

**Grassland irrigation and fertilisation decrease soil and within-  
vegetation temperatures, negatively impacting orthopteran  
populations**

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**Grassland irrigation and fertilisation decrease soil and within-vegetation temperatures,  
negatively impacting orthopteran populations**

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## **Abstract**

Traditional mountain meadows have been hosting an exceptionally rich biodiversity for centuries. They are now not only threatened by land abandonment, especially in remote areas, but also by massive intensification, notably via aerial irrigation and slurry application. As the consequences of this intensification on biodiversity are poorly understood a full-factorial experiment – whose design combines six management treatments with gradual levels of fertilization and irrigation – was conducted since 2010 at 12 meadow sites across the Swiss Alps. In 2013, we assessed the impact of these yearly applied management options on the community structure and population abundance of orthopterans. In parallel, we measured any changes in vegetation height and microclimate (both within the soil and just above the ground) in order to better appraise underlying mechanisms. Intensification had a negative impact on both orthopteran population densities (5000 individuals sampled in total) and species richness (21 species identified). Caelifera (grasshoppers) were generally more affected, with density and species richness drops of up to 70% and 50%, respectively, in the most intensively managed plots, i.e. those that combined high levels of slurry application and aerial irrigation. Intensification also induced a cooling of up to 4.5°C of above-ground, within-vegetation (air) temperature, and of 2.0°C in soil temperature, again within the most intensively managed plots, which could in part be related to an increase in vegetation height. This marked temperature drop is likely to have affected the development of orthopterans, leading to local extinction of thermophilous species. In contrast, fertilization and irrigation alone had only moderate effects on orthopterans and microclimate. These results will serve for defining best management practice for montane and subalpine meadows in the Alps, and possibly beyond.

**Keyword:** agriculture, Alps, arthropods, conservation, grasshoppers, meadow, microclimate

## 1. Introduction

In Europe, mountain meadows represent one of last remnant of exceptionally diverse semi-natural grassland types (Veen *et al.*, 2009). However two new management practices are spreading in alpine regions and threaten these biodiversity rich habitats: irrigation with sprinkler and fertilization with liquid manure (Maurer *et al.*, 2006; Riedener *et al.*, 2013). Both of these practices modify the vegetation community and structure which in turn affects the arthropod populations (Woodcock and Pywell, 2010; Andrey *et al.*, 2014). 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 process or pest control (Tschardt *et al.*, 2005) and are primordial food items for many vertebrates (e.g. Wilson *et al.*, 1999; Wickramasinghe *et al.*, 2004). This underlines the importance to preserve their abundance and diversity. So far fertilization has been shown to have a negative impact on arthropod species richness ensuing from a reduction of vegetation diversity (Haddad *et al.*, 2000; Haddad *et al.*, 2009). On the other hand it seems to boost herbivores abundance through an increase in plant tissue nitrogen and to have cascading effect on other arthropods functional groups (Haddad *et al.*, 2001; Kagata and Ohgushi, 2006). In contrast the effects of irrigation on arthropods remain poorly documented. Therefore current knowledge does not allow determining the irrigation and fertilization thresholds that should not be exceeded in order to maintain a functional and diverse arthropod community in mountain meadows.

The goal of the present study was to assess the response of orthopteran species richness and density to gradual levels of fertilization and irrigation in montane and subalpine meadows. In these grasslands orthopterans represent the most important insect group in term of biomass (Blumer and Diemer, 1996). They are a key component of the diet of many insectivorous species and an important decline in their density would have cascading effect on higher trophic level (Vickery *et al.*, 2001; Britschgi *et al.*, 2006). In addition, orthopterans are

recognized bioindicators for grasslands as they readily respond to management changes due to their sensitivity to a set of vegetation parameters (Baldi and Kisbenedek, 1997; Buri *et al.*, 2013).

First, orthopterans are sensitive to microclimate which varies with vegetation height and density (Song *et al.*, 2013). As ectotherms organisms, their development rate, body size, reproductive success and other physiological processes are depending on temperature. Each species has its own thermal sensitivity: for example eurythermal species such as *Chorthippus parallelus* are very tolerant and can adapt to a range of microclimatic conditions while thermophilous species such as *Stenobothrus lineatus* are restricted to warm and dry habitats (Van Wingerden *et al.*, 1991; Willott and Hassall, 1998). Microclimatic conditions influence thus the orthopteran community. Second, the habitat diversity hypothesis stipulates that more diverse a habitat is the more species it is likely to host (Baldi, 2008). At orthopteran scale microhabitat diversity is function of the vegetation structural heterogeneity which is to some extent correlated with plant diversity (e.g. Morris, 2000; Tews *et al.*, 2004; Woodcock and Pywell, 2010). Finally food availability is a limiting factor for the expansion of any organism. A sufficient proportion of grass is essential to maintain Caelifera density as they almost exclusively feed on it (Ibanez *et al.*, 2013). Ensifera on their side have a more diversified diet composed of small invertebrates and grasses and are thus less dependent on specific food resources (Baur *et al.*, 2006). The first aim of the present study was to investigate how orthopteran populations respond to gradual level of irrigation and fertilization and to determine whether an optimum management intensity maximising both density and species richness exist. The second aim was to measure the changes in vegetation height and soil and surface temperatures induced by intensification, and to determine whether orthopteran responses can be explained by these changes.

In the short term fertilization has been shown to increase vegetation structure (Andrey

*et al.*, 2014) while in the long term it induces a loss of plant species richness and a homogenisation of the vegetation cover (Marini *et al.*, 2008). In addition it induces a shift in plant community toward higher percentage of grass and legumes (Jacquemyn *et al.*, 2003) whereas irrigation favours grass species and increase nitrogen (N) mineralization by plants (Jeangros and Bertola, 2000; Wenninger and Inouye, 2008; Riedener *et al.*, 2013). Finally both inputs boost the productivity and thus create a denser and taller sward (Marini *et al.*, 2009; Bassin *et al.*, 2012). Consequently we expected soil and surface to gradually cool down along intensification gradient (Song *et al.*, 2013). Concerning the orthopterans we expected species richness to decrease steadily along intensification gradient due to the disappearance of thermophilous species (Van Wingerden *et al.*, 1991) and the loss of microhabitats (Tews *et al.*, 2004). In addition we expected densities to increase at mid-intensity as a consequence of better food quality (Ritchie, 2000; Hudewenz *et al.*, 2012) and to decrease in highly intensified plots due to the detrimental effect of microclimate cooling (Van Wingerden *et al.*, 1992).

A powerful advantage of the study is that it was realized in an experimental framework which allowed to get unbiased measurements on impacts of the investigated grassland management practices (six different treatments) on vegetation height, soil and surface temperatures, and orthopteran populations; i.e. that recorded relative differences between treatments were not influenced by the local and surrounding environmental characteristics. In addition this is the first study measuring precisely the effect of controlled levels of intensification on microclimate and orthopterans simultaneously. A clear novelty is that levels of intensification were based on site productivity potential, reflecting what farmers do, allowing direct transfer of the conclusions to the practice.

## 2. Material and methods

### 2.1 Study sites

The study was carried out in the canton of Valais, an inner Alps valley of Switzerland which experiences a continental climate with cold and wet winter and dry and hot summers: mean annual temperature amounts 10.7°C and mean annual precipitation achieves 517 mm (2000–2014 mean in Sion, 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 (Fig. 1, Appendix 1).

### 2.2 Experimental design

In 2010, within each meadows (n = 12), six different management treatments were randomly allocated to plots of 20 m in diameter spaced from each other by at least 5 m. The first plot served as a control (C). The second and third plots were only irrigated (I) or fertilized (F), and the fourth to sixth plots were irrigated and fertilized (I+F; Table 1). The exact amount of fertilizer applied at each site depended on the theoretical local hay production potential calculated using pre-experimental hay yield (when extensively managed) and site elevation (see table 3 in Sinaj *et al.*, 2009). Accordingly, I+F 3/3 treatments matched the norms recommended for intensively managed meadow, i.e. for groups 1, 2 and 3, respectively, 40, 60 and 80 [kg N·ha<sup>-1</sup>·yr<sup>-1</sup>]. Within group, mid-intensive (F and I+F 2/3) and low-intensive (I+F 1/3) treatments, received respectively two-thirds and one-third of the maximum fertilization dose. It has been decided to follow these prescriptions in order to obtain results within realistic agronomical systems. Fertilizer consisted 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 liquid manure (Sinaj *et al.*, 2009) consisting

namely of 2.4 kg of usable nitrogen, 2 kg of phosphate ( $P_2O_5$ ), and 8 kg of potassium oxide ( $K_2O$ ) per  $m^3$  of solution. Every year the plots were fertilized once in early spring and once after the first cut (June or July), each time half of the annual fertilizer amount was applied (except for the 1/3-plots that were fertilized only once in spring). Treatments I and I + F were additionally irrigated weekly from mid-May to end of August, except when heavy rainfall occurred ( $\geq 20$  mm over the previous week). Irrigation thresholds were chosen on the basis of Calame et al. (1992) experiment. Accordingly I and I+F 2/3 matched the recommendation 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 respectively half and one and an half of this dose (Table 1).

### *2.3 Orthopterans 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  $1\ m^2$  (as described in Humbert *et al.*, 2012). 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 August and 31 August). The date at which meadows were sampled was function of their altitude. During both sessions, eight samples were regularly taken per plot. All the individuals trapped within the biocenometer were caught and identified on site. Adults were identified to species level while juveniles were classified into suborders (Caelifera or Ensifera). All samplings were done on sunny days between 10 am and 5 pm.

### *2.4 Vegetation height record*

Vegetation height was measured as the average vegetation stratum height in a 10 cm radius around a ruler. Eight records were taken during the orthopterans samplings by randomly



dropping a ruler next to the area circled by the biocenometer. All the measurements were performed by the same person.

