

Grassland irrigation and fertilisation alter vegetation height and vegetation within temperature and negatively affect orthopteran populations

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1 **Abstract**

2 European mountain meadows are hosting an exceptionally rich biodiversity. While they have
3 long been exposed to land abandonment, they are nowadays additionally threatened by
4 agriculture intensification through aerial irrigation and slurry application. The consequences
5 of this intensification on arthropods are not well documented and studies are needed to fulfil
6 this knowledge gap. Six experimental management treatments combining a full factorial
7 design and a gradual level of fertilisation and irrigation were implemented in 2010 in twelve
8 different montane and subalpine Swiss meadows. In 2013, orthopterans were sampled to
9 assess the influence of the management practices on their population. In addition changes in
10 vegetation height and temperature induced by intensification were recorded in order to better
11 appraise underlying mechanisms. Intensification had a negative impact on Caelifera
12 (grasshoppers); with decreases of up to 70% in densities and 50% in species richness in the
13 most intensively managed treatment plots. In parallel intensification induced an increase in
14 mean vegetation height and a cooling of up to 4.2 °C (10 cm aboveground) within most
15 intensively managed plots. These microhabitat and microclimate changes are likely to have
16 affected Caelifera development, in particular thermophilous species. In contrast, Ensifera
17 (bush crickets) densities and species richness did not respond to the management treatments.
18 The use of irrigation (without fertilisation) had limited impacts on orthopterans and
19 microclimate. In conclusion, orthopterans, in particular Caelifera, are relatively sensitive to
20 grassland intensification and to conserve the full community, mountain agricultural systems
21 need to maintain extensively managed meadows.

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

23 **1. Introduction**

24 In Europe, mountain meadows represent one of last remnant of exceptionally diverse semi-
25 natural grassland types (Veen et al., 2009). However two new management practices are
26 spreading in alpine regions and threaten these biodiversity rich habitats: irrigation with
27 sprinkler and fertilisation with liquid manure (Maurer et al., 2006; Riedener et al., 2013).
28 Both of these practices modify the vegetation community and structure which in turn affects
29 the arthropod populations (Andrey et al., 2014; Schwab et al., 2002). Arthropods play an
30 important role in grassland systems and beyond; they provide or at least participate in a range
31 of ecosystem services such as pollination, decomposition process or pest control (e.g. Sutter
32 and Albrecht, 2016) and are primordial food items for many vertebrates (e.g. Arlettaz, 1996;
33 Wilson et al., 1999). This underlines the importance to preserve their abundance and
34 diversity. So far fertilisation has been shown to have a negative impact on arthropod species
35 richness ensuing from a reduction of vegetation diversity (Haddad et al., 2009; Haddad et al.,
36 2000). On the other hand it seems to boost herbivore abundances through an increase in plant
37 tissue nitrogen and to have cascading effect on other arthropods functional groups (Andrey et
38 al., 2016; Haddad et al., 2001; Hudewenz et al., 2012). In contrast the effects of irrigation on
39 arthropods remain poorly documented. Therefore current knowledge does not allow
40 determining the irrigation and fertilisation thresholds that should not be exceeded in order to
41 maintain a functional and diverse arthropod community in mountain meadows (but see
42 Andrey et al., 2016; Lessard-Therrien et al., 2018).

43 The goal of the present study was to assess the response of orthopteran species
44 richness and density to gradual levels of fertilisation and irrigation in montane and subalpine
45 meadows. In these grasslands, orthopterans represent the most important insect group in term
46 of biomass (Blumer and Diemer, 1996). They are a key component of the diet of many
47 insectivorous species and an important decline in their density would have cascading effect on

48 higher trophic level (Britschgi et al., 2006; Vickery et al., 2001). In addition, orthopterans are
49 recognized bioindicators for grasslands as they readily respond to management changes (Buri
50 et al., 2013) and are sensitive to a set of vegetation parameters (Le Provost et al., 2017). First,
51 orthopterans are sensitive to microclimate (Löffler and Fartmann, 2017) which varies with
52 vegetation height and density (Song et al., 2013). As ectotherms organisms, their development
53 rate, body size, reproductive success and other physiological processes are depending on
54 temperature. Each species has its own thermal sensitivity: for example eurythermal species
55 such as *Pseudochorthippus parallelus* are very tolerant and can adapt to a range of
56 microclimatic conditions while thermophilous species such as *Stenobothrus lineatus* are
57 restricted to warm and dry habitats (van Wingerden et al., 1991; Willott and Hassall, 1998).
58 Microclimatic conditions influence thus the orthopteran community. Second, the habitat
59 diversity hypothesis stipulates that more diverse a habitat is the more species it is likely to
60 host (Báldi, 2008). At an orthopteran scale microhabitat diversity is function of the vegetation
61 structural heterogeneity which is to some extent correlated with plant diversity (e.g. Morris,
62 2000; Woodcock et al., 2009) and vegetation height (Andrey et al., 2014). Finally food
63 availability is a limiting factor for the expansion of any organism. A sufficient proportion of
64 grass is essential to maintain Caelifera (grasshoppers) density as they almost exclusively feed
65 on it (Ibanez et al., 2013). Ensifera (bush crickets) on their side have a more diversified diet
66 composed of small invertebrates and grasses and are thus less dependent on specific food
67 resources (Baur et al., 2006). The first aim of the present study was to investigate how
68 orthopteran populations respond to gradual level of irrigation and fertilisation and to
69 determine whether an optimum management intensity maximising both density and species
70 richness exists. The second aim was to measure the changes in vegetation height and
71 aboveground temperatures induced by intensification, and to determine whether orthopteran
72 responses can be explained by these changes.

73 In the short term fertilisation has been shown to increase vegetation structure and
74 phytomass production (Andrey et al., 2014) while in the long term it induces a loss of plant
75 species richness and a homogenisation of the vegetation cover (e.g. Lessard-Therrien et al.,
76 2017; Marini et al., 2008; Socher et al., 2013). In addition it usually induces a shift in plant
77 community toward higher percentage of grass and legumes (Rudmann-Maurer et al., 2008;
78 Socher et al., 2013) whereas irrigation favours grass species and increase nitrogen (N)
79 mineralization by plants (Jeangros and Bertola, 2000; Riedener et al., 2013). Finally both
80 inputs boost the productivity and thus create a denser and taller sward (Bassin et al., 2012;
81 Marini et al., 2009). Consequently we expected aboveground temperature to gradually cool
82 down along the intensification gradient (Song et al., 2013). We expected orthopteran densities
83 to increase at mid-intensity as a consequence of better food quality (Hudewenz et al., 2012;
84 Joern et al., 2012) and to decrease in highly intensified plots due to the detrimental effect of
85 microclimate cooling (van Wingerden et al., 1992). Concerning orthopterans species richness,
86 we expected it to decrease steadily along the intensification gradient due to the disappearance
87 of thermophilous species and the loss of microhabitats (Fournier et al., 2017; van Wingerden
88 et al., 1991).

