

# Grassland intensification dramatically impacts grasshoppers: Experimental evidence for direct and indirect effects of fertilisation and irrigation

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## ABSTRACT

European mountain hay meadows are hosting an exceptionally rich biodiversity. They are currently threatened by both land abandonment and farming intensification via aerial irrigation and slurry application. The consequences of mountain grassland intensification on arthropods are still poorly documented, which is a serious handicap to proposing ecologically-friendly management guidance. Six experimental treatments mimicking a gradient of management intensity (including irrigation, fertilisation and various combinations thereof) were initiated in 2010 at twelve montane and subalpine Swiss meadow sites. In 2013, we sampled orthopterans to assess the influence of management practice on that taxonomic group. In parallel, the changes in vegetation height and ambient temperature (at 10 cm above ground level) induced by the intensification process were quantified in order to better appraise the underlying mechanisms. Intensification had a negative impact on Caelifera (grasshoppers), with decreases in densities and species richness reaching as much as 70% and 50%, respectively, in the most intensively managed treatment plots. Intensification furthermore led to a marked increase in mean vegetation height and a cooling of ambient temperature by up to 4.2 °C. Such microhabitat and microclimate alterations are likely to affect Caelifera development, in particular thermophilous species. In contrast, Ensifera (bushcrickets) densities and species richness showed no significant response to our experimental manipulations. Finally, the application of irrigation by sprinklers alone had limited impact on both orthopterans and meadow microclimate. We conclude that orthopterans, in particular Caelifera, are fairly sensitive to grassland management intensification: fertilisation should be avoided in focal areas for biodiversity conservation.

## 1. Introduction

In Europe, mountain hay meadows have for long ranked among the most biodiverse semi-natural grasslands (Veen et al., 2009). Yet, land abandonment and farming intensification have impacted them over the past decades to an extent that only fragments of these historical biodiversity hotspots remain today (e.g. Fischer and Stocklin, 1997; Spiegelberger et al., 2006; Hilpold et al., 2018; Löffler et al., 2019). Regarding grassland intensification, two newly spreading management practices are threatening these invaluable habitats in Alpine regions: irrigation with sprinkler and fertilisation with liquid manure (Crook and Jones, 1999; Maurer et al., 2006; Riedener et al., 2013). They modify the vegetation community and structure, which in turn affects invertebrate populations (Schwab et al., 2002; Perner et al., 2005; Andrey et al., 2014; Lessard-Therrien et al., 2017; Hilpold et al., 2018). Arthropods

play an important role in grassland systems and beyond: they provide or at least participate in a range of ecosystem services such as pollination, decomposition or pest control (e.g. Sutter and Albrecht, 2016) and represent primordial food sources for many vertebrates (e.g. Arlettaz, 1996; Wilson et al., 1999; Britschgi et al., 2006; Bowler et al., 2019). This underlines the importance of preserving not only speciose invertebrate communities but also abundant arthropod populations.

So far fertilisation has been shown to have a negative impact on arthropod species richness ensuing from a reduction of vegetation compositional and structural diversity (e.g. Marini et al., 2008; Haddad et al., 2009; Everwand et al., 2014). This happens despite the fact that fertilisation may boost the abundance of herbivores through an increase in plant tissue nitrogen, with cascading effects on other arthropod functional groups, in particular entomophagous guilds (Haddad et al., 2001; Hudewenz et al., 2012; Andrey et al., 2016; Welte et al., 2020). In

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contrast, the effects of irrigation on the arthropod communities of hay meadows remain poorly understood, which represents an impediment to providing proper management guidance for these rapidly degrading agro-ecosystems. More specifically, we still ignore whether modern management practice is compatible with the long term persistence of biodiversity-rich mountain hay meadows and if so, what would be acceptable thresholds of irrigation and fertilisation that enable maintaining their functionally diverse arthropod communities (but see Andrey et al., 2016; Lessard-Therrien et al., 2018).

The goal of the present study was to assess the response of orthopteran species richness and density to gradual levels of fertilisation and irrigation, and combination thereof, in montane and subalpine hay meadows. In these grasslands, orthopterans represent the most dominant insect group in terms of biomass (Blumer and Diemer, 1996). Orthopterans have moreover been recognised as key bioindicators for grassland ecosystems as they readily respond to changes in agricultural management (e.g. Buri et al., 2013), being sensitive to a broad set of vegetation parameters (Le Provost et al., 2017; Klein et al., 2020; Kurtogullari et al., 2020). First, orthopterans are sensitive to microclimate variation (Löffler and Fartmann, 2017), which itself heavily depends on vegetation height and density (Song et al., 2013). As ectothermic organisms, many physiological processes such as developmental rate, body size at maturity and reproductive success are dependent on external thermal conditions (e.g. Berner et al., 2004). The thermal sensitivity of orthopterans is also species-specific, with microclimatic conditions influencing the composition of orthopteran communities. For instance, eurythermal (i.e. warm tolerant) species such as *Pseudochorthippus parallelus* can adapt to a range of microclimatic conditions, while thermophilic and xerophilic species such as *Stenobothrus lineatus* are restricted to warm and dry habitats (van Wingerden et al., 1991; Willott and Hassall, 1998). Second, the habitat diversity hypothesis stipulates that more diverse the habitat, more speciose its community (Báldi, 2008). For orthopterans, microhabitat diversity is mainly a function of vegetation structural heterogeneity, which itself correlates with both plant species diversity (e.g. Morris, 2000; Woodcock et al., 2009) and vegetation height (Andrey et al., 2014; Kurtogullari et al., 2020). Third and last, as food availability is a limiting factor for any population, sufficient grass availability is essential to ensure the occurrence of dense Caelifera (grasshoppers) populations; in effect, these orthopterans almost exclusively feed on grass (Baur et al., 2006; Ibanez et al., 2013). Ensifera (here limited to bush crickets), on contrary, have a more diversified diet composed of a mix of small invertebrates and vegetation and thus depend on less specific food sources (Baur et al., 2006; Welti et al., 2020).

Changes in vegetation height and aboveground ambient temperature induced by intensification were also measured to determine whether orthopteran responses can be explained by modifications in the local microhabitat and microclimate conditions of a meadow. Ultimately, the goal was to identify whether an optimal trade-off exists in terms of degree of grassland management intensity and maintenance of biodiversity to provide evidence-based recommendations for sustainable management of mountain hay meadows.

Fertilisation of mountain grasslands has been shown to increase both vegetation structure and phytomass production in the short term (Andrey et al., 2014) and to induce a loss of plant species richness and a homogenisation of the vegetation cover in the long term (e.g. Marini et al., 2008; Lessard-Therrien et al., 2017; Boch et al., 2021). It also usually induces a shift in plant community composition toward a higher proportion of grass and legumes (Rudmann-Maurer et al., 2008). Irrigation, on the other hand, has been established to favour grass species and increase nitrogen (N) mineralisation by plants (Jeangros and Bertola, 2000; Riedener et al., 2013). Very often combined together, fertilisation and irrigation thus generally boost phytomass productivity (DeMalach et al., 2017; Boch et al., 2021), but create a denser and taller sward that is detrimental to many organisms (Marini et al., 2009; Bassin et al., 2012). Consequently, we predicted that: (1) aboveground

temperature would gradually cool down along the intensification gradient (Song et al., 2013; Kenyeres and Szentirmai, 2017); (2) orthopteran densities would increase at mid management intensity due to enhanced food supply and nutrient quality, but would decrease under high management intensity due to a cooler microclimate (van Wingerden et al., 1992; Hudewenz et al., 2012; Joern et al., 2012; Löffler and Fartmann, 2017; Klein et al., 2020; Welti et al., 2020); and (3) orthopteran species richness would steadily decrease all along the intensification gradient because of the loss of thermophilous species and variegated microhabitats (van Wingerden et al., 1991; Marini et al., 2008; Fartmann et al., 2012; Fournier et al., 2017).

## 2. Material and methods

### 2.1. Study sites

The study was carried out in the canton of Valais, an inner Alpine valley of SW Switzerland which experiences a continental climate with cold and wet winter and dry and hot summers: mean annual temperature and precipitation amount to 10.7 °C and 517 mm, respectively (2000–2014; Sion weather station, 482 m a.s.l.). In 2010, twelve extensively-managed meadows were selected within this region; they were situated between 790 and 1740 m a.s.l (Appendix A).

### 2.2. Experimental design

In 2010, in each meadow ( $n = 12$  spatial replicates), six different management treatments were randomly allocated to plots measuring 20 m in diameter and distant from each other by at least 5 m. One plot underwent neither fertilisation nor irrigation and served as a control (C). A second and third plot were only irrigated (I) or fertilised (F), respectively, while the fourth, fifth and sixth plots were irrigated and fertilised with various, increasing intensities of inputs (I+F; Table 1). The exact amount of fertiliser applied at each site depended on the theoretical maximum hay yield achievable locally with two harvests per year, which was estimated using expected hay yield and site elevation (for details see Appendix A in Andrey et al., 2016). Accordingly, sites were split in three categories, with I+F 3/3-plots (maximum quantity of inputs, i.e. high-intensification) receiving, respectively, 40, 60 or 80 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Mid-intensive (F and I+F 2/3) and low-intensive (I+F 1/3) plots, received two thirds and one third, respectively, of the maximum fertilisation dose. This adjustment was necessary to render our experiment as realistic as possible from the agronomical point of view and eventually drawing sound conservation management guidelines. Fertiliser was a mix consisting of organic dried manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium oxide (K<sub>2</sub>O) dissolved in water to reach the equivalent of standard-farm slurry, a solution that comprises 2.4 kg of usable nitrogen, 2 kg of phosphate (P<sub>2</sub>O<sub>5</sub>), and 8 kg of potassium oxide (K<sub>2</sub>O). The experimental plots were fertilised twice a year, once in early spring and once after the first grass cut (June or July). At each operation, half of the annual fertiliser amount was applied, except for the 1/3-plots that were fertilised only once in spring. Treatments I and I+F were additionally irrigated weekly from mid-May to the end of August, except when heavy rainfall occurred ( $\geq 20$  mm over the previous week). Irrigation thresholds were chosen on the basis of a previous experiment by Calame et al. (1992). Accordingly, I and I+F 2/3 matched the recommendations for the best profitability of water input (20 mm/week) while low-intensive (I+F 1/3) and high-intensive (I+F 3/3) management treatments received half and one and a half of this dose, respectively (Table 1).