### *2.5 Temperature record*

To record soil and surface temperatures I-buttons DS1921G-F ThermoChron (Maxim Integrated Products/Dallas) were used, which are self-sufficient systems measuring and recording temperature in 0.5°C increment. Two of those devices were randomly placed at 5 m above or below the centre of each plot: one thermometer was buried 5 cm belowground, the approximate depth at which eggs are laid (Bieringer and Zulka, 2003), and the other one was fixed on a stick 10 cm aboveground. I-buttons recorded temperature hourly from beginning of May to end of August. They were removed shortly before the first cut and replaced within a few days. The data from the ten days following mowing event were removed from the analysis to reduce noise due to the manipulation of the devices. Average daily temperature was calculated as the mean temperature between 12 am and 4 pm while average nocturnal temperature was calculated as the mean temperature between 12 pm and 4 am.

### *2.6 Statistical analyses*

Treatments effects were analysed with generalized linear mixed models (GLMMs) using the *lmer* function from the *lme4* package for R (Bates *et al.*, 2011). Response variables were orthopteran densities, species richness, vegetation height and temperatures; they were analysed with either Poisson (Caelifera densities and vegetation height) or Gaussian (others) distribution in order to achieve normal distribution of residuals. The fixed effects were the treatments (C, I, F, I+F 1/3, I+F 2/3, I+F 3/3), and the random effects were the study sites in all the analyses as well as the Julian dates for temperature analyses. When using the Poisson distribution, *P*-values were computed with the *pvals.fnc* function from the *languageR* package

using 100'000 Markov chain Monte Carlo iterations (Baayen, 2011). Caelifera and Ensifera responses were analysed separately as they differ in their ecology (Baur *et al.*, 2006). Temperature and density data were analysed per sampling session while species data were pooled as it was not possible to run separated analyses for the first session due to the low number of adults found during this period. All statistics were performed using R version 2.15.3 (R Core Team, 2013).

### 3 Results

#### 3.1 Orthopteran species richness

A total of 21 species was recorded within all plots, seven of which were Ensifera and fourteen of which were Caelifera (see Appendix 1 for detailed list). The minimum number of species found within a plot was one and the maximum was nine. Management practices significantly affected the Caelifera species richness. The highest Caelifera species richness was found within C-plots (mean  $\pm$  standard error (SE) =  $4.4 \pm 0.5$ ) that hosted similar species number than I-plots ( $4.0 \pm 0.4$ ) and F-plots ( $3.9 \pm 0.4$ ) but  $\sim 35\%$  more species than I+F 1/3-plots ( $2.8 \pm 0.4$ ,  $P < 0.001$ ) and I+F 2/3-plots ( $3.1 \pm 0.3$ ,  $P = 0.006$ ) and  $>50\%$  more species than I+F 3/3-plots ( $2.0 \pm 0.2$ ,  $P < 0.001$ ; see Fig. 2a and Appendix 2 for detailed model outputs). Contrariwise, no significant effect was detected on the Ensifera species richness (Fig. 2b and Appendix 2).

#### 3.2 Orthopterans 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 sampling session. Treatments were found to have significant effects on Caelifera densities while low densities of Ensifera limited the power of the analysis on this

suborder.

Before mowing the highest Caelifera densities were found within C-plots ( $8.42 \pm 2.76$ ) that hosted ~30–40% more individuals than I-plots ( $5.68 \pm 2.18$ ,  $P = 0.016$ ) and F-plots ( $4.77 \pm 1.89$ ,  $P < 0.001$ ) and >70% more individuals than I+F 1/3-plots ( $2.43 \pm 0.92$ ,  $P < 0.001$ ), I+F 2/3-plots ( $2.02 \pm 0.97$ ,  $P < 0.001$ ) and I+F 3/3-plots ( $2.26 \pm 0.85$ ,  $P < 0.001$ ; see Fig. 3a and Appendix 3 for detailed model outputs). Concerning the Ensifera, the highest densities were found within F-plots ( $0.94 \pm 0.17$ ) that hosted significantly more individuals than I+F 1/3-plots ( $0.53 \pm 0.24$ ,  $P = 0.033$ ) and I+F 3/3-plots ( $0.45 \pm 0.14$ ,  $P = 0.016$ ), while the C-plots ( $0.66 \pm 0.18$ ), I-plots ( $0.80 \pm 0.17$ ) and I+F 2/3-plots ( $0.57 \pm 0.17$ ) did not differ from any other plot (Fig. 3b and Appendix 3).

After mowing highest Caelifera densities were again found within C-plots ( $5.62 \pm 2.25$ ) which hosted ~40-45% more individuals than I+F 2/3-plots ( $3.17 \pm 0.68$ ,  $P = 0.006$ ) and I+F 3/3-plots ( $3.45 \pm 1.15$ ,  $P = 0.018$ ) while I-plots ( $3.81 \pm 1.11$ ), F-plots ( $4.64 \pm 1.23$ ) and I+F 1/3-plots ( $4.23 \pm 1.54$ ) densities were equivalent to other plots (see Fig. 3c and Appendix 3 for detailed model outputs). Ensifera densities did not respond the same way. Highest densities were found within I+F 3/3-plots ( $0.35 \pm 0.14$ ) that hosted significantly more individuals than I-plots ( $0.12 \pm 0.07$ ,  $P = 0.032$ ) while I+F 2/3-plots ( $0.30 \pm 0.10$ ), I+F 1/3-plots ( $0.25 \pm 0.09$ ), F-plots ( $0.17 \pm 0.06$ ) and C-plots ( $0.15 \pm 0.05$ ) did not differ from any other plots (Fig. 3d and Appendix 3).

### *3.3 Vegetation height*

Before mowing vegetation stratum height was the tallest in I+F 3/3-plots ( $61.8 \text{ cm} \pm 3.5 \text{ cm}$ ), it was slightly shorter in I+F 1/3-plots ( $52.1 \pm 7.7$ ,  $P = 0.084$ ), I+F 2/3-plots ( $51.9 \pm 2.3$ ,  $P = 0.092$ ) and F-plots ( $49.9 \pm 3.4$ ,  $P = 0.039$ ) while it grew half less in C-plots ( $31.8 \pm 2.9$ ,  $P < 0.001$ ) and I-plots ( $36.9 \pm 3.1$ ,  $P < 0.001$ ; see Fig. 4a and Appendix 4 for detailed model

outputs). After mowing the same trend was observed with tallest sward found within I+F 3/3-plots ( $25.0 \pm 1.9$ ), followed by I+F 2/3-plots ( $19.2 \pm 2.1$ ,  $P = 0.004$ ) and then I+F 1/3-plots ( $14.8 \pm 2.2$ ,  $P < 0.001$ ), F-plots ( $13.6 \pm 2.2$ ,  $P < 0.001$ ) and I-plots ( $12.8 \pm 1.2$ ,  $P < 0.001$ ), while C-plots vegetation ( $9.6 \pm 2.2$ ,  $P < 0.001$ ) was more than twice shorter (Fig. 4b and Appendix 4).

### 3.4 Temperature

Before mowing, mean diurnal surface temperature was the warmest in C-plots ( $22.4 \pm 1.0$  °C), then temperatures in I-plots ( $20.9 \pm 0.7$ ), I+F 1/3-plots ( $20.6 \pm 2.1$ ), I+F 2/3-plots ( $20.5 \pm 0.6$ ) and F-plots ( $20.3 \pm 0.8$ ) were 1.5-2.0°C colder (all  $P < 0.001$ ) while it was over 4.0°C colder in I+F 3/3-plots than in C-plot ( $18.2 \pm 0.5$ ,  $P < 0.001$ ). The soil temperature (5 cm belowground) was the warmest in C-plots ( $12.9 \pm 0.4$ ), I-plots ( $13.1 \pm 0.5$ ) and F-plots ( $13.0 \pm 0.8$ ), about 0.5° colder in the I+F 1/3-plots ( $12.3 \pm 0.5$ ) and I+F 2/3-plots ( $12.4 \pm 0.4$ ) compared to C-plot (both  $P < 0.001$ ) while I+F 3/3-plots ( $11.3 \pm 0.8$ ,  $P < 0.001$ ) were the coldest (see Fig. 4a and Appendix 5 for detailed model outputs).

After mowing, diurnal surface 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 ( $29.2 \pm 1.2$ ,  $P = 0.040$ ) were respectively ~1°C colder and I+F 3/3-plots ( $28.5 \pm 1.4$ ,  $P < 0.001$ ), I-plots ( $28.4 \pm 0.7$ ,  $P < 0.001$ ) and I+F 2/3-plots ( $28.3 \pm 1.1$ ,  $P < 0.001$ ) ~1.5°C colder than C-plots. The mean soil temperature was the warmest in C-plots ( $20.2 \pm 1.2$ ) and the coldest in I+F 3/3-plots ( $18.6 \pm 0.6$ ,  $P < 0.001$ ) while intermediately I-plots ( $19.8 \pm 0.7$ ,  $P < 0.001$ ), F-plots ( $19.4 \pm 0.7$ ,  $P < 0.001$ ), I+F 1/3-plots ( $19.2 \pm 0.8$ ,  $P < 0.001$ ) and I+F 2/3-plots ( $19.2 \pm 0.5$ ,  $P < 0.001$ ) soil temperatures were slightly decreasing from 0.6 to 1° colder than in C-plots (Fig. 5b and see Appendix 5 for detailed model outputs). Treatments did affect nocturnal temperatures but differences were not biologically relevant (in order of 0.1–0.2°) and are thus not further discussed.

## 4 Discussion

This study shows that grassland fertilization and irrigation combined greatly affects orthopterans by decreasing both their species richness and densities, but that the use of a single practice (irrigation or fertilization) has relatively limited impacts. The species loss along intensification gradient was expected but the associated drop in densities came as a surprise (Hudewenz *et al.*, 2012). The second important output of this study is the demonstration that intensification practices induce an important drop in soil and surface temperature. Microclimate cooling has often been suggested as a potential mechanism to explain responses of various arthropod groups to intensification (e.g. Schwab *et al.*, 2002; Dennis *et al.*, 2004; Marini *et al.*, 2009), but the link had never been clearly demonstrated.

