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Impacts of management intensification on ground-dwelling beetles and spiders in semi-natural mountain grasslands

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ABSTRACT

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

1. Introduction

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

Under the drier conditions of the large inner valleys of the European Alps, as typically encountered in the Rhone, Rhine and Danube catchments, grassland intensification involves irrigation via sprinklers (Crook and Jones, 1999) and the application of fertiliser, typically in the form of slurry from livestock wastes. These practices alter plant diversity because some species profit from enhanced nutrient and water supply by increasing phytomass production (Bassin et al., 2012; Fischer and Wipf, 2002) while others disappear through competitive exclusion (Grime, 1973), resulting in a homogenisation of plant community composition (Lessard-Therrien et al., 2017; Wesche et al., 2012). It is well established that grassland intensification is detrimental to plant diversity in mountain grasslands (e.g. Fischer et al., 2008; Humbert et al., 2016; Maurer et al., 2006; Niedrist et al., 2009; Peter et al., 2008). However, the response of invertebrates is much less clear as it seems to depend on the group targeted (Andrey et al., 2016; Grandchamp et al., 2005; Perner et al., 2005).

Arthropod predators are essential community components in grassland ecosystems because they occupy a variety of functional niches and thus fulfil important roles, for instance in the development of soil

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structure, as natural pest control agents feeding on a wide variety of prey and as food source for many insectivorous vertebrates (Altieri, 1999; Bianchi et al., 2006; Cole et al., 2006; Vickery et al., 2001; Vickery and Arlettaz, 2012). They rely on microhabitat structure such as vegetation architectural complexity, topography and soil conditions for habitat (Dennis et al., 1998; Gibson et al., 1992; Perner et al., 2005; Woodcock et al., 2007). They are essential for the proper functioning of grasslands, and because of top-down control on herbivorous arthropods (Hunter and Price, 1992), a decline in predatory species could be detrimental to primary production (Attwood et al., 2008; Perner et al., 2005). Arthropod predators have also been described as suitable bioindicators to assess the impact of land management on biodiversity (Kremen et al., 1993; Perner and Malt, 2003; Pfiffner and Luka, 2003; Rainio and Niemelä, 2003).

Previous studies addressing the impact of management intensification, and in particular fertilisation, in different types of grasslands have shown variable and contradictory effects on predatory arthropods. If fertilisation was generally found to have a negative effect on their taxonomic richness (Attwood et al., 2008; Birkhofer et al., 2015), abundance was affected either positively (Grandchamp et al., 2005; Siemann, 1998) or negatively (Dittrich and Helden, 2012). This calls for further controlled experimental approaches disentangling the specific impacts of irrigation and fertilisation on the biodiversity of mountain grasslands.

We investigated the response of arthropod predators, with a focus on ground beetles (Carabidae) and spiders (Araneae), to experimental intensification, via increased irrigation and fertilisation, of farming practices in montane and subalpine hay meadows. Our main objective was to identify the management intensity that would maintain rich arthropod diversity. Experimental irrigation was achieved with sprinklers and fertilisation through slurry application, mimicking the modern agricultural practices typically encountered in semi-natural meadows dedicated to hay production in the European Alps. After four years of manipulation, we quantified ground beetle and spider species richness and abundance, as well as changes in community composition and variability (a measure of β-diversity) under the different experimental treatments.

We predicted that, along the intensification gradient, ground beetle and spider abundance would increase, because of an increase in prey (herbivorous arthropods) density (Andrey et al., 2016, 2014; Blake et al., 1996; Di Giulio et al., 2001; Raworth et al., 2004). However, the abundance is not likely to increase indefinitely, and was expected to level off, or even reverse, towards higher level(s) of intensification due to micro-habitat deterioration (Dennis et al., 1998; Perner et al., 2005; Woodcock et al., 2007). Under high management intensity, only a few well adapted species would occur in high abundances, leading to a decrease in species richness and homogenisation of the community (i.e. a decrease in β-diversity) (Benton et al., 2003; Di Giulio et al., 2001; Gossner et al., 2016), as it was shown for the plant community (Lessard-Therrien et al., 2017). We hypothesized that fertilisation would be the main driver of these patterns (Birkhofer et al., 2015; Haddad et al., 2000). The effect of irrigation on ground-dwelling arthropods is less known, although moisture levels have been reported to be an important factor influencing ground beetle and spider assemblages (Blake et al., 1996; Entling et al., 2007; Eyre et al., 1990), therefore we predicted a positive effect on arthropod diversity.