### 2.3. Orthopteran sampling

Orthopterans were sampled in 2013 with a biocenometer (open trap) made of a net fastened around a strong circular wire so as to provide a total capture area of 1 m<sup>2</sup> (as described in Humbert et al., 2012). Two

**Table 1**

The six management treatments applied to our plots replicated at eleven locations in the SW Swiss Alps. Abbreviations for 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 maximum dose. The exact 3/3 dose of fertiliser applied at each site followed the management norm recommended to achieve maximum hay yield at any given locality (three categories). Note that I and F received the same amount of water or fertiliser as I+F 2/3. C-plots were mown once a year, the other plots twice a year using a sickle bar mower or a rotary mower.

Management treatment	Mowing regime (no. of cut yr <sup>-1</sup> )	Irrigation (mm week <sup>-1</sup> )	Fertilisation (kg N ha <sup>-1</sup> yr <sup>-1</sup> )		
			Category 1	Category 2	Category 3
C	1	0	0.0	0.0	0.0
I	2	20	0.0	0.0	0.0
F	2	0	53.3	40.0	26.6
I+F 1/3	2	10	26.6	20.0	13.3
I+F 2/3	2	20	53.3	40.0	26.6
I+F 3/3	2	30	80.0	60.0	40.0

sampling sessions were performed: one shortly before the first cut (between 12 June and 12 July) and one 4–6 weeks after it (between 13 and 31 August). The date at which meadows were sampled was a function of their elevation. Though, sampling was restricted to sunny days and took place between 10 am and 5 pm. During both sessions, eight biocenometer samples were regularly taken per treatment plot (see Fig. B1). All the individuals trapped within the biocenometer were caught and identified on the spot. Adults were identified to species level while juveniles were classified into suborders (Caelifera or Ensifera). Finally, the eight orthopteran samples stemming from a given experimental plot were merged, thus providing a single value per plot.

#### 2.4. Vegetation height record

Vegetation height was measured as the average vegetation stratum height in a 10-cm radius around a meterstick. Eight measurements were taken per plot at each orthopteran sampling session; they were averaged to obtain one value per plot. All measurements were performed by the same person.

#### 2.5. Temperature record

To record aboveground ambient temperature, I-buttons DS1921G-F Thermochron (Maxim Integrated Products/Dallas) were used ( $\pm 0.5$  °C accuracy). One I-button was randomly placed at 5 m from the centre of a plot and fixed on a stick 10 cm above the ground. I-buttons recorded temperature hourly from early May to late August. They were removed shortly before the first cut and replaced within a few days afterwards. The data collected during the first 10 days following a mowing event were discarded in order to eliminate any “noise” induced by the manipulation of the devices. Average daily and nocturnal temperatures were calculated as the mean hourly temperature between 12 am–4 pm and 0–4 am, respectively.

#### 2.6. Statistical analysis

The data were analysed with linear mixed models (LMMs) or generalised linear mixed models (GLMMs) using the *lmer* and *glmer* functions, respectively, from the *lme4* R package (Bates et al., 2015). Response variables were orthopteran densities (adults plus juveniles), species richness, vegetation height and temperature; they were fitted with either Poisson (Caelifera and Ensifera densities) or Gaussian (others) distributions. However, vegetation height had to be log-transformed in order to achieve normal distribution of residuals. The fixed effects were the various treatments (C, I, F, I+F 1/3, I+F 2/3, I+F 3/3) while the random intercept effect was the study site (meadow), this for all the analyses. When using the Gaussian distribution, *P*-values were obtained using the *lmerTest* package (Kuznetsova et al., 2017). Caelifera and Ensifera responses were analysed separately as these two taxonomic groups differ in their ecology (Baur et al., 2006). Vegetation height, temperature and density data were analysed separately per sampling

session, while data of both sampling sessions were pooled for the species analysis. Finally, post hoc tests were performed to assess pairwise differences between treatments. Models always fulfilled the underlying assumptions of normal distribution of residuals and homoscedasticity.

Structural equation modelling (SEM), using the *lavaan* package (Rosseel, 2012), were further used to determine if fertilisation and irrigation influence orthopterans directly or indirectly through changes in vegetation height or aboveground temperature. In the SEM analysis, water and slurry inputs were treated as two continuous variables with four levels: control with no input = 0; I+F 1/3 = 1; I, F and I+F 2/3 = 2; and I+F 3/3 = 3. As a first step, a set of candidate models was developed. Candidate models always included slurry and water inputs as two independent variables, and then their effects on orthopterans were considered as either direct, or indirect through vegetation height or aboveground temperature, or as a combination of both. In addition, the number of paths was set to a maximum of four, which led to a total of twenty candidate models (see Fig. B2 for a graphical representation of all SEM candidate models). In a second step, all models were run and kept only if the overall fit of the specific model was satisfactory. To assess model fit, the chi-square test (if  $P > 0.05$ ), the comparative fit index CFI (if CFI  $> 0.95$ ), the root mean square error of approximation RMSEA (if RMSEA  $< 0.07$ ) and the standardised root mean square residuals SRMR (if SRMR  $< 0.08$ ) were used (Hooper et al., 2008). In a third step, retained models were ranked based on AICc values (Akaike's Information Criterion corrected for small sample sizes) and the model with the lowest AICc plus the model(s) within a  $\Delta AIC < 6$  (following the suggestion of Harrison et al., 2018) were considered as the most plausible model(s). If several models were ranked within a  $\Delta AIC < 6$ , the model with the highest R-square was chosen as the best model. The *lavaan.survey* package, which applies robust maximum likelihood method to estimate standard errors, was used to include study site as a random effect in the SEM (Oberski, 2014). Prior to run the SEM, multivariate normality of the data was tested using Mardia's Skewness and Kurtosis tests (Korkmaz et al., 2014). All statistics were performed using R version 4.0.3 (R Core Team, 2020).

### 3. Results

Due to unfortunate field circumstances, orthopteran densities could not be sampled in one site (Cordona) before mowing. Similarly, no aboveground temperature was recorded at two sites (Eison and Grimentz) after mowing. Therefore, all related analyses were based on  $n = 11$  or  $n = 10$  sites, respectively.

#### 3.1. Orthopteran density

Mean density of orthopterans varied greatly among meadows and plots. It ranged from 0.13 to 24.38 individuals per m<sup>2</sup> during the first sampling session and from 0.65 to 27.38 individuals per m<sup>2</sup> during the second session. Treatments were found to have significant effects on Caelifera densities but no effect at all on Ensifera. Note that low densities

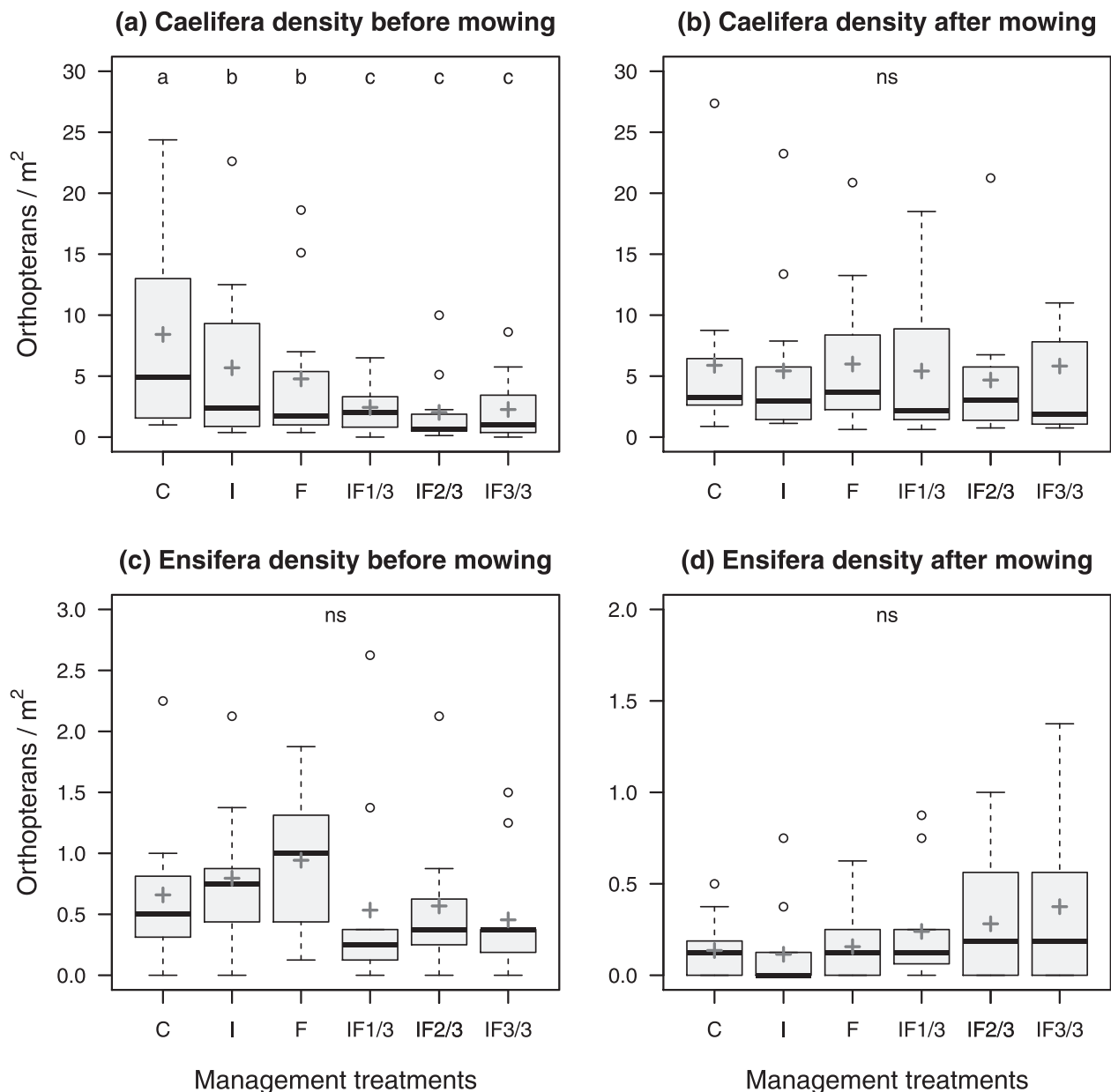
of Ensifera limited the power of the analysis on this suborder (Appendix A).

