



Functional response of leaf- and planthoppers to modern fertilisation and irrigation of hay meadows

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Abstract

In the drier regions of the European Alps, traditional land-use of montane and subalpine meadows, i.e. extensively managed with solid manure application and irrigation via water channels, is currently shifting towards application of slurry and aerial irrigation. The impact of these new practices upon biodiversity remains poorly understood and calls for quantitative assessments of their effects. Relying on a full block design, we tested the effects of six management treatments corresponding to an increasing gradient of farming intensification (fertilisation with slurry and/or irrigation with sprinklers) on Auchenorrhyncha (Hemiptera) communities occurring in the inner Swiss Alps. The experimental set up consisted of: control plots (no fertiliser, no irrigation; C-plots); plots that received only fertiliser (F-plots); plots that were only irrigated (I-plots); and plots that received low-, medium- and high-input of fertiliser and water (F + I 1/3-plots; F + I 2/3, F + I 3/3-plots; 3/3 corresponds here to the input level necessary for achieving maximum theoretical hay yield locally). After two years of experimental treatment (2012), plots that were only fertilised or only irrigated showed no change in the population sizes of Auchenorrhyncha, while plots that received low-, medium- and high-input of fertiliser and water harboured significantly higher abundances (1.9, 1.5 and 1.4 times higher, respectively), biomass (1.8, 1.6 and 1.8 times higher, respectively), as well as species richness (+27–30%, on average) than control plots. Abundances and species richness were also higher in plots with low-input of fertiliser and water compared to fertilised only plots. Monophagous and oligophagous species were most abundant in plots with low-input of fertiliser and water. Medium- and high-input treatments (F + I 2/3 and 3/3) increased the number of generalist (eurytopic) species, while only low-input treatment (F + I 1/3) boosted the more specialised (stenotopic) species. This provides support to the hump-shaped diversity-disturbance relationship and guidance for sustainable management of biodiversity-rich mountain hay meadows.

Zusammenfassung

In den trockeneren Gebieten des europäischen Alpenraums findet zurzeit eine Veränderung in der landwirtschaftlichen Nutzung von Wiesen der montanen und subalpinen Höhenstufen statt: Extensive Bewirtschaftungsformen wie das Einbringen von Feststoffdünger und eine Bewässerung mit Hilfe von Wasserkanälen werden dabei zunehmend durch den Einsatz von Gülle und Sprinkleranlagen ersetzt. Wie sich diese Bewirtschaftungsmaßnahmen auf die Biodiversität auswirken ist jedoch noch weitgehend unbekannt und quantitative Erhebungen dazu fehlen noch weitgehend. In einem Freilandversuch mit je 6

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unterschiedlich intensiv bewirtschafteten Probeflächen im Block-Design wurden die Auswirkungen von Flüssigdünger- und Sprinklereinsatz auf die Artengemeinschaften von Zikaden (Auchenorrhyncha, Hemiptera) im inneralpinen Gebiet der Schweiz untersucht. Das experimentelle Grundschema bestand jeweils aus einer Kontrollfläche (ohne Dünger und Bewässerung: C-Fläche), einer nur gedüngten Fläche (F-Fläche), einer nur bewässerten Fläche (I-Fläche) und weiteren 3 Flächen, die jeweils eine niedrige, mittlere oder hohe Dosis an Dünger und zusätzlichem Wasser (F+I 1/3, F+I 2/3, F+I 3/3) erhielten. Der Intensivierungsgrad F+I 3/3 entspricht dabei dem Wasser- und Düngemiteleintrag, der für einen maximalen, theoretisch an einem Standort erzielbaren Heuertrag benötigt würde. Nach zweijähriger Projektlaufzeit konnten auf Flächen, welche entweder nur gedüngt oder nur bewässert wurden, keine Veränderungen bei den Populationsgrößen der Zikaden festgestellt werden. Der Einsatz einer Kombination von Dünger und Bewässerung (niedriger, mittlerer und hoher Intensivierungsgrad) führten hingegen zu signifikant höherer Abundanz (1.9-, 1.5-, 1.4-fach), Biomasse (1.8-, 1.6-, 1.8-fach) und einem grösseren Artenreichtum (im Durchschnitt +27–30%) der Auchenorrhyncha. In Probeflächen mit niedriger Wasser und Düngemittelzugabe waren Abundanz und Artenreichtum höher als in nur gedüngten Flächen. Auch waren monophage und oligophage in diesen Flächen am häufigsten. Mittlere und hohe Intensivierungsgrade (F+I 2/3 und F+I 3/3) führten zudem zu einer Förderung der (eurytopen) Generalisten, während sich niedrige Dosen an Dünger und Wasser (F+I 1/3) positiv auf spezialisierte (stenotope) Arten auswirkten. Dieser Befund bestätigt die Theorie einer glockenförmig verlaufenden Beziehungskurve zwischen biologischer Diversität und Bewirtschaftungsintensität und eröffnet Möglichkeiten für eine nachhaltige Bewirtschaftung von artenreichen Heuwiesen im Berggebiet.