2. Materials and methods

2.1. Study sites

In 2010, eleven traditionally managed hay meadows were selected within the canton of Valais, in the inner Alps of SW Switzerland (Fig. A1 in Supplementary material). The region is characterized by a continental climate with cool and wet winters, as well as warm and dry summers. Average monthly ambient air temperature (2004–2014) in Sion, at valley bottom (482 m a.s.l.), ranged from a 0.3 °C in January to 20.5 °C in July (Federal Office of Meteorology and Climatology, 2016). The eleven meadows were situated within the montane and subalpine belts, between 880 and 1770 m a.s.l. (Table A1 in Supplementary material). All meadows had been extensively managed for at least the ten years preceding the experiment, harbouring on average 48 ± 8 (mean ± SD) plant species per 8 m^2 in the control plots in 2014 (Lessard-Therrien et al., 2017).

2.2. Experimental design

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

The experiment consisted of a gradient of management intensity including the control (C) and three plots that received a combination of aerial irrigation (I) via sprinklers and fertilisation (F) with slurry (i.e. liquid manure), with amounts varying in tandem with 1/3, 2/3 or 3/3 of the quantity theoretically needed to achieve maximum hay yield, under a mowing regime consisting of two cuts a year and according to site productivity potential (Sinaj et al., 2009). This created a 4-level management intensity gradient: C (no input); I + F 1/3 (low input), I + F 2/3 (medium input); and I + F 3/3 (high input). The experiment also included a 2 × 2 factorial design that allowed disentangling the effects of irrigation (I) and fertilisation (F) (both treatments applied separately at 2/3 of the maximal amount), by comparing controls (C, no input) to both irrigation and fertilisation combined (I + F 2/3). These I 2/3 and F 2/3 treatments are hereafter referred to as I and F, where appropriate.

The fertiliser consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4) dissolved into water so as to reach the same NPK nutrient-water concentration as of standard farm slurry (Sinaj et al., 2009). The amount of slurry applied per plot depended on the theoretical local hay production potential, calculated from site elevation and pre-experimental hay yield (see Appendix A in Supplementary material Andrey et al., 2016), which allowed the study sites to be categorized according to their potential productivity (Table A2 in Supplementary material).

2.3. Arthropod sampling

In each plot, ground-dwelling arthropods were sampled using three pitfall traps which consisted of plastic cups of 90 mm in diameter with a capacity of 500 ml that were buried flush with the ground surface. The three traps were arranged in a way that they formed a triangle, with triangle top situated 5 m above plot centre upslope, triangle lower tip located 5 m below the centre and side top situated 5 m left or right of centre (Fig. A2 in Supplementary material). Traps were filled with 0.25 l of propylene glycol (Weeks and McIntyre, 1997) diluted with water (ratio of 2:1) and a drop of detergent to reduce surface tension (Topping and Luff, 1995). Transparent covers measuring 20 × 20 cm were installed 5 cm above the traps, with three nails (at two extremities and in opposite edge centre) planted into to the soil, to prevent rain flooding. The traps were operated for two weeks, being emptied twice, once each week. Sampling was conducted before the first hay harvest, from May to July 2014 depending on elevation, starting from meadows situated at lower elevation and proceeding towards higher elevation. In each plot, we also measured mean vegetation height and visually estimated bare ground cover, two key habitat features that subsequently served as explanatory variables (Bell et al., 2001). Taxonomic nomenclature follows Freude et al. (2004) for ground beetles and Nentwig et al. (2016) for spiders.

2.4. Statistical analyses

2.4.1. Species abundance and richness

Statistical analyses were performed on the content of the three traps per plot pooled together. The effects of management treatment, vegetation height and bare ground cover on ground beetle and spider abundance and species richness were tested with generalized linear mixed effect models (GLMM), with a Poisson error distribution, using the R-package *lme4* (Bates et al., 2015). Analyses were conducted separately for the 2 × 2 factorial design and 4-level management intensity gradient. In the factorial design models, we fitted an interaction term between irrigation and fertilisation, which was retained only if significant. In our intensification gradient analysis, the four levels were treated as a single continuous variable: control with no input = 0; I + F 1/3 = 1; I + F 2/3 = 2; and I + F 3/3 = 3. In this analysis, we compared linear and quadratic regression models based on the lowest second-order corrected Akaike's information criterion (AICc), a measure corrected for small sample size (Burnham and Anderson 2002). The model with the lowest AICc value was retained. Study site (n = 11) was a random effect in all models. Concerning abundance data, we had to account for overdispersion by including an observation-level random effect in relevant models (Harrison, 2014). All analyses were conducted using R statistical software, version 3.1.2 (R Core Team, 2015).

