing piece of information would be essential to formulate final management prescriptions that represent an acceptable trade-off between biodiversity objectives and agricultural economy, i.e. for sustainable hay meadows farming.

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Supporting information

Appendix A. Description of the experimental treatments and study sites.

Table A.1. Description of the eleven meadows used as study sites with productivity category (A: meadows situated at higher elevation with lower productivity; B: meadows situated around mid-elevation with intermediate productivity; C: meadows situated at lower elevation with higher productivity). Fertiliser amount was adjusted for each category, elevation and geographic coordinates (see Table A.2).

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

Meadow management influence on arthropods

Table A.2. The experimental management treatments applied in our different meadow categories according to pre-experimental hay yield and altitudinal context. See Table A.1 for study site categorisation and Appendix A of Andrey et al. (2016, *Basic Appl Ecol.* 17 (7), 627-637) for more information on pre-experimental hay yield. Treatment abbreviations are as follows: (C) control; (I) irrigated, (F) fertilised, and (I+F) irrigated and fertilised. I+F 3/3 corresponds here to the quantity of inputs that would be necessary to achieve the local maximum hay yield; I+F 1/3 and I+F 2/3 refer to one third and two thirds of this quantity, respectively, according to Sinaj et al. (2009, *Rev. Suisse Agric.* 41, 1–98).

Treatment	No. of cut per year	Slurry fertilisation (kg ha ⁻¹ year ⁻¹)									Sprinkler irrigation (mm week ⁻¹)
		Category A			Category B			Category C			
		N	P	K	N	P	K	N	P	K	
C	1	0	0	0	0	0	0	0	0	0	0
I	2	0	0	0	0	0	0	0	0	0	20
F	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	0
I+F 1/3	2	13.3	4.8	36.9	20	7.3	55.4	26.7	9.7	73.8	10
I+F 2/3	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	20
I+F 3/3	2	40.0	14.5	110.6	60	21.8	166.0	80	29.1	221.4	30

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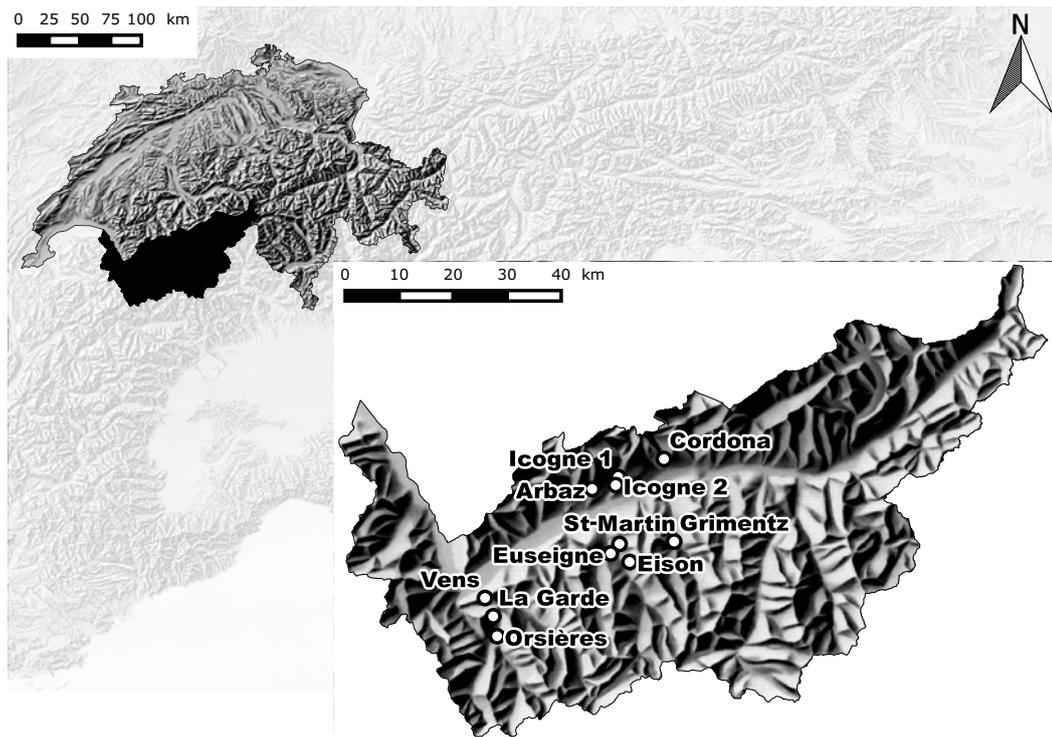


Figure A.1. Location of the eleven study sites in the canton of Valais (outlined in black on the country map), south-western Switzerland.

Meadow management influence on arthropods

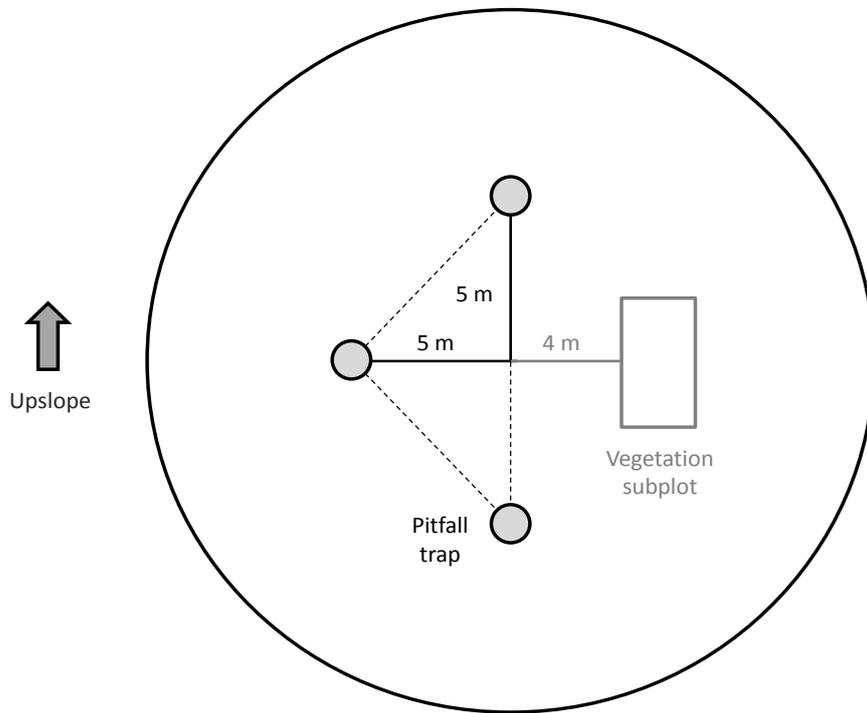


Figure A.2. Ground dwelling arthropod sampling design. Three pitfall traps were arranged in a triangle, its longest side parallel to the slope of the experimental plot. The plot diameter measured 20 m and the vegetation subplot measured 2 m x 4 m. The schema is not scaled.

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Appendix B. Species list

Table B. 1. List of ground beetles recorded at each study site.

Species	Family	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne 1	Icogne 2	La Garde	Orsieres	St-Martin	Vens
<i>Abax parallelepipedus</i> s.l. (Piller & Mitterpacher, 1783)	Carabidae		x		x				x	x		
<i>Amara aenea</i> (De Geer, 1774)	Carabidae		x				x	x	x	x	x	
<i>Amara aulica</i> (Panzer, 1796)	Carabidae					x		x			x	
<i>Amara communis</i> (Panzer, 1797)	Carabidae	x	x				x	x	x	x		x
<i>Amara convexior</i> Stephens, 1828	Carabidae	x	x	x			x	x		x		
<i>Amara curta</i> Dejean, 1828	Carabidae		x						x			x
<i>Amara equestris</i> (Duftschmid, 1812)	Carabidae								x			
<i>Amara eurynota</i> (Panzer, 1796)	Carabidae					x						
<i>Amara lunicollis</i> Schiödte, 1837	Carabidae	x	x	x		x	x	x	x	x	x	x
<i>Amara montivaga</i> Sturm, 1825	Carabidae						x	x		x		x
<i>Amara nitida</i> Sturm, 1825	Carabidae	x	x	x	x	x	x	x	x	x	x	x
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	Carabidae		x				x	x				x
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	Carabidae						x			x		
<i>Badister bullatus</i> (Schrank, 1798)	Carabidae		x	x		x		x	x	x	x	
<i>Badister lacertosus</i> Sturm, 1815	Carabidae					x						
<i>Bembidion lampros</i> (Herbst, 1784)	Carabidae	x	x		x	x	x	x		x	x	x
<i>Bembidion properans</i> Stephens, 1828	Carabidae							x				
<i>Brachinus expoldens</i> Duftschmid, 1812	Carabidae						x	x				
<i>Calathus melanocephalus</i> (Linnaeus, 1758)	Carabidae			x							x	
<i>Callistus lunatus lunatus</i> (Fabricius, 1775)	Carabidae					x						
<i>Carabus auratus auratus</i> Linnaeus, 1761	Carabidae				x					x		x
<i>Carabus auronitens</i> Fabricius, 1792	Carabidae				x						x	
<i>Carabus convexus</i> Fabricius, 1775	Carabidae										x	
<i>Carabus nemoralis</i> O.F. Müller, 1764	Carabidae									x		
<i>Cymindis axillaris</i> (Fabricius, 1794)	Carabidae								x			
<i>Tachyura sexstriata</i> (Duftschmid, 1812)	Carabidae	x										
<i>Harpalus affinis</i> (Schrank, 1781)	Carabidae				x							
<i>Harpalus anxius</i> (Duftschmid, 1812)	Carabidae	x						x				
<i>Harpalus dimidiatus</i> (P. Rossi, 1790)	Carabidae	x						x				
<i>Harpalus latus</i> (Linnaeus, 1758)	Carabidae				x						x	
<i>Harpalus luteicornis</i> (Duftschmid, 1812)	Carabidae						x					
<i>Harpalus rubripes</i> (Duftschmid, 1812)	Carabidae	x	x			x	x	x				
<i>Harpalus rufipalpis</i> Sturm, 1818	Carabidae		x				x					
<i>Harpalus tardus</i> (Panzer, 1796)	Carabidae	x	x	x			x	x		x	x	x
<i>Microlestes maurus</i> (Sturm, 1827)	Carabidae						x					
<i>Microlestes minutulus</i> (Goeze, 1777)	Carabidae									x		
<i>Notiophilus germinyi</i> Fauvel, 1863	Carabidae						x	x				x
<i>Notiophilus palustris</i> (Duftschmid, 1812)	Carabidae	x			x			x		x		
<i>Ophonus azureus</i> (Fabricius, 1775)	Carabidae					x						
<i>Platyderus depressus</i> (Audinet-Serville, 1821)	Carabidae								x			

Meadow management influence on arthropods

Table B. 1. *continued.*

Species	Family	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne 1	Icogne 2	La Garde	Orsieres	St-Martin	Vens
<i>Poecilus versicolor</i> (Sturm, 1824)	<i>Carabidae</i>	x	x	x	x	x	x	x	x	x	x	x
<i>Pterostichus burmeisteri</i> Heer, 1838	<i>Carabidae</i>					x					x	
<i>Pterostichus melanarius</i> (Illiger, 1798)	<i>Carabidae</i>			x		x					x	
<i>Pterostichus niger niger</i> (Schaller, 1783)	<i>Carabidae</i>										x	
<i>Pterostichus strenuus</i> (Panzer, 1796)	<i>Carabidae</i>					x						
<i>Pterostichus vernalis</i> (Panzer, 1796)	<i>Carabidae</i>				x					x		
<i>Syntomus truncatellus</i> (Linnaeus, 1761)	<i>Carabidae</i>		x	x	x		x	x	x	x		
<i>Synuchus vivalis vivalis</i> (Illiger, 1798)	<i>Carabidae</i>					x						
<i>Trechus quadristriatus</i> (Schrank, 1781)	<i>Carabidae</i>										x	
<i>Trichotichmus laevicollis</i> (Duftschmid, 1812)	<i>Carabidae</i>					x						

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Table B. 2. List of spiders recorded at each study site.