89

90 **2. Material and methods**

91 *2.1 Study sites*

92 The study was carried out in the canton of Valais, an inner Alps valley of Switzerland which
93 experiences a continental climate with cold and wet winter and dry and hot summers: mean
94 annual temperature amounts 10.7°C and mean annual precipitation achieves 517 mm (2000–
95 2014 mean in Sion, 482 m a.s.l.). In 2010, twelve extensively managed meadows were
96 selected within this region; they were situated between 790 and 1740 m a.s.l (Appendix 1).

97

98 *2.2 Experimental design*

99 In 2010, within each meadows (n = 12), six different management treatments were randomly
100 allocated to plots of 20 m in diameter spaced from each other by at least 5 m. The first plot
101 served as a control (C). The second and third plots were only irrigated (I) or fertilised (F), and
102 the fourth to sixth plots were irrigated and fertilised (I+F; Table 1). The exact amount of
103 fertiliser applied at each site depended on the theoretical maximum hay yield achievable
104 locally with two harvests per year, calculated using pre-experimental hay yield and site
105 elevation (for details see Appendix A in Andrey et al., 2016). Accordingly, sites were divided
106 in three groups; 1, 2 and 3, where I+F 3/3-plots received, respectively, 40, 60 or 80 [kg N·ha-
107 1·yr-1]. Within group, mid-intensive (F and I+F 2/3) and low-intensive (I+F 1/3) plots,
108 received respectively two-thirds and one-third of the maximum fertilisation dose. It has been
109 decided to follow these prescriptions in order to obtain results within realistic agronomical
110 systems. Fertiliser consisted of organic dried manure NPK pellets (MEOC SA, 1906 Charrat,
111 Switzerland), and mineral potassium oxide (K₂O) dissolved in water to reach the equivalent of
112 standard-farm liquid manure consisting namely of 2.4 kg of usable nitrogen, 2 kg of
113 phosphate (P₂O₅), and 8 kg of potassium oxide (K₂O) per m³ of solution. Every year the plots
114 were fertilised once in early spring and once after the first cut (June or July), each time half of
115 the annual fertiliser amount was applied (except for the 1/3-plots that were fertilised only
116 once in spring). Treatments I and I + F were additionally irrigated weekly from mid-May to
117 end of August, except when heavy rainfall occurred (≥ 20 mm over the previous week).
118 Irrigation thresholds were chosen on the basis of Calame Calame et al. (1992) experiment.
119 Accordingly I and I+F 2/3 matched the recommendation for the best profitability of water
120 input (20 mm/week) while low-intensive (I+F 1/3) and high-intensive (I+F 3/3) management
121 treatments received respectively half and one and an half of this dose (Table 1).

122

123 *2.3 Orthopterans sampling*

124 Orthopterans were sampled in 2013 with a biocenometer (open trap) made of a net fastened
125 around a strong circular wire so as to provide a total capture area of 1 m² (as described in
126 Humbert et al., 2012). Two sampling sessions were performed: one shortly before the first cut
127 (between 12 June and 12 July) and one 4–6 weeks after it (between 13 August and 31
128 August). The date at which meadows were sampled was function of their elevation. During
129 both sessions, eight samples were regularly taken per treatment plot. All the individuals
130 trapped within the biocenometer were caught and identified on site. Adults were identified to
131 species level while juveniles were classified into suborders (Caelifera or Ensifera). All
132 samplings were done on sunny days between 10 am and 5 pm.

133

134 *2.4 Vegetation height record*

135 Vegetation height was measured as the average vegetation stratum height in a 10 cm radius
136 around a meterstick. Eight records were taken per plot during the orthopterans samplings and
137 averaged to have one value per plot. All the measurements were performed by the same
138 person.

139

140 *2.5 Temperature record*

141 To record aboveground temperatures I-buttons DS1921G-F Thermochron (Maxim Integrated
142 Products/Dallas) were used, which are self-sufficient systems measuring and recording
143 temperature in 0.5 °C increment. In each plot one of those device was randomly placed at 5 m
144 from the centre, fixed on a stick 10 cm above the ground. I-buttons recorded temperature
145 hourly from beginning of May to end of August. They were removed shortly before the first
146 cut and replaced within a few days. The data from the ten days following mowing event were
147 removed from the analysis to reduce noise due to the manipulation of the devices. Average

148 daily temperature was calculated as the mean temperature between 12 am and 4 pm while
149 average nocturnal temperature was calculated as the mean temperature between 12 pm and 4
150 am.

151

152 *2.6 Statistical analyses*

153 Treatments effects were analysed with linear mixed models (LMMs) or generalized linear
154 mixed models (GLMMs) using the *lmer*, respectively *glmer*, functions from the *lme4* package
155 for R (Bates et al., 2015). Response variables were orthopteran densities, species richness,
156 vegetation height and temperatures; they were analysed with either Poisson (Caelifera and
157 Ensifera densities) or Gaussian (others) distribution. Though, vegetation height had to be log-
158 transformed in order to achieve normal distribution of residuals. The fixed effects were the
159 treatments (C, I, F, I+F 1/3, I+F 2/3, I+F 3/3), and the random intercept effects were the study
160 sites in all the analyses. When using the Gaussian distribution, p-values were obtained using
161 the *lmerTest* package Kuznetsova, 2017 #775}. Caelifera and Ensifera responses were
162 analysed separately as they differ in their ecology (Baur et al., 2006). Vegetation height,
163 temperature and density data were analysed per sampling session while species data were
164 pooled. Models always fulfilled model assumptions, notably residuals normal distribution and
165 homoscedasticity.

166 Structural equation modelling (SEM), using the *lavaan* package (Rosseel, 2012), were
167 further used to determine if fertilisation and irrigation influence orthopterans directly or/and
168 indirectly through changes in vegetation height or aboveground temperature. In this SEM
169 analysis, the water and slurry inputs were treated as two continuous variables with four levels:
170 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
171 set of candidate models was developed. Candidate models always included slurry and water
172 inputs as two independent variables, and then their effects on orthopterans were either direct,

173 indirect through vegetation height or aboveground temperature, or both. In addition, the
174 number of paths was set to maximum four which led to a total of twenty candidate models
175 (see Appendix 2 for a graphical representation of all SEM candidate models). Second, all
176 models were ran and kept only if the overall fit of the respective model was satisfactory. To
177 assess model fit, the chi-square test (if $P > 0.05$), the comparative fit index CFI (if CFI $>$
178 0.95), the root mean square error of approximation RMSEA (if RMSEA < 0.07) and the
179 standardised root mean square residuals SRMR (if SRMR < 0.08) were used (Hooper et al.
180 2008). Third, retained models were ranked based on AIC values (Akaike information
181 criterion) and the model with the lowest AIC plus the model(s) within a Δ AIC < 2 were
182 considered the most plausible model(s). If several models were ranked within a Δ AIC < 2 ,
183 the model with the highest R-square was chosen as best model. The *lavaan.survey* package,
184 which applies robust maximum likelihood method to estimate the standard errors, was used to
185 include the meadows as random effect in the SEM (Oberski, 2014). All statistics were
186 performed using R version 3.6.1 (R Core Team, 2019).

187

188 **3. Results**

189 Due to unfortunate field circumstances, orthopteran densities could not be sampled in site
190 Cordona before mowing. Similarly, no aboveground temperatures were recorded in Eison and
191 Grimentz after mowing. Therefore all related analyses were based on $n = 11$ or $n = 10$ sites
192 respectively.