In the following subsections we will first present the effects of the management practices on vegetation and microclimate. We will then discuss its effects on orthopterans density and species richness and show how these are linked to microclimate. Finally we will discuss the conservation implications of the present study.

### 4.1 Effects on vegetation and microclimate

Combined irrigation and fertilization led to twice taller swards in the most intensively managed plots (I+F 3/3) compared to control plots, which was expected as water and nitrogen are limiting factor for vegetation growth in dry subalpine region (e.g. Tasser and Tappeiner, 2002; Rigling *et al.*, 2003; Bassin *et al.*, 2012). Before the first cut irrigation alone had lesser effect, likely as a consequence of the wet 2013 spring. However after the cut both inputs had an equivalent positive effect on plants regrowth and their combination heightened their respective effects.

Soil and surface temperatures are linked to vegetation height: the taller and denser the sward becomes the less sunlight reaches the ground and the less it is warmed (Song *et al.*,

2013). Consequently the temperatures differences between the most intensively managed plots and the controls were of up to 2°C at 5 cm belowground and 4.3°C at 10 cm aboveground. After the cut vegetation regrew progressively which reduced the surface temperature differences among plots. Vegetation height is not the only factor explaining microclimate; other parameters such as vegetation density and canopy cover do influence quantity of sunshine reaching the soil and thus indirectly temperature (Van Wingerden *et al.*, 1992). This explains why surface temperatures were significantly colder in irrigated plot than in control plots while swards heights were similar.

#### *4.2 Effects on orthopteran species richness*

Overall orthopterans species richness decreased with management intensification. This trend is in line with previous observational studies done in the Italian Alps (Marini *et al.*, 2008), as well as conclusions from studies carried on in lowland regions (Knop *et al.*, 2006) and it confirms the general detrimental effects of grassland management intensification on orthopteran species richness. Nevertheless, different responses were observed between the two suborders, with stronger negative effects on Caelifera.

Highest Caelifera species richness was found in the control plots and was maintained in plots that were either irrigated or fertilized but the combination of both inputs had detrimental effects: species loss reached 50% in the most intensive plots (I+F 3/3). The parallel drop in species richness and temperatures suggests that either thermophile species chose deliberately not to oviposit within more intensive plots – showing a cumulative effect from previous year – or the eggs laid within colder plots poorly developed and never reached maturity (Willott and Hassall, 1998). Willot and Hassal (1998) showed that a difference of 5°C in ambient temperature – air temperature differences reached 4.3°C in our case – considerably affects Caelifera fitness: most sensitive species experiments a development time

50% longer, a reduction of 25% in body mass and a drop of 50% in pods production. This support the hypothesis that the microclimate conditions within intensively managed plots became too cold for thermophilous species. Although microclimate emerged as an important driver we do not claim that it is the only explanatory mechanism. De facto temperature changes do not explain the relatively lower Caelifera species richness found within low-intensity plots (I+F 1/3) compared to irrigated or fertilized only plots. It is known that in addition to soil and air temperature orthopteran community composition is related to several other parameters such as vegetation structural heterogeneity (Morris, 2000; Jerrentrup *et al.*, 2014), percentage of bare ground (Sliacka *et al.*, 2013; Weiss *et al.*, 2013) and plant species composition (Gardiner *et al.*, 2002; Ibanez *et al.*, 2013). Thus temperatures and sward height in I+F 1/3 plots might have been optimal, or at least similar to control plots, but vegetation too homogeneous and missing open patches depriving thermophilic species from essential basking sites.

Contrariwise to Caelifera, Ensifera species richness was not affected by intensification. This suborder is known to be less sensitive to microclimate than Caelifera and to depend more on vegetation structure (Bieringer and Zulka, 2003; Baur *et al.*, 2006; Schirmel *et al.*, 2010). However, a change in community composition accompanying intensification was noticed. Large species such as *Tettigonia viridissima* or generalists such as *Metrioptera roeselii* favoring tall vegetation which offers good singing spots and shelter (Baur *et al.*, 2006; Woodcock *et al.*, 2009) were more often found in intensively managed plots compared to extensively managed plots. In the contrary *Plactycleis albopunctata* or *Decticus verrucivorus* which are species associated with warm and dry habitat (Zschokke *et al.*, 2000; Baur *et al.*, 2006) were occasionally found in control plots, but not within intensively managed ones. This reflects the ecological diversity of Ensifera and might explain why their global species richness remained stable among experimental plots. It has to be noted that the power of the

analyses was constrained due to relatively low Ensifera densities (ranged between 0.5 to 1.0 individual per m<sup>2</sup>).

#### *4.3 Effects on orthopteran densities*

Management intensification had even stronger impacts on orthopteran densities than on species richness as detrimental effects were already visible in low intensity plots. Before mowing Caelifera densities dropped by 30–40% in plots that had been either irrigated or fertilized. The combination of both inputs was even worse leading to over 70% reduction in density regardless of quantities applied. As most individuals were low-mobile larvae during the first sampling session their distribution reflects their birth place. Therefore reasons for differences could be one or a combination of following factors: 1) females favored warmer sites to oviposit, 2) larval development was altered and survival rate was lower in colder plots (Willott and Hassall, 1998), 3) eggs hatching was delayed in colder plots and had not occurred yet at the time plots were sampled, which is detrimental to population as it reduces individuals chance to complete their life cycle and to reproduce (Van Wingerden *et al.*, 1991; Weiss *et al.*, 2013). Intensification also impacted Ensifera densities but to a lesser extent. This might reflect the fact that in average Ensifera species emerged earlier in the season compared to Caelifera, when vegetation height and thus microclimate differences were less pronounced among management practices. Moreover their development is globally less dependent on temperatures (Bieringer and Zulka, 2003).

The mowing event may have dispersed the individuals all over the meadow area (Humbert *et al.*, 2012) so the densities of adults orthopteran found during the second sampling session were not directly related to number of larvae found during the first sampling session. Nevertheless, the impact of intensification on Caelifera density was still substantial with 40% less individuals within moderately (I+F 2/3) and highly intensified (I+F 3/3) plots



than within control plots. A boom in eggs hatching probably occurred in the days following mowing due to warmer microclimate as about half of the individuals sampled during the second session were still at larval stage. However they were equally distributed among plots and it is adults that were more numerous within low intensity plots. We had hypothesized that at moderate management intensity level orthopteran densities would be maximized, benefiting from increased food supply without being impacted by microclimate changes (Hudewenz *et al.*, 2012; Spalinger *et al.*, 2012). However, results are not in accordance with our hypothesis and show that after the cut generalist species such as *C. parallelus* dispersed more or less evenly across the plots while the specialized thermophilous species such as *S. lineatus* or *Omocestus haemorrhoidales* recolonized the warmest plots (Baur *et al.*, 2006). Overall results seem to indicate that in the investigated mountain meadows food resource is not a limiting factor for Caelifera while temperature might be.

After mowing Ensifera were slightly more numerous in more intensively managed plots and there were virtually no more larvae. This pattern was due to the preponderant presence of adults *T. viridissima* and *M. roeseli* that favored the tall swards found in intensified plots. However densities remained very low with less than 0.5 Ensifera per m<sup>2</sup>.

#### *4.4 Conclusions and conservation implications*

Aerial irrigation and fertilization with liquid manure are two novel management practices currently spreading in dry alpine regions (Riedener *et al.*, 2013). While on one hand these practices benefit biodiversity in the sense that by increasing grass yield (Bassin *et al.*, 2012; Andrey *et al.*, 2014) they support continuity of local farming so as to keep montane and subalpine semi-natural grasslands open (Gellrich *et al.*, 2008), on the other hand they become a threat to biodiversity when too much inputs are applied. Currently, knowledge is missing to determine optimal management thresholds that would allow decent yield while preserving

functional diversity. The present study helps fulfilling this knowledge gap by appraising the effect of gradual grassland management intensification on key taxa.

In contrast to observational studies, the experimental approach adopted in this study has the advantage that measured differences between treatments were not affected (biased) by environmental parameters such as soil, altitude or surrounding landscape, neither by climate or past management history. In addition, results are based on controlled, quantitatively based, levels of grassland irrigation and fertilization that are related to what is done in the practice. On the other hand it has some limitations due to the size and proximity of the plots that could have blurred the signal. But despite the close proximity of the experimental plots, very clear evidences that intensification lower both Caelifera densities and species richness were found, which are then conservative findings. Results demonstrate that the use of one input alone, namely fertilization or irrigation, has moderate impacts on orthopterans and on microclimate while the combination of both inputs is harmful to orthopterans even at low dose. The first finding is good news for all stakeholders (including farmers, conservationists and policy-makers) as irrigation alone can increase hay yield without affecting biodiversity (Jeangros and Bertola, 2000; Andrey *et al.*, 2014) and is allowed in subsidized extensively managed meadows registered under Swiss agri-environment schemes. On the other hand the combination of both inputs heightens their respective effects and must be forbidden in grassland where conservation of invertebrate and vertebrate fauna is of concern as a drop in grassland invertebrate densities can have dramatic bottom-up effects on higher trophic levels (Vickery *et al.*, 2001). Whereas further investigations on the topic, including plants and other invertebrates measurements, are required to clearly assess the influence of management intensification on biodiversity, this study darken the optimist perspective to find an intermediate management intensity threshold (optimum) that provides decent agronomical yield and that has only limited negative effects on biodiversity.