Species	Family	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne 1	Icogne 2	La Garde	Orsieres	St-Martin	Vens
<i>Agroeca brunnea</i> (Blackwall, 1833)	<i>Liocranidae</i>								x			
<i>Agroeca cuprea</i> Menge, 1873	<i>Liocranidae</i>	x										
<i>Agyneta affinis</i> (Kulczyński, 1898)	<i>Linyphiidae</i>									x		x
<i>Agyneta fuscipalpa</i> (C. L. Koch, 1836)	<i>Linyphiidae</i>							x				
<i>Agyneta rurestris</i> (C. L. Koch, 1836)	<i>Linyphiidae</i>	x					x			x		
<i>Agyneta simplicatarsis</i> (Simon, 1884)	<i>Linyphiidae</i>	x	x			x	x	x				
<i>Alopecosa cuneata</i> (Clerck, 1757)	<i>Lycosidae</i>	x	x	x		x	x		x	x	x	x
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	<i>Lycosidae</i>		x					x			x	
<i>Alopecosa trabalis</i> (Clerck, 1757)	<i>Lycosidae</i>	x	x	x	x	x	x	x	x	x	x	x
<i>Arctosa figurata</i> (Simon, 1876)	<i>Lycosidae</i>	x	x	x			x		x			
<i>Arctosa lutetiana</i> (Simon, 1876)	<i>Lycosidae</i>	x	x				x		x	x		
<i>Argenna subnigra</i> (O. P.-Cambridge, 1861)	<i>Dictynidae</i>								x			
<i>Asagena phalerata</i> (Panzer, 1801)	<i>Theridiidae</i>		x			x	x	x			x	x
<i>Atypus piceus</i> (Sulzer, 1776)	<i>Atypidae</i>	x	x									
<i>Callobius claustrarius</i> (Hahn, 1833)	<i>Amaurobiidae</i>								x			
<i>Centromerita bicolor</i> (Blackwall, 1833)	<i>Linyphiidae</i>										x	
<i>Cheiracanthium campestre</i> Lohmander, 1944	<i>Eutichuridae</i>			x								
<i>Clubiona diversa</i> O. P.-Cambridge, 1862	<i>Clubionidae</i>				x							
<i>Clubiona neglecta</i> O. P.-Cambridge, 1862	<i>Clubionidae</i>											x
<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	<i>Linyphiidae</i>					x	x	x	x		x	x
<i>Dicymbium nigrum</i> (Blackwall, 1834)	<i>Linyphiidae</i>					x					x	
<i>Diplocephalus latifrons</i> (O. P.-Cambridge, 1863)	<i>Linyphiidae</i>										x	
<i>Diplostyla concolor</i> (Wider, 1834)	<i>Linyphiidae</i>									x		
<i>Drassodes lapidosus</i> (Walckenaer, 1802)	<i>Gnaphosidae</i>	x		x	x	x	x				x	x
<i>Drassodes pubescens</i> (Thorell, 1856)	<i>Gnaphosidae</i>	x		x				x				
<i>Drassyllus praeficus</i> (L. Koch, 1866)	<i>Gnaphosidae</i>	x					x	x				
<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	<i>Gnaphosidae</i>				x		x	x				x
<i>Drassyllus villicus</i> (Thorell, 1875)	<i>Gnaphosidae</i>							x				
<i>Dysdera erythrina</i> (Walckenaer, 1802)	<i>Dysderidae</i>					x						
<i>Enoplognatha thoracica</i> (Hahn, 1833)	<i>Theridiidae</i>	x	x				x			x		x
<i>Erigone dentipalpis</i> (Wider, 1834)	<i>Linyphiidae</i>	x	x			x	x	x	x	x		x
<i>Erigonella hiemalis</i> (Blackwall, 1841)	<i>Linyphiidae</i>				x							
<i>Euophrys frontalis</i> (Walckenaer, 1802)	<i>Salticidae</i>	x										
<i>Haplodrassus moderatus</i> (Kulczyński, 1897)	<i>Gnaphosidae</i>	x										
<i>Haplodrassus signifer</i> (C. L. Koch, 1839)	<i>Gnaphosidae</i>			x			x	x	x	x		x
<i>Heliophanus flavipes</i> (Hahn, 1832)	<i>Salticidae</i>			x			x	x				
<i>Iopecosa accentuata</i> (Latreille, 1817)	<i>Lycosidae</i>			x					x	x		x
<i>Mastigusa arietina</i> (Thorell, 1871)	<i>Dictynidae</i>		x									
<i>Mermessus trilobatus</i> (Emerton, 1882)	<i>Linyphiidae</i>		x		x		x	x		x	x	x
<i>Micaria formicaria</i> (Sundevall, 1831)	<i>Gnaphosidae</i>						x					
<i>Micaria fulgens</i> (Walckenaer, 1802)	<i>Gnaphosidae</i>		x		x	x		x				
<i>Micaria guttulata</i> (C. L. Koch, 1839)	<i>Gnaphosidae</i>		x	x			x		x	x		x
<i>Micrargus herbigradus</i> (Blackwall, 1854)	<i>Linyphiidae</i>							x				

Meadow management influence on arthropods

Table B. 2. *continued.*

Species	Family	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne 1	Icogne 2	La Garde	Orsieres	St-Martin	Vens
<i>Micrargus subaequalis</i> (Westring, 1851)	<i>Linyphiidae</i>											x
<i>Nematogmus sanguinolentus</i> (Walckenaer, 1841)	<i>Linyphiidae</i>				x							
<i>Neottiura suaveolens</i> (Simon, 1879)	<i>Theridiidae</i>	x	x									
<i>Ozyptila clavata</i> (Walckenaer, 1837)	<i>Thomisidae</i>		x		x				x	x		
<i>Ozyptila simplex</i> (O. P.-Cambridge, 1862)	<i>Thomisidae</i>	x			x		x			x		
<i>Pachygnatha clercki</i> Sundevall, 1823	<i>Tetragnathidae</i>							x	x		x	
<i>Pachygnatha degeeri</i> Sundevall, 1830	<i>Tetragnathidae</i>		x		x	x	x		x	x	x	x
<i>Panamomops sulcifrons</i> (Wider, 1834)	<i>Linyphiidae</i>				x		x				x	x
<i>Pardosa agrestis</i> (Westring, 1861)	<i>Lycosidae</i>								x			
<i>Pardosa bifasciata</i> (C. L. Koch, 1834)	<i>Lycosidae</i>	x	x	x			x	x	x			x
<i>Pardosa blanda</i> (C. L. Koch, 1833)	<i>Lycosidae</i>					x						
<i>Pardosa hortensis</i> (Thorell, 1872)	<i>Lycosidae</i>	x										
<i>Pardosa lugubris</i> (Walckenaer, 1802)	<i>Lycosidae</i>	x	x						x			
<i>Pardosa palustris</i> (Linnaeus, 1758)	<i>Lycosidae</i>	x		x			x	x	x	x	x	x
<i>Pardosa prativaga</i> (L. Koch, 1870)	<i>Lycosidae</i>				x					x		x
<i>Pardosa pullata</i> (Clerck, 1757)	<i>Lycosidae</i>	x			x		x		x	x		x
<i>Pardosa riparia</i> (C. L. Koch, 1833)	<i>Lycosidae</i>			x		x			x		x	
<i>Pardosa saltans</i> Töpfer-Hofmann, 2000	<i>Lycosidae</i>		x					x	x			
<i>Pellenes tripunctatus</i> (Walckenaer, 1802)	<i>Salticidae</i>								x			
<i>Phlegra fasciata</i> (Hahn, 1826)	<i>Salticidae</i>	x	x				x					
<i>Pisaura mirabilis</i> (Clerck, 1757)	<i>Pisauridae</i>		x									
<i>Pocadicnemis juncea</i> Locket & Millidge, 1953	<i>Linyphiidae</i>				x							
<i>Pocadicnemis pumila</i> (Blackwall, 1841)	<i>Linyphiidae</i>									x		
<i>Robertus lividus</i> (Blackwall, 1836)	<i>Theridiidae</i>				x	x						
<i>Robertus neglectus</i> (O. P.-Cambridge, 1871)	<i>Theridiidae</i>					x						
<i>Sibianor aurocinctus</i> (Ohlert, 1865)	<i>Salticidae</i>							x				
<i>Talavera aequipes</i> (O. P.-Cambridge, 1871)	<i>Salticidae</i>								x			
<i>Tapinocyba praecox</i> (O. P.-Cambridge, 1873)	<i>Linyphiidae</i>			x								
<i>Tapinocyboides pygmaeus</i> (Menge, 1869)	<i>Linyphiidae</i>							x				x
<i>Tegenaria silvestris</i> L. Koch, 1872	<i>Agelenidae</i>								x			
<i>Tenuiphantes mengei</i> (Kulczyński, 1887)	<i>Linyphiidae</i>				x							
<i>Thanatus formicinus</i> (Clerck, 1757)	<i>Philodromidae</i>	x						x				
<i>Tiso vagans</i> (Blackwall, 1834)	<i>Linyphiidae</i>			x	x	x	x		x		x	
<i>Trachyzelotes pedestris</i> (C. L. Koch, 1837)	<i>Gnaphosidae</i>	x	x					x				
<i>Trichoncus hackmani</i> Millidge, 1955	<i>Linyphiidae</i>											x
<i>Trochosa ruricola</i> (De Geer, 1778)	<i>Lycosidae</i>							x	x	x		
<i>Trochosa terricola</i> Thorell, 1856	<i>Lycosidae</i>	x	x				x		x			x
<i>Walckenaeria antica</i> (Wider, 1834)	<i>Linyphiidae</i>									x		x
<i>Walckenaeria dysderoides</i> (Wider, 1834)	<i>Linyphiidae</i>				x						x	
<i>Xerolycosa nemoralis</i> (Westring, 1861)	<i>Lycosidae</i>		x									
<i>Xysticus bifasciatus</i> C. L. Koch, 1837	<i>Thomisidae</i>				x	x	x	x		x	x	
<i>Xysticus cristatus</i> (Clerck, 1757)	<i>Thomisidae</i>				x							
<i>Xysticus erraticus</i> (Blackwall, 1834)	<i>Thomisidae</i>	x	x	x						x	x	x
<i>Xysticus gallicus</i> Simon, 1875	<i>Thomisidae</i>					x						

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Table B. 2. *continued.*

Species	Family	Arbaz	Cordona	Eison	Euseigne	Grimentz	Icogne 1	Icogne 2	La Garde	Orsieres	St-Martin	Vens
<i>Xysticus kochi</i> Thorell, 1872	<i>Thomisidae</i>	x	x			x	x	x	x			x
<i>Xysticus luctator</i> L. Koch, 1870	<i>Thomisidae</i>			x		x						
<i>Xysticus ninnii</i> Thorell, 1872	<i>Thomisidae</i>	x					x					
<i>Zelotes apricorum</i> (L. Koch, 1876)	<i>Gnaphosidae</i>								x			
<i>Zelotes latreillei</i> (Simon, 1878)	<i>Gnaphosidae</i>				x	x						
<i>Zelotes petrensis</i> (C. L. Koch, 1839)	<i>Gnaphosidae</i>	x		x					x	x		x
<i>Zodariion italicum</i> (Canestrini, 1868)	<i>Zodariidae</i>						x	x				

Meadow management influence on arthropods

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Appendix C. Non-metric multidimensional scaling (NMDS) graphical projections of ground-dwelling arthropod communities.

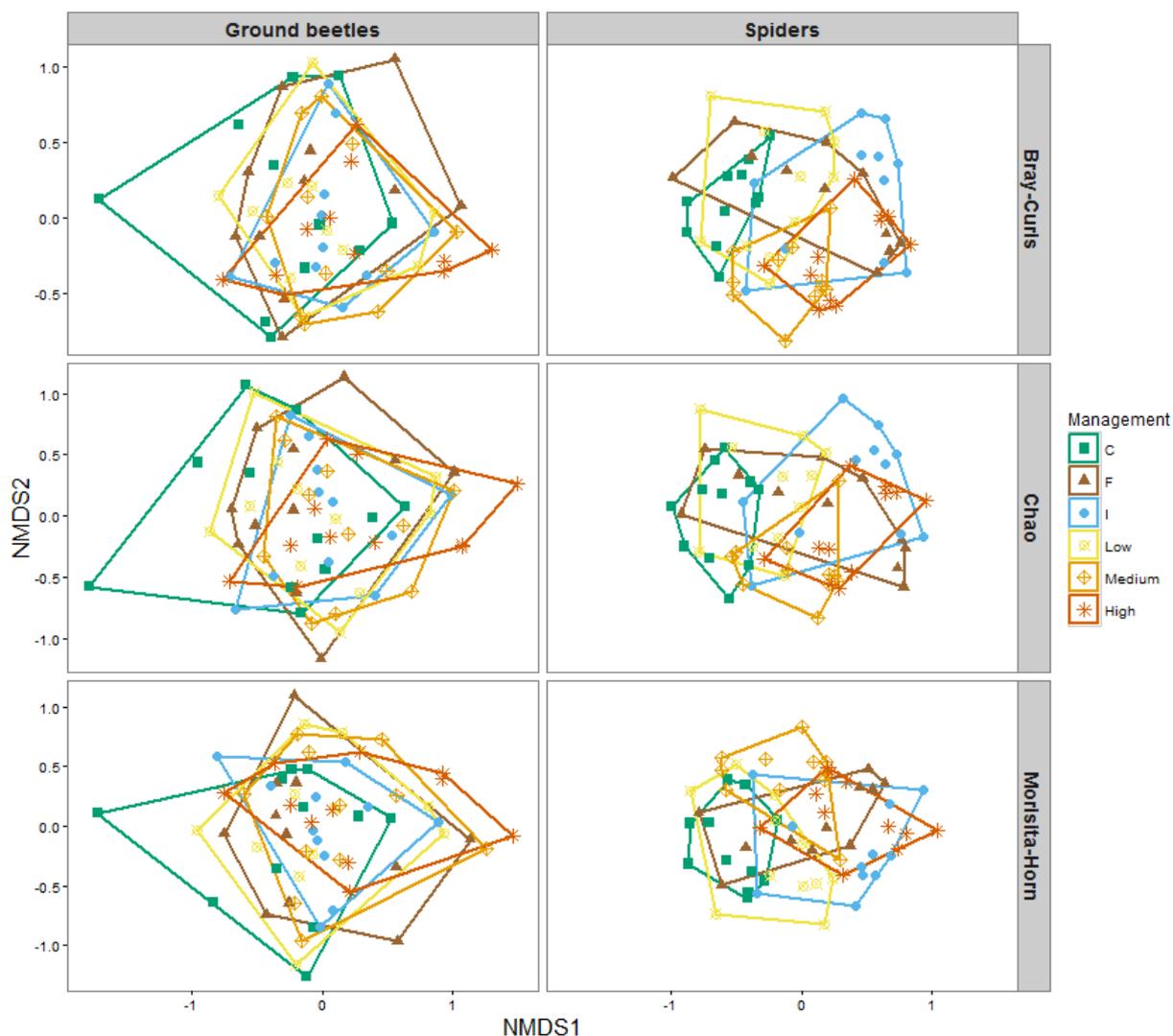


Fig. C.1. Ground beetle and spider community composition according to management treatment using three abundance-based dissimilarity indices; Bray-Curtis, Chao and Morisita-Horn. C = Control (no input), I = irrigation, F = fertilisation, Low= irrigation + fertilisation 1/3, Medium = irrigation + fertilisation 2/3, High= irrigation + fertilisation 3/3. Fractions of I+F refer to the relative amount of fertiliser applied in comparison to the input necessary to achieve maximum hay yield locally (the latter corresponding to I+F 3/3) according to Sinaj et al. (2009).