2.4.2. Community analyses

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

To test for the magnitude of changes in arthropod communities between experimental treatments and study sites we used the function *adonis* in *vegan* R-library, which performs a multivariate analysis of variance using simple distance matrices (Anderson, 2001). A p-value was obtained by permuting the least absolute deviation residuals (Anderson et al., 2006a). Three measures of inter-community distance were then used (Bray-Curtis, Chao, and Morisita-Horn) to assess changes in community composition between treatments and sites. We used three dissimilarity indices to cover the whole range of possible community variation from emphasising species composition to abundance changes in communities (Anderson et al., 2006b). First, the widely used Bray-Curtis dissimilarity index (Bray and Curtis, 1957) is a version of the Sørensen index (see Magurran, 2004), modified to include abundance. Based on absolute differences in species proportions, it captures variation in community structure (Anderson et al., 2006b). The second metric, Chao's dissimilarity index (Chao et al., 2005), is a probabilistic abundance-based measure that controls for species undetected during sampling. In effect, it is unlikely to census an entire arthropod community during only two weeks of pitfall trapping at only three locations per plot. It is based on the probability that two individuals randomly drawn from two distinct samples belong to any of the species shared by these two samples, but not to the very same shared species, contrary to other dissimilarity indices (Chao et al., 2005). This index is therefore particularly appropriate for species-rich communities that include a large fraction of rare species. The third index, the Morisita-Horn index (Horn, 1966) is another abundance-based dissimilarity metric for measuring spatial variation in diversity, which is fairly sensitive to species richness and sample size (Barwell et al., 2015; Chao et al., 2006; Magurran, 2004).

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

3. Results

3.1. Abundance and species richness

A total of 3840 ground beetles belonging to 50 species were captured (Table B1 in Supplementary material). The two most abundant species were *Poecilus versicolor* and *Bembidion lampros*, contributing 47.3% and 15.6%, respectively, to the total number of individuals (all other species each accounted for less than 10% of the total). We sampled 9620 spiders in total. All individuals were considered for abundance data. However, for the analysis of species richness, due to logistic constraints, we randomly selected two traps out of the three sampled per plot (for a total of 4668 individuals of 94 species; Table B2 in Supplementary material). The most abundant species were *Alopecosa trabalis* and *Pardosa palustris* accounting for 49.1% and 12.8% of the individuals, respectively. All other species again contributed < 10% each to the total catch.

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

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

The 2 × 2 factorial analysis revealed that fertilisation had a positive effect on both ground beetle and spider abundance (Fig. 3 and Table 2), but no effect on species richness for either taxonomic group (Fig. 4 and Table 2). Irrigation had a positive effect on ground beetle abundance (Table 2) while it had no effect on spider abundance. Species richness of

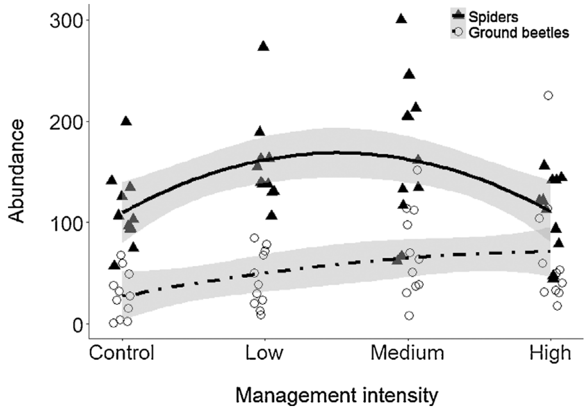

Fig. 1. Effects of combined irrigation and fertilisation on ground-dwelling predatory arthropod abundance with respect to management intensity. The 4-level management intensity gradient consists of control (no input), low, medium and high input levels, i.e. fertilisation and irrigation at, respectively,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