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Introduction

In the past 50 years, management of montane and sub-alpine meadows of Western and Central Europe has shifted from traditional practices with no or low input of solid animal manure to more mechanised practices with higher input of fertilisers, essentially in the form of liquid manure (Strijker, 2005). In addition, in the drier inner and southern valleys of mountain massifs such as the European Alps, hay meadows are also irrigated. For centuries, gravitational, terrestrial irrigation systems conducting water from the main tributaries to the cultivated slopes have been used. Yet, this traditional system has been progressively abandoned and replaced by underground water pipe networks conducting water to aerial sprinklers, which require far less maintenance (Crook & Jones, 1999). These marked changes of farming practices have negatively impacted the biodiversity of plants, arthropods and vertebrates found in traditionally managed mountain meadows (e.g. Britschgi, Spaar, & Arlettaz, 2006; Riedener, Rusterholz, & Baur, 2013).

Farming intensification in mountain grasslands results from increasing fertiliser and/or water inputs, which enhances phytomass production but induces a reduction of plant species richness (Dietschi, Holderegger, Schmidt, & Linder, 2007; Homburger & Hofer, 2012; Humbert, Dwyer, Andrey, & Arlettaz, 2016). The resulting alteration of vegetation structure (Andrey, Humbert, Pernollet, & Arlettaz, 2014) and microclimate can in turn positively or negatively affect arthropod abundance, biomass and species richness, with the direction of response depending on the taxon (e.g. Delley, 2014; Grandchamp et al., 2005). In line with the hump-shaped hypothesis (Mittelbach et al., 2001), several

studies have suggested that an intermediate level of grassland management intensity, notably a low or moderate input of fertiliser and/or water, may indeed benefit productivity and fodder nutritional quality, as well as plant species richness (Bowman, Gartner, Holland, & Wiedermann, 2006; Jeangros & Bertola, 2000; Peter, Gigon, Edwards, & Lüscher, 2009). Although this might in turn boost resources for herbivorous arthropods (Andrey et al. 2014; Grandchamp et al., 2005; Haddad, Haarstad, & Tilman, 2000), a recent meta-analysis by Humbert et al. (2016) pointed out a lack of experimental studies on the effects of intensification upon grassland arthropod communities.

To fill this knowledge gap, we launched a series of controlled experiments with the objective to quantitatively define whether an optimal trade-off exists in terms of degree of grassland management intensity, looking in particular at hay production versus maintenance of biodiversity and related ecosystem functions. The research was conducted at 12 replicated sites in the SW Swiss Alps, among traditionally managed montane and subalpine hay meadows (no or low input of solid manure, and occasional terrestrial irrigation). Six different experimental treatments were applied to the study plots from 2010 onwards, generating a full factorial design and a gradual level of fertilisation and irrigation. The study plots were sufficiently large (20 m diameter; 314 m²) to allow investigating the responses of plant and arthropod populations to experimental manipulation of management type and intensity. As study models, we selected Auchenorrhyncha (Hemiptera: Fulgoromorpha and Cicadomorpha), also known as plant-, frog- and leafhoppers. This taxon is highly diverse and fairly abundant in grasslands, and is considered an excellent bioindicator, notably of

land-use change (reviewed in Biedermann, Achtziger, Nickel, & Stewart, 2005). In addition, these primary consumers play an important role both as prey for upper trophic levels in the food chain (Moreby & Stoate, 2001) and in nutrient cycling (Andrzejewska, 1979). Finally, their diversity of ecological traits, notably in terms of trophic specialisation (mono-, oligo- and polyphagous) and species-specific habitat associations (steno- and eurytopic) provides opportunities for mechanistic investigations of ecological functionalities.

The plots had all been very extensively managed for years before the onset of our experiments. We thus expected a marked response of Auchenorrhyncha (abundance, biomass and species richness) to the intensity gradient of our experimental manipulations. More specifically, we predicted an increase of food resources and niche availability for non-graminoid feeders and generalist Auchenorrhyncha (polyphagous and eurytopic species), which should both increase in abundance and species richness (Di Giulio, Edwards, & Meister, 2001). This prediction is based on the findings by Andrey et al. (2014), drawn from the same experimental set up as here, who showed that irrigating and fertilising increased the relative cover of non-graminoid plants (mostly legumes). Although the relative coverage of grasses decreased in Andrey et al. (2014), Humbert et al. (2016) found that grass biomass generally increases with nitrogen addition, thus we expected no detectable or positive effects of intensification on graminoid-feeding Auchenorrhyncha. Conversely, a negative impact of intensification was predicted for specialists (monophagous and stenotopic species) that are known for their higher sensitivity to even slight modifications of their habitat (Nickel & Hildebrandt, 2003). Based on our results we shall frame concrete recommendations for biodiversity-friendly management of mountain hay meadows, notably as concerns slurry application and sprinkler irrigation.

Materials and methods

Study sites

Twelve traditionally managed montane and subalpine hay meadows (790–1740 m above sea level) were selected within the inner Alps (Central Valais, SW Switzerland) in 2010, primarily based on farming history: they had to be managed extensively since at least the year 2000, with no or very low levels of fertilisation and irrigation and only a single cut per year (Tables 1 and 2). In reality, most study meadows had probably been managed traditionally for decades if not centuries. Meadow area (>4000 m²) was an additional selection criterion. Central Valais is characterised by a continental climate, with cold winters, and dry and hot summers.