Meadow management influence on arthropods

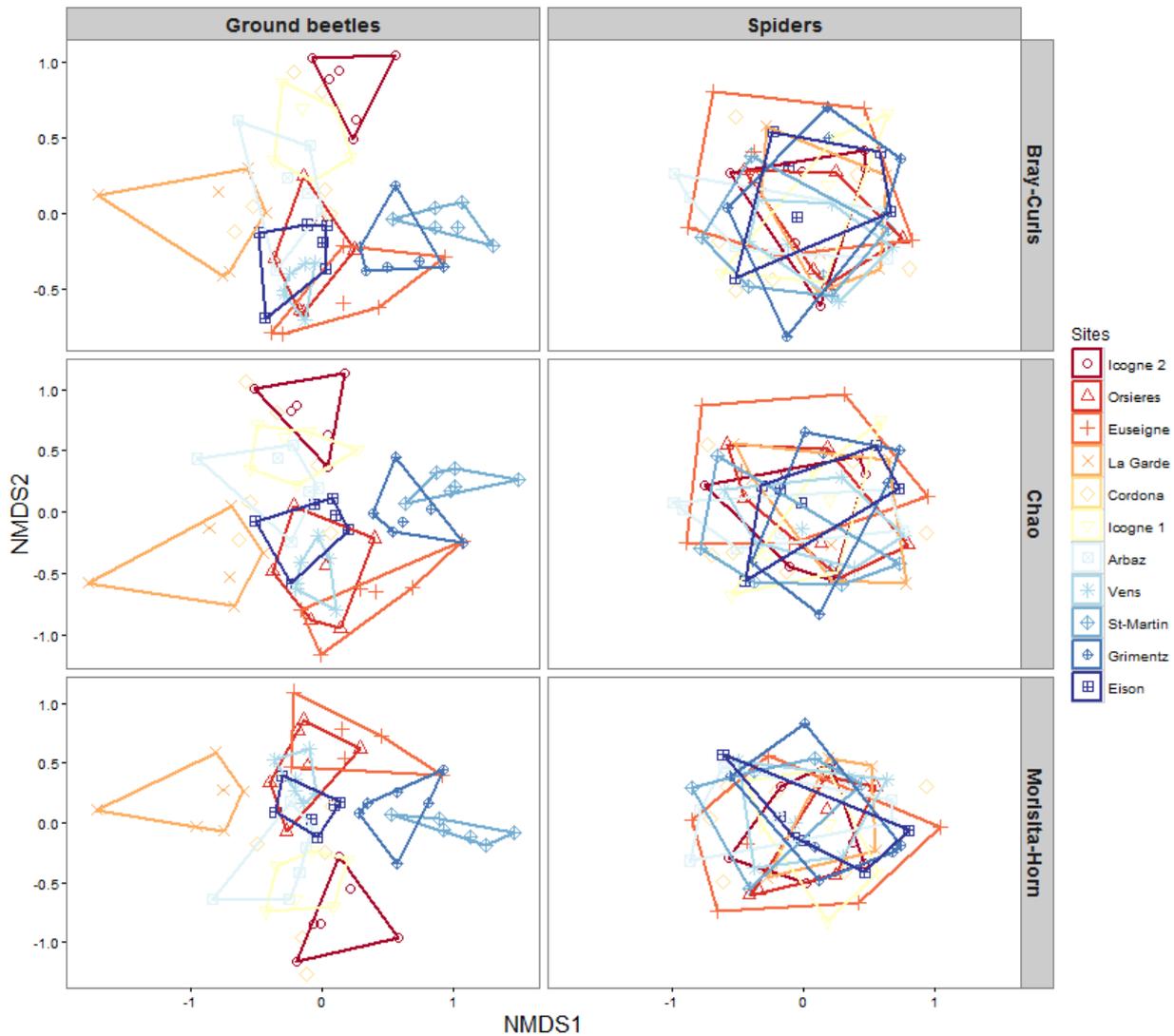


Fig. C.2. Ground beetle and spider community composition according to study site using three abundance-based dissimilarity indices: Bray-Curtis, Chao and Morisita-Horn. Study sites are ordered according to elevation, from red with open circle being lowest and blue with crossed square being highest.



Sustainable biodiversity-productivity management trade-offs in semi-natural mountain grasslands

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ABSTRACT

Over the last few decades, management practices in mountain hay meadows have been intensified in the quest for greater forage production which threatens mountain grassland biodiversity. In order to identify sustainable trade-offs between hay yield and biodiversity, we experimentally tested the effects of six different management regimes, each applied to one of six plots within a meadow across 11 spatial replicates in the SW Swiss Alps. A plot was therefore either 1) only irrigated with a sprinkler; 2) fertilised with slurry; 3-5) receiving low, medium or high amounts of both fertiliser and water respectively, again in the form of slurry and sprinkler water; 6) receiving no input of either water or fertiliser (control plot). In 2015, after five years of this experimental treatment, we measured various agronomic aspects of meadow productivity including phytomass (in terms of dry mass; DM yield), phytomass nitrogen (N) content, annual N yield, total soil N and phosphorus (P) content as well as legume, grass and forb cover, and plant species richness. Our main results were that phytomass and nitrogen yields increased along the intensification gradient (irrigation and fertilisation combined), but the pattern was driven mainly by fertilisation. Plant species richness decreased linearly along the intensification gradient (irrigation and fertilisation combined), i.e. with increase in phytomass productivity. Thus, the intensification of mountain meadows increased hay production, but at the cost of plant diversity. There was no single level of management intensity that simultaneously maximized phytomass yield and plant biodiversity. However, a biodiversity-productivity trade-off emerged at one third of the quantity of water and slurry inputs necessary to achieve maximum local hay yield. Under this intensity level, 95% of plant species richness was maintained while phytomass yield was increased by 26% compared to control meadows. Given that phytomass yield is 73% lower in high-input meadows compared to the most suitable intensity level for biodiversity, agricultural policies must support sustainable management practices. This support would ensure the conservation of species-rich mountain grasslands, while also taking into account the opportunity costs from the potential hay production losses faced by the farming community.

Chapter 3

INTRODUCTION

The semi-natural grasslands situated below the tree line in European mountain ranges is the result of a long history of traditional exploitation to support local livestock rearing (Fischer & Wipf 2002; Maurer et al. 2006; Baur et al. 2006). The traditional low intensity management applied in these grasslands created open, species-rich habitats that are today considered as major biodiversity hotspots in Europe and of high conservation value (Poschlod & Wallis de Vries 2002; Väre et al. 2003; Fischer et al. 2008).

In recent decades, many mountain hay meadows that are easily accessible for agricultural machinery have been farmed more intensively in the quest for greater forage production (Tasser & Tappeiner 2002; Graf et al. 2014). This intensification has involved fertilisation with livestock liquid waste (slurry), and also irrigation via sprinklers in drier regions of the Alps (Crook & Jones 1999). Intensification has led to a loss of mountain grassland floral and faunal diversity, notably resulting from the increase in fertiliser inputs (Maurer et al. 2006; Marini et al. 2008; Fischer et al. 2008; Humbert et al. 2016). Addition of nutrients leads to community shifts from specialised, less competitive species to nitrophilous, competitive species, which is causing considerable biodiversity loss in formerly species-rich and nutrient-poor traditional grasslands (Bobbink 1991), as well as a homogenization of plant communities across agricultural landscapes (Gossner et al. 2016). Competition for light is the main mechanism driving this biodiversity loss (Hautier et al. 2009). When seedlings emerge, the reduced light intensity at ground level due to the dense overhead vegetation canopy hinders their persistence and inhibits the growth of less competitive species (Verkaar & Schenkeveld 1984; Borer et al. 2014; DeMalach et al. 2017).

Restoring and maintaining biodiversity of semi-natural grasslands is a top priority of the Common Agricultural Policy (CAP) in Europe, and triggered numerous research initiatives (Hejcman et al. 2007; Fischer et al. 2010; Lamarque et al. 2011; Kampmann et al. 2012). The enhancement of grassland biodiversity usually requires a reduction in management intensity (typically a reduction of fertiliser inputs; Schellberg et al. 1999), but this inevitably lowers forage production (Isselstein et al. 2005). Grassland biodiversity conservation furthermore requires a certain degree of management to prevent progressive vegetation succession towards forest. Meadow abandonment is a rapidly

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ongoing process affecting mountain grasslands and leads to a loss of plant and other species typical of open habitats because of encroachment by shrubs and trees (e.g. Gellrich et al. 2008; Graf et al. 2014). Since the primary goal of semi-natural grassland management by farmers is to produce forage in good quantity and quality for their livestock (Tasser & Tappeiner 2002) and the species-rich grasslands are of great conservation value, there is an urgent need to identify a viable trade-off between agronomic production and biodiversity maintenance in semi-natural grasslands under modern exploitation.

We hypothesise that an intermediate level of management intensity between high intensification and land abandonment could emerge as a good trade-off between biodiversity conservation, the maintenance of key ecological functions and services, and hay production (Tasser & Tappeiner 2002; Niedrist et al. 2009). In order to identify and quantify such a trade-off, we carried out a field experiment testing combinations of fertilisation through slurry application and irrigation via sprinklers, a widespread practice to increase hay production often disregarded in mountain grassland studies (but see Riedener et al. 2013; Melliger et al. 2014). We experimentally manipulated fertilisation and irrigation among species-rich montane and subalpine semi-natural grasslands in order to create a realistic farming intensification gradient, while applying a 2 x 2 factorial design to disentangle the effect of fertilisation and irrigation.

To date, several biodiversity indicators have been studied as part of this field experiment. The main results have demonstrated that, under low to medium intensity farming management, a good diversity of plant and arthropod species can be retained in these mountain grasslands (Lessard-Therrien et al. in press; Andrey et al. 2014; Andrey et al. 2016), confirming observational studies in mountain areas (Grandchamp et al. 2005; Marini et al. 2008). Yet, quantitative studies of changes in yield and nutrient content in response to mountain grassland intensification remain scarce although essential to have an accurate depiction of modern farming viability compatible with biodiversity preservation.

Here, we aim to quantify these agronomic outputs with respect to a gradient in management intensity (i.e. increasing levels of irrigation and fertilisation) with customized experimental treatments adapted to the meadows' productivity potential. After five years of experimental

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manipulation, we studied phytomass (as a proxy for hay) production and nitrogen (N) yield (a measure of the crude protein content, essential for livestock nutrition) produced per unit area. Second, soil nutrient content was assessed by measuring N and phosphorus (P) – the main growth-limiting nutrients for plants under natural circumstances (Vitousek & Howarth 1991; Koerselman & Meuleman 1996) – in order to evaluate nutrient dynamics along our intensification gradient. Third, the cover of three plant functional groups (grasses, legumes and forbs) was also recorded, as the proportions of these groups in the plant community plays an important role in the quality of hay harvested in semi-natural grasslands (Pontes et al. 2007; Duru et al. 2008) and may change with intensification (Leto et al. 2008; Brum et al. 2009). These variables represent important agronomic components of the provisioning services delivered by grassland ecosystems. Fourth, we assessed changes in plant species richness in order to link vegetation patterns between productivity and species richness during the same growing season. Here, we expected a pattern conforming to the hump-shaped model, which posits that plant species richness of managed grasslands peaks at intermediate levels of agricultural productivity where above-ground phytomass was used as a proxy for annual net primary productivity (Grime 1973; Guo & Berry 1998; Mittelbach et al. 2001; Fraser et al. 2015). This peak in species richness is driven by two opposing processes. First, in low productivity systems with low phytomass, species richness is limited by abiotic stresses (such as insufficient water and/or nutrients) which are conditions that a few specialized species can tolerate. In contrast, in highly productive systems generating high phytomass, species richness is constrained through competitive exclusion by a few dominant species that eliminate many others (Grime 1973; Al-Mufti et al. 1977; Guo & Berry 1998).

We predicted, first, that phytomass production would increase linearly with farming intensification, a typical pattern in mountain grasslands subjected to N addition (Humbert et al. 2016). We predicted that this linear increase would not reach a plateau as the gradient was designed to prevent over-intensification, at which point fertiliser input exceeds the potential production limit of the site (Bai et al. 2010). We also predicted an increase in N yield along the intensification gradient because as plants grow, their intake of nutrients increases as long as extra nutrients are available (Reid 1978). Third, grass cover was expected to increase along the intensification

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gradient, mainly as a consequence of fertilisation (Leto et al. 2008). In effect, legume species, which have symbiotic relationships with N fixing bacteria, are expected to show a hump-shaped relationship in terms of percent cover along the intensification gradient. Legumes would benefit from nutrient input because P and potassium (K) were also included in the fertiliser used (Mountford et al. 1993), but they are typically outcompeted by grasses under high intensification (Leto et al. 2008). Forb cover was expected to expand as some forb species with faster growth rates and large aerial structures respond positively to management intensification (Mountford et al. 1993), even though other species grow at slower rates and/or occupy specific microhabitats, therefore progressively vanishing from the plant community after nutrient addition (Mountford et al. 1993; Onipchenko et al. 2012). The experiment took place in species-rich meadows, and an increase in both phytomass and species richness was observed under medium intensification management after one year of experimentation (Andrey et al. 2014). After five years, the cumulative effect of intensification might have surpassed its beneficial influence on species richness. Therefore, our fourth prediction was that the increase in phytomass would now lead to a linear decline in species richness, being on the right-hand side of the hump-shape relationship, as often found in studies comparing species richness and live phytomass (Fraser et al. 2015).

MATERIALS AND METHODS

Study sites

In 2010, eleven traditionally managed hay meadows were selected within the canton of Valais, in the inner Alps of SW Switzerland (Fig. S.1). The region is characterized by a continental climate with cool, wet winters and warm, dry summers. Mean monthly ambient air temperature (2004-2014) at valley bottom in Sion (482 m a.s.l.), ranged from 0.3 °C in January to 20.5 °C in July (Federal Office of Meteorology and Climatology 2016). The eleven meadows were situated within the montane and subalpine belts, between 880 and 1770 m a.s.l. (Table A. 1), and all had been extensively managed i.e. had either been fertilised with solid manure and/or irrigated from water brought to the meadows along traditional open gravitational channels, for at least the ten years preceding the initiation of the experiment or longer.