The second important contribution of this study is the quantitative assessment of changes in microclimate induced by intensification. The effective cooling (up to 2°C 5 cm in the soil and more than 4°C at 10 cm above ground) measured exceeded expectations and can have huge impacts on the development of local micro-fauna (Logan *et al.*, 2006). While we acknowledge that we do not prove the causal connection, but only show a correlation between cooling and orthopteran decline, it is highly probable that changes in soil and aboveground temperatures play an important underlying mechanistic role explaining intensification impact on this group (see also Van Wingerden *et al.*, 1992; Bieringer and Zulka, 2003; Marini *et al.*, 2008), as well as on other grassland invertebrate taxa such as butterflies (Kramer *et al.*, 2012) and beetles (Gillingham *et al.*, 2012).

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**Table 1:** Management practices applied to the six different experimental plots (treatments).

The exact amount of fertilizer applied at each site followed the local management norm recommended in Sinaj *et al.* (2009), and were classed in three groups. Irrigation thresholds were selected on the basis of Calame *et al.* (1992) experiment. Note that I and F, received the same amount of water or fertilisers as I+F 2/3.

| Management treatment | Mowing regime [no. of cut·yr <sup>-1</sup> ] | Irrigation [mm·week <sup>-1</sup> ] | Fertilization [kg N·ha <sup>-1</sup> ·yr <sup>-1</sup> ] |         |         |
|----------------------|--|-------------------------------------|--|---------|---------|
|                      |  |                                     | Group 1  | Group 2 | Group 3 |
| C                    | 1  | -                                   | -  | -       | -       |
| I                    | 2  | 20                                  | -  | -       | -       |
| F                    | 2  | -                                   | 53.3   | 40      | 26.6    |
| I+F 1/3              | 2  | 10                                  | 26.6   | 20      | 13.3    |
| I+F 2/3              | 2  | 20                                  | 53.3   | 40      | 26.6    |
| I+F 3/3              | 2  | 30                                  | 80   | 60      | 40      |

## Figures legends

**Fig.1.** Location of the 12 study sites in the canton of Valais (dark grey) in Switzerland.

**Fig.2.** Responses of Caelifera (a) and Ensifera (b) species richness to the six different management treatments. Abbreviations for treatments: C = control, F = fertilization only, I = irrigation only, I+F 1/3 = irrigation + fertilization at 1/3 of maximum intensity, I+F 2/3 = irrigation + fertilization at 2/3 of maximum intensity, I+F 3/3 = irrigation + fertilization at maximum intensity level. 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 quantiles.

**Fig.3.** Responses of orthopteran densities (individuals/m<sup>2</sup>) to the six different management treatments: a) Caelifera densities before mowing; b) Ensifera densities before mowing; c) Caelifera densities after mowing (Note that in the control, a point at 27.4 individuals/m<sup>2</sup> does not appear on the figure); d) Ensifera densities after mowing. For treatment abbreviations and boxplot descriptions see legend of figure 2.

**Fig.4.** Soil and air diurnal temperature and mean vegetation height responses to the six different management treatments, before (a) and after mowing (b). Open crossed circles represent air temperatures, filled circles represent soil temperatures and triangles represent mean vegetation heights. Different letters indicate significant differences between treatments at an alpha rejection value set to 0.05, and error bars represent 95% confidence intervals. For treatment abbreviations see legend of figure 2.

Fig.1

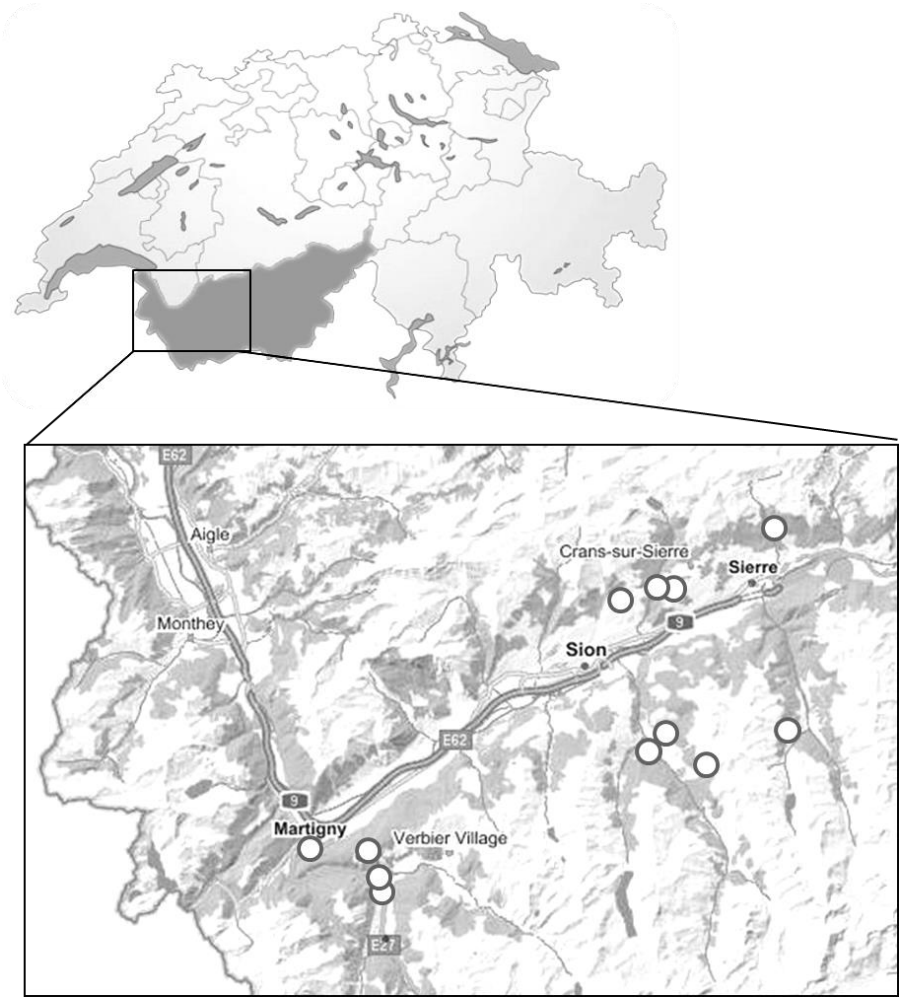
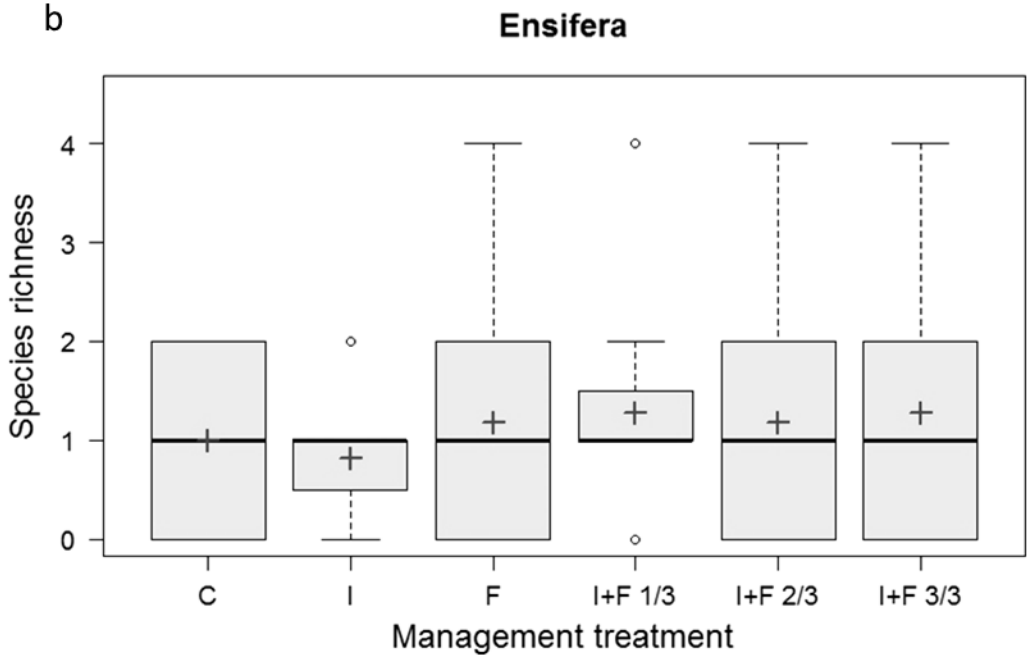
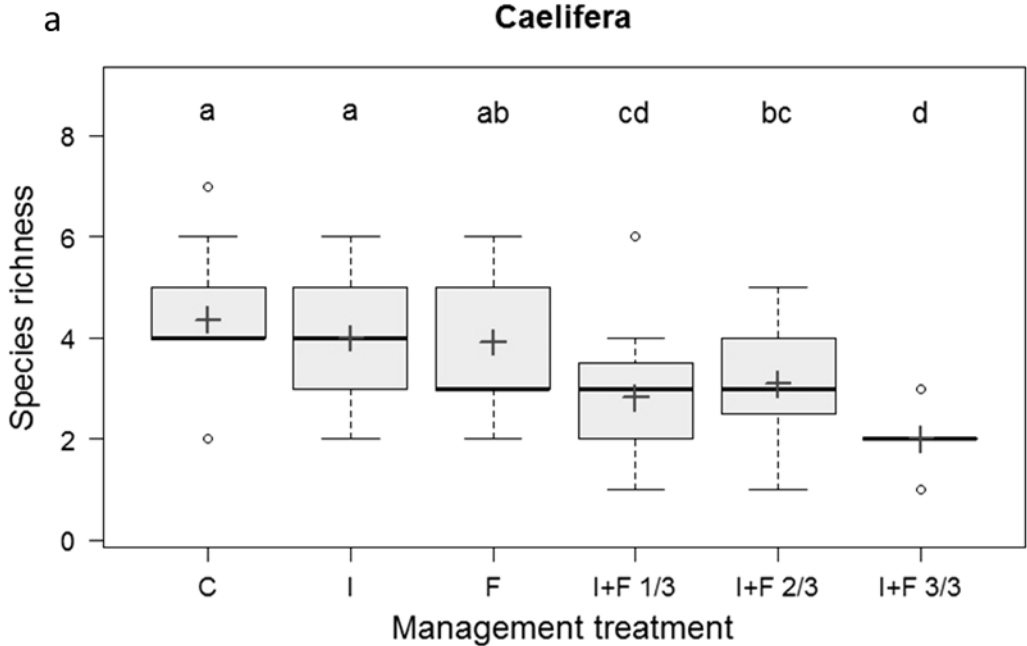