193

194 *3.1 Orthopterans density*

195 Mean density of orthopterans varied greatly among meadows and plots. It ranged from 0.13 to
196 24.38 individuals per m^2 during the first sampling session and from 0.65 to 27.38 individuals
197 per m^2 during the second sampling session. Treatments were found to have significant effects

198 on Caelifera densities while none were detected on Ensifera. Note that low densities of
199 Ensifera limited the power of the analysis on this suborder.

200 Before mowing the highest Caelifera densities were found within C-plots, mean \pm
201 standard error (SE) = 8.42 ± 2.73 , that hosted ~30–40% more individuals than I-plots ($5.68 \pm$
202 2.05 , $P = 0.016$) and F-plots (4.77 ± 1.82 , $P < 0.001$) and >70% more individuals than I+F
203 1/3-plots (2.43 ± 0.66 , $P < 0.001$), I+F 2/3-plots (2.02 ± 0.87 , $P < 0.001$) and I+F 3/3-plots
204 (2.26 ± 0.81 , $P < 0.001$; see Fig. 1a and Appendix 3 for detailed model outputs). Concerning
205 the Ensifera, the highest densities were found within F-plots (0.94 ± 0.16) and the lowest
206 within I+F 3/3-plots (0.45 ± 0.14), though differences were not statistically significant (Fig.
207 1b and Appendix 3). C-plots (0.66 ± 0.18), I-plots (0.80 ± 0.16), I+F 1/3-plots (0.53 ± 0.23)
208 and I+F 2/3-plots (0.57 ± 0.17) had intermediate densities. After mowing Caelifera and
209 Ensifera densities did not differ across treatments (Fig. 1c, Fig. 1d and Appendix 3).

210

211 *3.2 Orthopteran species richness*

212 A total of 21 species was recorded within all plots, seven of which were Ensifera and fourteen
213 of which were Caelifera (see Appendix 1 for detailed list). The minimum number of species
214 found within a plot was one and the maximum was nine. Management practices significantly
215 affected the Caelifera species richness. The highest Caelifera species richness was found
216 within C-plots (4.6 ± 0.5), that hosted similar species number than I-plots (4.25 ± 0.5) and F-
217 plots (4.2 ± 0.5) but ~30% more species than I+F 1/3-plots (3.2 ± 0.5 , $P < 0.001$) and I+F 2/3-
218 plots (3.5 ± 0.5 , $P = 0.004$) and 50% more species than I+F 3/3-plots (2.3 ± 0.4 , $P < 0.001$;
219 see Fig. 2a and Appendix 4 for detailed model outputs). Contrariwise, no significant effects
220 were detected on the Ensifera species richness (see Fig. 2b and Appendix 4).

221

222 *3.3 Vegetation height*

223 Before mowing vegetation stratum height was the tallest in I+F 3/3-plots ($61.8 \text{ cm} \pm 3.5 \text{ cm}$),
224 it was slightly shorter in I+F 1/3-plots (52.1 ± 7.7 , $P = 0.016$), I+F 2/3-plots (51.9 ± 2.3 , $P =$
225 0.080) and F-plots (49.9 ± 3.4 , $P = 0.023$) while it grew half less in C-plots (31.8 ± 2.9 , $P <$
226 0.001) and I-plots (36.9 ± 3.1 , $P < 0.001$; see Fig. 3a and Appendix 5 for detailed model
227 outputs). After mowing the same trend was observed with tallest sward found within I+F 3/3-
228 plots (24.2 ± 2.0), followed by I+F 2/3-plots (18.3 ± 2.2 , $P = 0.006$) and then I+F 1/3-plots
229 (14.0 ± 2.2 , $P < 0.001$), F-plots (12.8 ± 2.2 , $P < 0.001$) and I-plots (12.3 ± 1.2 , $P < 0.001$),
230 while C-plots vegetation (9.0 ± 2.2 , $P < 0.001$) was more than twice shorter (Fig. 3b and
231 Appendix 5).

232

233 *3.4 Temperature*

234 Before mowing, mean diurnal aboveground temperature was the warmest in C-plots ($22.4 \pm$
235 $0.9 \text{ }^\circ\text{C}$), then temperatures in I-plots (20.9 ± 0.7), I+F 1/3-plots (20.6 ± 1.4), I+F 2/3-plots
236 (20.5 ± 0.6) and F-plots (20.3 ± 0.7) were $1.5\text{--}2.1 \text{ }^\circ\text{C}$ colder (all $P < 0.05$ except for I-plots)
237 while it was over $4.2 \text{ }^\circ\text{C}$ colder in I+F 3/3-plots than in C-plot (18.2 ± 0.5 , $P < 0.001$). See
238 Fig. 3a and Appendix 6 for detailed model outputs. Given the noticeable negative relationship
239 between temperatures and vegetation heights, an additional LMM was run between both (Fig.
240 4; Estimate = -3.383 , SE = 0.894 , $P < 0.001$).

241 After mowing, diurnal aboveground temperature was the highest in C-plots ($29.9 \pm$
242 0.9) and F-plots (30.2 ± 0.9). I+F 1/3-plots (29.5 ± 1.2), I+F 3/3-plots (28.5 ± 1.4), I-plots
243 (28.4 ± 0.7) and I+F 2/3-plots (28.3 ± 1.1) were respectively 0.4 to $1.7 \text{ }^\circ\text{C}$ colder than C-plots,
244 but differences were not statistically significant (Fig. 3b and Appendix 6). Treatments did
245 affect nocturnal temperatures but differences were not biologically relevant (in order of 0.1--
246 $0.2 \text{ }^\circ\text{C}$) and are thus not further discussed.

247

248 3.5 Structural equation modeling (SEM)

249 As treatments did not affect Ensifera densities nor species richness SEMs were run only on
250 Caelifera. Before mowing the best SEM model (chi-square = 0.084, d.f. = 1, $P = 0.772$; CFI =
251 1; RMSEA < 0.001; SRMR = 0.006) explaining changes in Caelifera densities included both
252 indirect effects of slurry and water inputs through vegetation height plus a direct effect of
253 water input (Fig. 5a). The best SEM models explaining Caelifera densities after mowing (chi-
254 square = 0.612, d.f. = 1, $P = 0.434$; CFI = 1; RMSEA < 0.001; SRMR = 0.013) and Caelifera
255 species richness (chi-square = 0.612, d.f. = 1, $P = 0.434$; CFI = 1; RMSEA < 0.001; SRMR =
256 0.014) were the same. They included both direct effects of slurry and water inputs plus an
257 indirect effect of water input through aboveground temperature measured after mowing (Fig.
258 5b and 5c). However, for the density after mowing, only one path was statistically significant;
259 i.e. the effect of water input on aboveground temperature. For species richness the direct
260 effect of slurry input on Caelifera species richness was significant, as well as the effect of
261 water input on aboveground temperature coupled with a non-significant effect ($P = 0.253$) of
262 aboveground temperature on Caelifera species richness. For Caelifera species richness, all
263 combination of SEM models with vegetation height and aboveground temperature measured
264 before and after the first mowing were tried.