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Experimental design

Replicated across the eleven meadows, six different experimental management treatments were randomly assigned to six 20 m diameter plots per meadow, with one treatment per plot, and a distance of at least 5 m between the boundaries of adjacent plots. The same treatment was applied consistently each year over five years (2010-2015), before measurements took place in 2015. Irrigation was carried out using sprinklers and fertilisation consisted of dried bovine manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4) dissolved into water so as to reach the same nutrient (NPK)-water concentration as standard farm slurry from cattle (Sinaj et al. 2009). This solution will be referred to as slurry hereafter. The experiment consisted of various management intensity including the control (C) and three plots that received a combination of aerial irrigation (I) via sprinklers and fertilisation (F) with slurry, with amounts varying in tandem from 1/3, through 2/3 to 3/3 of the quantity theoretically needed to achieve maximum hay yield, under a mowing regime consisting of two hay harvests per year and according to site productivity potential (Sinaj et al. 2009). This created a four-level management intensity gradient: C (no input); I+F 1/3 (low input), I+F 2/3 (medium input); and I+F 3/3 (high input). The experiment also included a 2 x 2 factorial design that allowed disentangling the effects of irrigation (I) and fertilisation (F) (both treatments applied separately at 2/3 of the maximal input amount), by comparing controls (C, no input) to both irrigation and fertilisation combined (I+F 2/3). These I 2/3 and F 2/3 treatments are hereafter referred to as I (irrigation) and F (fertilisation), where appropriate. The amount of slurry applied per plot depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site elevation a.s.l. (see Appendix A in Andrey et al. 2016; Sinaj et al. 2009), which allowed the study sites to be categorized according to their potential productivity. As the latter is highly correlated with elevation, we adjusted the amount of added fertiliser according to elevation, following Sinaj et al. (2009) (Table 1).

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Table 1. Experimental management treatments as operated in three different categories of meadow according to elevation and productivity (see Table A.1 for site coordinates and elevation). Category A: meadows situated at higher elevation with lower productivity (St-Martin, Grimentz, Eison); B: meadows situated at mid-elevation with intermediate productivity (La Garde, Cordona, Icogne1, Arbaz, Vens); C: meadows situated at lower elevation with higher productivity (Icogne2, Orsières, Euseigne). Treatment abbreviations are as follows: (C) control; (I) irrigated, (F) fertilised, and (I+F) irrigated and fertilised. Fractions of I+F refer to the relative amount of fertiliser applied in comparison to the input necessary to achieve maximum hay yield, according to the theoretical productivity potential of the site with two hay harvests per year (according to Sinaj et al. 2009).

Treatment	No. of cut per year	Slurry fertilisation (kg ha ⁻¹ year ⁻¹)									Sprinkler irrigation (mm week ⁻¹)
		Category A			Category B			Category C			
		N	P	K	N	P	K	N	P	K	
C	1	0	0	0	0	0	0	0	0	0	0
I	2	0	0	0	0	0	0	0	0	0	20
F	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	0
I+F 1/3	2	13.3	4.8	36.9	20	7.3	55.4	26.7	9.7	73.8	10
I+F 2/3	2	26.7	9.7	73.8	40	14.5	110.6	53.3	19.4	147.5	20
I+F 3/3	2	40.0	14.5	110.6	60	21.8	166.0	80	29.1	221.4	30

Data collection

Phytomass was measured by sampling 3.2 m² of vegetation cut at 6 cm above the ground in each plot, just before the first (mid-June to mid-July) and second hay harvests (mid-August to mid-September) by farmers. The total fresh mass of the phytomass was first measured and its dry mass (DM) was then calculated by retaking the mass of three randomly chosen 250 g subsamples after drying at 105° C for 48 h to estimate productivity. The N content, which is a measure of the crude protein content of the DM, was calculated by analysing other subsamples dried at 60° C for 48 h for their total percentage nitrogen (% N). The annual values of DM yield (i.e. productivity during the growing season) were obtained by summing the two harvest values for each plot. N yield, the total annual yield of crude protein in harvested aboveground phytomass per surface area, was calculated by multiplying the DM yield with the N content. Soil nutrient content was measured as total N and P by taking five sub-samples of the top soil layer (0-10 cm deep, then removing the first 2 cm to avoid pollution contamination), which provides a sample of ca 1 kg of soil per study plot. All N measurements (from phytomass

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and soil) were conducted using the Kjeldahl method (Kjeldahl 1883) while total P was measured following (Saunders & Williams 1955) by Sol-Conseil, an external lab (<http://www.sol-conseil.ch>).

All vascular plants were identified to species level and each species' percent coverage was visually estimated by two observers and then averaged if different. The surveys were conducted in an 8 m² (4 x 2 m) subplot within each experimental plot between early June and early July, progressing from meadows at lower to higher elevation so as to follow vegetation phenology. We calculated percentage cover of three functional groups; legumes (Fabaceae), graminoids (Poaceae, Cyperaceae and Juncaceae; hereafter called grasses), and forbs (all other families) by summing cover values for species belonging to the appropriate functional group. Relative percentage cover was calculated so the total cover would sum up to 100%. Prior to statistical analysis, functional group relative cover values were log-transformed to meet assumptions of the test requirement for normally distributed residual error terms.

Statistical analyses

Due to some logistic issues encountered in the field during harvest, phytomass quantity data were missing for four treatments (I, F, I+F 2/3 and I+F 3/3) at one study site (Euseigne) at first harvest, and for all treatments at a second study site (Eison) at second harvest. Analyses were therefore performed based on the data from nine meadows. The effects of the experimental management treatments on DM yield, phytomass N content, total N yield, soil total N and P content, plant species richness and plant functional group cover were tested with linear mixed-effect models (LMM) using the R-package *lme4* (Bates et al. 2015). The great variability in responses observed between study sites (e.g. Fig. 1) reflects a wide spatial heterogeneity of biotic and abiotic conditions encountered in the study area, hence 'study site' was added to all models as a random factor. In the intensification gradient analysis, the four intensification levels were treated as a single continuous variable: control with no input = 0; I+F 1/3-plots = 1; I+F 2/3-plots = 2; and I+F 3/3-plots = 3. Given the N fixing abilities of legumes, their cover was expected to be positively correlated with N yield (Dooley et al. 2015) and this relationship was tested in a separate mixed-effect model, again with site as random factor. We compared linear and quadratic models involving the functional group coverage and the

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intensification gradient using the Akaike information criterion (AIC, Akaike 1987). The model with the lowest AIC value was retained. In the 2 x 2 factorial design models, an interaction term between irrigation and fertilisation was added and was retained only if significant. Comparisons between DM yield and N content between harvests were tested using a LMM with harvest session (first vs second harvest in the season) as a fixed effect, and treatment as a random factor. The relationship between plant species richness and DM yield was tested with a LMM with treatment and study site both as random factors. We also compared linear and quadratic models between species richness and DM yield using AIC (Akaike 1987). Linear models were also conducted to test for this relationship within a single treatment (e.g. within control plots) using the `lm` R-function. All analyses were conducted using the R statistical software, version 3.1.2 (R Core Team 2015).

RESULTS

The means and standard errors (SE) of all measured variables are shown in Table 2. Across meadows, dry mass (DM) yield was about 2.5 times higher at first harvest than at the second (LMM; $t = -15.41$, $df = 67.71$, $P < 0.001$), whereas the DM N content was about 1.6 times higher for the second harvest (LMM; $t = 15.87$, $df = 70.00$, $P < 0.001$; Fig. 1). Model outputs on the effects of the intensification gradient on the variables measured are reported in Table 3 and on the effects of the 2 x 2 factorial design in Table 4. DM yield was positively correlated with management intensity levels for both harvests. Along the intensification gradient, annual DM yield increased by 26%, 45% and 73% in the low (I+F 1/3), medium (I+F 2/3) and high (I+F 3/3) intensity levels respectively, relative to the DM yield mean in the control (Fig. 2). The N content did not change along the intensification gradient at either the first or the second harvest. Annual N yield increased linearly along the intensification gradient, of 40%, 60% and 89% in the low, medium and high intensity levels, respectively, relative to the N yield mean in the control (Fig. 2). Total soil N and P content did not vary along the intensification gradient. Legume relative cover peaked at medium levels of the intensification gradient (from 5% of relative cover in the control, up to 18% at medium intensity, and down to 10% under high intensity), for which the quadratic model showed a significant relationship and gave the lowest AIC value (LMM_{quadratic}; $t = -2.12$, $df =$

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25.00, $P = 0.04$, Table 2 and Fig. 3). There was no correlation between relative legume cover and DM N yield along the intensification gradient (LMM; $t = 1.707$, $df = 34.00$, $P = 0.097$) There was no significant effect of management intensity on either grass or forb relative coverage. When summed, although still not significant, grass and forb cover showed the opposite pattern of legume relative cover, with the quadratic model giving the lowest AIC value (LMM_{quadratic}; $t = 1.88$, $df = 25.00$, $P = 0.07$, Table 2). Plant species richness decreased linearly along the intensification gradient, by 5%, 7% and 20% in the low, medium and high intensity levels, respectively, relative to the mean species richness across control plots (Fig. 2).

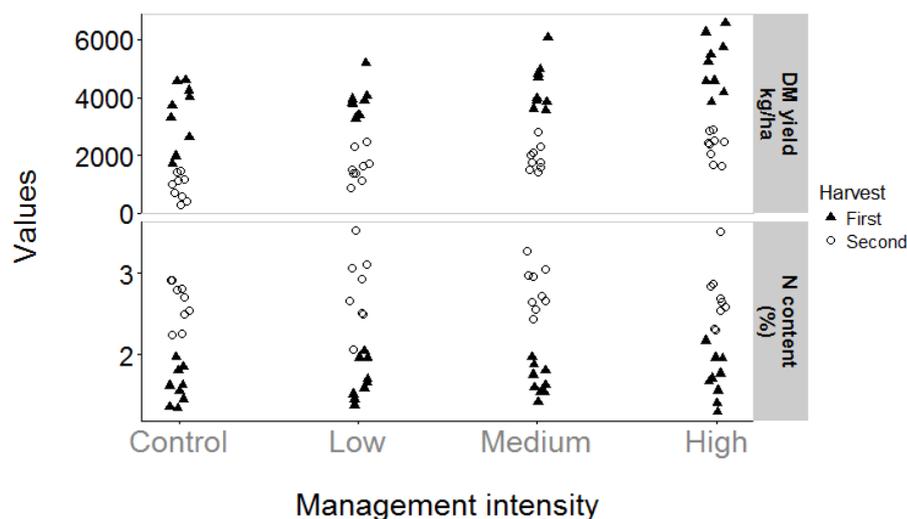


Fig. 1. Vegetation dry mass (DM) yield and N content at first and second harvest along the intensification gradient: control (no input), low, medium and high intensity levels with, respectively, 1/3, 2/3 and 3/3 of the dose that would be necessary to achieve the maximum local hay yield with two hay harvests per year. See Table 3 for statistical analyses.

Table 2. Management treatment effects on vegetation dry mass (DM) yield, DM N content, N yield, total soil N and P, legume, grass and forb covers as well as plant species richness. The annual values of DM yield were obtained by summing the two harvests for each plot. N yield, the total annual yield of crude protein in harvested aboveground phytomass per surface area, was calculated by multiplying DM yield with N content. Means and SE are shown. For more details on treatment abbreviations, see legend of Table 1.

	Management treatments					
	Control (C)	Irrigation (I)	Fertilisation (F)	Low (I+F 1/3)	Medium (I+F 2/3)	High (I+F 3/3)
Yield (kg DM ha ⁻¹)						
First harvest	3409.79 ± 362.11	2639.82 ± 108.91	4979.16 ± 258.34	3846.49 ± 190.34	4377.22 ± 275.06	5155.99 ± 312.23
Second harvest	912.93 ± 142.44	1259.42 ± 98.01	1641.28 ± 182.21	1600.60 ± 170.41	1911.07 ± 148.30	2314.34 ± 148.52
Annual harvest	4322.72 ± 488.97	3899.24 ± 183.53	6620.43 ± 319.33	5447.09 ± 275.10	6288.29 ± 309.40	7470.33 ± 382.73
DM N content (%)						
First harvest	1.62 ± 0.07	1.71 ± 0.05	1.54 ± 0.07	1.70 ± 0.08	1.68 ± 0.06	1.72 ± 0.09
Second harvest	2.63 ± 0.09	2.62 ± 0.13	2.76 ± 0.10	2.81 ± 0.14	2.81 ± 0.09	2.70 ± 0.12
Annual N yield (kg N ha ⁻¹)	79.09 ± 9.49	77.70 ± 3.76	121.11 ± 5.62	110.68 ± 7.51	126.65 ± 6.01	149.14 ± 5.80
Total soil N (%)	0.60 ± 0.06	0.57 ± 0.04	0.52 ± 0.06	0.55 ± 0.04	0.55 ± 0.03	0.61 ± 0.04
Total soil P (mg P/kg)	4.29 ± 0.44	3.64 ± 0.37	5.00 ± 0.68	4.12 ± 0.34	4.78 ± 0.65	4.40 ± 0.65
Legume cover (%)	4.66 ± 0.93	9.40 ± 2.26	12.65 ± 4.27	7.95 ± 1.34	18.00 ± 4.70	9.81 ± 2.73
Grass cover (%)	55.83 ± 8.65	53.12 ± 5.83	51.60 ± 6.37	45.39 ± 5.97	45.12 ± 5.07	55.46 ± 6.90
Forb cover (%)	39.50 ± 8.47	37.48 ± 5.38	35.75 ± 5.47	46.66 ± 6.23	36.88 ± 6.74	34.74 ± 7.12
Plant species richness	49.11 ± 3.45	48.22 ± 2.16	45.00 ± 3.01	46.89 ± 3.66	45.56 ± 2.14	39.22 ± 3.34

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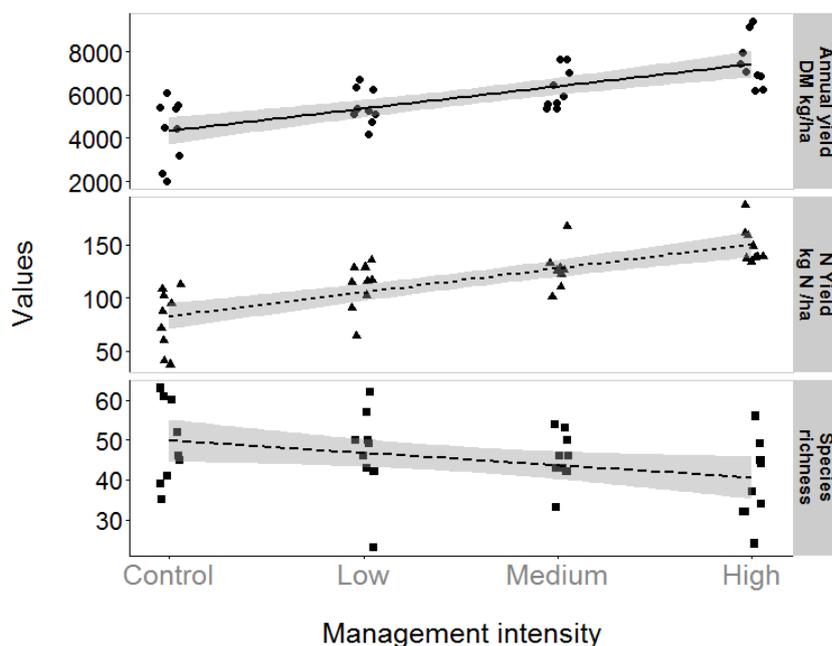


Fig. 2. Effect of management intensification on annual vegetation dry mass (DM) and N yields, and plant species richness, with SE indicated by shaded area: control (no input), low, medium and high intensity levels with, respectively, 1/3, 2/3 and 3/3 of the dose that would be necessary to achieve the maximum local hay yield with two hay harvests per year. See Table 3 for statistical analyses.