Table 1. Description of the twelve study sites with altitude and exact geographical coordinates.

Sites	Name	Altitude [m]	Coordinates	
			Latitude	Longitude
1	Sembrancher	798	46°4'24" N	7°8'36" E
2	Orsières	1022	46°1'44" N	7°9'8" E
3	Euseigne	1028	46°10'9" N	7°25'27" E
4	Icogne 2	880	46°16'42" N	7°26'10" E
5	La Garde	980	46°3'45" N	7°8'35" E
6	Vens	1373	46°5'7" N	7°7'24" E
7	Arbaz	1270	46°16'42" N	7°22'47" E
8	Icogne 1	1200	46°17'56" N	7°26'31" E
9	Cordona	1153	46°19'45" N	7°33'8" E
10	Eison	1768	46°9'18" N	7°28'10" E
11	Saint-Martin	1589	46°11'8" N	7°26'43" E
12	Grimontz	1738	46°11'22" N	7°34'35" E

Experimental design

Within each of the 12 meadows, six circular plots of 20 m diameter were delineated, with at least 5 m distance between the boundaries of adjacent plots (Fig. 1). One out of six different management treatments were randomly assigned to each of the six plots in a given meadow. The first plot served as a control (C-plot: neither fertilisation nor irrigation); the second plot received only fertilisation with slurry (F-plot); the third plot received only regular aerial irrigation from a sprinkler (I-plot); and the three other plots received low, medium or high inputs of fertiliser and water, with respectively 1/3, 2/3 or 3/3 of a quantity that had been estimated to allow maximum hay yield at a given locality (F+I 1/3, F+I 2/3, F+I 3/3-plots). C-plots and F+I 1/3-plots were mown once a year, which corresponds to local standards for extensively managed meadows, while F, I, F+I 2/3 and F+I 3/3-plots, which received higher input of slurry and/or water, had to be mown twice a year. I, F+I 1/3, F+I 2/3 and F+I 3/3-plots were irrigated weekly from mid-May to the beginning of September, except under heavy rainfall (>20 mm during the previous week). Weekly sprinkler irrigation amounted to 10 mm in F+I 1/3-plots, 20 mm in I and F+I 2/3-plots or 30 mm in F+I 3/3-plots.

The fertiliser consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium oxide (K₂O) dissolved into water so as to reach the viscosity of standard farm slurry (Sinaj, Richner, Fleisch, & Charles, 2009). One m³ of this solution contained 2.4 kg of monopolisable nitrogen (N), 0.872 kg of phosphorus (P) and 6.64 kg of potassium (K). Liquid manure was applied four times during the experiment (each time with half of the corresponding yearly dose), in August 2010, May 2011, August 2011 and May 2012. The exact amount of manure applied per plot depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site elevation (see Appendix A). As a reference base,

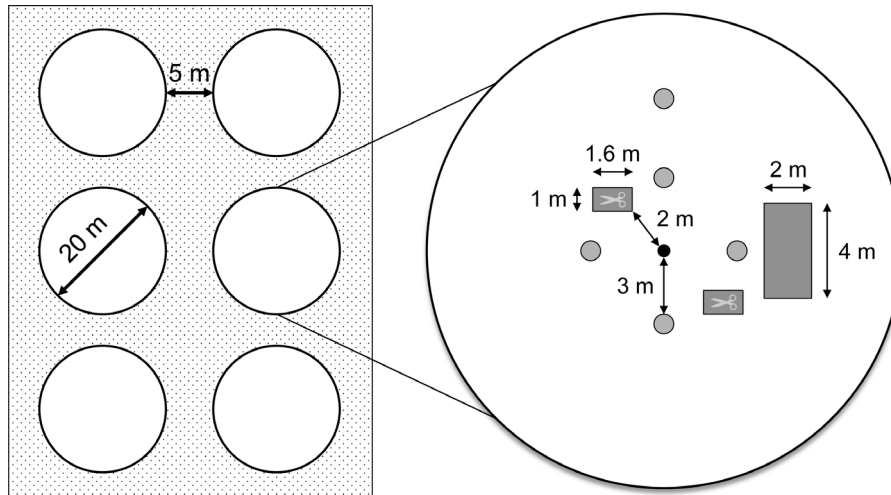


Fig. 1. Experimental design. The six management treatments were applied randomly to six 20-m-diameter plots delineated within each meadow, with a minimum 5 m buffer zone between the plots. In each plot, we sampled plant species richness and coverage of each functional group, i.e. Fabaceae, Poaceae and other plants (within a subplot of 4 m × 2 m), hay yield (grass cut along two horizontal strips of 1 m × 1.6 m) and Auchenorrhyncha (five light-grey circular sub-samples of 0.2 m²).

the F+I 3/3-plots would correspond to the criteria of mid-intensive management described by Sinaj et al. (2009), with a maximum nitrogen fertilisation of 80 kg ha⁻¹ year⁻¹. In other words, the chosen design created a site-adapted management intensification gradient ranging from extensive (C treatment) to mid-intensive (F+I 3/3 treatment) management (Table 2). Expressing our results in site-relative terms (matching between inputs and maximum possible local hay yield, see above) renders them extrapolable to the management of montane and subalpine meadows occurring in similar environmental contexts beyond the inner Swiss Alps.