265

266 4. Discussion

267 This study shows that mountain grassland fertilisation and irrigation combined, greatly affects
268 Caelifera (grasshoppers) by decreasing their densities and species richness, but that the use of
269 irrigation only (at two-thirds of the maximum dose) has relatively limited impacts. On the
270 other hand, overall Ensifera (bush crickets) densities and species richness did not respond to
271 the management treatments. This study also demonstrates that intensification practices induce
272 an important drop in aboveground temperatures parallel to an increase in vegetation heights.

273 Microclimate cooling has often been suggested as a potential mechanism to explain responses
274 of various arthropod groups to intensification (e.g. Gardiner et al., 2002; Löffler and
275 Fartmann, 2017; Marini et al., 2009), but the link had never been clearly demonstrated.

276 In the following subsections we first present the effects of the management practices
277 on vegetation and microclimate. We then state its effects on orthopteran density and species
278 richness and discuss how these are linked to vegetation height and microclimate. Finally we
279 discuss the conservation implications of the present study.

280

281 *4.1 Effects on vegetation and microclimate*

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

288 Aboveground temperatures were linked to vegetation height: the taller the sward
289 became the less sunlight reached the ground and the less it was warmed (see also Song et al.,
290 2013). Consequently the temperatures differences between the most intensively managed
291 plots and the controls were of up to 4.2°C at 10 cm aboveground. After the cut, vegetation
292 regrew progressively which reduced the surface temperature differences among plots.

293 Vegetation height is not the only factor explaining microclimate; other parameters such as
294 vegetation density and canopy cover do influence quantity of sunshine reaching the soil and
295 thus indirectly temperature (van Wingerden et al., 1992), as well as sprinkler irrigation as
296 demonstrated here. This explains why surface temperatures varied more along the
297 intensification gradient than swards heights.

298

299 *4.2 Effects on orthopteran densities*

300 Different responses were observed between the two suborders. Before mowing Caelifera
301 densities were respectively 30 to 40% lower in plots that had been either irrigated or fertilised.
302 The combination of both inputs was even worse leading to over 70% reduction in density
303 regardless of quantities applied (i.e. densities were divided by three). Our SEM indicates that
304 this negative effect is due to a combination of a direct negative effect of water input and an
305 indirect effect of slurry input through vegetation height. As most individuals were low-mobile
306 larvae during the first sampling session their distribution reflects their birth place. Therefore
307 reasons for differences could be one or a combination of following factors: 1) females
308 favoured lower sward sites to oviposit; 2) larval development was altered and survival rate
309 was lower in plots with tall vegetation (Willott and Hassall, 1998); or 3) eggs hatching was
310 delayed in taller vegetation and had not occurred yet at the time plots were sampled, which is
311 detrimental to population as it reduces individuals chance to complete their life cycle and to
312 reproduce (van Wingerden et al., 1991; Weiss et al., 2013). Management intensification did
313 not impact Ensifera densities. This might reflect the fact that in average Ensifera emerged
314 earlier in the season compared to Caelifera, when vegetation height and thus microclimate
315 differences were less pronounced among management practices. Moreover their development
316 is globally less dependent on temperatures (Bieringer and Zulka, 2003).

317 The mowing event may have dispersed the individuals all over the meadow area
318 (Humbert et al., 2012) so the densities of Caelifera found during the second sampling session
319 were not directly related to number found during the first sampling session. Nevertheless, we
320 observed that generalist species such as *P. parallelus* dispersed more or less evenly across the
321 plots while the specialized thermophilous species such as *S. lineatus* or *Omocestus*
322 *haemorrhoidales* recolonized the warmest plots. A boom in Caelifera eggs hatching probably

323 occurred in the days following mowing due to warmer microclimate as about half of the
324 individuals sampled during the second session were still at larval stage. After mowing
325 Ensifera were slightly, though not statistically, more numerous in more intensively managed
326 plots and there were virtually no more larvae. This pattern was due to the preponderant
327 presence of adults *Tettigonia viridissima* and *Roeseliana roeselii* that favoured the tall swards
328 found in intensified plots. However densities remained very low with less than 0.5 Ensifera
329 per m².

330 We had hypothesized that at moderate management intensity level orthopteran
331 densities would be maximized, benefiting from increased food supply without being impacted
332 by microclimate changes (Hudewenz et al., 2012). However, results are not in accordance
333 with our hypothesis. Overall results seem to indicate that in the investigated mountain
334 meadows food resource is not a limiting factor for Caelifera while temperature might be.

335

336 *4.3 Effects on orthopteran species richness*

337 Highest Caelifera species richness was found in the control plots and was maintained in plots
338 that were either irrigated or fertilised but the combination of both inputs had detrimental
339 effects: species loss reached 50% in the most intensive plots, i.e. richness was divided by two.
340 This trend is in line with previous observational studies done in the Alps or Prealps (Marini et
341 al., 2008; Schlegel and Schnetzler, 2018), as well as conclusions from studies carried on in
342 lowland regions (e.g. Chisté et al., 2016; Knop et al., 2006) and it confirms the general
343 detrimental effects of grassland management intensification on orthopteran species richness.

344 The SEM indicates strong direct negative effects of slurry and water input, plus an
345 indirect effect of water input through changes in aboveground temperature, though the last
346 path between aboveground temperature and Caelifera species richness was not statistically
347 significant. The direct effect of slurry and water input should not be interpreted as strictly

348 direct, it could also be indirect through variables not included in the model. It is known that in
349 addition to aboveground temperature, orthopteran community composition is related to
350 several other parameters such as vegetation structural heterogeneity (Jerrentrup et al., 2014),
351 percentage of bare ground (Weiss et al., 2013), plant species composition (Fournier et al.,
352 2017; Gardiner et al., 2002; Ibanez et al., 2013), and management regime (e.g. our control
353 plots were cut once a year while irrigated and fertilised plots twice; see also Buri et al., 2013).
354 The parallel drop in species richness and temperatures suggests that either thermophile
355 species chose deliberately not to oviposit within more intensive plots – showing a cumulative
356 effect from previous year – or the eggs laid within colder plots poorly developed and larvae
357 never reached maturity (Willott and Hassall, 1998). Willott and Hassall (1998) showed that a
358 difference of 5°C in ambient temperature – air temperature differences reached 4.2°C in our
359 case – considerably affects Caelifera fitness: most sensitive species experiments a
360 development time 50% longer, a reduction of 25% in body mass and a drop of 50% in pods
361 production. Altogether, our findings support the hypothesis that the microclimate conditions
362 within intensively managed plots became too cold for thermophilous species. Though, we do
363 not claim that it is the only explanatory mechanism. *De facto* temperature changes do not
364 explain the relatively lower Caelifera species richness found within low-intensity plots (I+F
365 1/3) compared to irrigated or fertilised only plots.