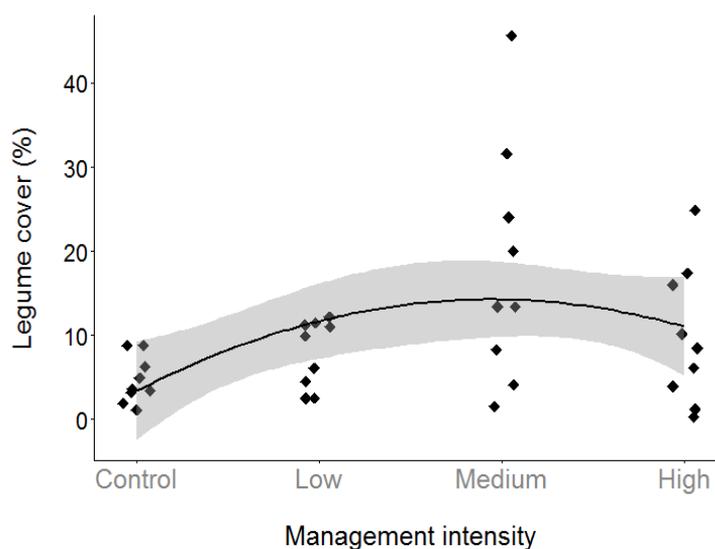


Fig. 3. The effect of management intensification on legume cover, with SE indicated by shaded area: control (no input), low, medium and high intensity levels with, respectively, 1/3, 2/3 and 3/3 of the dose that would be necessary to achieve the maximum local hay yield with two hay harvests per year. Grass and forb cover showed the opposite trend when summed. See Table 3 for statistical analysis.

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Table 3. Outputs of the generalized linear mixed models on the effect of the management intensity gradient on vegetation dry mass (DM) yield, DM N content, N yield, total soil N and P, legume, grass and forb covers as well as plant species richness. Intercept refers to the estimated value of the control adjusted by the random factor (i.e. the study site), estimates for functional group cover are on a log-scale, SE stands for standard error and significant effects are highlighted in bold.

	Estimate	SE	P
Yield (kg DM ha ⁻¹)			
First harvest			
Intercept	3331.97	264.73	<0.001
Management intensity	576.93	93.95	<0.001
Second harvest			
Intercept	1007.53	129.21	<0.001
Management intensity	451.47	64.87	<0.001
Annual harvest			
Intercept	4339.50	325.23	<0.001
Management intensity	1028.40	137.17	<0.001
DM N content (%)			
First harvest			
Intercept	1.63	0.06	<0.001
Management intensity	0.02	0.03	0.345
Second harvest			
Intercept	2.70	0.10	<0.001
Management intensity	0.02	0.03	0.543
N yield (kg N ha ⁻¹)			
Annual harvest			
Intercept	82.47	6.11	<0.001
Management intensity	22.61	3.16	<0.001
Total soil N (%)			
Intercept	0.56	0.04	<0.001
Management intensity	0.01	0.01	0.533
Total soil P (mg P/kg)			
Intercept	4.24	0.50	<0.001
Management intensity	0.09	0.14	0.512
Legume cover (log scale)			
Intercept	1.28	0.33	<0.001
Management intensity	1.19	0.50	0.026
Management intensity ²	-0.34	0.16	0.043
Grass cover (log scale)			
Intercept	3.80	0.13	<0.001
Management intensity	0.02	0.05	0.853
Forb cover (log scale)			
Intercept	3.60	0.18	<0.001
Management intensity	-0.05	0.05	0.371
Plant species richness			
Intercept	49.84	2.84	<0.001
Management intensity	-3.10	1.13	0.011

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Table 4. Outputs of the generalized linear mixed models testing the 2 x 2 factorial design to separate the effects of irrigation or fertilisation on vegetation dry mass (DM) yield, DM N content, DM N yield, total soil N and P, legume, grass and forb covers as well as plant species richness. Intercept refers to the estimated value of the control adjusted by the random factor (i.e. the study sites), estimates for functional group cover are on the log-scale, SE stands for standard error and significant effects are highlighted in bold.

	Estimate	SE	P
Yield (kg DM ha ⁻¹)			
First harvest			
Intercept	3367.78	246.40	<0.001
Irrigation	-685.95	196.46	0.002
Fertilisation	1653.38	196.46	<0.001
Second harvest			
Intercept	932.11	125.66	<0.001
Irrigation	308.14	140.18	0.038
Fertilisation	689.99	140.18	<0.001
Annual harvest			
Intercept	4299.89	313.90	<0.001
Irrigation	-377.81	260.95	0.160
Fertilisation	2343.38	260.95	<0.001
DM N content (%)			
First harvest			
Intercept	1.60	0.05	<0.001
Irrigation	0.11	0.047	0.019
Fertilisation	-0.05	0.047	0.241
Second harvest			
Intercept	2.61	0.09	<0.001
Irrigation	0.01	0.07	0.797
Fertilisation	0.16	0.07	0.031
N yield (kg N ha ⁻¹)			
Annual harvest			
Intercept	77.35	5.77	<0.001
Irrigation	2.07	5.97	0.731
Fertilisation	45.48	5.97	<0.001
Total soil N (%)			
Intercept	0.58	0.05	<0.001
Irrigation	0.00	0.04	0.978
Fertilisation	-0.04	0.04	0.268
Total soil P (mg P/kg)			
Intercept	4.18	0.51	<0.001
Irrigation	-0.43	0.38	0.274
Fertilisation	0.92	0.38	0.025
Legume cover (log scale)			
Intercept	1.57	0.27	<0.001
Irrigation	0.70	0.31	0.032
Fertilisation	0.72	0.31	0.027

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Table 4. *continued.*

	Estimate	SE	<i>P</i>
Grass cover (log scale)			
Intercept	3.91	0.13	<0.001
Irrigation	-0.03	0.13	0.785
Fertilisation	-0.08	0.13	0.546
Forb cover (log scale)			
Intercept	3.49	0.16	<0.001
Irrigation	0.02	0.12	0.848
Fertilisation	-0.01	0.12	0.884
Plant species richness			
Intercept	48.75	2.51	<0.001
Irrigation	-0.16	2.07	0.937
Fertilisation	-3.38	2.07	0.116

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Irrigation alone had a negative effect on DM yield at the first harvest, but a positive effect at the second harvest. Fertilisation alone had a positive effect on the DM yield of both harvests. DM N increased under irrigation only at first harvest, and increased under fertilisation only at second harvest. Throughout the growing season, DM and N yields increased mainly because of fertilisation (Fig. 4). Total soil N was affected neither by fertilisation nor by irrigation, while total soil P increased only with fertilisation. Fertilisation and irrigation applied separately both had positive effects on relative legume cover, but not on grass or forb relative cover. There was no effect of irrigation or fertilisation applied separately on plant species richness (Fig. 4). Moreover, none of the interactions between irrigation and fertilisation were significant in the 2 x 2 factorial design models. Across experimental treatments, species richness declined in a linear way as DM yield increased ($\Delta AIC=33.20$, LMM_{linear} ; $t = 3.83$, $df = 47.76$, $P < 0.001$; $n=54$, Fig. 5), but no significant trends were found within single treatments, e.g. across meadows in the control plots ($n = 9$; Fig. 5).

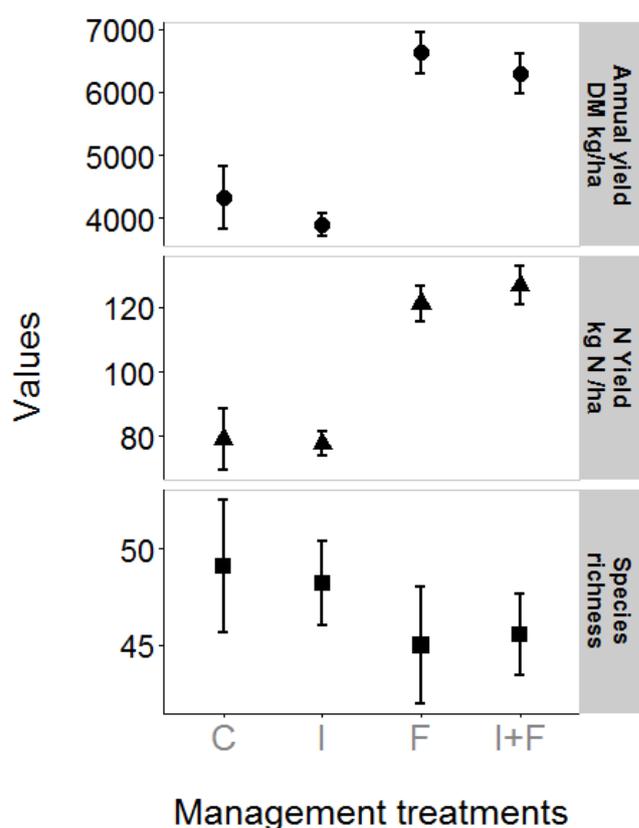


Fig. 4. The separate effects of irrigation and fertilisation tested by the 2 x 2 factorial design on annual vegetation dry mass (DM) and N yields, and plant species richness. C = control (no input); I = irrigation, F = fertilisation, I+F = irrigation + fertilisation. Mean values \pm SE are shown. See Table 4 for statistical analyses.

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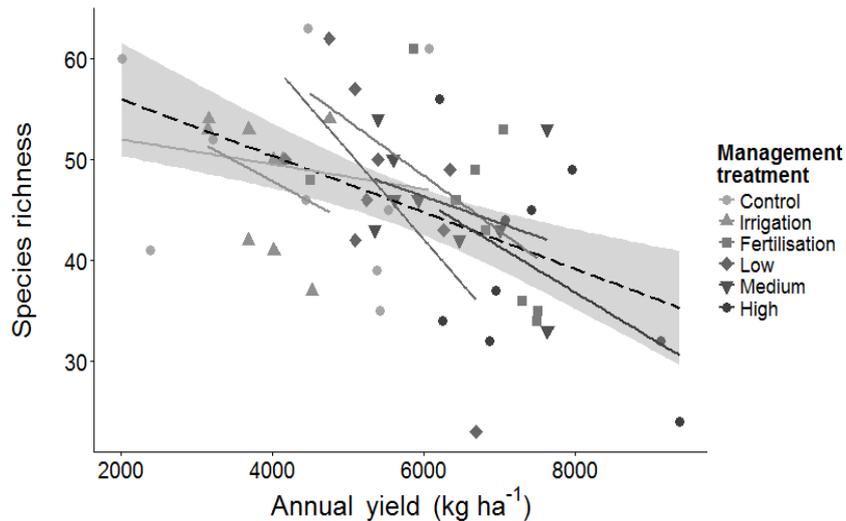


Fig. 5. Relationship between plant species richness (assessed in 8 m² subplots) and annual yield (productivity). The data shown include the 4-level management intensity gradient (consisting of the control without input, the low, medium and high input levels that were fertilised and irrigated at respectively 1/3, 2/3 or 3/3 of the dose that would be necessary to achieve the maximum local hay yield with two hay harvests per year) and the solely irrigated and fertilised treatments. Shorter lines represent the trends within treatments (none significant, $n = 9$ for each) and the dashed line represent the mean trend across treatments ($n = 54$, LMM with treatment and site as random factor; $t = 3.83$, $df = 47.76$, $P < 0.001$), with SE indicated by shaded area.

DISCUSSION

This study experimentally shows that intensification via modern irrigation (sprinklers) and fertilisation (slurry) techniques increases phytomass and N yields, but at the cost of plant species richness. These results are consistent with the large body of literature reporting the effects of agricultural intensification. Grass and forb percentage cover did not vary, but legume cover peaked at medium intensification. Contrary to previous biodiversity and agronomic studies of farming intensification among mountain semi-natural grasslands, which have focused solely on fertilisation (Schellberg et al. 1999; Bassin et al. 2012; Humbert et al. 2016), our research also considers irrigation, separately or in combination with fertilisation. Its originality also resides in experimentally testing a full gradient of farming intensification options, which enables framing concrete recommendations for a sustainable management of mountain hay meadows, from the viewpoint of both agricultural productivity and biodiversity.

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Above-ground agronomic aspects

After five years of experimental management intensification, we evidenced an average increase in phytomass yield of approximately 73% (from ca 4300 to 7500 kg ha⁻¹) when comparing the high-intensity management to the control, confirming our first prediction and in line with former studies. Similar to our current findings, Bassin et al. (2012) obtained an increase in yield of 61% under an N input of 50 kg N ha⁻¹yr⁻¹. In more productive systems than the Alps, where temperatures are warmer and/or precipitation higher, which improves nutrient uptake by plants and can play a strong role in upland grassland productivity (Mamolos et al. 2005), the increase in phytomass yield with nutrient addition is less pronounced, as reported by Brum et al. (2009). These authors found a linear increase in annual DM yield of 18% with N inputs from 0 to 180 kg N ha⁻¹, in a system with two annual harvests after seven years of experimental manipulation in Spanish mountain grasslands. Eventually, a threshold or plateau can be reached after which extra N addition has no further effect on plant growth (Bai et al. 2010). In high plateau grasslands in Inner Mongolia, Bai et al. (2010) tested a gradient of N application ranging from 0 to 175 kg N ha⁻¹yr⁻¹ and found a linear increase in phytomass yield of 271% up to 105 kg N ha⁻¹yr⁻¹, but above this level no further increase in yield was observed.