Auchenorrhyncha sampling

Auchenorrhyncha were collected using a suction sampler equipped with a gauze in its nozzle to retain arthropods (Sanders & Entling, 2011). Each plot was sampled twice during the vegetation period (2012), before the two grass mowing events. At each sampling session, five subsamples were collected: four at 3 m distance from plot centre along or perpendicular to the slope gradient and one at 6 m distance from plot centre, positioned along the slope axis (Fig. 1). Sub-samples were vacuumed from the standing vegetation present within an open metal cylinder of 50 cm height and 50.5 cm diameter that was placed on the ground (0.2 m² area). Sampling was conducted between 11:00 and 17:00, only under dry vegetation conditions and with low or moderate wind. Nymphs and adults were deep-frozen at -20 °C before being identified under the microscope to species level according to the key by Biedermann and Niedringhaus (2009). The number of individuals was counted prior to drying the material in an oven at 60 °C for 72 h, which allowed estimating dry biomass (±0.1 mg). For statistical analyses, all the subsamples from a plot were summed while the samples from the two

sampling sessions were pooled together. The samples thus provided information about abundance, biomass and species richness over an area of 1 m² (5 subsamples of 0.2 m²) sampled twice during the vegetation period. Auchenorrhyncha were further categorised according to:

- 1) feeding guild: graminoid-feeders (including grasses, sedges and rushes in their diet) versus non-graminoid-feeders (including all vascular plants that are not graminoids, such as legumes);
- 2) trophic specialisation: monophagous species (feeding on a single plant species or genus: 1st or 2nd degree monophagy); oligophagous species (feeding on one or two plant families, or exploiting less than five plant species from less than five families (Nickel et al. 2003; Nickel & Remane, 2002); and polyphagous species (foraging upon a broad spectrum of plant genera and species);
- 3) habitat specialisation: eurytopic species (broadly adapted species that can occur in a wide spectrum of habitats), which are usually oligophagous or polyphagous, and stenotopic species (tolerating only a small range of habitat conditions), which mainly comprise monophagous species (Maczey 2004; Nickel 2003; Rombach 2000) (see Appendix B).

Vegetation sampling

In each plot, a 4 m × 2 m permanent subplot was established at a distance of 4 m from the plot centre, randomly placed along the axis of the meadow slope (Fig. 1). In 2012, just before the first mowing, we assessed plant species richness and coverage (%) of three different functional species groups (Fabaceae, Poaceae and other families). Before the first cut (all plots) and just before the second cut (I, F, F+I 2/3 and F+I 3/3-plots only; C and F+I 1/3 were mown just

Table 2. Management intensities applied on each study site (see Table 1 for a list of sites) according to initial conditions. Abbreviations for experimental treatments: C = control; F = fertilised; I = irrigated; F + I 1/3, F + I 2/3 and F + I 3/3 = fertilised and irrigated at respectively 1/3, 2/3 or 3/3 of the dose that would be necessary to achieve the maximum theoretical local hay yield. For each treatment indications are provided for: quantity of nitrogen (N), phosphorus (P) and potassium (K) fertiliser applied per hectare and year; water column applied via sprinkler irrigation per week; and number of grass cuts per year. The fertiliser consisted of organic NPK pellets and mineral K₂O dissolved in water to reach the equivalent of standard-farm liquid manure.

Treatments	Sites 1–4				Sites 5–9				Sites 10–12			
	Fertiliser applied [kg ha ⁻¹ year ⁻¹]		Water irrigation [mm/week]	Number of cuts per year	Fertiliser applied [kg ha ⁻¹ year ⁻¹]		Water irrigation [mm/week]	Number of cuts per year	Fertiliser applied [kg ha ⁻¹ year ⁻¹]		Water irrigation [mm/week]	Number of cuts per year
	N	P			N	P			N	P		
C	0.0	0.0	0	1	0.0	0.0	0	1	0.0	0.0	0	1
F	53.3	19.4	147.5	0	40.0	14.5	110.6	0	2	26.7	9.7	73.8
I	0.0	0.0	0	2	0.0	0.0	0	2	0.0	0.0	20	2
F + I 1/3	26.7	9.7	73.8	10	20.0	7.3	55.4	10	1	13.3	4.8	36.9
F + I 2/3	53.3	19.4	147.5	20	40.0	14.5	110.6	20	2	26.7	9.6	73.8
F + I 3/3	80.0	29.1	221.4	30	60.0	21.8	166.0	30	2	40.0	14.5	110.6

once), hay production was estimated by clipping two strips (1 m × 1.6 m) of grass at 6 cm above the ground (total area per plot: 3.2 m²; Fig. 1). The collected plant material was dried in an oven at 105 °C for 72 h and then weighed to ±0.1 g. Measures such as plant species richness and hay production served as co-variables in the analyses.