Before mowing, the highest Caelifera densities were found within C-plots (mean  $\pm$  standard error [SE] =  $8.42 \pm 2.73$ ) that hosted ~30–40% more individuals than I-plots ( $5.68 \pm 2.05$ ,  $P = 0.016$ ) and F-plots ( $4.77 \pm 1.82$ ,  $P < 0.001$ ) and > 70% more individuals than I+F 1/3-plots ( $2.43 \pm 0.66$ ,  $P < 0.001$ ), I+F 2/3-plots ( $2.02 \pm 0.87$ ,  $P < 0.001$ ) and I+F 3/3-plots ( $2.26 \pm 0.81$ ,  $P < 0.001$ ; see Fig. 1a and Table B1 for detailed model outputs). Concerning the Ensifera, the highest densities were found within F-plots ( $0.94 \pm 0.16$ ) and the lowest within I+F 3/3-plots ( $0.45 \pm 0.14$ ), although differences were not statistically significant (Fig. 1b and Table B1). C-plots ( $0.66 \pm 0.18$ ), I-plots ( $0.80 \pm 0.16$ ), I+F 1/3-plots ( $0.53 \pm 0.23$ ) and I+F 2/3-plots ( $0.57 \pm 0.17$ ) had

intermediate densities. After mowing, Caelifera and Ensifera densities did not differ across treatments (Fig. 1c, d and Table B1).

### 3.2. Orthopteran species richness

A total of 21 species was recorded within all plots, seven of which were Ensifera and 14 of which were Caelifera (see Appendix A for detailed list). The minimum number of species found within a plot was one and the maximum was nine. Management practices significantly affected Caelifera species richness. The highest Caelifera species richness was found within C-plots ( $4.6 \pm 0.5$ ) that hosted similar species number to I-plots ( $4.25 \pm 0.5$ ) and F-plots ( $4.2 \pm 0.5$ ) but ~30% more species than I+F 1/3-plots ( $3.2 \pm 0.5$ ,  $P < 0.001$ ) and I+F 2/3-plots



**Fig. 1.** Orthopteran density (individuals/m<sup>2</sup>) in response to the six different management treatments: (a) Caelifera density before mowing; (b) Caelifera density after mowing (note that in the IF3/3-plot a point at 31.9 individuals/m<sup>2</sup> lies outside the frame of the figure); (c) Ensifera density before mowing; (d) Ensifera density after mowing. Abbreviations for treatments: C = control; F = fertilisation only; I = irrigation only, IF1/3 = irrigation and fertilisation at low dose, IF2/3 = irrigation and fertilisation at medium dose, IF3/3 = irrigation and fertilisation at high dose. Different letters indicate significant differences between treatments at an alpha rejection value set to 0.05. Bold lines represent medians, cross the means; boxes the first and third quartiles.

( $3.5 \pm 0.5$ ,  $P = 0.004$ ) and 50% more species than I+F 3/3-plots ( $2.3 \pm 0.4$ ,  $P < 0.001$ ; see Fig. 2a and Table B2 for detailed model outputs). Contrariwise, no significant effects were detected on Ensifera species richness (see Fig. 2b and Table B2).

### 3.3. Vegetation height

Before mowing, vegetation stratum height was the tallest in I+F 3/3-plots ( $61.6 \text{ cm} \pm 3.4 \text{ cm}$ ), it was slightly shorter in I+F 2/3-plots ( $51.8 \pm 2.3$ ), I+F 1/3-plots ( $44.7 \pm 2.7$ ), and F-plots ( $49.6 \pm 3.3$ ), while it grew to only half the height of intensively-managed plots in I- ( $36.8 \pm 3.1$ ) and C-plots ( $31.8 \pm 2.9$ ). After mowing the same trend was observed, with tallest sward found within I+F 3/3-plots ( $24.2 \pm 2.0$ ), followed by I+F 2/3-plots ( $18.5 \pm 2.1$ ) and then I+F 1/3-plots ( $14.0 \pm 2.2$ ), F-plots ( $12.8 \pm 2.2$ ) and I-plots ( $12.3 \pm 1.2$ ), while C-

plots vegetation ( $7.7 \pm 1.2$ ) was relatively short. Except for I-plots before mowing ( $P = 0.050$ ), they all significantly differed from C-plots at  $P < 0.001$  (see Fig. 3 and Table B3 for detailed model outputs).

### 3.4. Temperature

Before mowing, mean diurnal aboveground temperature was the warmest in C-plots ( $22.4 \pm 0.9^\circ\text{C}$ ), while temperatures in I-plots ( $20.9 \pm 0.7$ ), I+F 1/3-plots ( $20.6 \pm 1.4$ ), I+F 2/3-plots ( $20.5 \pm 0.6$ ) and F-plots ( $20.3 \pm 0.7$ ) were  $1.5\text{--}2.1^\circ\text{C}$  cooler than in C-plots (all  $P < 0.05$  except for I-plots). Finally, temperature was even over  $4.2^\circ\text{C}$  colder in I+F 3/3-plots ( $18.2 \pm 0.5$ ) than in C-plot ( $P < 0.001$ ). See Fig. 3a and Table B4 for detailed model outputs. Given the noticeable negative

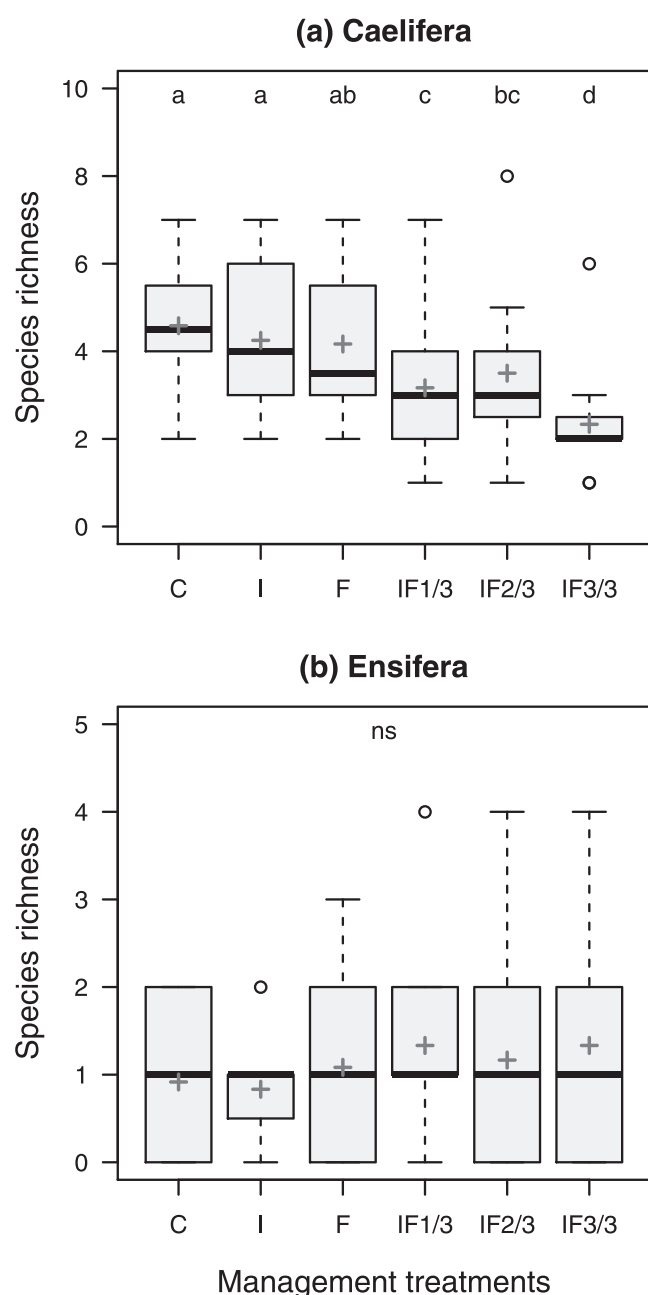


Fig. 2. Responses of Caelifera (a) and Ensifera (b) species richness to the six different management treatments. For treatment abbreviations and boxplot descriptions see legend of Fig. 1.

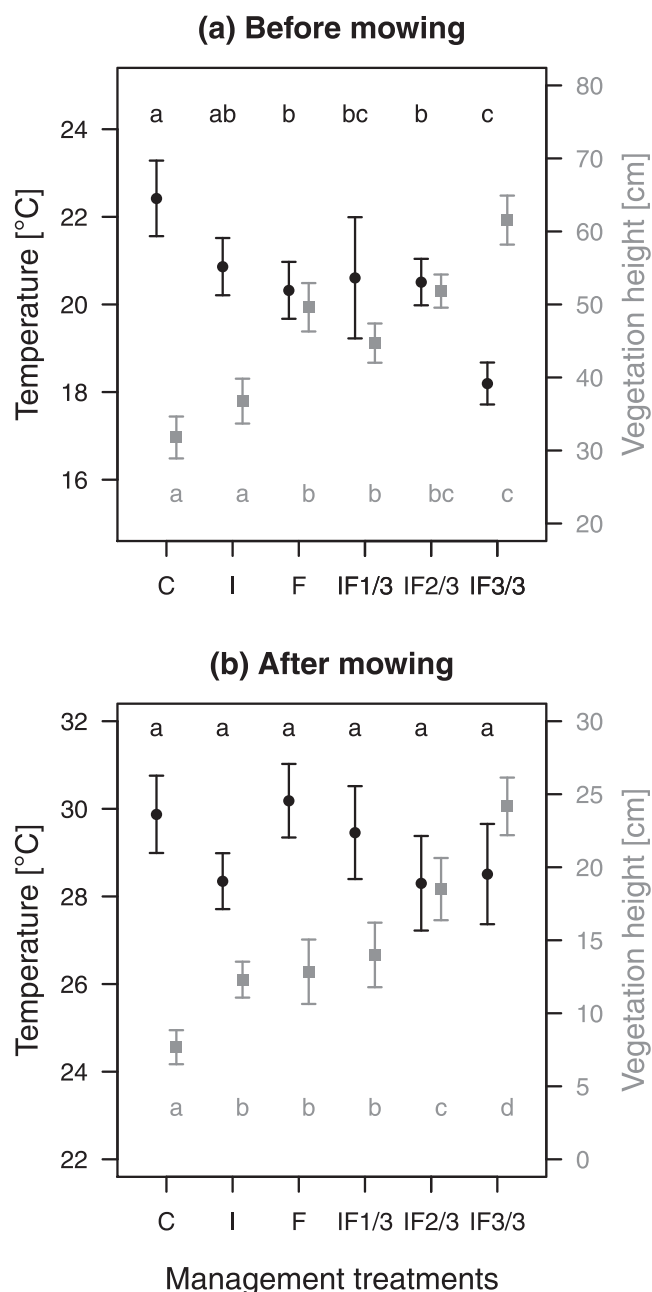


Fig. 3. Aboveground diurnal temperature (black circles) and vegetation height (grey squares) with respect to the six different management treatments, before (a) and after mowing (b). Mean values  $\pm$  SE of the raw data are shown. Different letters indicate significant differences between treatments at an alpha rejection value set to 0.05. For treatment abbreviations see legend of Fig. 1.