Fertilisation increased phytomass yield, as expected, but irrigation had contrasting effects at different harvests; a negative effect at the first and a positive effect at the second. This may reflect different large-scale environmental conditions at different times of the season. For instance, the combination of snow-melt and rain as well as mild temperatures (average of 18° C and 75 mm of rain for May and June 2015; Federal Office of Meteorology and Climatology, 2016) may mean that water is likely to be less limiting during the first part of the growing season, therefore irrigation will have less influence on yield. Later in the season, when the climate becomes hotter and drier (average of 23° C and 57 mm of rain for July and August 2015; (Federal Office of Meteorology and Climatology 2016), which is a general rule in the inner Alps, irrigation may have more impact on yield. It is thus likely that irrigation contributed to an increase in yield at the second harvest, releasing plants from hydric stress. In mountain ranges, inter-annual weather variation may further interact with irrigation in such way that during drier years,

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irrigation increases phytomass yield, as found by Andrey et al., 2014 in the same experimental set up as in this study. During other years that are drier, irrigation does not have an effect, as reported here for annual yield, and also by Fahnestock & Detling (1999).

In all management treatments, vegetation N content was higher in the second than at the first harvest, as usually found in meadows where two hay harvests occur per year (Schellberg et al. 1999). The phytomass of the second harvest thus produces a forage of higher crude protein content for livestock (Pontes et al. 2007). As plants grow, their tissues contain increasing proportions of structural and storage materials that contain little N, so that plant protein content progressively declines over time (Greenwood et al. 1990). Before the first harvest, the plants had most likely reached an advanced stage of maturity and thus contained less protein. Under management aiming at increasing yield without adding fertilisers, such as irrigation alone, an increase in hay yield accompanied by a decrease in N content might be expected since no additional nutrients were available for plant's uptake (Duru & Ducrocq 1996). However, our results do not support this, as plant N content did not change despite that phytomass production at second harvest increased with irrigation. Finally, our hypothesis that there would be an increase in N yield (i.e. vegetation N content per unit area) along the intensification gradient since plants would be able to increase their intake of nutrients was supported, and similar results have also been reported in other experimental fertilisation gradients (Reid 1978; Nevens & Rehuél 2003). We should note here that we assessed forage quality by measuring total N yield (e.g. Reid 1978; Dooley et al. 2015), and further analysis to assess forage nutritive value could be done by measuring digestibility (Tallowin & Jefferson 1999; Pontes et al. 2007) which would need further investigation.

Total N and P soil content

There are many factors influencing nutrient retention or buffering the changes in soil N and P content in agricultural ecosystems such as soil texture, aggregate structure, organic matter content or pH (Bauer & Black 1981; Campbell & Souster 1982; Breeuwsma & Silva 1992; Turner & Haygarth 2000). Total nitrogen (N) content in the soil did not differ between the management treatments probably because the soil N pool is very large compared to the

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amount of N added with fertilisation. As mentioned above, Bai et al. (2010) found that a critical threshold of $105 \text{ kg N ha}^{-1}\text{yr}^{-1}$ was reached where the production potential of the existing plant community was saturated with N. Above this concentration, there was little additional increase in aboveground phytomass and N began to accumulate in the soil, as light, water and other nutrients likely became limiting. This finding suggests that soil N saturation for the plant community is not likely to happen in mountain semi-natural grasslands under similar fertiliser concentrations as used in our experiment, where the maximum amount was $40\text{-}80 \text{ kg N ha}^{-1}\text{yr}^{-1}$.

Our results on higher soil P content under solely fertilisation contrasts with the stable soil P content found along the intensification gradient combining both fertilisation and irrigation. Perhaps the total P content in the fertilisation treatment was higher than in the intensification gradient soil because there was no addition of water through irrigation to render soil P more available for plants. Irrigation (i.e. water availability) can play a major role in P uptake by plants. An NP experiment in upland grassland in northern Greece showed that phytomass production was limited by both N and P in dry grasslands, but by N only in inundated grasslands (Mamolos et al. 2005). Irrigation seems to be a good practice to render soil P more available to increase phytomass in mountain grasslands, but we did not find evidence for this in our experiment as total P content was the same in the control and in the irrigated treatment. If we had measured N and P in the forms that are directly available to plant instead of total N and P content in the soil, maybe we would have been able to detect different patterns.

Plant functional group percent cover

A peak in legume relative cover at medium management intensity levels has also been reported in other studies involving a fertilisation gradient (Mountford et al. 1993; Nevens & Rehuel 2003). As N fixers, legume species also need P and K for optimal growth, but compete poorly against grasses under high N levels (Leto et al. 2008; Brum et al. 2009). There is evidence that increased N fertilisation has a negative effect on symbiotic N fixation in several legume species (Nesheim & Øyen 1994; Carlsson & Huss-Danell 2003), as it reduces nodulation and nitrogenase activity in their root systems (Oliveira et al. 2004). This explains the curvilinear pattern observed, namely

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the decrease of legume cover at high N inputs. However, the relative cover of grasses and forbs remained constant along the intensification gradient and this was also the case when testing absolute cover values (data not shown). A closer look at patterns within meadows reveals that forb or grass cover had contrasting patterns from one meadow to another. Also, if forb or grass cover was high in the control, there was a decrease in cover in low and medium intensity level, probably due to specialised species decline and high cover values again under high intensity where competitive species increase in abundance illustrating a turnover in plant community. Plant community composition changes along the intensification gradient, with stress-tolerant species being replaced by competitive species which thrive with high nutrient addition. Therefore, the relative cover of some species increases, while others decrease, resulting in an overall similar total cover within the functional groups. As the plant community is unlikely to be stable after only a 5 year experimental manipulation (Bowman et al. 2006; Clark & Tilman 2008; Yang et al. 2011), grass and some forb species are expected to out-compete legume species under high intensification in the longer term, translating into greater proportional grass and forb cover as we predicted (Mountford et al. 1993; Leto et al. 2008; Brum et al. 2009). The lack of correlation between legume cover and N yield may indicate that the greater proportion of legumes at medium management intensity had a positive effect on phytomass quantity rather than quality, as reported by Spehn et al. (2002).

Plant species richness

Plant species richness declined by 20% along the intensification gradient (from 49 ± 3 to 39 ± 3 species per 8 m^2) across all study sites. Farming intensification has been repeatedly shown to cause plant diversity decline (Díaz et al. 2006; Niedrist et al. 2009; Duru et al. 2015). Furthermore, the greater phytomass production is in response to intensification, the greater decrease in species richness is observed (Humbert et al. 2016). This trend is generally regarded as being principally driven by fertilisation, namely N addition (Maurer et al. 2006; Fischer et al. 2008; Humbert et al. 2016). Yet, in this study we did not find a negative effect of fertilisation on plant species richness when applied alone (2 x 2 factorial design), but only when combined with irrigation (intensity gradient). Irrigation applied alone also

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did not have any effect on plant species richness, confirming other studies findings in mountain hay meadows (Riedener et al. 2013; Melliger et al. 2014). After one year of the experiment onset, fertilisation had a much lesser effect than irrigation on plant species richness (Andrey et al. 2014), but the dry conditions that prevailed in that first season and the short time frame may have led to that peculiar outcome. The present study assessed plant communities five years after the experiment started, meaning that the effects observed here integrate the conditions of several vegetation seasons with varied weather circumstances. As we applied relatively low doses of fertiliser in the “fertilised-only” treatment (ca 50 kg N ha⁻¹yr⁻¹, see Table 1), N inputs was possibly insufficient to trigger a response in species richness after 5 years. However, as found in other studies in mountain grasslands, low doses of N applied over long periods can also lead to similar species richness declines as do high N doses applied for short periods, so N addition could lead to a decrease in species richness because of a cumulative effect on the longer term (De Schrijver et al. 2011; Humbert et al. 2016). It is also possible that there is too little statistical power to detect a trend due to our low number of replicates as other studies found a significant decrease in plant species richness within five years of experimental fertilisation under lower or similar N doses in grasslands (Clark & Tilman 2008; Yang et al. 2011).

Productivity-diversity relationship

The linear decline in species richness with increasing phytomass yield along the intensification gradient across the study meadows (Fig. 5), suggests that our experimental design encompasses above all the right-hand side of the hump-shape relationship between productivity and diversity first described by Grime (1973) and later confirmed in many studies (Mittelbach et al. 2001; Pärtel et al. 2007; Whittaker 2010; Fraser et al. 2015). Given the high variability of ecological characteristics among meadows, we can also observe a negative relationship between productivity and species richness within treatments, with the strength of the trend typically increasing with management intensity (shorter lines on Fig. 5). Although not significant, probably because of lack of statistical power (n=9), these trends also confirm our expectations and suggest that this relationship could be independent of fertilisation and water input. A posteriori, it appears thus that the species-rich

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meadows where we conducted our experiments were probably at the peak of the hump-back productivity-diversity hump-back relationship prior to the start of the experiment, i.e. at an optimal intermediate level of management for plant diversity. In other words, the long-term traditional and extensive management of these mountain meadows, with fertilisation with limited quantities of solid manure and irrigation by gravitational channels, had probably reached an optimum between biodiversity and productivity.

Conclusion

The present results, adding to previous findings from the same experimental research set up, allow framing recommendations for a sustainable balance under modern management practice. As for leaf-and planthoppers (Andrey et al. 2016), plants (Chapter 1) and ground-dwelling arthropods (Chapter 2), slurry fertilisation and sprinkler irrigation at levels corresponding to 1/3 to 2/3 of the inputs necessary to achieve a theoretical maximum hay yield locally seem to represent the best compromise between biodiversity and agronomic objectives in situations where traditional management is given up. These low to medium intensity levels (I+F 1/3 to 2/3) would increase phytomass yield by 26% to 45%, N yield by 40 to 60%, while plant species richness would decrease by 5 to 7%. As it is reasonable to assume that the manipulated plant community will not be stable after the five year duration of this study, and that species richness would likely continue to decrease under steady fertilisation in the longer term, application of the precautionary principle leads to the conclusion that low intensity combining irrigation and fertilisation (I+F 1/3) rather than medium intensity (I+F 2/3) that would be preferred in trading off biodiversity loss against yield increase.

In many situations, farmers who continue to manage the semi-natural grasslands on their farms in a traditional way or at low intensity act against their economic interests. Phytomass yield was 73% greater in high-input meadows compared to the most suitable intensity level for biodiversity in this study. Political support (financial compensation in the form of direct payment) to compensate the cost that production losses represents, is therefore an essential component in mountain grassland biodiversity conservation and should target sustainable management practices.

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Supporting information

Table S.1. Description of the eleven meadows used as study sites with productivity category, elevation and geographic coordinates. Category A: meadows situated at higher elevation with lower productivity; B: meadows situated around mid-elevation with intermediate productivity; C: meadows situated at lower elevation with higher productivity. Fertiliser amount was adjusted for each category (see Table 1) according to the theoretical productivity potential of the site with two hay harvests per year, based on Sinaj et al. (2009). Data from the two meadows in italics; Euseigne and Eison, were incomplete due to logistic practicalities, so they were not included in the analyses.

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

Biodiversity-productivity management tradeoffs

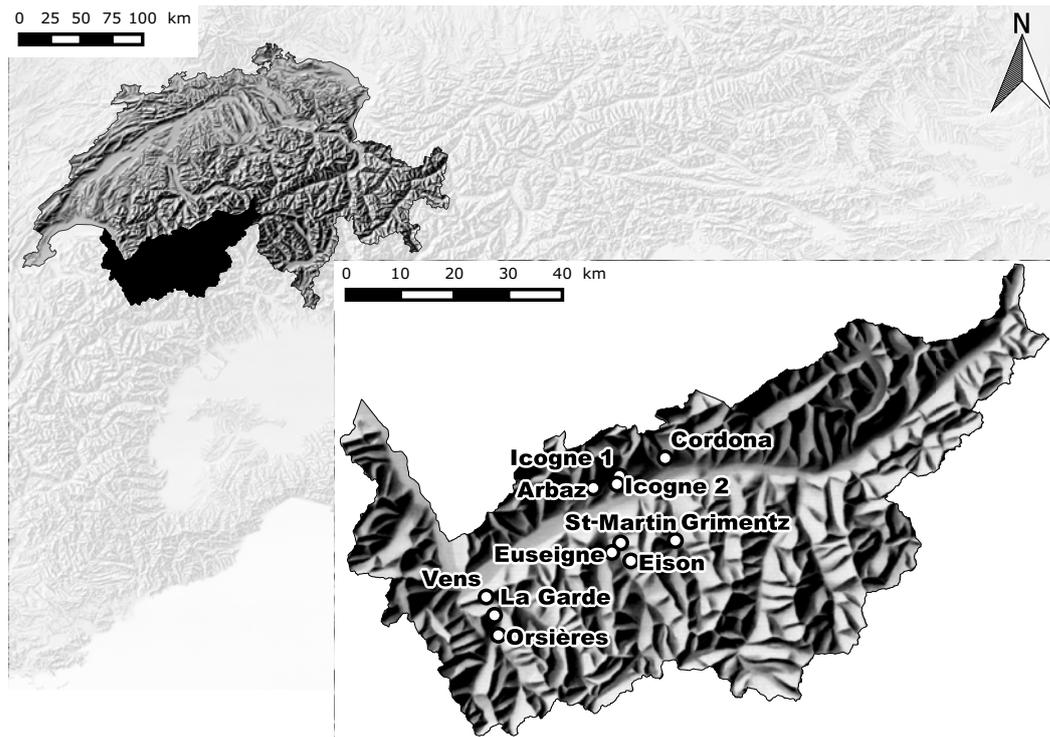


Figure S.1. Location of the eleven study sites in the canton of Valais (outlined in black on the country map), south-western Switzerland. Data from Euseigne and Eison were incomplete due to logistic practicalities, so were not included in the analyses.