Statistical analysis

Treatment effects were analysed with linear mixed-effects models (LMMs) using the *lmer* function from the *lme4* library (Bates, Maechler, Bolker, & Walker, 2013) implemented in R 3.1.2 (R Core Team, 2014). Response variables were: (1) Auchenorrhyncha abundance (log-transformed); (2) Auchenorrhyncha biomass (no transformation); (3) Auchenorrhyncha species richness (log-transforming $x + 1$); (4) abundance of non-graminoid- and graminoid-feeders (log-transforming $x + 1$); (5) abundance of monophagous, oligophagous and polyphagous species (log-transforming $x + 1$); (6) species richness of eurytopic and stenotopic species (log-transformed); (7) abundance of dominant Auchenorrhyncha species (we chose species that occurred in at least six meadows) (log-transforming $x + 1$). In order to avoid pseudoreplication, Auchenorrhyncha subsamples stemming from a given plot were pooled in all analyses, thus providing a single value per plot and meadow (n total = 72).

Following Johnson and Omland (2004), six candidate models were generated. A first model included only the six different treatments as fixed effect (C, F, I, or F + I 1/3, F + I 2/3 and F + I 3/3-plots), while the five other models alternately included in addition one of the measured covariables (plant species richness; hay production; coverage of Fabaceae, Poaceae and other families, respectively) that could influence Auchenorrhyncha responses to the treatments. Study site ($n = 12$) was designated as a random intercept effect. The model with the lowest Akaike's Information Criterion (AIC) value, regarded as the best-supported model, was retained. In order to assess to which extent management treatments differed in their effects, planned orthogonal comparisons were additionally conducted by successfully removing: (1) the C-plots; (2) the C and F-plots; (3) the C, F and I-plots; (4) the C, F, I and F + I 1/3-plots. Models always fulfilled model assumptions, notably residuals normal distribution and homoscedasticity.

Results

Overall, 5570 Auchenorrhyncha (3752 adults and 1818 nymphs) were collected: 4552 individuals could be identified to species ($n = 73$), and 1017 to genus, sub-family or family level. All identified individuals belonged to the three families Cicadellidae, Aphrophoridae or Delphacidae. The species *Philaenus spumarius* (12.4% of all individuals), *Ditropsis*

flavipes (9.8%), *Evacanthus interruptus* (6.3%) and *Eupteryx heydenii* (6.2%) were most abundant (see Appendix B).

Forty-five species were allocated to the guild of graminoid-feeders, 18 to non-graminoid-feeders. In terms of trophic specialisation, 27 species were monophagous, 30 oligophagous and 14 polyphagous. With respect to habitat specialisation, 40 species were classified as stenotopic and 30 as eurytopic. Note that some species could not be categorised due to lack of knowledge of their ecological requirements (for more details see Appendix B). In any statistical analysis of all six response variables, the best models always included only the treatment among the retained fixed effects, i.e. vegetation co-variables were never included in best-supported models.

Auchenorrhyncha abundance, biomass and species richness

Mean abundance and biomass were significantly higher in the three treatments combining fertilisation and irrigation than in the C-plots (see Fig. 2 and Table 3). In relative terms, this represents increases in abundance and biomass of, respectively, 86% and 77% (F+I 1/3-plots), 45% and 63% (F+I 2/3-plots) and 41% and 81% (F+I 3/3-plots). In contrast, the treatments including either fertilisation or irrigation (F and I-plots) did not differ from the controls (C-plots), both for abundance and biomass. Similarly, there was no difference, neither in abundance nor in biomass, among the three levels of combined fertilisation and irrigation. Beside these general patterns there were, however, further pairwise differences between treatments. As regards abundance, fertilisation alone did not differ from the combined treatments F+I 2/3 and F+I 3/3, while F+I 1/3 did. In terms of biomass, the combined treatments (F+I 1/3, 2/3 and 3/3) did not differ from fertilisation and irrigation treatments alone. For species richness, there were two main differences: F+I 1/3, F+I 2/3, and F+I 3/3-plots harboured, on average, more species than C-plots (increase by respectively 30%, 27% and 27%), and F+I 1/3-plots harboured more species than F-plots (increase by 28%).

Auchenorrhyncha feeding guilds, trophic and habitat specialisation, and dominant species

The influence of experimental treatment on feeding guilds, trophic specialisation and habitat specialisation is presented in Appendix C. The mean abundance of non-graminoid-feeders differed only between F+I 1/3 and I-plots (they were more numerous in the former), contrary to graminoid-feeders, which were more abundant in F+I 1/3, F+I 2/3 and F+I 3/3 than in both C and I-plots. Abundance of graminoid-feeders was also greater in F+I 1/3-plots than in F-plots. Trophic specialisation analyses showed a greater abundance of monophagous and oligophagous species in F+I 1/3-plots compared to C, F and I-plots. F+I 2/3-plots also showed a