Fig.2



**Fig.3**

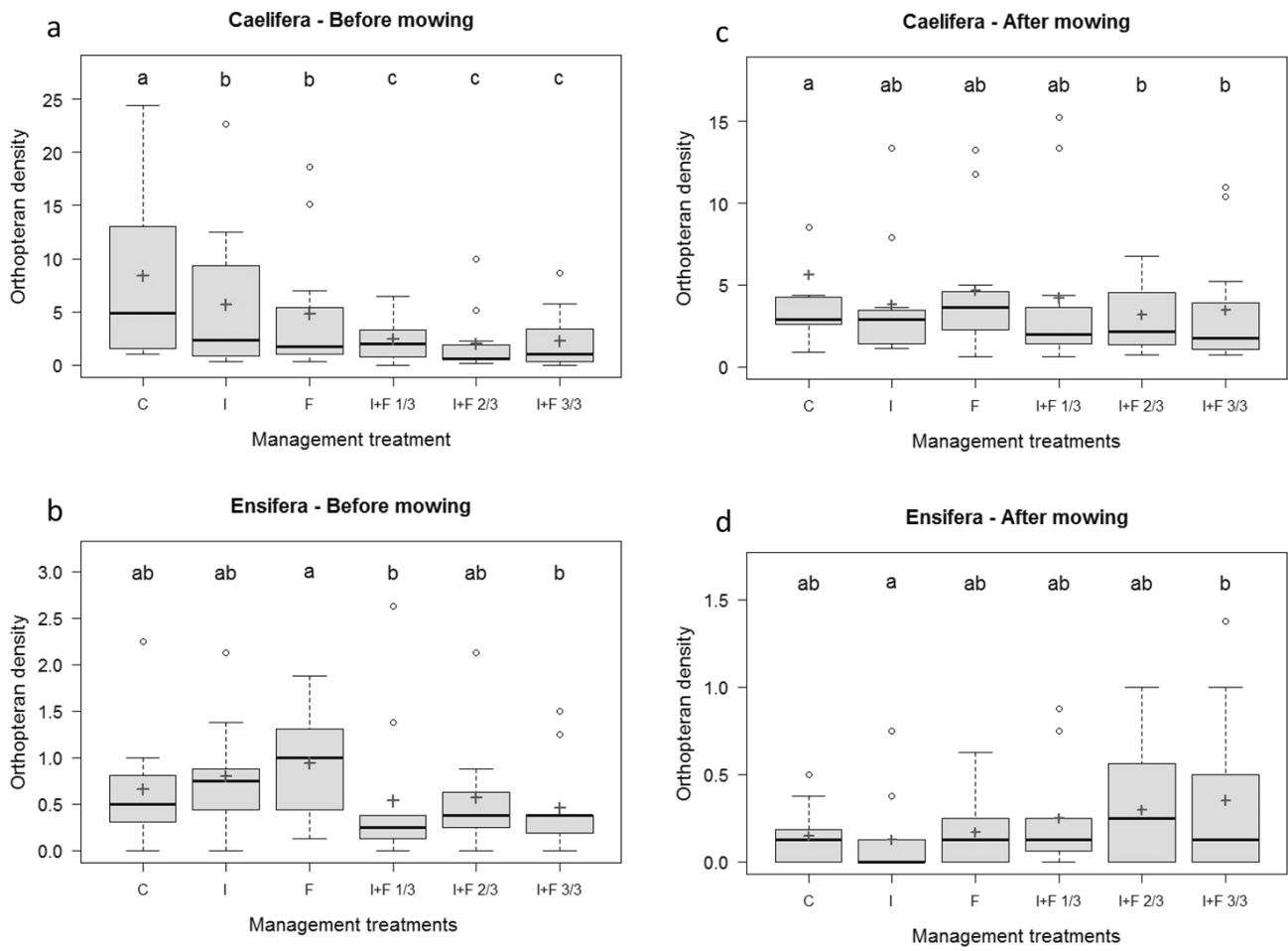
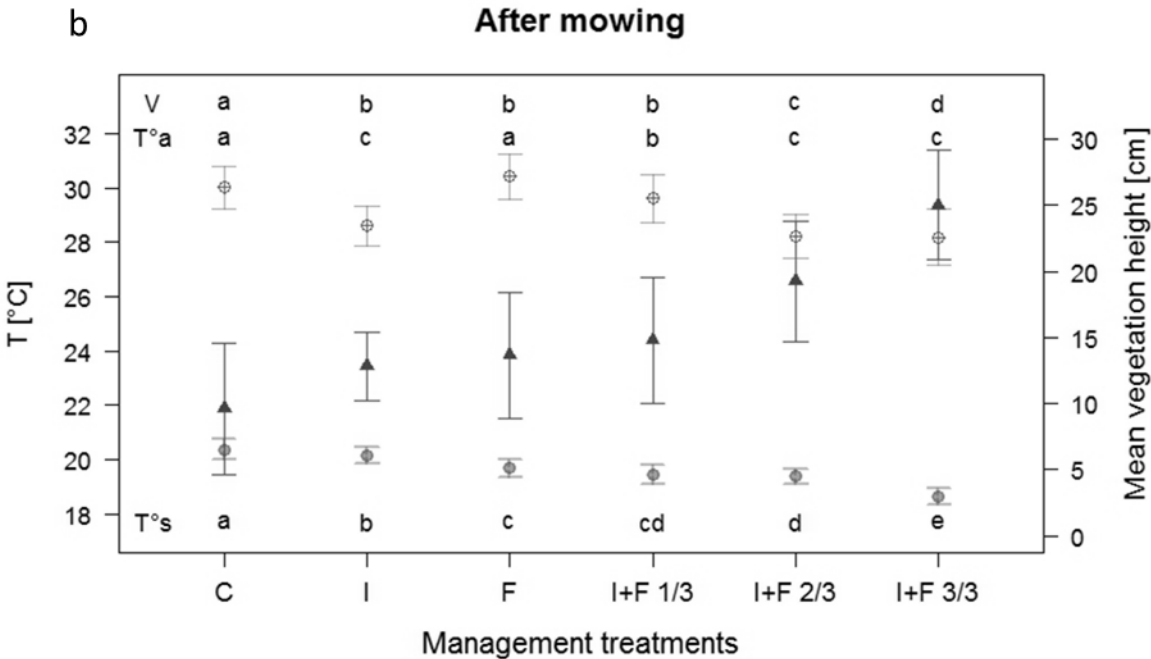
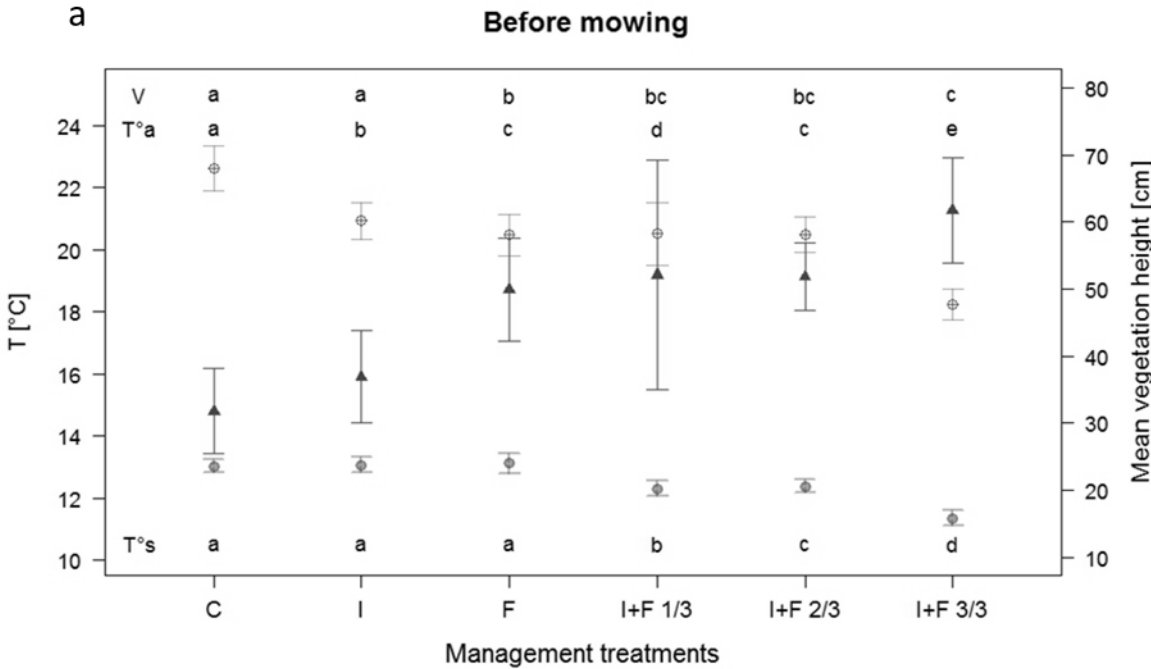


Fig. 4





## **Appendices**

**Appendix 1:** Location of all study sites and indication on the number of orthopterans of each species caught during the two sampling sessions in each site.

**Appendix 2:** Results of the GLMMs carried out on the effects of fertilization and irrigation on Caelifera and Ensifera species richness.

**Appendix 3:** Results of the GLMMs carried out on the effects of fertilization and irrigation on Caelifera and Ensifera densities.

**Appendix 4:** Results of the GLMMs carried out on the effects of fertilization and irrigation on vegetation height.

**Appendix 5:** Results of the GLMMs carried out on the effects of fertilization and irrigation on soil and surface temperature.