General discussion

The effect of grassland intensification on biodiversity have been well researched and the mechanisms behind biodiversity decline are well understood (Fridley 2001; Benton et al. 2003; Suding et al. 2005; Kleijn et al. 2009; Fischer et al. 2010; Kelemen et al. 2013; DeMalach et al. 2017). Numerous actions have been taken to reverse biodiversity decline on farmland, but with little success (Kleijn et al. 2001; Zechmeister et al. 2003; Kleijn & Sutherland 2003; Kleijn et al. 2006; Wilson et al. 2007; Kleijn et al. 2011). The search for a sustainable management have also received attention in mountain areas, targeting the effects of mowing and grazing, with or without fertilisation on plants (Fischer & Wipf 2002; Pecháčková et al. 2010; Valkó et al. 2012), or on insects (Grandchamp et al. 2005; Marini et al. 2008) and targeting the effects of irrigation on plants (Melliger et al. 2014) and plants and gastropods (Riedener et al. 2013). The goal of this project was to investigate the effect of irrigation and fertilisation combined, on a broad range of indicators while also considering agronomic aspects. The aim of this thesis was to provide concrete and practical recommendations for a conservation-productivity balance in mountain semi-natural grasslands, i.e. a sustainable management that would preserve biodiversity while maintaining acceptable levels of hay production. This aim was addressed by experimentally assessing the effect of an intensification gradient, mimicking modern agricultural practices, as well as a 2 x 2 factorial design that allowed disentangling the separate effects of irrigation with sprinklers and slurry fertilisation in eleven species-rich hay meadows in the montane-subalpine belt. The effects of grassland intensification are divided among essential components in the conservation-productivity balance: plants (Chapter 1), and ground-dwelling arthropods (Chapter 2) on the side of biodiversity conservation, and phytomass as well as nitrogen yields on the side of agronomic aspects (Chapter 3).

MAIN OUTCOMES

A better understanding of how various grassland management regimes affect biodiversity is a prerequisite to develop guidelines for regional agriculture policies that efficiently protect the remaining biodiversity (Fischer et al. 2008). This fully controlled field experiment complements and builds on previous observational

studies that evaluated the response of montane and subalpine grassland plant and arthropod communities to intensification (Tasser & Tappeiner 2002; Grandchamp et al. 2005; Marini et al. 2008; Fischer et al. 2008; Niedrist et al. 2009; Humbert et al. 2016). This project also included effects on agronomic aspects, an important component for biodiversity targeted management (Isselstein et al. 2005), which play a critical role in semi-natural grassland preservation as a habitat in the Alps.

First, there is a consensus that grassland plant diversity (Fischer et al. 2008; Niedrist et al. 2009; Humbert et al. 2016; Chapter 1) and phylogenetic diversity (Egorov et al. 2014; Rader et al. 2014, Chapter 1) are declining at local and landscape level because of grassland intensification. Nutrient addition leads to community shifts from specialised, less competitive species to nitrophilous, competitive species, as well as a homogenization of plant communities across agricultural landscapes (Gossner et al. 2016). Competition for light is the main mechanism driving this biodiversity loss (Hautier et al. 2014; DeMalach et al. 2017), where nitrophilous species form a dense overhead vegetation canopy which inhibits the growth of less competitive species (Verkaar & Schenkeveld 1984; Borer et al. 2014). Water addition doesn't seem to have an effect on plant species diversity, confirming the findings of observational studies on irrigation techniques in mountain areas (Riedener et al. 2013; Melliger et al. 2014). The reduction in phylogenetic diversity means that not only the plant community found under high management intensity is poorer in species number, but the species composing this community are more closely related. This plant community's gene pool and evolutionary potential is thus reduced and this can have negative impact on adaptation's possibilities to environment variation (Cadotte et al. 2012), notably with climate change. Therefore, to preserve grassland plant diversity, I recommend a very low intensity management involving one hay harvest a year, without additional input of fertilizer where meadows are still managed as such and with or without irrigation. When flora preservation is of concern, if added, water and nutrients inputs must be limited to 1/3–2/3 of what would be necessary to achieve the maximum hay yield possible locally.

Second, intensification had a positive effect on ground-dwelling arthropod communities, as long as its level remained moderate, as also previously found in observational studies (Pfiffner & Luka 2003; Grandchamp et al. 2005, Chapter 2). Increase in prey density is the most likely explanation (Siemann 1998; Raworth et al. 2004; Andrey et al. 2014). The decrease of spider abundance and the

levelling-off of ground beetle abundance under high intensification might be due to the homogenisation of the vegetation architectural complexity (Greenstone 1984; Luff & Rushton 1989; Woodcock et al. 2007). Therefore, to preserve grassland ground-dwelling arthropod diversity, I recommend a medium intensity management involving two hay harvests a year and irrigation and fertilisation at levels corresponding to two-thirds of the quantity necessary to achieve local maximum hay yield.

Third, as expected, grassland intensification increased phytomass productivity and nitrogen (N) yield (Reid 1978; Brum et al. 2009, Chapter 3). As widely demonstrated in the literature, when soil nutrients are no longer limiting, plant species richness was negatively correlated with phytomass across the intensity gradient (Grime 1973; Guo & Berry 1998; Fraser et al. 2015, Chapter 3). The hump-shaped productivity-diversity hypothesis posits that plant diversity peaks at intermediate levels of phytomass production (Grime 1973; Mittelbach et al. 2001; Fraser et al. 2015). On the left-hand side of the hump-back curve where phytomass productivity is low, it has been experimentally demonstrated that, in nutrient-limited soil (without artificial inputs, as in natural circumstances), grassland plant diversity has a positive effect on productivity, soil nutrient use and nutrient retention thanks to niche complementarity (Tilman & Downing 1996; Tilman 1999; Marquard et al. 2009). The mechanisms proposed are that interspecific differences in the use of resources by plants allow more diverse plant communities to utilize more fully limiting resource and thus attain greater productivity (Naeem et al. 1994; 1995). In addition, greater nutrient utilization at higher species diversity results in lower leaching of soil nitrogen, contributing to the sustainability of nutrient cycling and soil fertility in these ecosystems that maintains this favourable environment for high biodiversity at all trophic levels (Vitousek et al. 1993; Grigulis et al. 2013). On the right-hand side of the hump-back curve where phytomass productivity is high, only a few nitrophilous, highly competitive species that thrive with high nutrient addition predominate and form a thick canopy obstructing light for the lower ground vegetation. Competition for light is the main mechanism driving the decrease in plant species richness (Hautier et al. 2009; DeMalach et al. 2017), as explained above for Chapter 1. As shown in Chapter 3, plant species richness was negatively correlated with phytomass across the intensity gradient, confirming that this agro-ecosystem is situated on the right-hand side of the hump-shape relationship, as often found in studies comparing

species richness and live phytomass (Fraser et al. 2015). There is no single level of management intensity that simultaneously maximizes phytomass yield, which was greatest under high intensification and plant biodiversity which was greatest without intensification (i.e. control). However, a biodiversity-productivity trade-off emerged at one third of the quantity of water and slurry inputs necessary to achieve maximum local hay yield.

The different components of semi-natural grasslands investigated in this thesis responded differently to grassland intensification, as found when merging the findings from the three chapters together (Fig 1).

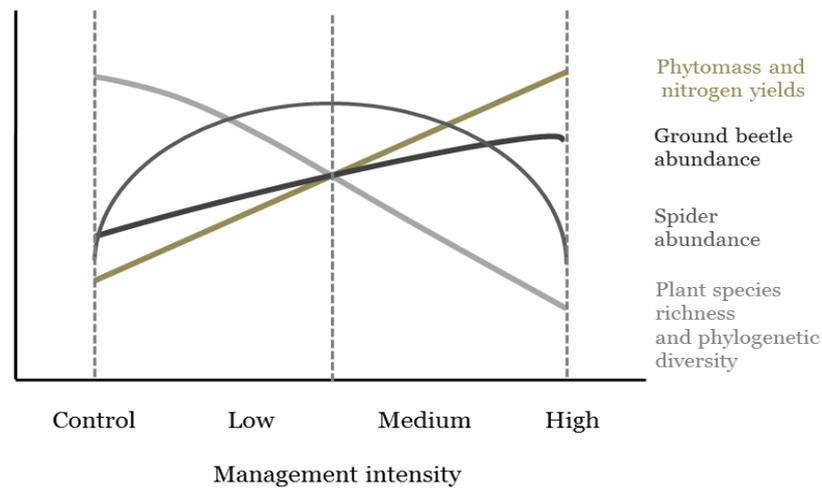


Figure 1. Schema of significant trends detected for biodiversity and agronomic aspects of semi-natural grassland along an experimental management intensity gradient involving irrigation and fertilisation in this thesis.

Grassland intensification also had different impact on various indicators measured at different time in the same research project. After the first year of the experiment, in 2011, plant species richness, vegetation structure, plant-associated arthropod abundance and biomass as well as phytomass production increased with irrigation and fertilisation combined (Andrey et al. 2014). The overall impacts of intensification were positive on biodiversity and agronomic outputs in the short term. Medium intensification as applied then might have indeed promoted high plant species richness because it rapidly offered favourable conditions to species thriving with high nutrient availability, normally absent on nutrient-poor

and dry soils, adding to the community composed of stress-tolerant species. The increase in plant-associated arthropod biodiversity might be associated with the gain in vegetation structure (Dittrich & Helden 2012). In 2012, during the second year of the experiment, leaf- and plant-hopper species richness, abundance and biomass increased with low intensification and remained stable under medium and high intensification (Andrey et al. 2016). Low intensification was likely to boost the biomass and nutritional quality of plants, increasing the survival or the reproductive performance of leaf- and plant-hoppers, and so being beneficial for their biodiversity (Sedlacek et al. 1988). In 2013, intensification had a negative impact on both orthopteran density and species richness, most probably because of temperature decrease in the plant canopy (Delley 2014). Arthropods depend on microhabitat temperature for their development, activity and reproduction, which varies with vegetation height and density (Song et al. 2013). This pattern was also found for caterpillar abundance in 2014, likely for the same reason related to temperature (Dosch 2014). In 2015, land snail abundance responded positively to intensification (Dani, unpublished), but species richness did not change. Snails are strongly dependent on moisture for survival in grasslands (Dvořáková & Horsák 2012) and moisture level is probably highest under a thick vegetation canopy, as found under high intensity management. For arbuscular mycorrhizal fungi (AMF), grassland intensification only had a negative impact under high intensity management, also in 2015 (Herzog 2016). AMF create a symbiotic relationship with the majority of terrestrial plants and their mycelia colonise plant roots, enhancing water and nutrient uptake in exchange for supply of sugars (Brachmann & Parniske 2006). Under high management intensification, plants are less likely to invest resources in creating a symbiosis with AMF as nutrients are less limiting with high inputs of fertilisers. The coexistence of all targeted species, which served here as indicators, would thus be maximized thanks to different management intensities across mountain and subalpine semi-natural grasslands.

REFLECTIONS/THOUGHTS/INSIGHTS

Four to five years might appear to be a rather short time period for evaluating arthropod and plant communities within the experimental setup. However, studies of the impact of management intensification on hay meadow biodiversity have detected stabilisation of botanic composition after 3-8 years, depending on the level of fertilisation applied (Bowman et al. 2006; Clark & Tilman 2008;

Yang et al. 2011). Also the short reaction time of ground-dwelling arthropods to changes in land use have been emphasized in previous studies (Perner & Malt 2003; Gerlach et al. 2013). These organisms are thus powerful indicators to assess grassland intensification impacts (Pfiffner & Luka 2003). The time frame of this experiment is therefore reasonable, and appears to be sufficient to detect impacts that can be used to support management advice. However, the trends described here for each indicator might change if the experiment would continue further. Long-term experiments, observational studies and monitoring are thus very important to understand grassland diversity dynamics.

In the Chapter 1, the experimental treatments were the fixed effects in the models, and were considered as categorical variables (C, I, F, I+F 1/3, I+F 2/3, I+F 3/3), illustrating changes in plant diversity from one treatment to the next. The `relevel` function in R, which allows changing the reference level of the fixed effects, was used to carry out multiple comparisons between treatments when performing the linear mixed-effect models. I intentionally did not apply any correction for multiple comparisons because, in a conservation context, I opted for the risk of making a type I rather than a type II error. In effect, the precautionary principle states that a false positive (a difference erroneously found between treatments) is better than a false negative (a true difference between treatment not detected) (Underwood & Chapman 2003). This ensures that any recommendations are conservative in the context of preservation of grassland biodiversity (Noss 1994). However, analysing the data in this way, I detected significant changes in plant species richness only between the control and the high intensity level treatment (I+F 3/3), whereas when considering experimental treatment as a continuous variable, as in Chapter 3, I could detect a significant drop in species richness as management intensification increased. I acknowledge that these data were taken during different years (2014 in first chapter and 2015 in third chapter). However, after re-running the analysis with phylogenetic diversity (2014 data) and experimental treatments as continuous variable, the same pattern was indicated as for plant species richness (i.e. a significant drop in phylogenetic diversity as management intensification increased). These results highlight the fact that different ways of analysing the data can influence the outcomes and have important implications including changing management recommendations.

In Chapter 2, the response of ground-dwelling arthropods to grassland management was clearer when considering abundance rather than species richness

data because it takes longer for species to disappear than to become rarer. I could also detect a change in community variability among sites when using the Chao or Morisita-Horn indices, but not with the Bray-Curtis index. This highlights that the trend detected in different diversity analyses will depend on the form of data that are collected (species counts vs abundance) or type of index used. This can in turn have serious implications for data interpretation and the preparation of conservation advice (Gering et al. 2003; Dahms et al. 2010). This emphasizes the need for considering a variety of diversity measures, indices and indicators when aiming at conserving biodiversity, as achieved in this thesis.

In studies on nutrient addition impacts, atmospheric N deposition has proved to contribute to the disruption of ecosystem properties (Vitousek 1997) as well as plant biodiversity decline (Stevens et al. 2004), and could have an effect on grassland soil nutrient dynamics. According to governmental studies, atmospheric N deposition is considered to be low in Swiss montane and subalpine areas (5 to 10 kg N ha⁻¹yr⁻¹; FOEN 2015). This is especially the case in dry inner-Alpine valleys with low wet deposition rates and low local emissions (Rihm & Kurz 2001). In another study, observed species richness of plant species targeted for conservation in mountain grassland was negatively related to modelled N deposition, so the authors claim that airborne N deposition may counteract conservation efforts (Roth et al. 2013). In developing guidelines regarding mountain grassland management, atmospheric N deposition should therefore also be considered in addition to fertiliser amounts allowed if the goal is to maintain plant species richness. In this study, the effect of atmospheric N deposition were not studied, but were implicitly included in the control plots, so it can be argued that our management recommendations do take this factor into account.