366 Contrariwise to Caelifera, Ensifera species richness was not affected by
367 intensification. This suborder is known to be less sensitive to microclimate than Caelifera and
368 to depend more on vegetation structure (Baur et al., 2006; Bieringer and Zulka, 2003).
369 However, a change in community composition accompanying intensification was noticed.
370 Large species such as *T. viridissima* or generalists such as *R. roeselii* favouring tall vegetation
371 which offers good singing spots and shelter (Baur et al., 2006; Buri et al., 2013) were more
372 often found in intensively managed plots compared to extensively managed plots. In the

373 contrary *Plactycleis albopunctata* or *Decticus verrucivorus* which are species associated with
374 warm and dry habitat (Baur et al., 2006) were occasionally found in control plots, but not
375 within intensively managed ones. This reflects the ecological diversity of Ensifera and might
376 explain why their global species richness remained stable among experimental plots. It has to
377 be noted that the power of the analyses was constrained due to relatively low Ensifera species
378 richness (the average \pm standard deviation was 1.1 ± 1.0 across all plots).

379

380 *4.4 Conclusions and conservation implications*

381 Aerial irrigation and fertilisation with liquid manure are two novel management practices
382 currently spreading in dry alpine regions (Riedener et al., 2013). While on one hand these
383 practices benefit biodiversity in the sense that by increasing grass yield (Andrey et al., 2014;
384 Bassin et al., 2012) they support continuity of local farming so as to keep montane and
385 subalpine semi-natural grasslands open (Riedener et al., 2014; Rudmann-Maurer et al., 2008),
386 on the other hand they become a threat to biodiversity when too much inputs are applied (this
387 study).

388 In contrast to observational studies, the experimental approach adopted in this study
389 has the advantage that measured differences between treatments were not affected (biased) by
390 environmental parameters such as soil, elevation or surrounding landscape, neither by climate
391 or past management history. In addition, results are based on controlled, quantitatively based,
392 levels of grassland irrigation and fertilisation that are related to what is done in the practice.
393 On the other hand it has some limitations due to the size and proximity of the plots that could
394 have blurred the signal. Despite the close proximity of the experimental plots, very clear
395 evidences that intensification lower both Caelifera densities and species richness were found,
396 which are then conservative findings.

397 Results demonstrate that the use of irrigation input alone has moderate impacts on
398 orthopterans and on microclimate while the combination of irrigation and fertilisation inputs
399 is harmful to orthopterans even at low dose. The first finding is good news for all stakeholders
400 (including farmers, conservationists and policy-makers) as irrigation alone can increase hay
401 yield without affecting biodiversity (see also Jeangros and Bertola, 2000; Riedener et al.,
402 2013) and is allowed in subsidized extensively managed meadows registered under Swiss
403 agri-environment schemes. On the other hand fertilisation alone and the combination of both
404 inputs must be forbidden in grasslands where conservation of invertebrate and vertebrate
405 fauna is of concern as a drop in grassland invertebrate densities can have dramatic bottom-up
406 effects on higher trophic levels (Britschgi et al., 2006). Management intensification had even
407 stronger impacts on Caelifera densities than on species richness as detrimental effects were
408 already visible in low intensity plots. Combine with our precedent findings on plants (REF
409 (Andrey et al., 2014; Lessard-Therrien et al., 2017), bryophytes (Boch et al., 2018),
410 Auchenorrhyncha (Andrey et al., 2016), spiders and ground beetles (Lessard-Therrien et al.,
411 2018), this study darkens the optimistic perspective to find an intermediate management
412 intensity threshold that provides decent agronomical yield and that has only limited negative
413 effects on biodiversity.

414 The second important contribution of this study is the quantitative assessment of
415 changes in microhabitat and -climate induced by intensification. The effective cooling (more
416 than 4 °C at 10 cm above ground) measured exceeded expectations and can have huge
417 impacts on the development of local micro-fauna (Logan et al., 2006). While we acknowledge
418 that we only prove a causal connection between changes in vegetation height and Caelifera
419 densities before mowing, aboveground temperature was retained (regardless of its non-
420 statistically significant last path) in the best SEMs to explain Caelifera density after mowing
421 and species richness, and the models showed very good fitting properties. In addition there

422 was a strong negative correlation between vegetation height and sward temperature which
423 highlights that both effects can hardly be separated.

424

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433

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585

586

587

588 **Tables**

589 **Table 1:** Management practices applied to the six different experimental treatment plots.

590 Abbreviations for treatments: C = control; F = fertilised; I = irrigated; F+I 1/3, F+I 2/3 and

591 F+I 3/3 = fertilised and irrigated at respectively 1/3, 2/3 or 3/3 of the maximum dose. The

592 exact 3/3 dose of fertiliser applied at each site followed the management norm recommended

593 to achieve maximum hay yield at a given locality, and were classed in three groups. Note that

594 I and F, received the same amount of water or fertiliser as I+F 2/3.

Management treatment	Mowing regime [no. of cut·yr ⁻¹]	Irrigation [mm·week ⁻¹]	Fertilisation [kg N·ha ⁻¹ ·yr ⁻¹]		
			Group 1	Group 2	Group 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

595

596 **Figures legends**

597 **Fig. 1.** Responses of orthopteran densities (individuals / m²) to the six different management
598 treatments: a) Caelifera densities before mowing; b) Caelifera densities after mowing (note
599 that in the IF3/3-plot a point at 31.9 individuals / m² do not appear on the figure); c) Ensifera
600 densities before mowing; d) Ensifera densities after mowing. Abbreviations for treatments: C
601 = control; F = fertilisation only; I = irrigation only, IF1/3 = irrigation and fertilisation at low
602 dose, IF2/3 = irrigation and fertilisation at medium dose, IF3/3 = irrigation and fertilisation at
603 high dose. Different letters indicate significant differences between treatments at an alpha
604 rejection value set to 0.05. Bold lines represent medians, cross the means; boxes the first and
605 third quantiles.