relationship between temperature and vegetation height, we modelled the temperature as a function of log-transformed vegetation height using LMM with study site as random intercept effect (Fig. 4; Estimate =  $-3.530$ , SE =  $1.004$ ,  $P = 0.001$ ).

After mowing, diurnal aboveground temperature was the highest in C-plots ( $29.9 \pm 0.9$ ) and F-plots ( $30.2 \pm 0.9$ ). I+F 1/3-plots ( $29.5 \pm 1.2$ ), I+F 3/3-plots ( $28.5 \pm 1.4$ ), I-plots ( $28.4 \pm 0.7$ ) and I+F 2/3-plots ( $28.3 \pm 1.1$ ) were  $0.4$ – $1.7$  °C colder than C-plots, but differences were not statistically significant (Fig. 3b and Table B4). Treatments did affect nocturnal temperature but differences were not biologically relevant (in order of  $0.1$ – $0.2$  °C) and are thus not further discussed.

### 3.5. Structural equation modelling (SEM)

As treatments affected neither Ensifera densities nor species richness, SEMs were run only on Caelifera. Before mowing, the best SEM model (number of observations = 66, chi-square = 0.189, d.f. = 1,  $P = 0.663$ ; CFI = 1; RMSEA < 0.001; SRMR = 0.010) explaining changes in Caelifera densities included both indirect effects of slurry and water inputs through vegetation height (Fig. 5a). The best SEM models explaining Caelifera densities after mowing (number of observations = 60, chi-square = 0.612, d.f. = 1,  $P = 0.434$ ; CFI = 1; RMSEA < 0.001; SRMR = 0.013) as well as Caelifera species richness (number of observations = 60, chi-square = 0.612, d.f. = 1,  $P = 0.434$ ; CFI = 1; RMSEA < 0.001; SRMR = 0.014) were structurally similar. They included both direct effects of slurry and water inputs plus an indirect effect of water input through aboveground temperature measured after mowing (Fig. 5b and c). However, for the density after mowing, only one path was statistically significant, pinpointing the effect of irrigation on aboveground temperature. For Caelifera species richness, the direct effects of slurry and water input were significant, as well as the effect of water input on aboveground temperature coupled with a non-significant effect ( $P = 0.253$ ) of aboveground temperature on species richness. Note that for Caelifera species

richness, we tried all combinations of SEM models with vegetation height and aboveground temperature measured before and after the first mowing. See Table B5 for more details on the SEM outputs including results of the multivariate normality tests.

## 4. Discussion

This study shows that mountain grassland fertilisation, especially when combined with irrigation, greatly affects Caelifera (grasshoppers) by decreasing their densities and species richness. In contrast, irrigation alone seems to have a fairly limited impact, although still significant on Caelifera density. Concerning Ensifera (bush crickets), densities and species richness did not respond to our experimental manipulations. Our results also demonstrate that grassland intensification can induce an important drop in aboveground ambient temperature, probably due to the parallel increase in vegetation heights, i.e. canopy shading effects. This important finding corroborates numerous studies which have claimed, without providing clear evidence, that microclimate cooling through farming intensification is a major trigger of grassland arthropods decline (e.g. Gardiner et al., 2002; Marini et al., 2009; Kenyeres and Szentirmai, 2017; Löffler and Fartmann, 2017). Hereafter, we shall first discuss the effects of management practice on vegetation and microclimate, then move to its effects on orthopteran density and species richness, and eventually discuss their interlinks. Finally, we shall address the conservation implications of our findings.

### 4.1. Effects on vegetation and microclimate

Combined irrigation and fertilisation led to twice taller swards in the most intensively managed plots (I+F 3/3) compared to control plots, which was expected since access to water and nitrogen are the main limiting factors for vegetation growth in dry mountain regions (Tasser and Tappeiner, 2002; Bassin et al., 2012). Before the first hay cut, irrigation alone had a less pronounced effect than fertilisation, probably as a consequence of the wet spring of 2013. However, after the initial cut both inputs had an equivalent positive effect on plant regrowth, with their combination even amplifying their respective effects.

Aboveground temperature was linked to vegetation height: the taller the sward, the greater the ground shading and colder the aboveground temperature (see also Song et al., 2013; Kenyeres and Szentirmai, 2017). Consequently, the temperature difference between the most intensively managed plots and the controls reached  $4.2$  °C at 10 cm above ground level. After the first cut, vegetation regrew progressively, which reduced the temperature difference among plots. Yet, vegetation height is not the only factor ruling grassland microclimate. Indeed, other parameters such as vegetation density and canopy cover do influence solar radiation on soil-level in meadows, indirectly determining its aboveground temperature (van Wingerden et al., 1992). Sprinkler irrigation was also relevant for microclimatic variation, as demonstrated in this study.

### 4.2. Effects on orthopteran density

The two suborders of orthopterans responded totally differently to the experimental manipulations. Before mowing, Caelifera densities were 30% and 40% lower in plots that had been either irrigated or fertilised, respectively. The combination of both inputs had even more dramatic effects, with a > 70% reduction in Caelifera density regardless of the quantities applied; in other terms, densities were divided by three! The structural equation modelling (SEM) indicates that this negative effect is mostly an indirect effect of slurry and water input mediated by vegetation height (see also Kenyeres and Szentirmai, 2017). As most Caelifera individuals were still nymphs at the first sampling session, i.e. little mobile, sampling location is likely to match birthplace. The mechanisms responsible for this variation may derive from three alternative scenarios: (1) females favoured shorter sward sites to lay their eggs; (2) the quality of nymph development was altered and/or survival

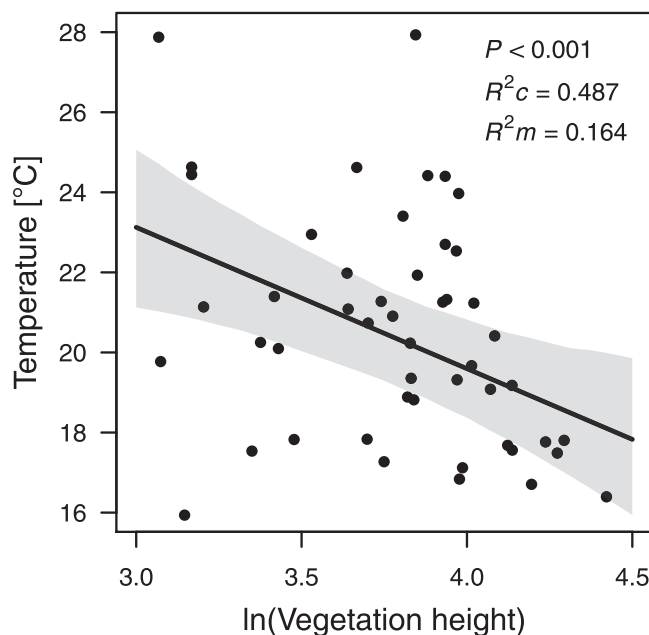
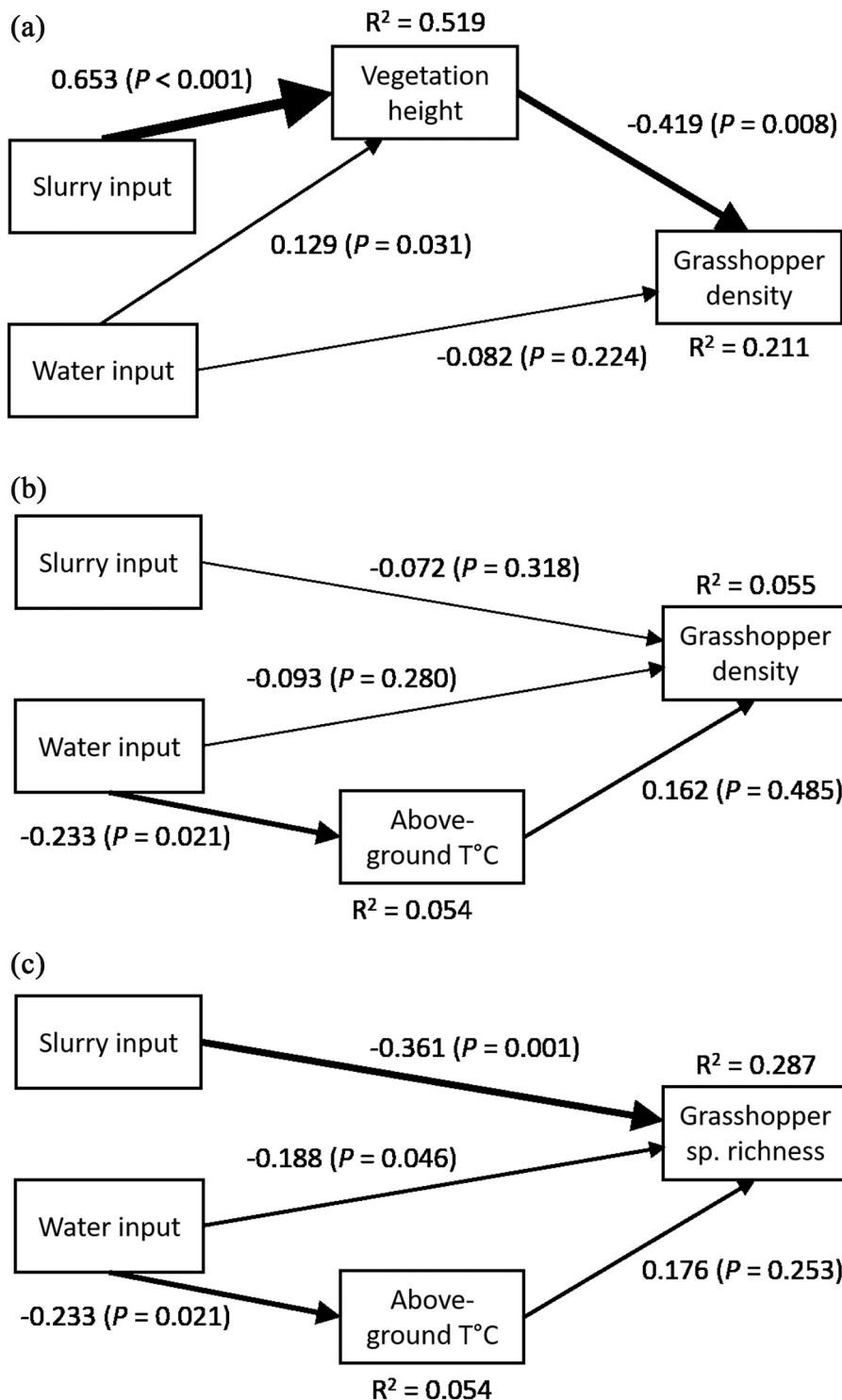