COLLABORATIVE FRAMEWORK WITH STAKEHOLDERS

Central Europe is composed of human-dominated landscapes, and conservation strategies are a matter of public debate over which type of ecosystem or landscape is wanted and should have priority for conservation (Tscharntke et al. 2005). Since social and political decision-making plays a large role in managed ecosystems, researchers must involve land managers, politicians and other stakeholders to engage with both the ecological and socioeconomic factors that determine biodiversity conservation, its functions, and the tradeoffs between different

management scenarios (Suding et al. 2005; Ban et al. 2013). On the other hand, stakeholders must also acknowledge that conservation measures must be based on objective scientific evidence if they are to be effective (Sutherland et al. 2004; Soulé et al. 2005; Svancara et al. 2005).

To optimise the likelihood that the results presented in this thesis would be taken into consideration in the establishment of regional guidelines for sustainable farming management, this research project was carried out within the collaborative framework of an accompanying group. The members of the accompanying group included representatives of associations for Agriculture Development and Rural Affairs (AGRIDEA), cantonal authorities and Federal Offices for the Environment (FOEN) and Agriculture (FOAG), and scientists with agronomic and conservation backgrounds (AGROSCOPE and Bern University). This framework was used to link the themes and issues faced by conservation science and practices as well as to bridge the gap between research outputs and public actions (Arlettaz et al. 2010; Braunisch et al. 2012; Cook et al. 2013).

CONCRETE MANAGEMENT RECOMMENDATIONS

In the light of the results from each chapter in this thesis linked with the results found for the other indicators studied within this research project, I conclude that there is no single management regime that favours all grassland agro-ecosystem components investigated. Therefore, I suggest a heterogeneous management regime applied across the mountain agricultural landscape. Accommodating various forms of diversity is important to ensure that the remaining semi-natural grasslands harbour the greatest possible array of species ecologies, which provide multiple functions that sustain and regulate services that benefit the human population. I thus agree with other authors that heterogeneity at multiple spatial scales (i.e. within farm or landscape) is considered as a major factor contributing to the preservation of biodiversity in farmland areas (Kruess & Tschardt 2002; Benton et al. 2003; Fischer et al. 2008; Vickery & Arlettaz 2012; Rader et al. 2014).

More specifically, diverse management regimes ranging from no inputs with one hay harvest per year to irrigation and fertilisation using up to 2/3 of the amount that would be necessary to achieve the maximum theoretical local hay yield at the farm to landscape level would allow the maintenance of a broad range

of biodiversity indicators in mountain semi-natural grasslands. Where meadows are still extensively managed, roughly equivalent to the control (no inputs with one hay harvest a year) or irrigated- only plots, management must remain extensive to maintain high plant species richness, phylogenetic diversity, as well as caterpillars, orthopterans and AMF diversity. Where traditional management is progressively abandoned, low to medium management intensity (1/3-2/3 I+F) with modern farming techniques (slurry spraying and aerial irrigation) is preferable to high intensification or land abandonment in order to maintain a somewhat species-rich plant community, high abundance of plant-and ground-dwelling arthropods, and snails typical of open habitats.

A medium management intensity (2/3 I+F) is also preferable to high intensification or land abandonment according to our results as it would retain 93% of plants species present in meadows under extensive management, as well as high ground-dwelling arthropod diversity. However, given the cumulative effect of nitrogen addition over time (De Schrijver et al. 2011; Humbert et al. 2016), the precautionary principle leads to the conclusion that irrigation and fertilisation combined at low rather than medium intensity would be preferable in trading off biodiversity loss against yield increase. Indeed, it is reasonable to assume that the manipulated plant community is not yet stable after the five year duration of this study, and that species richness would likely continue to decrease under steady fertilisation in the longer term (Yang et al. 2011).

Local agricultural policies must support evidence-based recommendations, for example by offering financial compensation adapted to the potential hay production loss to farmers willing to apply a low to medium intensity management (Strijker 2005; Marini et al. 2008). Frequent biodiversity surveys could be conducted in the meadows belonging to the farmers who receive compensation to ensure that grassland diversity is maintained in the long term. This would ensure the sustainable exploitation of mountain grasslands, achieving a compromise between biodiversity preservation and hay production.

DIRECTIONS FOR FUTURE RESEARCH

In this thesis, results on diversity of plant and predatory arthropods as well as agronomic aspects are presented after four to five years of experimental grassland management intensification in order to develop management recommendations.

As the field experiment finished in 2015, the management recommendations were formulated based on longest time possible within the frame of the research project. A further way to explore the data would be to make a temporal study of the impact of grassland management intensification on biodiversity, comparing datasets from 2010 (baseline data before the onset of the experiment), and onwards within this research project. The changes in species richness and abundance of various indicators could thereby be quantified with intensification through time (Table 1).

Table 1. Biodiversity indicators and agronomic aspects were measured at different times during the experimental research project testing grassland intensification in mountain semi-natural grasslands. Symbols in the table represent the trend for various taxa diversity comparing to the baseline data in 2010 or to data from the control within the same year.

	Baseline data 2010	2011	2012	2013	2014	2015
Plants	√	+	=		-	-
Biomass quantity	√	+	+			+
Biomass quality	√		+			+
Cicadas (Auchenorrhyncha)	√		+			=
Orthoptera					-	
Snails	√					+
Caterpillars					-	-
Spiders					+	
Ground beetles					+	
Arbuscular mycorrhizal fungi						-

Biodiversity is described as “the totality of the species (including the genetic variation represented in the species populations) across the full range of organisms, i.e. invertebrate animals, protists, bacteria and fungi, above- and below-ground, as well as the vertebrates and plants” (Swift et al. 2004). Along this line, a recent study proposed a multidiversity approach, measuring species richness and abundance of nine trophic groups from primary producers, passing through above- and below-ground herbivores and predators, detritivores, soil microbial decomposers, plant symbionts, to bacterivores, to investigate links between grassland biodiversity and functionality (Soliveres et al. 2016). Such an approach could also be used to assess the impact of farming intensification on mountain semi-natural grassland biodiversity with more time and resources.

The importance of protecting grasslands in mountainous regions is increasingly being recognised worldwide (International Mountain Society 2003;

Hurni et al. 2013; Newbold et al. 2016). As mountain farmland intensification is a phenomenon common to many countries (e.g. Tasser & Tappeiner 2002; Fischer et al. 2008; Niedrist et al. 2009), a pan-European action plan could be developed to address mountain semi-natural grassland protection. Some authors and organisations have shown interest in portraying the situation of semi-natural grassland on a European scale (Strijker 2005; Emanuelsson 2008). The European Commission (2008) launched the LIFE Programme to support environmental, nature conservation and climate action projects throughout the European Union. Several initiatives have been developed to protect mountain *Nardus* grasslands and steppes in individual countries. To better understand the problem at a wide scale, further research could link geographic information systems (GIS), such as orthophotographs, with visits in the field and interviews with farmers, to quantify the proportion of species-rich grassland remaining across the Alps. The progression in proportion of grasslands that were abandoned, intensified or remained under low-intensification in recent decades could be also described with GIS, in a similar way that Lachat et al. (2011) applied at the country scale for Switzerland, but for the whole Alps. A consortium could thus be created to gather researchers and stakeholders from the different countries involved to develop a plan to protect remaining species-rich semi-natural mountain grasslands.

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“What you do makes a difference, and you have to decide what kind of difference you want to make“

– Jane Goodall



Pour que fleurs et
criquets repeuplent la
prairie

AURÉLIE COULON

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: **Lessard-Therrien Malie**
Matrikelnummer: **13-140-678**
Studiengang: **Phil.-nat. Ökologie und Evolution**

Bachelor Master Dissertation

Titel der Arbeit: **A balance between productivity and biodiversity conservation in montane and subalpine semi-natural grasslands**

Leiter der Arbeit: Prof. Dr. R. Arlettaz
Dr. Jean-Yves Humbert

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Bern,
Ort/Datum

.....
Unterschrift

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INTERESTS AND AMBITIONS ---

I became a field biologist because of my love for the outdoors and my curiosity towards the natural world. My research is driven by an interest in current anthropogenic impact on ecosystems and methods to combine resources exploitation/land use and preservation of biodiversity. I want to develop an international career with hands on experiences in conservation ecology, working towards providing evidence based recommendations on sustainable management practices.

EDUCATION ---

- Ph.D. 2014-2017 (finishing in April), **Bern University**, Switzerland
Conservation Biology, thesis title: A balance between productivity and biodiversity in mountain semi-natural grasslands
- M.Sc. 2011- 2013, **McGill University**, Canada
Biology, thesis title: A phylogenetic study of flowering phenology in tundra plants of the Canadian sub-Arctic
- B.Sc. 2007-2010, **Sherbrooke University**, Canada
BSc degree in Ecology, COOP program

PUBLICATIONS ---

- Lessard-Therrien, M.**, Humbert, JY., & Arlettaz, R. (2017). Experiment-based recommendations for biodiversity-friendly management of mountain hay meadows. *Applied Vegetation Science*, in press. doi: 10.1111/avsc.12309
- Lavanchy, G., Strehler, M., Llanos Roman, M. N., **Lessard-Therrien, M.**, Humbert, J. Y., Dumas, Z., ... & Schwander, T. (2016). Habitat heterogeneity favors asexual reproduction in natural populations of grasthrips. *Evolution*, 70(8), 1780-1790.

Lessard-Therrien, M., Bolmgren, K., & Davies, T. J. (2014). Predicting flowering phenology in a subarctic plant community. *Botany*, 92(10), 749-756.

Lessard-Therrien, M., Davies, T. J., & Bolmgren, K. (2014). A phylogenetic comparative study of flowering phenology along an elevational gradient in the Canadian subarctic. *International Journal of Biometeorology*, 58(4), 455-462.

GRANTS AND AWARDS

- 2017 Best student talk in Conservation and Systematics, Biology17, Bern University
- 2013 International Internship Award, FQRNT
- 2013 Graduate Excellence Award, McGill University
- 2012 QCBS Excellence Award
- 2012 Mobility Award, McGill University
- 2012 Graduate Travel Award, McGill University
- 2012 Northern Scientific Training Program Grant, Departement of Indian Affairs and Northern Development Canada
- 2011 Graduate Excellence Fellowship, McGill University
- 2009 Ministère des Loisirs et du Sport Grant, Québec
- 2009 Paul Desmarais Award, Université de Sherbrooke
- 2007 Gaspésie-Les-Iles Grant

TEACHING EXPERIENCE

2014 - 2016 Teaching assistant at Bern University, Switzerland

- 417310 Statistics for biology, practical
- 100329 Conservation biology, practical
- 100329 Conservation biology, statistics

2011 – 2013 Teaching assistant at McGill University, Canada

- BIOL310 Biodiversity and Ecosystems, practical
- BIOL112 Cell and Molecular Biology, practical
- BIOL111 Principles: Organismal Biology, practical

WORKSHOP ORGANISATION

- 2017 Linear Model Workshop Using Bayesian Methods, University of Bern
- 2017 Data management for evolutionary ecologists, University of Bern
- 2016 Data wrangling and plotting with R, University of Bern

Malie Lessard-Therrien, CV

PRESENTATIONS

Invited seminars (host indicated in parentheses)

- 2015 University of Lausanne, Switzerland (Dr. Jonathan Rolland & Prof. Nicolas Salamin)
- 2015 Agroscope, Switzerland (Prof. Marcel van der Heijden)
- 2014 University of Siedlce, Poland (Dr. Marzena Stańska & Prof. Barbara Kot)
- 2014 Institute of Plant Science at Bern University, Switzerland (Prof. Markus Fischer)

Conference and symposiums (presentation type indicated in parentheses)

- 2017 Biology17, Bern, Switzerland (talk)
- 2016 Ecological Society of Germany, Austria and Switzerland annual meeting, Marburg, Germany (talk)
- 2016 British Ecological Society symposium, Cambridge, United Kingdom (poster)
- 2015 International Congress for Conservation Biology, Montpellier, France (poster)
- 2015 Student Conference on Conservation Science, Cambridge, United Kingdom (poster)
- 2014 Québec Center for Biodiversity Science, Montréal, Canada (talk)
- 2013 Québec Center for Biodiversity Science, Montréal, Canada (talk)
- 2012 Phenology, Future Climate and the Living Earth, Milwaukee, United States (poster)

Public outreach

- 2017 PhD project results, Agriculture Service, Sion, Switzerland
- 2016 Meeting with farmers, Vétroz, Switzerland
- 2010 Eastern Grey Kangaroos, Gerald McShane Elementary School, Canada
- 2009 Blue whale behavior, Sherbrooke University, Canada

PROFESSIONAL EXPERIENCE

- 2011 Research assistant McGill Sub-Arctic Research Station, Canada
 - Responsible for set up of experimental design on Mount Irony, Labrador
 - Completed and extensive flora survey and herbarium montage
 - Demonstrated excellent team work and leadership in remote locations and extreme weather
- 2009 Research assistant in Wilson's Promontory Park, Australia
 - Aided in capturing and marking Eastern Gray Kangaroos
 - Compiled behavioral observations and morphological data
- 2009 Research assistant at CICIMAR, Mexico
 - Monitored blue whale population in Gulf of California
 - Responsible for collecting tissues samples and behavioral observations
 - Participation in photographic documentation of blue and fin whales

2008 Guide at the National Parc Ile-Bonaventure-et-du-Rocher-Percé in Percé (Qc), Canada

- Gave group presentations on marine wildlife
- Demonstrated excellent public communication
- Monitored seal population on Bonaventure island

ACADEMIC EXPERIENCE

2016 Volunteer at BIOLOGY16 conference, Lausanne, Switzerland

2015 Organization of PACE15 (Plant and Animal Conservation Ecology) conference, Dübendorf, Switzerland

2013 AB-326 Graduate course on Arctic Plant Ecology at UNIS, Svalbard, Norway

2012 Volunteer at the annual Québec Center for Biodiversity Science symposium, Montreal, Canada

2012-2013 Research collaboration at Stockholm University, Sweden

- Use of phylogenetic statistical tools
- Specialized phenology analysis
- Research network development