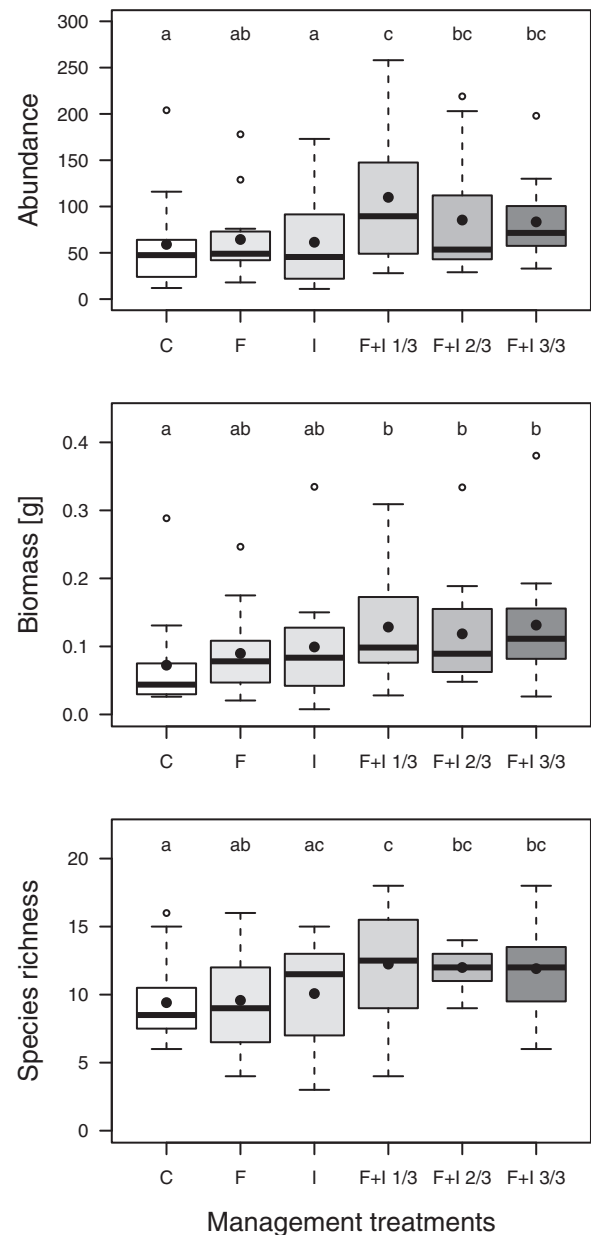


Fig. 2. Auchenorrhyncha abundance, biomass and species richness in response to the different experimental treatments. Bold lines represent medians, solid points the means, boxes the first and third quartiles, whiskers the inter-quartile distance multiplied by 1.5, and open dots the outliers. Different letters indicate significant differences among treatments at an alpha rejection level of 0.05. For management treatment abbreviations, see legend of Table 2. For statistical analyses see Table 3.

higher abundance of monophagous species compared to I-plots, while a higher abundance of polyphagous species was observed in F+I 3/3-plots compared to C-plots. Finally, when considering habitat specialisation, stenotopic Auchenorrhyncha had a greater species richness in F+I 1/3-plots compared to C, F and I-plots, and eurytopic species richness was higher in F+I 2/3 and F+I 3/3-plots compared to C and F-plots.

Table 3. Outputs of the linear mixed-effects models used to measure the impact of experimental treatments on Auchenorrhyncha abundance, biomass and species richness. For treatment abbreviations, see legend of Table 2. Estimate, standard error (SE) and *P*-value (*P*) are provided. Significant *P*-values are highlighted in bold. The intercept represents the respective reference treatment (in brackets) and the random effect reports the estimated standard deviation for the random intercept effect (i.e. study site).

Treatments	Abundance (log scale)			Biomass [g]			Species richness (log scale)		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Intercept (C)	3.780	0.204	<0.001	−2.917	0.212	<0.001	9.417	0.992	<0.001
F vs C	0.193	0.185	0.300	0.279	0.203	0.174	0.167	1.227	0.893
I vs C	0.039	0.185	0.832	0.273	0.203	0.184	0.667	1.227	0.589
F+I 1/3 vs C	0.683	0.185	0.001	0.631	0.203	0.003	2.833	1.227	0.025
F+I 2/3 vs C	0.454	0.185	0.017	0.608	0.203	0.004	2.583	1.227	0.040
F+I 3/3 vs C	0.520	0.185	0.007	0.706	0.203	0.001	2.500	1.227	0.046
Random effect	0.543			0.542			1.668		
Intercept (F)	3.973	0.199	<0.001	−2.638	0.213	<0.001	9.583	1.005	<0.001
I vs F	−0.154	0.192	0.428	−0.006	0.214	0.977	0.500	1.238	0.688
F+I 1/3 vs F	0.490	0.192	0.015	0.351	0.214	0.108	2.667	1.238	0.037
F+I 2/3 vs F	0.260	0.192	0.182	0.329	0.214	0.132	2.417	1.238	0.057
F+I 3/3 vs F	0.327	0.192	0.096	0.427	0.214	0.052	2.333	1.238	0.066
Random effect	0.502			0.520			1.712		
Intercept (I)	3.819	0.202	<0.001	−2.644	0.215	<0.001	10.083	1.000	<0.001
F+I 1/3 vs I	0.643	0.203	0.003	0.358	0.235	0.138	2.167	1.306	0.106
F+I 2/3 vs I	0.414	0.203	0.049	0.335	0.235	0.164	1.917	1.306	0.152
F+I 3/3 vs I	0.481	0.203	0.024	0.433	0.235	0.074	1.833	1.306	0.170
Random effect	0.493			0.471			1.332		
Intercept (F+I 1/3)	4.463	0.186	<0.001	−2.286	0.192	<0.001	12.250	0.950	<0.001
F+I 2/3 vs F+I 1/3	−0.229	0.144	0.125	−0.023	0.179	0.899	−0.250	1.220	0.840
F+I 3/3 vs F+I 1/3	−0.162	0.144	0.270	0.076	0.179	0.677	−0.333	1.220	0.787
Random effect	0.540			0.501			1.373		
Intercept (F+I 2/3)	4.234	0.170	<0.001	−2.309	0.179	<0.001	12.000	0.795	<0.001
F+I 3/3 vs F+I 2/3	0.067	0.133	0.627	0.098	0.150	0.524	−0.083	1.125	0.942
Random effect	0.492			0.500			0.000		