Fig. 4. Negative relationship between diurnal temperature at 10 cm above ground level (in °C) and log-transformed vegetation height (in cm) before mowing. The regression line is drawn from the LMM outputs with 95% confidence intervals. Marginal  $R^2$  ( $R^2m$ ) represents the percentage of variance explained by the fixed effects only, whereas conditional  $R^2$  ( $R^2c$ ) is the percentage explained by both the fixed and random effects together (Nakagawa and Schielzeth, 2013).



**Fig. 5.** Best structural equation model (SEM) explaining the influences of slurry and water inputs on: (a) Caelifera density before mowing; (b) Caelifera density after mowing; and (c) Caelifera species richness. Standardised path coefficients are shown beside each path, with the level of statistical significance indicated by asterisks (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). The width of the arrows depicts the strength of the effect and  $R^2$  values represent the proportion of variance explained for each dependent variable. More details on the model outputs can be found in [Table B5](#).

rate was lower in plots harbouring tall vegetation (Willott and Hassall, 1998); or (3) hatching was delayed under taller vegetation circumstances, i.e. it had not been initiated at the time of the sampling session; the latter phenomenon would thus compromise the chance to complete life cycle and to reproduce (van Wingerden et al., 1991; Berner et al., 2004; Weiss et al., 2013). At this stage, it is impossible to disentangle these non-exclusive scenarios. Concerning Ensifera, we could not evidence any impact of management intensification on density. Yet, their densities were comparatively much lower compared to Caelifera, providing limited statistical power. They may also have emerged earlier

in the season, i.e. when vegetation height and thus microclimate differences were less pronounced among management practices.

The mowing operations may have triggered a dispersal of the surviving individuals beyond the plots (Humbert et al., 2012) so that Caelifera density at the second sampling session may no longer properly mirror the situation prevailing initially (before mowing). Nevertheless, we observed that generalist species such as *P. parallelus* dispersed more or less evenly across the plots while the specialised thermophilous species such as *S. lineatus* or *Omocestus haemorrhoidalis* recolonised the warmest plots in priority. These specialists depend more on the

suitability of habitats than generalists do in central European calcareous grasslands (König and Krauss, 2019). Surprisingly, about half of the individuals sampled at the second sampling session were nymphs. This suggests that a boom in Caelifera hatching occurred on the days following mowing, probably due to a sudden warmer soil surface temperature. After mowing, Ensifera appeared to be slightly more numerous in more intensively managed plots (no significant difference, however), while there were virtually no nymphs any longer. This pattern was due to the preponderant presence of adults *Tettigonia viridissima* and *Roeseliana roeselii* (despite very low density altogether: 0.5 Ensifera per m<sup>2</sup>), two species that typically favoured the taller swards that by then occurred mostly in the intensified plots.

We had hypothesised that orthopteran density would peak at moderate management intensity, benefitting from an increased vegetation structure and food supply (phytomass) without being impacted by the unsuitable microclimatic conditions induced by excessive shading (Fartmann et al., 2012; Hudewenz et al., 2012). However, results are not in accordance with that hypothesis, suggesting that in mountain hay meadows food supply is not a limiting factor for Caelifera that are mostly restrained by thermal conditions (see also Löffler and Fartmann, 2017; Löffler et al., 2019; Kurtogullari et al., 2020). Klein et al. (2020) – a study that was also carried out in Valais – found a hump-shaped relationship between orthopteran abundance and grassland management intensity. However, their management gradient started with arid unmanaged grasslands (*Stipo-Poion*), while our experiment was run exclusively in agricultural productive mesic hay meadows (average annual dry phytomass production in control-plots equalled 340 g/m<sup>2</sup>; Boch et al., 2021). The general findings are thus corroborating each other; with traditional low intensity management associated with the highest abundance.

#### 4.3. Effects on orthopteran species richness

The highest species richness for Caelifera was found in the control plots and remained high in plots that were only subjected to experimental irrigation and fertilisation. It is above all the combination of these two factors that generated detrimental effects: species richness was halved in the most intensive plots. A drop in species richness following grassland intensification had been reported not only by previous observational studies from the Alps and Prealps (Marini et al., 2008; Schlegel and Schnetzler, 2018) but also for lowland regions (e.g. Knop et al., 2006; Chisté et al., 2016).

The SEM indicates strong direct negative effects of slurry and water input, plus an indirect effect of water input through changes in aboveground temperature, though the path between aboveground temperature and Caelifera species richness was not statistically significant. Yet, the direct effects evidenced for slurry and water input might not be strictly direct as they could be mediated by other variables that were not included in the model. Actually, it is known that in addition to aboveground temperature, orthopteran community composition is related to several other parameters such as vegetation structural heterogeneity (Jerrentrup et al., 2014; Kurtogullari et al., 2020), percentage of bare ground (Weiss et al., 2013), plant species composition (Gardiner et al., 2002; Ibanez et al., 2013; Fournier et al., 2017), and management regime (Buri et al., 2013). The parallel drop in species richness and temperature suggests either that thermophilous species chose deliberately not to oviposit in more intensive plots – with therefore egg laying decisions taken in the previous year influencing the current year situation – or that eggs laid within colder plots poorly develop and/or that their larvae never reach maturity (Willott and Hassall, 1998). Willott and Hassall (1998) showed that a difference of 5 °C in ambient temperature – the delta in air temperature reached 4.2 °C in the present study – considerably affects Caelifera fitness: the most thermo-sensitive species experience an elongation of development time up to 50%, a 25% reduction in body mass and a 50% drop in egg pod production. In line with this, our findings support the hypothesis that the conditions

prevailing in our intensively managed plots may have become too cold for ensuring the persistence of thermophilous species.

Contrariwise to Caelifera, Ensifera species richness was not affected by management intensification. This suborder is known to be less sensitive to microclimatic conditions than Caelifera and to depend more on vegetation structure (Bieringer and Zulka, 2003; Baur et al., 2006; Buri et al., 2013). Notwithstanding, a change in community composition concomitant with intensification was evidenced. Large species such as *T. viridissima* and generalists such as *R. roeselii* favour tall vegetation which offers good singing posts and shelter (Baur et al., 2006; Buri et al., 2013). Not surprisingly, both were more abundant in intensively managed than in extensively managed plots. On the contrary, *Platycleis albopunctata* or *Decticus verrucivorus*, typically associated with warm and dry habitat (Baur et al., 2006), were occasionally encountered in control plots, but not in intensively managed plots. Ensifera have overall more versatile and variegated ecological niches than Caelifera, which might explain the stability of species richness among the six experimental treatments. However, statistical power is here limited due to the small number of species (mean of 1.1) recorded per experimental plot.

#### 4.4. Conclusions and conservation implications

Aerial irrigation and fertilisation with liquid manure are two farming practices rapidly spreading in montane and subalpine grassland ecosystems (Riedener et al., 2013). If this contributes to combat land abandonment and woody vegetation encroachment, the resulting habitat changes nevertheless massively impact biodiversity (this study; see also Hilpold et al., 2018; Boch et al., 2021). An important contribution of this study is certainly the experimental demonstration of the alterations undergone by the microhabitat and microclimate of meadows subjected to agricultural intensification. The effective cooling we measured (> 4 °C at 10 cm above ground) was beyond any predictions. At that magnitude of change, huge impacts on the development of the local micro-fauna are to be expected (Logan et al., 2006).

In contrast to observational studies of farmland biodiversity which are plethora, the experimental approach adopted here – in which various realistic management treatments were randomly allocated to plots and compared to controls – avoids the biases typically inherent in mere correlational investigations. In effect, correlative approaches are easily “polluted” by confounding environmental factors such as soil and climate conditions, elevation, surrounding landscape and the management history of any given study site to mention just a few. Our experimental manipulations also perfectly mirrored the modern management practices prevailing nowadays in mountain hay meadows: our slurry solution mimicked real liquid manure composition while water additions were delivered from sprinklers. The quantities of inputs were moreover adjusted according to local bio-agronomical circumstances, consistent with actual agricultural practice. Yet, there are some limitations to our experimental approach. For instance, the reduced size and proximity of our treatment plots might have somewhat blurred the signal given the mobility of our study model organisms, orthopterans. This could have influenced our results, especially as concerns the second session. In this sense, the differences we observed between treatments might be judged conservative.