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

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

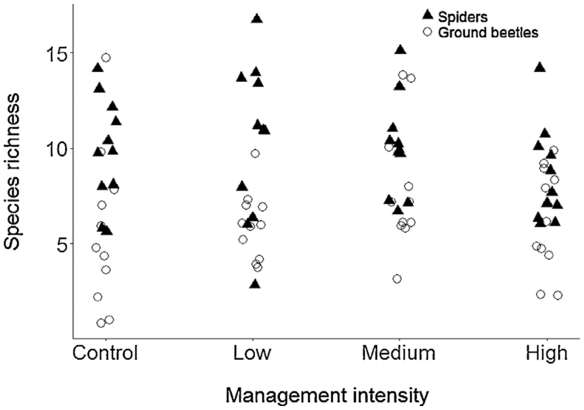

Fig. 2. Absence of effects of management intensity on ground beetle and spider species richness. For more details, see legend of Fig. 1. For statistical analyses see Table 1.

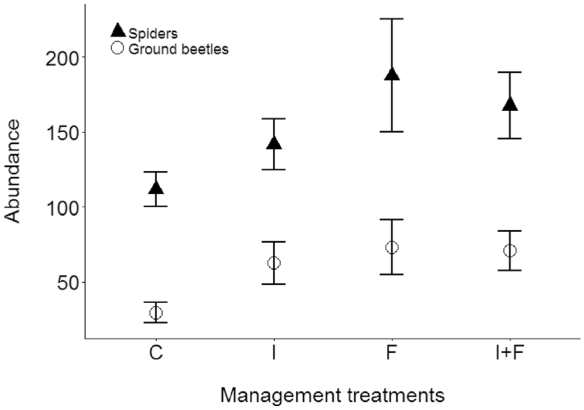

Fig. 3. Separate effects of irrigation and fertilisation tested by the 2 × 2 factorial design on ground beetle and spider abundance. C = control (no input); I = irrigation, F = fertilisation, I + F = irrigation + fertilisation. Mean values ± SE are shown. See Table 2 for statistical analyses.

neither taxon was affected by irrigation. A significant interactive effect between fertilisation and irrigation was revealed only for ground beetle abundance (Table 2), indicating that the effects of the two factors were not additive (Fig. 3 and Table 2).

Table 2
Outputs of the generalized linear mixed-models of the 2 × 2 factorial design to disentangle the effect of fertilisation and irrigation on ground beetle and spider abundance and species richness. Study site was included as a random effect in all models. Observation level was included as a random effect in abundance models, so as to cope with overdispersed data. All estimates are on the log-scale, SE stands for standard error. Significant effects are highlighted in bold.

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

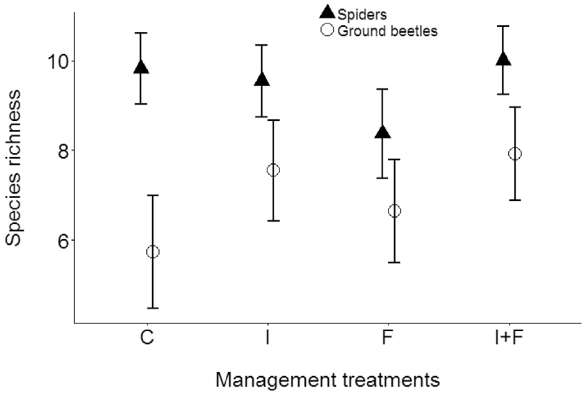

Fig. 4. Absence of separate effects of irrigation and fertilisation tested by the 2 × 2 factorial design on ground beetle and spider species richness. For management treatment description, see legend of Fig. 3. Mean values ± SE are shown. See Table 2 for statistical analyses.

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

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

3.2. Arthropod community composition

The multivariate analysis of variance performed on the distance matrices using the Bray-Curtis index showed that the ground beetle community was not altered by the experimental treatments (Table 3 and Fig. C1 in Supplementary material), but differed significantly between study sites (Table 3 and Fig. C2 in Supplementary material). However, the Chao and Morisita-Horn indices indicated that the ground beetle community was significantly influenced by both treatment and site, although the amount of variation explained by the experimental treatment was much lower than by site, based on R^2 values (Table 3).