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

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

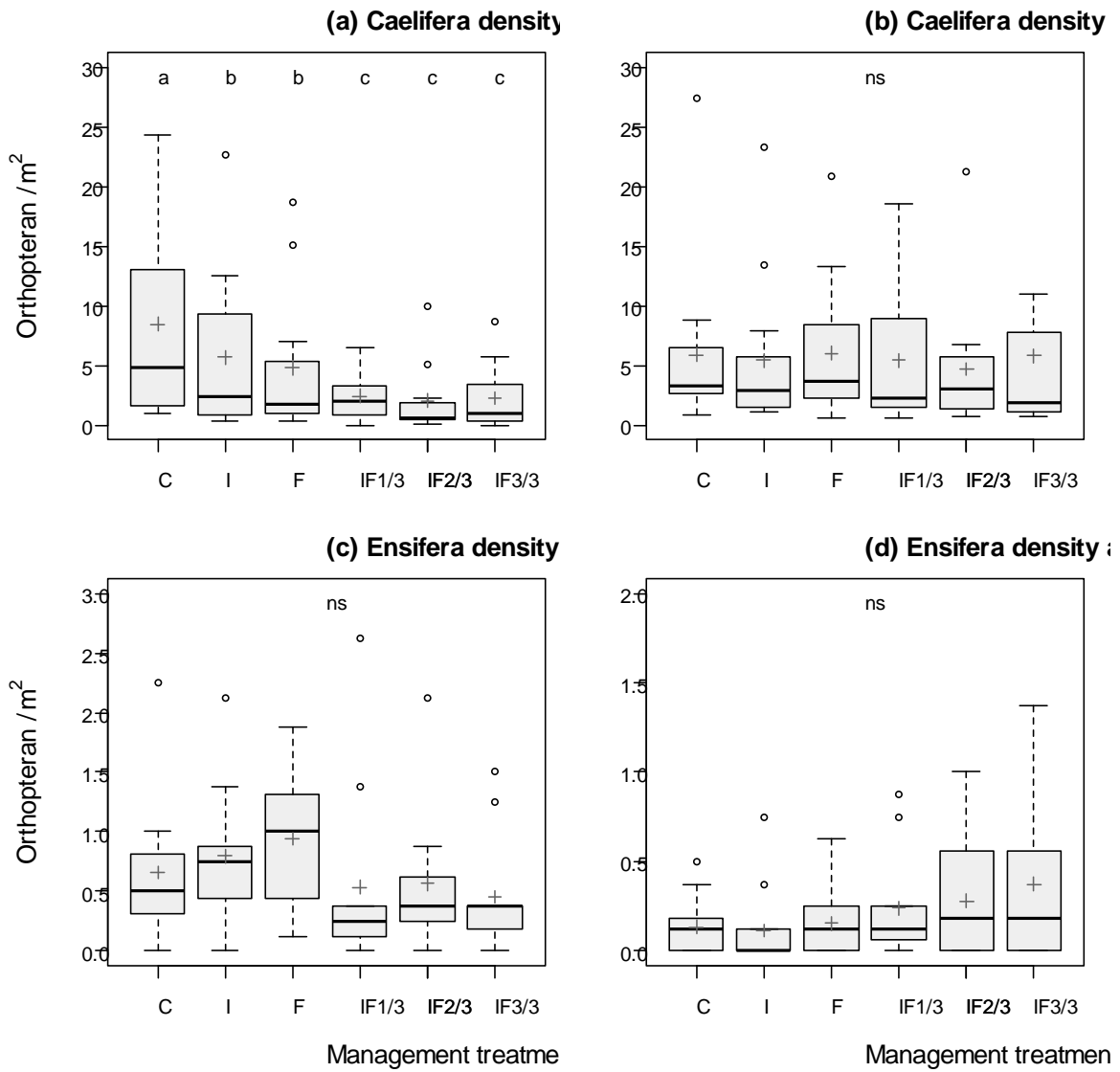
614 **Fig. 4.** Negative relationship between aboveground diurnal temperature and log-transformed
615 vegetation height (in cm) before mowing. The regression line is drawn from the LMM outputs
616 with 95% confidence intervals. Marginal r² (R2m) represents the percentage of variance
617 explained by the fixed effects only, whereas conditional r² (R2c) is the percentage explained
618 by both fixed and random effects grouped (Nakagawa and Schielzeth, 2013).

619

620 **Fig. 5.** Best structural equation model (SEM) explaining the influences of slurry and water
621 inputs on: (a) Caelifera density before mowing; (b) Caelifera density after mowing; and (c)
622 Caelifera species richness. Standardized path coefficients are shown beside each path, with
623 the level of statistical significance indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P <$
624 0.001). The width of the arrows depicts the strength of the effect and R^2 values represent the
625 proportion of variance explained for each dependent variable. All candidate SEM models can
626 be found in Appendix 2.