Results demonstrate that irrigation and fertilisation, when applied exclusively, had a moderate although significant impact on Caelifera density and, for fertilisation, meadow microclimate. Yet, it is above all the combination of irrigation and fertilisation which was particularly harmful to orthopterans, this even at low dose. That irrigation per se is not that detrimental to entomofauna will certainly please farmers, conservationists and policy-makers as it confirms former views that hay yield can be increased at reduced cost for biodiversity (see also Jeangros and Bertola, 2000; Riedener et al., 2013). As a matter of fact, irrigation of hay meadows with sprinklers is allowed in extensively-managed meadows subsidised under the Swiss agri-environment scheme. However, in the irrigation-alone treatment, we observed a drop of 30% of

grasshopper (Caelifera) density, which might already cause negative bottom-up effects on higher trophic levels, notably insectivorous vertebrates (e.g. Britschgi et al. 2006). For keeping integral communities and abundant populations of orthopterans as well as functional food chains the best option would thus be to renounce to both irrigation and fertilisation in hay meadows where biodiversity conservation is the target of the agri-environmental measures.

When combining the present results with our previous findings on other taxonomic groups from the same experimental set up (plants: Andrey et al., 2014; Auchenorrhyncha: Andrey et al., 2016; Lessard-Therrien et al., 2017; bryophytes Boch et al., 2018; spiders and ground beetles: Lessard-Therrien et al., 2018; Boch et al., 2021) we realise that it is difficult if not impossible to find an optimal trade-off between agro-nomical yield and biodiversity maintenance across all plant and invertebrate taxa. Our initial hope was that there is an intermediate level of agricultural intensification that may provide decent revenue to farmers without too much compromising biodiversity. Grasshoppers represent a real challenge from that viewpoint because they definitely prefer dry and nutrient poor grasslands. We conclude that if moderate intensification is not detrimental to plants and a majority of invertebrates (Riedener et al., 2013; Andrey et al., 2016; Lessard-Therrien et al., 2018), there are some taxa, notably orthopterans, which would suffer in agri-environmental measures that tolerate intermediate levels of farming intensity.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107412.

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**Appendix A:** Location name of all study sites (or meadows n = 12), geographic coordinates (WGS84), elevation, sampling date, and number of orthopterans of each species caught during the two sampling sessions (i.e. before and after mowing). In addition, meadows were classified in three groups according to the maximum hay productivity potential of the site (see Material and Methods section for more details). Data are missing for the first session in Cordona due to technical problems.

	Study site	Coordinates		Group	Elevation [m]	Sampling date	Caelifera larvae	Ensifera larvae	<i>Pseudochorthippus parallelus</i>	<i>Chortippus biguttulus</i>	<i>Chortippus dorsatus</i>	<i>Chortippus brunneus</i>	<i>Stauroderus scalaris</i>	<i>Stenobothrus lineatus</i>	<i>Euthysira brachyptera</i>	<i>Omocestus rufipes</i>	<i>Omocestus viridulus</i>	<i>Omocestus haemorrhoidalis</i>	<i>Acryptera fusca</i>	<i>Chrysochraon dispar</i>	<i>Mecostethus parapleurus</i>	<i>Tettigonia viridissima</i>	<i>Roesellana roeselii</i>	<i>Metriopectera saussuriana</i>	<i>Decticus verrucivorus</i>	<i>Platycleis albopunctata</i>	<i>Pholidoptera griseoaptera</i>	<i>Conocephalus fuscus</i>	<i>Leptophyes punctatissima</i>
		Latitude	Longitude																										
Before mowing	Euseigne	46°10'9"N	7°25'27"E	1	1028	02/07/2013	36	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Icogne 1	46°17'56"N	7°26'31"E	1	880	13/06/2013	56	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
	Orsières	46°1'44"N	7°9'8"E	1	1022	19/06/2013	90	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
	Sembrancher	46°4'24"N	7°8'36"E	1	798	12/06/2013	27	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Arbaz	46°16'42"N	7°22'47"E	2	1270	26/06/2013	27	22	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	3	0	0	0	0	0
	Cordona	46°19'45"N	7°33'8"E	2	1153	12/06/2013	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Icogne 2	46°16'42"N	7°26'10"E	2	1200	26/06/2013	48	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
	La Garde	46°3'45"N	7°8'35"E	2	980	18/06/2013	267	73	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	14	2	0	0	0	0
	Vens	46°5'7"N	7°7'24"E	2	1373	12/06/2013	119	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Eison	46°9'18"N	7°28'10"E	3	1768	12/07/2013	708	29	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	4	0	0	0	0	0
	Grimentz	46°11'22"N	7°34'35"E	3	1738	08/07/2013	360	6	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	St-Martin	46°11'8"N	7°26'43"E	3	1589	02/07/2013	488	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
After mowing	Euseigne	46°10'9"N	7°25'27"E	1	1028	22/08/2013	30	0	39	3	42	7	0	5	1	0	0	0	4	0	0	1	2	3	0	0	1	0	0
	Icogne 1	46°17'56"N	7°26'31"E	1	880	14/08/2013	39	0	7	0	0	0	8	4	2	2	0	0	0	1	0	1	3	0	0	1	1	0	0
	Orsières	46°1'44"N	7°9'8"E	1	1022	21/08/2013	63	3	29	22	1	0	3	1	11	0	0	1	0	0	4	1	4	0	0	0	0	2	0
	Sembrancher	46°4'24"N	7°8'36"E	1	798	13/08/2013	17	0	33	0	5	0	3	3	7	0	0	0	0	0	0	1	2	0	0	0	0	0	0
	Arbaz	46°16'42"N	7°22'47"E	2	1270	23/08/2013	190	0	2	11	0	0	1	1	5	0	0	0	0	0	0	0	0	2	3	0	0	0	0
	Cordona	46°19'45"N	7°33'8"E	2	1153	23/08/3013	280	1	305	15	10	4	7	6	2	2	0	1	0	0	1	2	15	0	3	0	0	0	8
	Icogne 2	46°16'42"N	7°26'10"E	2	1200	14/08/2013	419	0	36	0	0	0	9	1	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
	La Garde	46°3'45"N	7°8'35"E	2	980	13/08/2013	20	0	48	2	2	0	52	8	3	0	0	5	0	0	0	1	4	1	6	10	9	0	0
	Vens	46°5'7"N	7°7'24"E	2	1373	21/08/2013	36	0	0	8	0	4	13	2	0	5	0	0	4	0	0	0	6	0	0	0	1	0	0
	Eison	46°9'18"N	7°28'10"E	3	1768	31/08/2013	477	0	191	12	24	0	116	117	18	0	0	26	2	0	0	1	3	3	0	0	0	0	0
	Grimentz	46°11'22"N	7°34'35"E	3	1738	26/08/2013	35	0	13	2	16	3	46	1	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
	St-Martin	46°11'8"N	7°26'43"E	3	1589	31/08/2013	27	0	6	3	0	0	59	0	6	1	0	0	6	0	0	0	7	4	3	0	0	0	0

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## **Appendix B**

**Figure B.1:** Orthopteran sampling design.

**Figure B.1:** Initial full structural equation model used to build all candidate models.

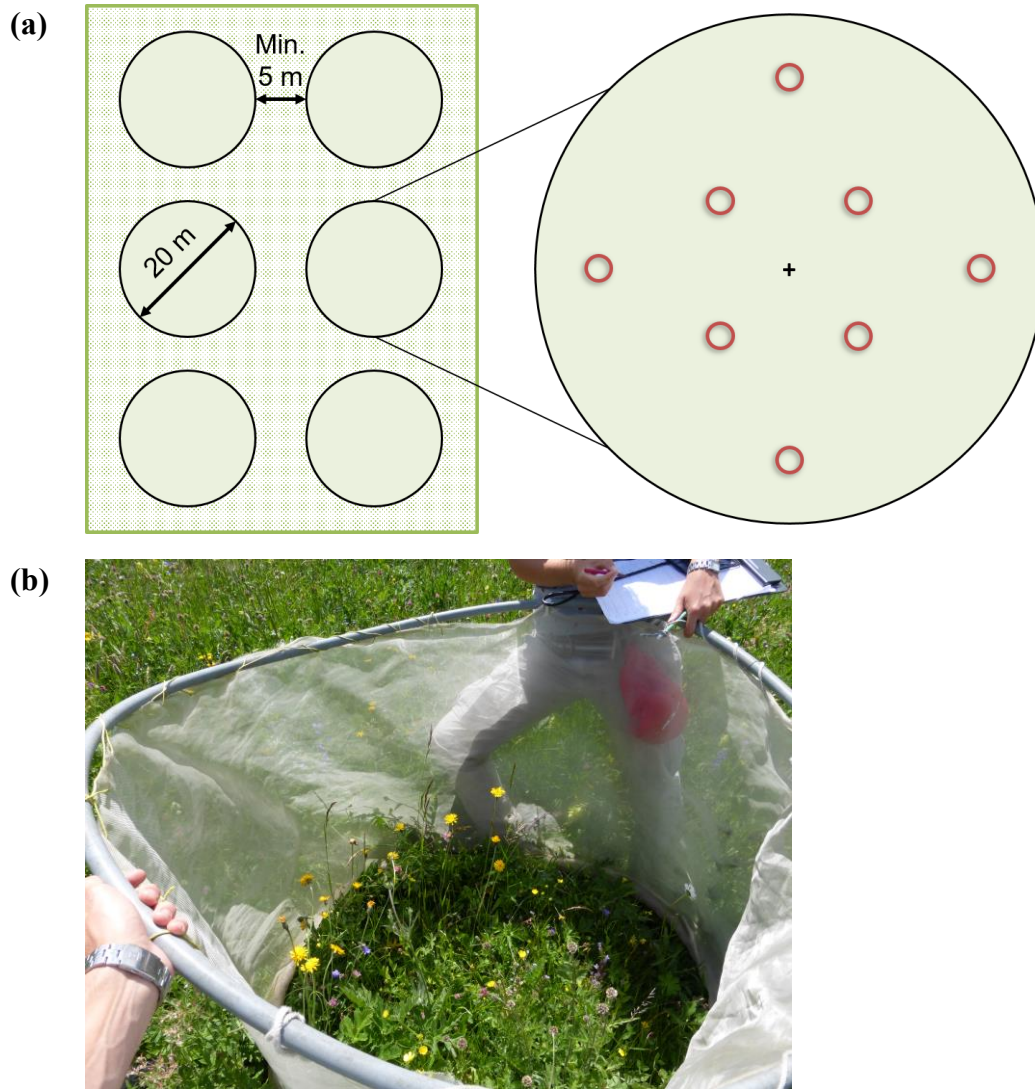
**Table B.1:** Results of the GLMMs carried out on the effects of fertilisation and irrigation on Caelifera and Ensifera densities.