## Appendix 1

Location name of all study sites (n = 12), sampling date, geographic coordinates (Swiss grid system), altitude and number of orthopterans of each species caught during the two sampling sessions. In addition, meadows were classified in three groups according to the maximum 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.

|               | Site        | Coordinates |        | Group | Altitude | Date       | Caelifera larvae | Ensifera larvae | <i>Chortippus parallelus</i> | <i>Chortippus biguttulus</i> | <i>Chortippus dorsatus</i> | <i>Chortippus brunneus</i> | <i>Stauroderus scalaris</i> | <i>Stenobothrus lineatus</i> | <i>Euthystira brachyptera</i> | <i>Omocestus rufipes</i> | <i>Omocestus viridulus</i> | <i>Omocestus haemorrhoidalis</i> | <i>Acryptera fusca</i> | <i>Chrysopa dispar</i> | <i>Mecostethus parapleurus</i> | <i>Tettigonia viridissima</i> | <i>Metrioptera rosellii</i> | <i>Metrioptera saussuriana</i> | <i>Decticus verrucivorus</i> | <i>Plactycleis albopunctata</i> | <i>Pholidoptera grisoptera</i> | <i>Conocephalus fuscus</i> | <i>Leptophyes punctatissima</i> |    |
|---------------|-------------|-------------|--------|-------|----------|------------|------------------|-----------------|------------------------------|------------------------------|----------------------------|----------------------------|-----------------------------|------------------------------|-------------------------------|--------------------------|----------------------------|----------------------------------|------------------------|------------------------|--------------------------------|-------------------------------|-----------------------------|--------------------------------|------------------------------|---------------------------------|--------------------------------|----------------------------|---------------------------------|----|
|               |             | x           | Y      |       |          |            |                  |                 |                              |                              |                            |                            |                             |                              |                               |                          |                            |                                  |                        |                        |                                |                               |                             |                                |                              |                                 |                                |                            |                                 |    |
| Before mowing | Arbaz       | 595461      | 125245 | 2     | 1270     | 26.06.2013 | 27               | 22              | 0                            | 0                            | 0                          | 0                          | 0                           | 0                            | 7                             | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 0                            | 3                               | 0                              | 0                          | 0                               | 0  |
|               | Cordona     | 608758      | 130885 | 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                              | NA |
|               | Eison       | 602397      | 111514 | 3     | 1768     | 12.07.2013 | 708              | 29              | 0                            | 0                            | 0                          | 0                          | 0                           | 0                            | 15                            | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 4                            | 0                               | 0                              | 0                          | 0                               |    |
|               | Euseigne    | 598898      | 113104 | 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                               | 0  |
|               | Grimentz    | 610641      | 115352 | 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                               | 0  |
|               | Icogne 1    | 599817      | 125975 | 1     | 880      | 13.06.2013 | 56               | 41              | 0                            | 0                            | 0                          | 0                          | 0                           | 0                            | 0                             | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 4                            | 0                               | 0                              | 0                          | 0                               |    |
|               | Icogne 2    | 600271      | 127509 | 2     | 1200     | 26.06.2013 | 48               | 40              | 0                            | 0                            | 0                          | 0                          | 0                           | 0                            | 0                             | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 8                            | 0                               | 0                              | 0                          | 0                               |    |
|               | La Garde    | 577142      | 101280 | 2     | 980      | 18.06.2013 | 267              | 73              | 0                            | 1                            | 0                          | 0                          | 0                           | 0                            | 0                             | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 14                           | 2                               | 0                              | 0                          | 0                               |    |
|               | Orsieres    | 577775      | 97591  | 1     | 1022     | 19.06.2013 | 90               | 15              | 0                            | 0                            | 0                          | 0                          | 0                           | 0                            | 0                             | 0                        | 0                          | 0                                | 0                      | 0                      | 0                              | 0                             | 0                           | 0                              | 2                            | 0                               | 0                              | 0                          | 0                               |    |
|               | Sembrancher | 577171      | 102476 | 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                               |    |
|               | Suen        | 600525      | 114908 | 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                               |    |
|               | Vens        | 575624      | 104732 | 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                               |    |
| After mowing  | Arbaz       | 595461      | 125245 | 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                          |                                 |    |
|               | Cordona     | 608758      | 130885 | 2     | 1153     | 23.08.2013 | 280              | 1               | 305                          | 15                           | 10                         | 4                          | 7                           | 6                            | 2                             | 2                        | 0                          | 1                                | 0                      | 0                      | 1                              | 2                             | 15                          | 0                              | 3                            | 0                               | 0                              | 0                          | 8                               |    |
|               | Eison       | 602397      | 111514 | 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                               |    |

|             |        |        |   |      |            |     |   |    |    |    |   |    |   |    |   |   |   |   |   |   |   |   |   |   |    |   |   |   |
|-------------|--------|--------|---|------|------------|-----|---|----|----|----|---|----|---|----|---|---|---|---|---|---|---|---|---|---|----|---|---|---|
| Euseigne    | 598898 | 113104 | 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 |
| Grimentz    | 610641 | 115352 | 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 |
| Icogne 1    | 599817 | 125975 | 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 |
| Icogne 2    | 600271 | 127509 | 2 | 1200 | 14.08.2013 | 419 | 0 | 36 | 0  | 0  | 0 | 9  | 1 | 0  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0  | 0 | 0 | 0 |
| La Garde    | 577142 | 101280 | 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 |
| Orsieres    | 577775 | 97591  | 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 | 577171 | 102476 | 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 |
| Suen        | 600525 | 114908 | 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 |
| Vens        | 575624 | 104732 | 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 |

**Appendix 2.** Results of the linear mixed effects models carried out on the effects of fertilization and irrigation on Caelifera and Ensifera species richness. Table refers to figure 2 in the main text. Both sampling sessions were analyzed together. The fixed factors were the experimental treatments (C: control plots; F: fertilized; I: irrigated; I+F: fertilization and irrigation at 1/3 of the maximal doses; I+F 2/3: fertilization and irrigation at 2/3 of the maximal doses, I+F 3/3: fertilization and irrigation at maximal doses). *P*-values and 95% confidence intervals (CI) were computed with 100'000 Markov chain Monte Carlo (MCMC) iterations. Significant contrasts are highlighted in bold.

| Response variable and comparison  | MCMC mean | Lower 95% CI | Upper 95% CI | MCMC <i>P</i> -value |
|-----------------------------------|-----------|--------------|--------------|----------------------|
| <b>Caelifera species richness</b> |           |              |              |                      |
| I vs. C                           | -0.361    | -1.201       | 0.488        | 0.383                |
| F vs. C                           | -0.455    | -1.282       | 0.388        | 0.283                |
| I+F 1/3 vs. C                     | -1.547    | -2.426       | -0.763       | <b>&lt;0.001</b>     |
| I+F 2/3 vs. C                     | -1.273    | -2.086       | -0.427       | <b>0.006</b>         |
| I+F 3/3 vs. C                     | -2.358    | -3.185       | -1.532       | <b>&lt;0.001</b>     |
| F vs. I                           | -0.091    | -0.906       | 0.773        | 0.829                |
| I+F 1/3 vs. I                     | -1.181    | -2.006       | -0.357       | <b>0.008</b>         |
| I+F 2/3 vs. I                     | -0.914    | -1.791       | -0.097       | <b>0.038</b>         |
| I+F 3/3 vs. I                     | -1.995    | -2.823       | -1.160       | <b>&lt;0.001</b>     |
| I+F 1/3 vs. F                     | -1.096    | -1.927       | -0.281       | <b>0.013</b>         |
| I+F 2/3 vs. F                     | -0.815    | -1.625       | 0.045        | 0.058                |
| I+F 3/3 vs. F                     | -1.909    | -2.758       | -1.105       | <b>&lt;0.001</b>     |
| I+F 2/3 vs. I+F 1/3               | 0.275     | -0.556       | 1.083        | 0.509                |
| I+F 3/3 vs. C I+F 1/3             | -0.817    | -1.613       | 0.046        | 0.054                |
| I+F 3/3 vs. C I+F 2/3             | -1.095    | -1.903       | -0.239       | <b>0.008</b>         |
| <b>Ensifera species richness</b>  |           |              |              |                      |
| I vs. C                           | -0.189    | -0.941       | 0.607        | 0.624                |
| F vs. C                           | 0.182     | -0.568       | 0.975        | 0.636                |
| I+F 1/3 vs. C                     | 0.270     | -0.485       | 1.061        | 0.481                |
| I+F 2/3 vs. C                     | 0.178     | -0.579       | 0.976        | 0.640                |
| I+F 3/3 vs. C                     | 0.270     | -0.484       | 1.047        | 0.486                |
| F vs. I                           | 0.361     | -0.395       | 1.155        | 0.361                |
| I+F 1/3 vs. I                     | 0.450     | -0.310       | 1.266        | 0.249                |
| I+F 2/3 vs. I                     | 0.359     | -0.407       | 1.147        | 0.365                |
| I+F 3/3 vs. I                     | 0.450     | -0.328       | 1.214        | 0.250                |
| I+F 1/3 vs. F                     | 0.101     | -0.652       | 0.910        | 0.794                |
| I+F 2/3 vs. F                     | 0.000     | -0.795       | 0.792        | 0.994                |
| I+F 3/3 vs. F                     | 0.095     | -0.683       | 0.874        | 0.803                |
| I+F 2/3 vs. I+F 1/3               | -0.094    | -0.851       | 0.704        | 0.801                |
| I+F 3/3 vs. C I+F 1/3             | 0.000     | -0.775       | 0.753        | 0.989                |
| I+F 3/3 vs. C I+F 2/3             | -0.093    | -0.879       | 0.704        | 0.808                |