Regarding dominant species, only 20 matched our selection criterion (occurrence in at least six meadows; see Appendix D). For three species only, some combinations of fertilisation and irrigation positively affected abundance, in comparison to C-plots: *Adarrus multinotatus*, *Agallia brachyptera* and *Megadelphax sordidula* (see Appendix E).

Discussion

This research establishes that a moderate fertilisation (slurry) and irrigation (sprinklers) of traditional, very low-input montane and subalpine hay meadows is beneficial, at least in the short term (2 years), for the abundance, biomass and species richness of Auchenorrhyncha. Most previous investigations of the impact of fertilisation and irrigation on the biodiversity of mountain hay meadows have been observational (e.g. Grandchamp et al. 2005; Riedener et al., 2013). A first originality of the present study resides in its fully randomised block design, which minimises any biases due to

possible confounding factors, thereby providing conclusive evidence. Second, we applied different doses of fertiliser and water, whose quantities were adjusted to the potential productivity of a given study site so as to mimic realistic, regional farming practices. This means that the conclusions drawn from this study are generalisable, thus providing concrete guidance for sustainable, i.e. more biodiversity-friendly, management of mountain hay meadows.

Auchenorrhyncha abundance, biomass and species richness

Auchenorrhyncha abundance, biomass and mean species richness were significantly increased in plots combining fertilisation and irrigation (+41%–86% for abundance and biomass, and +27%–30% for species richness, depending on F+I level) compared to no-input, control plots (C-plots). In comparison, fertilisation and irrigation alone (F and I-plots) had no effect on any of the three above metrics. Auchenorrhyncha were also more abundant and diverse in low-input

plots (F+I 1/3) than in F and I-plots, while differences between medium- and high-input plots (F+I 2/3 and F+I 3/3) and F and I-plots were non-significant, indicating that an intermediate management intensity would represent an optimum for the conservation of these invertebrates.

Based on previous studies (Prestidge 1982; Sedlacek, Barrett, & Shaw, 1988), we had expected that fertiliser application alone would have a positive effect on Auchenorrhyncha. Fertilisation is likely to boost the nutritional quality of plants, increasing the survival or the reproductive performance of Auchenorrhyncha, or overall plant biomass, theoretically providing them with a greater diversity of feeding, oviposition and refuge opportunities (Sedlacek et al., 1988). However, the absence of such an effect in our experiment rather indicates that fertilisation alone is not sufficient to induce these benefits for Auchenorrhyncha. Interestingly, Körösi, Batary, Orosz, Redei, and Baldi (2012) claimed that vegetation structural complexity is the main determinant of Auchenorrhyncha communities because it offers a greater range of micro-climates. This result would indeed be in line with our finding that fertilisation does not enhance vegetation structure, at least in the short term (Andrey et al., 2014). However, vegetation structure is unlikely to be the only factor influencing Auchenorrhyncha. As a matter of fact, even irrigation, which alone has been demonstrated to increase vegetation structure (Andrey et al., 2014), did not promote Auchenorrhyncha in this study. In conclusion, the fact that fertilisation and irrigation in isolation did not have any effect on Auchenorrhyncha, whereas their combination did, confirms that it is the interaction between these two factors which, via agricultural intensification, induces changes in grassland biodiversity, and this is likely to apply beyond the sole inner Alps (see also Gaujour, Amiaud, Mignolet, & Plantureux, 2012; Riedener et al., 2013).

Auchenorrhyncha feeding guilds, trophic and habitat specialisation, and dominant species

The species collected belonged mainly to the guild of graminoid-feeders that were ca 1.5 times more abundant than the non-graminoid-feeders. In opposition to our prediction, we only observed an effect of the experimental treatments on the former guild: graminoid-feeders were 61–135% (depending on F+I level) more abundant in plots combining fertilisation and irrigation. Auchenorrhyncha have often been described as being especially sensitive to the nitrogen content of their food sources. Their reproductive output, for instance, is often much increased around a rather narrow, optimal nitrogen content of the host plants (Prestidge 1982; Prestidge & McNeill, 1983). The distinct responses of the two foraging guilds would thus indirectly support the view that farming intensification affects the nitrogen content of grasses and non-grasses in different ways: Turner and Knapp (1996) found that under similar levels of nitrogen addition, the nitrogen concentration in forb (Lamiaceae and Asteraceae) tissues

is, on average, higher than in grasses. As graminoid-feeders were more abundant under all combinations of fertilisation and irrigation than under irrigation alone (note that a similar pattern occurred in non-graminoid-feeders for F+I 1/3-plots versus I-plots), while their abundance did not differ from F-plots (but see F+I 1/3), we conclude that fertiliser input is the ultimate factor at play.