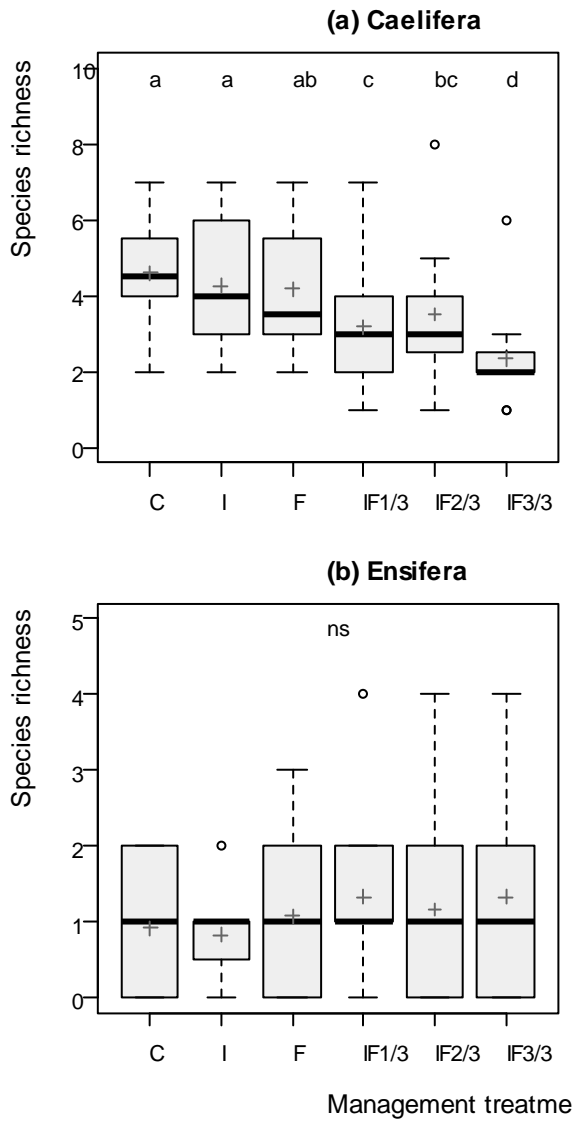
627 **Figures**

628 **Fig. 1**



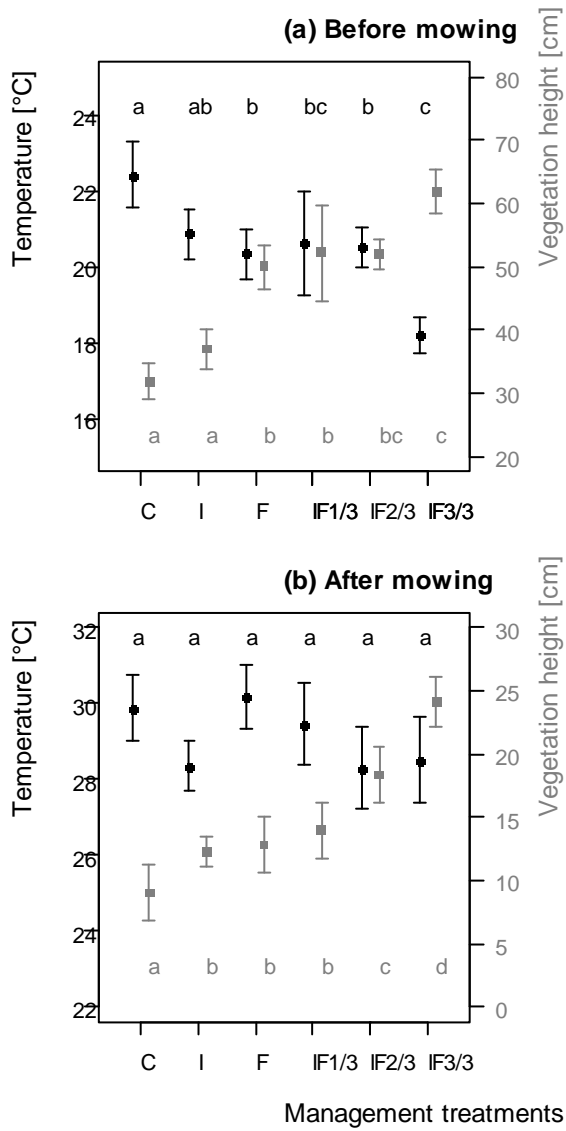
629

630 **Fig. 2**



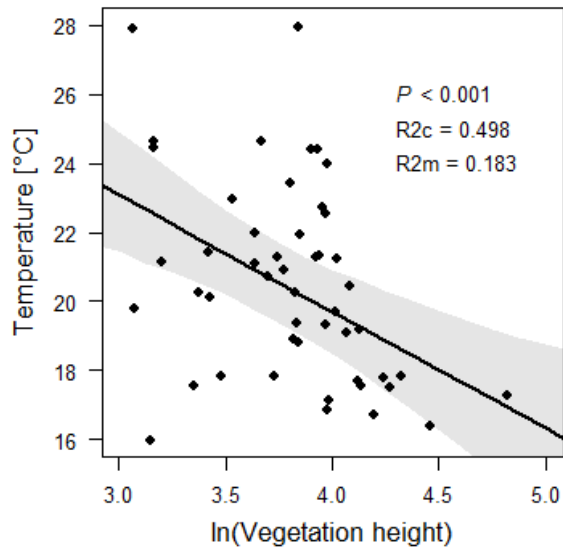
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632 **Fig. 3**



633

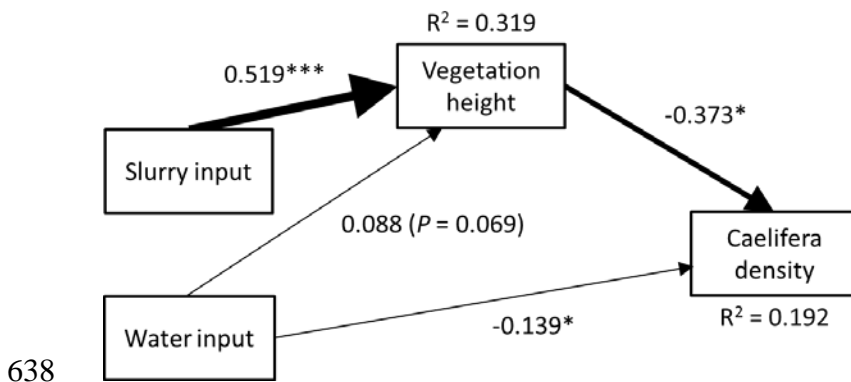
634 **Fig. 4**



635

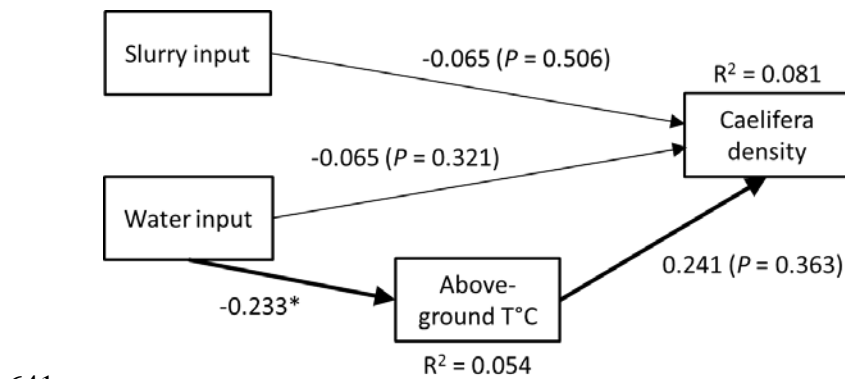
636 **Fig. 5**

637 **(a) Caelifera density before mowing**



639

640 **(b) Caelifera density after mowing**

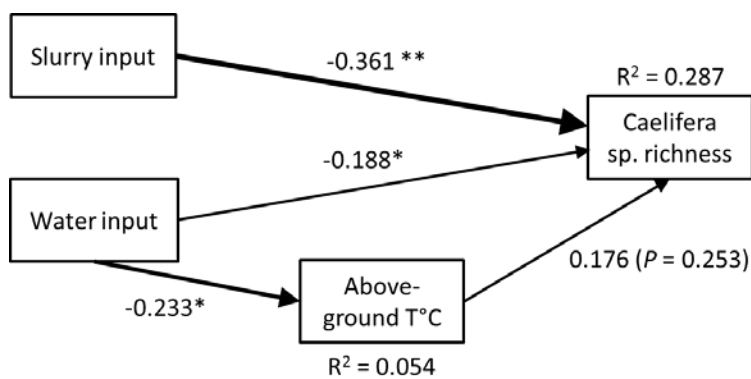


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642

643 **(c) Caelifera species richness**

644



645

646

647 **Appendices**

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

650 **Appendix 2:** Initial full structural equation model used to build all candidate models.

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

653 **Appendix 4:** Results of the LMMs carried out on the effects of fertilisation and irrigation on
654 Caelifera and Ensifera species richness.

655 **Appendix 5:** Results of the LMMs carried out on the effects of fertilisation and irrigation on
656 vegetation height.

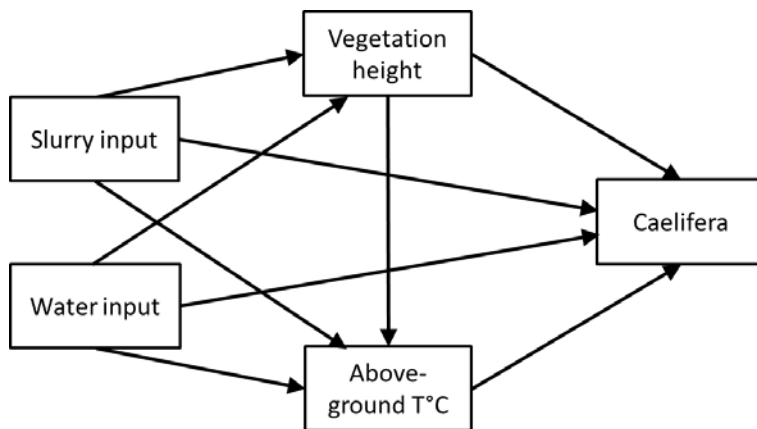
657 **Appendix 6:** Results of the LMMs carried out on the effects of fertilisation and irrigation on
658 aboveground diurnal temperature.

659

Appendix 1. Location name of all study sites (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.

See Supplemental File.

Appendix 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. 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 ran on Caelifera densities before and after mowing and on Caelifera species richness (pooled sampling session).



Appendix 3. 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 factors 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). The random factors were the study sites. Parameter estimates (differences between expected mean abundances on the log scale) are given for paired regime comparisons and significant differences are highlighted in bold.