**Appendix 3.** Results of the linear mixed effects models carried out on the effects of fertilization and irrigation on Caelifera and Ensifera densities. Table refers to figure 3 in the main text. Each sampling sessions was analyzed separately. The fixed factors were the experimental treatments (see legend of Appendix 2 for abbreviations). For Ensifera, *P*-values and 95% confidence intervals (CI) were computed with 100'000 Markov chain Monte Carlo (MCMC) iterations. Significant contrasts are highlighted in bold.

| Response variable and comparison               | Estimate  | Standard error | z value      | Pr(< z )<br><i>P</i> -value |
|--|-----------|----------------|--------------|-----------------------------|
| <b>Caelifera density Session 1 (log scale)</b> |           |                |              |                             |
| I vs. C  | -0.393    | 0.164          | -2.402       | <b>0.016</b>                |
| F vs. C  | -0.568    | 0.173          | -3.284       | <b>&lt;0.001</b>            |
| I+F 1/3 vs. C                                  | -1.242    | 0.219          | -5.655       | <b>&lt;0.001</b>            |
| I+F 2/3 vs. C                                  | -1.426    | 0.236          | -6.037       | <b>&lt;0.001</b>            |
| I+F 3/3 vs. C                                  | -1.315    | 0.226          | -5.818       | <b>&lt;0.001</b>            |
| F vs. I  | -0.174    | 0.187          | -0.931       | 0.351                       |
| I+F 1/3 vs. I                                  | -0.849    | 0.231          | -3.671       | <b>&lt;0.001</b>            |
| I+F 2/3 vs. I                                  | -1.033    | 0.247          | -4.181       | <b>&lt;0.001</b>            |
| I+F 3/3 vs. I                                  | -0.921    | 0.237          | -3.884       | <b>&lt;0.001</b>            |
| I+F 1/3 vs. F                                  | -0.674    | 0.238          | -2.837       | <b>0.004</b>                |
| I+F 2/3 vs. F                                  | -0.858    | 0.253          | -3.391       | <b>&lt;0.001</b>            |
| I+F 3/3 vs. F                                  | -0.747    | 0.244          | -3.067       | <b>0.002</b>                |
| I+F 2/3 vs. I+F 1/3                            | -0.184    | 0.287          | -0.642       | 0.521                       |
| I+F 3/3 vs. I+F 1/3                            | -0.073    | 0.279          | -0.261       | 0.794                       |
| I+F 3/3 vs. I+F 2/3                            | 0.111     | 0.292          | 0.382        | 0.702                       |
| <b>Caelifera density Session 2 (log scale)</b> |           |                |              |                             |
| I vs. C  | -0.390    | 0.200          | -1.949       | 0.051                       |
| F vs. C  | -0.193    | 0.189          | -1.021       | 0.307                       |
| I+F 1/3 vs. C                                  | -0.286    | 0.194          | -1.470       | 0.141                       |
| I+F 2/3 vs. C                                  | -0.573    | 0.212          | -2.705       | <b>0.006</b>                |
| I+F 3/3 vs. C                                  | -0.487    | 0.206          | -2.363       | <b>0.018</b>                |
| F vs. I  | 0.197     | 0.209          | 0.944        | 0.345                       |
| I+F 1/3 vs. I                                  | 0.105     | 0.213          | 0.491        | 0.623                       |
| I+F 2/3 vs. I                                  | -0.183    | 0.229          | -0.797       | 0.425                       |
| I+F 3/3 vs. I                                  | -0.097    | 0.224          | -0.433       | 0.665                       |
| I+F 1/3 vs. F                                  | -0.092    | 0.203          | -0.455       | 0.649                       |
| I+F 2/3 vs. F                                  | -0.380    | 0.220          | -1.728       | 0.084                       |
| I+F 3/3 vs. F                                  | -0.294    | 0.214          | -1.372       | 0.170                       |
| I+F 2/3 vs. I+F 1/3                            | -0.288    | 0.224          | -1.283       | 0.199                       |
| I+F 3/3 vs. I+F 1/3                            | -0.202    | 0.219          | -0.922       | 0.356                       |
| I+F 3/3 vs. I+F 2/3                            | 0.086     | 0.235          | 0.365        | 0.715                       |
| <hr/>  |           |                |              |                             |
| Response variable and comparison               | MCMC mean | Lower 95% CI   | Upper 95% CI | MCMC <i>P</i> -value        |
| <b>Ensifera density Session 1</b>              |           |                |              |                             |
| I vs. C  | 0.135     | -0.244         | 0.522        | 0.486                       |

|                     |        |        |        |              |
|---------------------|--------|--------|--------|--------------|
| F vs. C             | 0.284  | -0.107 | 0.660  | 0.155        |
| I+F 1/3 vs. C       | -0.127 | -0.518 | 0.254  | 0.518        |
| I+F 2/3 vs. C       | -0.093 | -0.480 | 0.283  | 0.636        |
| I+F 3/3 vs. C       | -0.206 | -0.579 | 0.199  | 0.281        |
| F vs. I             | 0.148  | -0.244 | 0.514  | 0.433        |
| I+F 1/3 vs. I       | -0.260 | -0.643 | 0.125  | 0.181        |
| I+F 2/3 vs. I       | -0.228 | -0.604 | 0.157  | 0.238        |
| I+F 3/3 vs. I       | -0.342 | -0.733 | 0.026  | 0.079        |
| I+F 1/3 vs. F       | -0.408 | -0.782 | -0.028 | <b>0.033</b> |
| I+F 2/3 vs. F       | -0.374 | -0.756 | 0.005  | 0.055        |
| I+F 3/3 vs. F       | -0.490 | -0.891 | -0.111 | <b>0.016</b> |
| I+F 2/3 vs. I+F 1/3 | 0.036  | -0.346 | 0.412  | 0.845        |
| I+F 3/3 vs. I+F 1/3 | -0.076 | -0.453 | 0.303  | 0.694        |
| I+F 3/3 vs. I+F 2/3 | -0.114 | -0.491 | 0.275  | 0.561        |

### Ensifera density Session 2

|                     |        |        |       |              |
|---------------------|--------|--------|-------|--------------|
| I vs. C             | -0.023 | -0.232 | 0.181 | 0.824        |
| F vs. C             | 0.023  | -0.188 | 0.226 | 0.832        |
| I+F 1/3 vs. C       | 0.103  | -0.105 | 0.308 | 0.323        |
| I+F 2/3 vs. C       | 0.148  | -0.061 | 0.354 | 0.156        |
| I+F 3/3 vs. C       | 0.205  | 0.003  | 0.416 | 0.052        |
| F vs. I             | 0.045  | -0.168 | 0.255 | 0.667        |
| I+F 1/3 vs. I       | 0.125  | -0.085 | 0.323 | 0.226        |
| I+F 2/3 vs. I       | 0.171  | -0.036 | 0.372 | 0.100        |
| I+F 3/3 vs. I       | 0.228  | 0.027  | 0.444 | <b>0.032</b> |
| I+F 1/3 vs. F       | 0.082  | -0.125 | 0.292 | 0.434        |
| I+F 2/3 vs. F       | 0.128  | -0.075 | 0.333 | 0.217        |
| I+F 3/3 vs. F       | 0.182  | -0.021 | 0.395 | 0.087        |
| I+F 2/3 vs. I+F 1/3 | 0.047  | -0.157 | 0.255 | 0.653        |
| I+F 3/3 vs. I+F 1/3 | 0.101  | -0.105 | 0.311 | 0.330        |
| I+F 3/3 vs. I+F 2/3 | 0.057  | -0.161 | 0.263 | 0.599        |

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**Appendix 4.** Results of the linear mixed effects models carried out on the effects of fertilization and irrigation on mean vegetation height. Table refers to figure 4 in the main text. Each sampling sessions was analyzed separately. The fixed factors were the experimental treatments (see legend of Appendix 2 for abbreviations). For session 1, P-values and 95% confidence intervals (CI) were computed with 100'000 Markov chain Monte Carlo (MCMC) iterations. Significant contrasts are highlighted in bold.

| Response variable and comparison        | MCMC mean | Lower 95% CI | Upper 95% CI | MCMC P-value     |
|---|-----------|--------------|--------------|------------------|
| <b>Mean vegetation height Session 1</b> |           |              |              |                  |
| I vs. C                                 | 5.027     | -6.055       | 16.450       | 0.376            |
| F vs. C                                 | 18.052    | 6.806        | 29.340       | <b>0.002</b>     |
| I+F 1/3 vs. C                           | 20.258    | 8.744        | 31.220       | <b>&lt;0.001</b> |
| I+F 2/3 vs. C                           | 20.131    | 9.025        | 31.540       | <b>0.001</b>     |
| I+F 3/3 vs. C                           | 29.935    | 18.568       | 40.900       | <b>&lt;0.001</b> |
| F vs. I                                 | 12.968    | 1.554        | 23.645       | <b>0.024</b>     |
| I+F 1/3 vs. I                           | 15.199    | 4.273        | 26.335       | <b>0.009</b>     |
| I+F 2/3 vs. I                           | 14.965    | 3.486        | 26.281       | <b>0.012</b>     |
| I+F 3/3 vs. I                           | 24.860    | 13.561       | 35.857       | <b>&lt;0.001</b> |
| I+F 1/3 vs. F                           | 2.209     | -9.396       | 13.190       | 0.692            |
| I+F 2/3 vs. F                           | 2.079     | -9.295       | 12.851       | 0.715            |
| I+F 3/3 vs. F                           | 11.941    | 0.834        | 23.333       | <b>0.039</b>     |
| I+F 2/3 vs. I+F 1/3                     | -0.230    | -11.014      | 11.267       | 0.966            |
| I+F 3/3 vs. C I+F 1/3                   | 9.658     | -1.518       | 20.794       | 0.092            |
| I+F 3/3 vs. C I+F 2/3                   | 9.849     | -1.409       | 21.025       | 0.084            |