**Table B.2:** Results of the LMMs carried out on the effects of fertilisation and irrigation on Caelifera and Ensifera species richness.

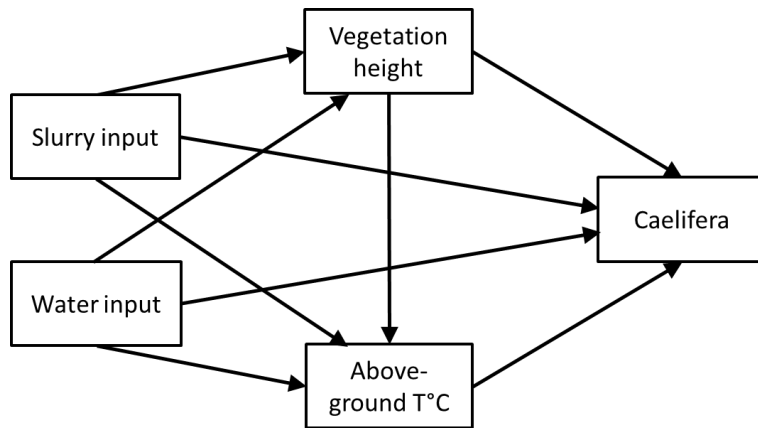
**Table B.3:** Results of the LMMs carried out on the effects of fertilisation and irrigation on vegetation height.

**Table B.4:** Results of the LMMs carried out on the effects of fertilisation and irrigation on aboveground diurnal temperature.

**Table B.5:** Detailed structural equation model (SEM) outputs



**Fig. B.1.** Orthopteran sampling design. (a) The six management treatments were applied randomly to six 20 m-diameter plots delineated within each meadow ( $n = 12$  meadows or spatial replicates), with a minimum 5 m buffer zone between the plots. In each plot, orthopterans were sampled within eight biocenometer samples regularly taken (red open circles). Two sampling sessions were performed: one shortly before the first cut (between 12 June and 12 July) and one 4–6 weeks after it (between 13 and 31 August). (b) Orthopterans sampling with a biocenometer made of a net fastened around a strong circular wire so as to provide a total capture area of  $1 \text{ m}^2$ . Here in the control plot of St-Martin, on 2 July 2013.



**Fig. B.2.** Structural equation modelling (SEM) were used to determine if fertilisation and irrigation influence orthopterans directly or/and indirectly through changes in vegetation height or aboveground temperature (at 10 cm above ground level). The chart represents the full structural equation model including all potential paths. However, the number of paths of the candidate models was set to maximum four and they always included slurry and water inputs which led to a total of twenty candidate models. SEMs were run on Caelifera densities before and after mowing and on Caelifera species richness (pooled sampling session).

**Table B.1.** Results of the GLMMs carried out on the effects of fertilisation and irrigation on Caelifera and Ensifera densities for both sampling sessions (i.e. before and after mowing). Table refers to figure 1 in the article. The fixed effects were the experimental treatments (C = control plots; F = fertilised; I = irrigated; I+F 1/3 = irrigation and fertilisation at low dose; I+F 2/3 = irrigation and fertilisation at medium dose; I+F 3/3 = irrigation and fertilisation at high dose). Parameter estimates (differences between expected mean abundances on the log scale) are given for paired regime comparisons and significant differences are highlighted in bold. Marginal  $R^2$  ( $R^2m$ ) represents the percentage of variance explained by the fixed effects only, whereas conditional  $R^2$  ( $R^2c$ ) is the percentage explained by both fixed and random effects together (Nakagawa and Schielzeth 2013 *Methods Ecol. Evol.*). The random effect reports the estimated standard deviation for the random intercept effect (i.e. the study site).

Response variable	Estimate	SE	$P(> z )$
<b>(a) Caelifera density before mowing (log scale)</b>			
I vs C	-0.393	0.164	<b>0.016</b>
F vs C	-0.568	0.173	<b>0.001</b>
I+F 1/3 vs C	-1.242	0.220	<b>&lt;0.001</b>
I+F 2/3 vs C	-1.426	0.236	<b>&lt;0.001</b>
I+F 3/3 vs C	-1.315	0.226	<b>&lt;0.001</b>
F vs I	-0.174	0.187	0.352
I+F 1/3 vs I	-0.849	0.231	<b>&lt;0.001</b>
I+F 2/3 vs I	-1.033	0.247	<b>&lt;0.001</b>
I+F 3/3 vs I	-0.921	0.237	<b>&lt;0.001</b>
I+F 1/3 vs F	-0.674	0.238	<b>0.005</b>
I+F 2/3 vs F	-0.859	0.253	<b>0.001</b>
I+F 3/3 vs F	-0.747	0.243	<b>0.002</b>
I+F 2/3 vs I+F 1/3	-0.184	0.287	0.521
I+F 3/3 vs I+F 1/3	-0.073	0.279	0.794
I+F 3/3 vs I+F 2/3	0.112	0.292	0.702
Random effect	1.105		
$R^2m$	0.166		
$R^2c$	0.869		

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Response variable	Estimate	SE	<i>P</i> (>  <i>z</i>  )
<b>(b) Caelifera density after mowing (log scale)</b>			
I vs C	-0.081	0.172	0.637
F vs C	0.018	0.168	0.917
I+F 1/3 vs C	-0.083	0.172	0.629
I+F 2/3 vs C	-0.230	0.179	0.199
I+F 3/3 vs C	-0.011	0.169	0.950
F vs I	0.099	0.171	0.564
I+F 1/3 vs I	-0.002	0.175	0.991
I+F 2/3 vs I	-0.149	0.182	0.414
I+F 3/3 vs I	0.070	0.172	0.683
I+F 1/3 vs F	-0.101	0.171	0.557
I+F 2/3 vs F	-0.247	0.178	0.165
I+F 3/3 vs F	-0.028	0.168	0.867
I+F 2/3 vs I+F 1/3	-0.147	0.182	0.420
I+F 3/3 vs I+F 1/3	0.072	0.172	0.675
I+F 3/3 vs I+F 2/3	0.219	0.179	0.222
Random effect	0.843		
<i>R</i> <sup>2</sup> <i>m</i>	0.008		
<i>R</i> <sup>2</sup> <i>c</i>	0.792		
<b>(c) Ensifera density before mowing (log scale)</b>			
I vs C	0.188	0.502	0.708
F vs C	0.358	0.484	0.459
I+F 1/3 vs C	-0.210	0.555	0.705
I+F 2/3 vs C	-0.148	0.546	0.786
I+F 3/3 vs C	-0.372	0.581	0.523
F vs I	0.170	0.459	0.711
I+F 1/3 vs I	-0.398	0.533	0.455
I+F 2/3 vs I	-0.337	0.524	0.521
I+F 3/3 vs I	-0.560	0.561	0.318
I+F 1/3 vs F	-0.569	0.516	0.271
I+F 2/3 vs F	-0.507	0.506	0.317
I+F 3/3 vs F	-0.730	0.544	0.180
I+F 2/3 vs I+F 1/3	0.062	0.575	0.914
I+F 3/3 vs I+F 1/3	-0.161	0.608	0.791
I+F 3/3 vs I+F 2/3	-0.223	0.600	0.710
Random effect	0.421		
<i>R</i> <sup>2</sup> <i>m</i>	0.035		
<i>R</i> <sup>2</sup> <i>c</i>	0.136		

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Response variable	Estimate	SE	<i>P</i> (>  <i>z</i>  )
<b>(d) Ensifera density after mowing (log scale)</b>			
I vs C	-0.167	1.159	0.885
F vs C	0.143	1.072	0.894
I+F 1/3 vs C	0.571	0.981	0.561
I+F 2/3 vs C	0.731	0.955	0.444
I+F 3/3 vs C	1.019	0.915	0.266
F vs I	0.310	1.123	0.782
I+F 1/3 vs I	0.738	1.037	0.477
I+F 2/3 vs I	0.898	1.012	0.375
I+F 3/3 vs I	1.186	0.974	0.224
I+F 1/3 vs F	0.427	0.939	0.649
I+F 2/3 vs F	0.588	0.911	0.519
I+F 3/3 vs F	0.876	0.869	0.314
I+F 2/3 vs I+F 1/3	0.160	0.803	0.842
I+F 3/3 vs I+F 1/3	0.448	0.755	0.553
I+F 3/3 vs I+F 2/3	0.288	0.720	0.690
Random effect	0.314		
<i>R</i> <sup>2</sup> <i>m</i>	0.037		
<i>R</i> <sup>2</sup> <i>c</i>	0.057		

**Table B.2.** Results of the LMMs carried out on the effects of fertilisation and irrigation on Caelifera and Ensifera species richness. Table refers to figure 2 in the article. Both sampling sessions were analysed together. Abbreviations and parameter estimates as in Table B.1.