The majority of the 27 monophagous Auchenorrhyncha species (i.e. trophic specialists) found in this study are typically associated with common host plants. In our plots, *Festuca rubra*, for instance, hosted *Acanthodelphax spinosa*, *Dicranotropis divergens* and *Rhopalopyx adumbrata*. This plant has a broad ecological tolerance, frequently occurring in intensively managed grasslands (Pavlů, Gaisler, Pavlů, Hejzman, & Ludvíková, 2012). As *F. rubra*, most plants hosting monophagous species did actually not disappear from plots subjected to increased fertilisation and irrigation. In contrast, only three species of Auchenorrhyncha exhibited very narrow trophic niches: *Batracomorphus irrotatus* (43 individuals, host plant: *Helianthemum nummularium*), *Eupelix cuspidata* (one individual, host plant: *Festuca ovina*) and *Kelisia haupti* (one individual, host plant: *Carex humilis*). The observation that abundances of both monophagous and oligophagous species were higher where intensification was low (F+I 1/3) compared to control plots and to plots submitted to fertilisation and irrigation in isolation, and that it also tended to be greater at F+I 1/3 than in the more intensive treatments, might be indicative of an optimal trade-off between host plant diversity and plant nutritional quality. Oligophagous Auchenorrhyncha, in contrast, tended to be more abundant at higher levels of intensification, which supports the view that they benefitted more from an increase in overall phytomass. Yet, the short duration of our study (two years) and the relatively moderate quantities of fertiliser and water applied, even at the higher intensity levels, may have enabled the cohabitation of both nitrophilous and more specialised species, as a result of the availability of a broad spectrum of trophic niches.

Overall, habitat specialists, i.e. stenotopic Auchenorrhyncha (44% of total abundance), were slightly more abundant than eurytopic species (38%; while 18% of species remained undefined), which is in line with the observation that stenotopic Auchenorrhyncha usually predominate among low-input mountain meadows (Nickel & Achatziger, 2005). Interestingly, the number of stenotopic species was increased only under low input management (F+I 1/3) compared to no input, fertiliser alone and water alone input treatments (+39% on average). In contrast, eurytopic species richness progressively increased with increased fertilisation and irrigation (+38% and +44% in F+I 2/3 and F+I 3/3-plots, respectively, compared to controls). As our experiment progresses (ongoing) we expect eurytopic species to further increase in more intensified plots in the near future (Nickel 2003; Nickel et al. 2005; Nickel et al. 2003).

Regarding dominant Auchenorrhyncha species, fertilisation and irrigation increased the abundance of *Adarrus*

multinotatus and *M. sordidula*. This was expected as both species tightly depend on *Brachypodium pinnatum* and *Arrhenaterum elatius*, respectively, two grasses known to profit from fertilisation (Bobbink, Bik, & Willems, 1988; Liancourt, Viard-Cr  tat, and Michalet (2009)). The abundance of *Agallia brachyptera* – a ground living Auchenorrhyncha of the litter layer that plays the role of an umbrella species (Maczey, 2004) – was promoted by low intensity treatment conditions (F+I 1/3), whereas it did less well in F+I 2/3-plots.

Finally, some remarkable species were collected during this study. *Arboridia simillima*, *Bobacella corvina* and *Athysanus quadrum* were recorded for the first time in Switzerland, while *Emeljanovianus medius* was collected for the second time (Trivellone et al., 2015). Moreover, four species that are considered to be of conservation concern in Germany were collected (there is no Swiss red list for Auchenorrhyncha): *Arboridia simillima*, *Athysanus quadrum*, *D. flavipes* (all endangered), and *Eupteryx heydenii* (vulnerable) (Nickel, Witsack, & Remane, 1999).

Conclusions and management recommendations

Shallow fertilisation with slurry and irrigation with sprinklers promptly enhanced conditions for Auchenorrhyncha in very low-input mountain hay meadows in the short term, notably by increasing the abundance of monophagous and oligophagous species and the richness of stenotopic species. A greater application of fertiliser and water still enhanced abundance and species richness of Auchenorrhyncha, but exclusively through an increase of trophic and habitat generalists. We predict that a prolonged application of our experimental manipulation beyond two years would further negatively impact plant species richness (due to a growing accumulation of fertiliser; Humbert et al., 2016); this would further impoverish the palette of host-plants for Auchenorrhyncha, leading to more detrimental effects for monophagous and stenotopic species.

In many mountainous regions of Europe, the management of hay meadows on flat and accessible terrain is currently undergoing massive intensification, whereas meadows on steep, less accessible slopes are progressively being abandoned (Tasser & Tappeiner, 2002). This dichotomous, negative trend should be reversed. Based on this research on a key indicator taxon of mountain biocenoses, we can already recommend applying doses of fertiliser and water roughly equivalent to one third of the amount that would be necessary to achieve the maximum theoretical local hay yield (our figures for F+I 1/3 can serve as reference, see Table 2). Future results of our ongoing experiment will certainly help fine-tune these prescriptions. Finally, future studies should also investigate to which extent organisms situated higher up along the food chain (predatory arthropods, vertebrates) might benefit from the management recommendations that promote emblematic taxa such as Auchenorrhyncha,

especially given the staple food resource that they represent for higher trophic levels.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.07.002>.

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