| Response variable and comparison                    | Estimate | Standard error | z value | Pr(< z ) P-value |
|---|----------|----------------|---------|------------------|
| <b>Mean vegetation height Session 2 (log scale)</b> |          |                |         |                  |
| I vs. C   | 0.287    | 0.129          | 2.230   | <b>0.026</b>     |
| F vs. C   | 0.350    | 0.127          | 2.754   | <b>0.006</b>     |
| I+F 1/3 vs. C                                       | 0.431    | 0.125          | 3.449   | <b>0.001</b>     |
| I+F 2/3 vs. C                                       | 0.694    | 0.119          | 5.826   | <b>&lt;0.001</b> |
| I+F 3/3 vs. C                                       | 0.956    | 0.115          | 8.352   | <b>&lt;0.001</b> |
| F vs. I   | 0.063    | 0.117          | 0.540   | 0.593            |
| I+F 1/3 vs. I                                       | 0.144    | 0.115          | 1.250   | 0.211            |
| I+F 2/3 vs. I                                       | 0.407    | 0.109          | 3.740   | <b>&lt;0.001</b> |
| I+F 3/3 vs. I                                       | 0.669    | 0.104          | 6.460   | <b>&lt;0.001</b> |
| I+F 1/3 vs. F                                       | 0.081    | 0.113          | 0.720   | 0.473            |
| I+F 2/3 vs. F                                       | 0.344    | 0.107          | 3.220   | <b>0.001</b>     |
| I+F 3/3 vs. F                                       | 0.607    | 0.102          | 5.970   | <b>&lt;0.001</b> |
| I+F 2/3 vs. I+F 1/3                                 | 0.263    | 0.104          | 2.520   | <b>0.012</b>     |
| I+F 3/3 vs. C I+F 1/3                               | 0.525    | 0.099          | 5.310   | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 2/3                               | 0.262    | 0.092          | 2.860   | <b>0.004</b>     |

**Appendix 5.** Results of the linear mixed effects models carried out on the effects of fertilization and irrigation on soil and surface temperature. Table refers to figure 4 in the main text. Each sampling sessions was analyzed separately. The fixed factors were the experimental treatments (see legend of Appendix 2 for abbreviations). P-values and 95% confidence intervals (CI) were computed with 100'000 Markov chain Monte Carlo (MCMC) iterations. Significant contrasts are highlighted in bold.

| Response variable and comparison  | MCMC mean | Lower 95% CI | Upper 95% CI | MCMC P-value     |
|-----------------------------------|-----------|--------------|--------------|------------------|
| <b>Air temperature Session 1</b>  |           |              |              |                  |
| I vs. C                           | -1.367    | -1.802       | -0.904       | <b>&lt;0.001</b> |
| F vs. C                           | -2.189    | -2.678       | -1.714       | <b>&lt;0.001</b> |
| I+F 1/3 vs. C                     | -2.890    | -3.463       | -2.272       | <b>&lt;0.001</b> |
| I+F 2/3 vs. C                     | -2.307    | -2.791       | -1.873       | <b>&lt;0.001</b> |
| I+F 3/3 vs. C                     | -4.510    | -4.942       | -4.043       | <b>&lt;0.001</b> |
| F vs. I                           | -0.820    | -1.287       | -0.302       | <b>0.002</b>     |
| I+F 1/3 vs. I                     | -1.525    | -2.116       | -0.966       | <b>&lt;0.001</b> |
| I+F 2/3 vs. I                     | -0.938    | -1.364       | -0.478       | <b>&lt;0.001</b> |
| I+F 3/3 vs. I                     | -3.135    | -3.576       | -2.680       | <b>&lt;0.001</b> |
| I+F 1/3 vs. F                     | -0.705    | -1.330       | -0.089       | <b>0.025</b>     |
| I+F 2/3 vs. F                     | -0.117    | -0.576       | 0.406        | 0.648            |
| I+F 3/3 vs. F                     | -2.318    | -2.816       | -1.826       | <b>&lt;0.001</b> |
| I+F 2/3 vs. I+F 1/3               | 0.586     | 0.017        | 1.173        | <b>0.045</b>     |
| I+F 3/3 vs. C I+F 1/3             | -1.614    | -2.211       | -1.033       | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 2/3             | -2.196    | -2.669       | -1.750       | <b>&lt;0.001</b> |
| <b>Soil temperature Session 1</b> |           |              |              |                  |
| I vs. C                           | 0.028     | -0.145       | 0.201        | 0.759            |
| F vs. C                           | 0.085     | -0.091       | 0.261        | 0.347            |
| I+F 1/3 vs. C                     | -0.884    | -1.084       | -0.695       | <b>&lt;0.001</b> |
| I+F 2/3 vs. C                     | -0.648    | -0.825       | -0.474       | <b>&lt;0.001</b> |
| I+F 3/3 vs. C                     | -1.849    | -2.045       | -1.663       | <b>&lt;0.001</b> |
| F vs. I                           | 0.059     | -0.113       | 0.235        | 0.501            |
| I+F 1/3 vs. I                     | -0.910    | -1.098       | -0.716       | <b>&lt;0.001</b> |
| I+F 2/3 vs. I                     | -0.676    | -0.846       | -0.499       | <b>&lt;0.001</b> |
| I+F 3/3 vs. I                     | -1.875    | -2.067       | -1.680       | <b>&lt;0.001</b> |
| I+F 1/3 vs. F                     | -0.971    | -1.165       | -0.779       | <b>&lt;0.001</b> |
| I+F 2/3 vs. F                     | -0.733    | -0.905       | -0.563       | <b>&lt;0.001</b> |
| I+F 3/3 vs. F                     | -1.934    | -2.125       | -1.739       | <b>&lt;0.001</b> |
| I+F 2/3 vs. I+F 1/3               | 0.236     | 0.042        | 0.422        | <b>0.015</b>     |
| I+F 3/3 vs. C I+F 1/3             | -0.966    | -1.167       | -0.753       | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 2/3             | -1.203    | -1.393       | -1.005       | <b>&lt;0.001</b> |
| <b>Air temperature Session 2</b>  |           |              |              |                  |
| I vs. C                           | -1.529    | -2.072       | -1.002       | <b>&lt;0.001</b> |
| F vs. C                           | 0.200     | -0.339       | 0.750        | 0.472            |
| I+F 1/3 vs. C                     | -0.563    | -1.087       | -0.024       | <b>0.040</b>     |
| I+F 2/3 vs. C                     | -1.859    | -2.399       | -1.356       | <b>&lt;0.001</b> |
| I+F 3/3 vs. C                     | -1.681    | -2.296       | -1.083       | <b>&lt;0.001</b> |
| F vs. I                           | 1.727     | 1.181        | 2.305        | <b>&lt;0.001</b> |



|                       |        |        |        |                  |
|-----------------------|--------|--------|--------|------------------|
| I+F 1/3 vs. I         | 0.964  | 0.417  | 1.515  | <b>0.001</b>     |
| I+F 2/3 vs. I         | -0.332 | -0.864 | 0.244  | 0.243            |
| I+F 3/3 vs. I         | -0.151 | -0.759 | 0.474  | 0.647            |
| I+F 1/3 vs. F         | -0.768 | -1.310 | -0.205 | <b>0.008</b>     |
| I+F 2/3 vs. F         | -2.065 | -2.604 | -1.478 | <b>&lt;0.001</b> |
| I+F 3/3 vs. F         | -1.889 | -2.482 | -1.256 | <b>&lt;0.001</b> |
| I+F 2/3 vs. I+F 1/3   | -1.299 | -1.845 | -0.748 | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 1/3 | -1.124 | -1.757 | -0.499 | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 2/3 | 0.177  | -0.430 | 0.791  | 0.568            |

### Soil temperature Session 2

|                       |        |        |        |                  |
|-----------------------|--------|--------|--------|------------------|
| I vs. C               | -0.515 | -0.720 | -0.301 | <b>&lt;0.001</b> |
| F vs. C               | -0.871 | -1.073 | -0.667 | <b>&lt;0.001</b> |
| I+F 1/3 vs. C         | -1.050 | -1.263 | -0.837 | <b>&lt;0.001</b> |
| I+F 2/3 vs. C         | -1.175 | -1.372 | -0.971 | <b>&lt;0.001</b> |
| I+F 3/3 vs. C         | -1.902 | -2.105 | -1.691 | <b>&lt;0.001</b> |
| F vs. I               | -0.357 | -0.560 | -0.158 | <b>0.001</b>     |
| I+F 1/3 vs. I         | -0.535 | -0.748 | -0.329 | <b>&lt;0.001</b> |
| I+F 2/3 vs. I         | -0.663 | -0.871 | -0.461 | <b>&lt;0.001</b> |
| I+F 3/3 vs. I         | -1.388 | -1.587 | -1.182 | <b>&lt;0.001</b> |
| I+F 1/3 vs. F         | -0.178 | -0.388 | 0.022  | 0.090            |
| I+F 2/3 vs. F         | -0.305 | -0.496 | -0.106 | <b>0.001</b>     |
| I+F 3/3 vs. F         | -1.032 | -1.217 | -0.835 | <b>&lt;0.001</b> |
| I+F 2/3 vs. I+F 1/3   | -0.128 | -0.337 | 0.072  | 0.216            |
| I+F 3/3 vs. C I+F 1/3 | -0.855 | -1.056 | -0.646 | <b>&lt;0.001</b> |
| I+F 3/3 vs. C I+F 2/3 | -0.726 | -0.926 | -0.533 | <b>&lt;0.001</b> |

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## **Erklärung**

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: Sarah Delley  
Matrikelnummer: 09-505-132  
Studiengang: Master of Science in Ecology and Evolution with special qualification  
in Animal Ecology and Conservation, Universität Bern  
Titel der Arbeit: Grassland irrigation and fertilisation decrease soil and within vegetation  
temperatures and negatively affect orthopteran populations  
LeiterIn der Arbeit: Jean-Yves Humbert and Raphaël Arlettaz

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

Ich gewähre hiermit Einsicht in diese Arbeit.

Bern, 14 September 2014

Sarah Delley