Response variable	Estimate	SE	df	<i>P</i> (> t )
<b>(a) Caelifera species richness</b>				
I vs C	-0.333	0.358	55	0.355
F vs C	-0.417	0.358	55	0.249
I+F 1/3 vs C	-1.417	0.358	55	<b>&lt;0.001</b>
I+F 2/3 vs C	-1.083	0.358	55	<b>0.004</b>
I+F 3/3 vs C	-2.250	0.358	55	<b>&lt;0.001</b>
F vs I	-0.083	0.357	55	0.817
I+F 1/3 vs I	-1.083	0.357	55	<b>0.004</b>
I+F 2/3 vs I	-0.750	0.357	55	<b>0.041</b>
I+F 3/3 vs I	-1.917	0.357	55	<b>&lt;0.001</b>
I+F 1/3 vs F	-1.000	0.357	55	<b>0.007</b>
I+F 2/3 vs F	-0.667	0.357	55	0.068
I+F 3/3 vs F	-1.833	0.357	55	<b>&lt;0.001</b>
I+F 2/3 vs I+F 1/3	0.333	0.358	55	0.355
I+F 3/3 vs I+F 1/3	-0.833	0.358	55	<b>0.023</b>
I+F 3/3 vs I+F 2/3	-1.167	0.358	55	<b>0.002</b>
Random effect	1.379			
<i>R</i> <sup>2</sup> <i>m</i>	0.181			
<i>R</i> <sup>2</sup> <i>c</i>	0.765			
<b>(b) Ensifera species richness</b>				
I vs C	-0.083	0.332	55	0.803
F vs C	0.167	0.332	55	0.618
I+F 1/3 vs C	0.417	0.332	55	0.215
I+F 2/3 vs C	0.250	0.332	55	0.455
I+F 3/3 vs C	0.417	0.332	55	0.215
F vs I	0.250	0.332	55	0.455
I+F 1/3 vs I	0.500	0.332	55	0.138
I+F 2/3 vs I	0.333	0.332	55	0.320
I+F 3/3 vs I	0.500	0.332	55	0.138
I+F 1/3 vs F	0.250	0.332	55	0.455
I+F 2/3 vs F	0.083	0.332	55	0.803
I+F 3/3 vs F	0.250	0.332	55	0.455
I+F 2/3 vs I+F 1/3	-0.167	0.332	55	0.618
I+F 3/3 vs I+F 1/3	0.000	0.332	55	1.000
I+F 3/3 vs I+F 2/3	0.167	0.332	55	0.618
Random effect	0.661			
<i>R</i> <sup>2</sup> <i>m</i>	0.032			
<i>R</i> <sup>2</sup> <i>c</i>	0.417			

**Table B.3.** Results of the LMMs carried out on the effects of fertilisation and irrigation on average vegetation height for both sampling sessions (i.e. before and after mowing). Table refers to figure 3 in the article. Abbreviations and parameter estimates as in Table B.1.

Response variable	Estimate	SE	df	<i>P</i> (> t )
<b>(a) Vegetation height before mowing</b>				
I vs C	0.151	0.075	50	0.050
F vs C	0.463	0.075	50	<b>&lt;0.001</b>
I+F 1/3 vs C	0.357	0.075	50	<b>&lt;0.001</b>
I+F 2/3 vs C	0.519	0.075	50	<b>&lt;0.001</b>
I+F 3/3 vs C	0.685	0.075	50	<b>&lt;0.001</b>
F vs I	0.313	0.075	50	<b>&lt;0.001</b>
I+F 1/3 vs I	0.206	0.075	50	<b>0.008</b>
I+F 2/3 vs I	0.368	0.075	50	<b>&lt;0.001</b>
I+F 3/3 vs I	0.534	0.075	50	<b>&lt;0.001</b>
I+F 1/3 vs F	-0.107	0.075	50	0.161
I+F 2/3 vs F	0.055	0.075	50	0.466
I+F 3/3 vs F	0.221	0.075	50	<b>0.005</b>
I+F 2/3 vs I+F 1/3	0.162	0.075	50	<b>0.036</b>
I+F 3/3 vs I+F 1/3	0.328	0.075	50	<b>&lt;0.001</b>
I+F 3/3 vs I+F 2/3	0.166	0.075	50	<b>0.032</b>
Random effect	0.145			
<i>R</i> <sup>2</sup> <i>m</i>	0.506			
<i>R</i> <sup>2</sup> <i>c</i>	0.705			
<b>(b) Vegetation height after mowing</b>				
I vs C	0.545	0.096	55	<b>&lt;0.001</b>
F vs C	0.487	0.096	55	<b>&lt;0.001</b>
I+F 1/3 vs C	0.591	0.096	55	<b>&lt;0.001</b>
I+F 2/3 vs C	0.941	0.096	55	<b>&lt;0.001</b>
I+F 3/3 vs C	1.237	0.096	55	<b>&lt;0.001</b>
F vs I	-0.058	0.096	55	0.549
I+F 1/3 vs I	0.047	0.096	55	0.628
I+F 2/3 vs I	0.396	0.096	55	<b>&lt;0.001</b>
I+F 3/3 vs I	0.692	0.096	55	<b>&lt;0.001</b>
I+F 1/3 vs F	0.105	0.096	55	0.281
I+F 2/3 vs F	0.454	0.096	55	<b>&lt;0.001</b>
I+F 3/3 vs F	0.750	0.096	55	<b>&lt;0.001</b>
I+F 2/3 vs I+F 1/3	0.349	0.096	55	<b>0.001</b>
I+F 3/3 vs I+F 1/3	0.646	0.096	55	<b>&lt;0.001</b>
I+F 3/3 vs I+F 2/3	0.296	0.096	55	<b>0.003</b>
Random effect	0.393			
<i>R</i> <sup>2</sup> <i>m</i>	0.418			
<i>R</i> <sup>2</sup> <i>c</i>	0.847			

**Table B.4.** Results of the LMMs carried out on the effects of fertilisation and irrigation on aboveground diurnal temperature for both sampling sessions (i.e. before and after mowing).

Table refers to figure 3 in the article. Abbreviations and parameter estimates as in Table B.1.

Response variable	Estimate	SE	df	$P(> t )$
<b>(a) Temperature before mowing</b>				
I vs C	-1.300	0.850	39	0.134
F vs C	-2.111	0.920	39	<b>0.027</b>
I+F 1/3 vs C	-2.305	1.098	40	<b>0.042</b>
I+F 2/3 vs C	-2.099	0.876	39	<b>0.021</b>
I+F 3/3 vs C	-4.317	0.866	39	<b>&lt;0.001</b>
F vs I	-0.810	0.914	39	0.381
I+F 1/3 vs I	-1.005	1.081	40	0.358
I+F 2/3 vs I	-0.799	0.849	39	0.353
I+F 3/3 vs I	-3.017	0.849	39	<b>0.001</b>
I+F 1/3 vs F	-0.195	1.133	40	0.865
I+F 2/3 vs F	0.012	0.929	39	0.990
I+F 3/3 vs F	-2.207	0.930	39	<b>0.023</b>
I+F 2/3 vs I+F 1/3	0.206	1.094	40	0.851
I+F 3/3 vs I+F 1/3	-2.012	1.099	40	0.075
I+F 3/3 vs I+F 2/3	-2.218	0.875	39	<b>0.015</b>
Random effect	1.597			
$R^2m$	0.232			
$R^2c$	0.547			
<b>(b) Temperature after mowing</b>				
I vs C	-1.612	0.949	38	0.097
F vs C	0.181	0.949	38	0.850
I+F 1/3 vs C	-0.503	0.949	38	0.599
I+F 2/3 vs C	-1.636	0.948	38	0.092
I+F 3/3 vs C	-1.228	1.028	39	0.240
F vs I	1.793	0.979	39	0.075
I+F 1/3 vs I	1.109	0.968	38	0.259
I+F 2/3 vs I	-0.024	0.978	39	0.981
I+F 3/3 vs I	0.385	1.060	39	0.719
I+F 1/3 vs F	-0.684	0.979	39	0.489
I+F 2/3 vs F	-1.817	0.978	39	0.071
I+F 3/3 vs F	-1.408	1.046	39	0.186
I+F 2/3 vs I+F 1/3	-1.133	0.978	39	0.254
I+F 3/3 vs I+F 1/3	-0.724	1.060	39	0.499
I+F 3/3 vs I+F 2/3	0.409	1.058	39	0.702
Random effect	2.098			
$R^2m$	0.061			
$R^2c$	0.541			

**Table B.5.** Detailed structural equation model (SEM) outputs for: (a) Caelifera density before mowing; (b) Caelifera density after mowing; and (c) Caelifera species richness. For each regression path, estimate (i.e. equivalent to unstandardized path coefficient in our case), standard error (SE), respective z- and p-values, as well as standardized path coefficient (Std coef.) are provided. Results of the Mardia's Skewness and Kurtosis multivariate normality tests are also given (here, p-values greater than 0.05 indicate multivariate normal distribution). Table refers to figure 5 in the article.

Response	Predictor	Estimate	SE	Z-value	P-value	Std coef.
<b>(a) Caelifera density before mowing (log scale)</b>						
Vegetation height	~ Slurry input	8.001	1.351	5.923	<b>&lt;0.001</b>	0.653
Vegetation height	~ Water input	1.575	0.729	2.158	<b>0.031</b>	0.129
Grasshopper density	~ Vegetation height	-0.027	0.010	-2.640	<b>0.008</b>	-0.419
Grasshopper density	~ Water input	-0.065	0.054	-1.216	0.224	-0.082
<i>Multivariate normality tests</i>						
Mardia Skewness		39.879			0.262	
Mardia Kurtosis		-1.750			0.080	
<b>(b) Caelifera density after mowing (log scale)</b>						
Aboveground T°C	~ Water input	-0.584	0.253	-2.311	<b>0.021</b>	-0.233
Grasshopper density	~ Slurry input	-0.044	0.044	-0.999	0.318	-0.072
Grasshopper density	~ Water input	-0.056	0.052	-1.081	0.280	-0.093
Grasshopper density	~ Aboveground T°C	0.039	0.056	0.699	0.485	0.162
<i>Multivariate normality tests</i>						
Mardia Skewness		40.385			0.244	
Mardia Kurtosis		-1.050			0.294	
<b>(c) Caelifera species richness</b>						
Aboveground T°C	~ Water input	-0.584	0.253	-2.311	<b>0.021</b>	-0.233
Grasshopper sp. richness	~ Slurry input	-0.467	0.140	-3.325	<b>0.001</b>	-0.361
Grasshopper sp. richness	~ Water input	-0.244	0.122	-1.999	<b>0.046</b>	-0.188
Grasshopper sp. richness	~ Aboveground T°C	0.091	0.079	1.143	0.253	0.176
<i>Multivariate normality tests</i>						
Mardia Skewness		41.244			0.216	
Mardia Kurtosis		-0.915			0.360	