Response variable and comparison	Estimate	SE	<i>P</i> (> z)
(a) Caelifera density before mowing (log scale)			
I vs C	-0.393	0.164	0.016
F vs C	-0.568	0.173	0.001
I+F 1/3 vs C	-1.242	0.220	<0.001
I+F 2/3 vs C	-1.426	0.236	<0.001
I+F 3/3 vs C	-1.315	0.226	<0.001
F vs I	-0.174	0.187	0.352
I+F 1/3 vs I	-0.849	0.231	<0.001
I+F 2/3 vs I	-1.033	0.247	<0.001
I+F 3/3 vs I	-0.921	0.237	<0.001
I+F 1/3 vs F	-0.674	0.238	0.005
I+F 2/3 vs F	-0.859	0.253	0.001
I+F 3/3 vs F	-0.747	0.243	0.002
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
(b) Caelifera density after mowing (log scale)			
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

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Response variable and comparison	Estimate	SE	<i>P</i> (> z)
(c) Ensifera density before mowing (log scale)			
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
(d) Ensifera density after mowing (log scale)			
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

Appendix 4. 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. The fixed factors 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). The random factors were the study sites. Parameter estimates (differences between expected mean species richness) are given for paired regime comparisons and significant differences are highlighted in bold.

Response variable and comparison	Estimate	SE	<i>P</i> (> t)
(a) Caelifera species richness			
I vs C	-0.333	0.358	0.355
F vs C	-0.417	0.358	0.249
I+F 1/3 vs C	-1.417	0.358	<0.001
I+F 2/3 vs C	-1.083	0.358	0.004
I+F 3/3 vs C	-2.250	0.358	<0.001
F vs I	-0.083	0.357	0.817
I+F 1/3 vs I	-1.083	0.357	0.004
I+F 2/3 vs I	-0.750	0.357	0.041
I+F 3/3 vs I	-1.917	0.357	<0.001
I+F 1/3 vs F	-1.000	0.357	0.007
I+F 2/3 vs F	-0.667	0.357	0.068
I+F 3/3 vs F	-1.833	0.357	<0.001
I+F 2/3 vs I+F 1/3	0.333	0.358	0.355
I+F 3/3 vs I+F 1/3	-0.833	0.358	0.023
I+F 3/3 vs I+F 2/3	-1.167	0.358	0.002
(b) Ensifera species richness			
I vs C	-0.083	0.332	0.803
F vs C	0.167	0.332	0.618
I+F 1/3 vs C	0.417	0.332	0.215
I+F 2/3 vs C	0.250	0.332	0.455
I+F 3/3 vs C	0.417	0.332	0.215
F vs I	0.250	0.332	0.455
I+F 1/3 vs I	0.500	0.332	0.138
I+F 2/3 vs I	0.333	0.332	0.320
I+F 3/3 vs I	0.500	0.332	0.138
I+F 1/3 vs F	0.250	0.332	0.455
I+F 2/3 vs F	0.083	0.332	0.803
I+F 3/3 vs F	0.250	0.332	0.455
I+F 2/3 vs I+F 1/3	-0.167	0.332	0.618
I+F 3/3 vs I+F 1/3	0.000	0.332	1.000
I+F 3/3 vs I+F 2/3	0.167	0.332	0.618

Appendix 5. 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. The fixed factors 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 medium at dose; I+F 3/3 = irrigation and fertilisation at high dose). The random factors were the study sites. Parameter estimates (differences between expected mean) are given for paired regime comparisons and significant differences are highlighted in bold.

Response variable and comparison	Estimate	SE	<i>P</i> (> <i>t</i>)
(a) Before mowing			
I vs C	0.154	0.094	0.106
F vs C	0.468	0.094	<0.001
I+F 1/3 vs C	0.454	0.094	<0.001
I+F 2/3 vs C	0.520	0.094	<0.001
I+F 3/3 vs C	0.687	0.094	<0.001
F vs I	0.314	0.094	0.002
I+F 1/3 vs I	0.300	0.094	0.002
I+F 2/3 vs I	0.366	0.094	<0.001
I+F 3/3 vs I	0.533	0.094	<0.001
I+F 1/3 vs F	-0.014	0.094	0.881
I+F 2/3 vs F	0.052	0.094	0.580
I+F 3/3 vs F	0.219	0.094	0.023
I+F 2/3 vs I+F 1/3	0.066	0.094	0.482
I+F 3/3 vs I+F 1/3	0.233	0.094	0.016
I+F 3/3 vs I+F 2/3	0.167	0.094	0.080
(b) After mowing			
I vs C	0.479	0.107	<0.001
F vs C	0.421	0.107	<0.001
I+F 1/3 vs C	0.520	0.107	<0.001
I+F 2/3 vs C	0.864	0.107	<0.001
I+F 3/3 vs C	1.171	0.107	<0.001
F vs I	-0.058	0.107	0.592
I+F 1/3 vs I	0.041	0.107	0.706
I+F 2/3 vs I	0.385	0.107	0.001
I+F 3/3 vs I	0.692	0.107	<0.001
I+F 1/3 vs F	0.099	0.107	0.362
I+F 2/3 vs F	0.443	0.107	<0.001
I+F 3/3 vs F	0.750	0.107	<0.001
I+F 2/3 vs I+F 1/3	0.344	0.107	0.002
I+F 3/3 vs I+F 1/3	0.652	0.107	<0.001
I+F 3/3 vs I+F 2/3	0.307	0.107	0.006

Appendix 6. 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. The fixed factors 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 medium at dose; I+F 3/3 = irrigation and fertilisation at high dose). The random factors were the study sites. Parameter estimates (differences between expected mean) are given for paired regime comparisons and significant differences are highlighted in bold.

Response variable and comparison	Estimate	SE	<i>P</i> (> t)
(a) Before mowing			
I vs C	-1.300	0.850	0.134
F vs C	-2.111	0.920	0.027
I+F 1/3 vs C	-2.305	1.098	0.042
I+F 2/3 vs C	-2.099	0.876	0.021
I+F 3/3 vs C	-4.317	0.866	<0.001
F vs I	-0.810	0.914	0.381
I+F 1/3 vs I	-1.005	1.081	0.358
I+F 2/3 vs I	-0.799	0.849	0.353
I+F 3/3 vs I	-3.017	0.849	0.001
I+F 1/3 vs F	-0.195	1.133	0.865
I+F 2/3 vs F	0.012	0.929	0.990
I+F 3/3 vs F	-2.207	0.930	0.023
I+F 2/3 vs I+F 1/3	0.206	1.094	0.851
I+F 3/3 vs I+F 1/3	-2.012	1.099	0.075
I+F 3/3 vs I+F 2/3	-2.218	0.875	0.015
(b) After mowing			
I vs C	-1.612	0.949	0.097
F vs C	0.181	0.949	0.850
I+F 1/3 vs C	-0.503	0.949	0.599
I+F 2/3 vs C	-1.636	0.948	0.092
I+F 3/3 vs C	-1.228	1.028	0.240
F vs I	1.793	0.979	0.075
I+F 1/3 vs I	1.109	0.968	0.259
I+F 2/3 vs I	-0.024	0.978	0.981
I+F 3/3 vs I	0.385	1.060	0.719
I+F 1/3 vs F	-0.684	0.979	0.489
I+F 2/3 vs F	-1.817	0.978	0.071
I+F 3/3 vs F	-1.408	1.046	0.186
I+F 2/3 vs I+F 1/3	-1.133	0.978	0.254
I+F 3/3 vs I+F 1/3	-0.724	1.060	0.499
I+F 3/3 vs I+F 2/3	0.409	1.058	0.702