The spider community changed significantly under the experimental treatments when applying both the Bray-Curtis and Chao indices (Table 3 and Fig. C1 in Supplementary material), but study site had no effect (Table 3 and Fig. C2 in Supplementary material). When considering the Morisita-Horn index, the spider community was significantly influenced by both treatment and study site (Table 3).

The taxon-specific differences due to study site are clearly visible on the NMDS graphical projections (Fig. C2 in Supplementary material): the polygons representing the various ground beetle communities are more distant from one another compared to those of spider communities that overlap a lot.

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

4. Discussion

In this study, we experimentally quantified the response of key predatory arthropod communities to modern grassland irrigation and fertilisation, applied either separately or in combination, within mountain hay meadows. Both ground beetle and spider abundance showed curvilinear relationships with the intensification gradient, but spider populations peaked at moderate intensity whereas ground beetle abundance was greatest at a high level of intensification. In contrast, we found no evidence for any effects of the experimental treatments on species richness. Although we observed some change in arthropod community composition with intensification, community variability remained largely unaltered by the treatments in both taxonomic groups. The observed changes were driven by both irrigation and fertilisation for ground beetles, but only by fertilisation for spiders.

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

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

4.1. Abundance and species richness

In agreement with our prediction, arthropod abundance increased with grassland management intensification up to a given threshold (significant quadratic effects for the two taxa), showing a hump-shaped relationship between predatory invertebrate abundance and management intensity. Such a curvilinear relationship was already reported for plant species richness (Chalcraft et al., 2009; Fraser et al., 2015; Kelemen et al., 2013) and for arthropod abundance (Simons and Weisser, 2017) along a phytomass productivity gradient. A similar hump-shaped relationship is also commonly found between species richness and disturbance (e.g. sessile organisms Connell, 1978; plants Grime, 1973; Huston, 1979; Wilson and Tilman, 2002; invertebrates Pöyry et al., 2009; Uchida and Ushimaru, 2014). As no disturbance gradient was tested here, the hump-shaped diversity-productivity relationship may be at play in the present case.

Organic fertilisation was the main underlying driver, apparently playing a more important role than irrigation. Fertilisation boosts phytomass production (see Appendix D in Supplementary material), providing more abundant food resources for herbivorous arthropods (Andrey et al., 2014, 2016; Perner et al., 2005; Prestidge, 1982), soil micro-organisms and mesofauna (Pfiffner and Luka, 2003; Purvis and Curry, 1984). Intensification thus leads to an increase in prey density, with positive cascading bottom-up effects along the food chain (Hunter and Price, 1992). Additionally, a thicker canopy layer resulting from a denser plant cover also better protects ground-dwelling arthropods from vertebrate predators such as insectivorous birds (Atkinson et al., 2005), potentially reducing top-down control on their populations (Hunter and Price, 1992).

Yet, there is a notable discrepancy in the responses of our two taxonomic groups to grassland intensification. While spider abundance peaked at low–medium farming intensity (47% higher than in the control or high input treatments), the curvilinear pattern found for ground beetles is hardly visible on the graphical projection (Fig. 1). This suggests that spider populations are more affected by intensification than those of ground beetles. Biotic and abiotic conditions seem to start to degrade beyond a given threshold of intensity, which leads to a drop (spiders) or a levelling off (ground beetles) in abundance. For spiders, the ecological conditions prevailing beyond that threshold might have significantly decreased habitat suitability. Indeed, changes in microhabitat such as a homogenisation of the vegetation three-dimensional structure are especially detrimental to some web-building spider families (Samu et al., 1999; Sunderland and Samu, 2000). The levelling off in ground beetle abundance might be linked with prey density dynamics. In effect, in the same experimental set up as ours, Andrey et al. (2016) showed that the abundance of leaf- and planthoppers (Auchenorrhyncha), a typical prey of ground beetles (Thiele, 1977), start levelling off from low intensity onwards. These findings are in line with the results by Britschgi et al. (2006) who show that hay meadow intensification leads to a progressive impoverishment of the arthropod community, i.e. of the prey supply for insectivorous birds.

The lack of effect on species richness along the intensification gradient contradicted our expectations. A higher species richness is often found in least intensive agricultural systems (Attwood et al., 2008; Pfiffner and Luka, 2003; Uchida and Ushimaru, 2014). As our experimental plots were relatively small (20 m diameter) and embedded within extensively managed hay meadows, immigration into the plots by these mobile arthropods might have blurred the pattern and consequently reduced the power to detect any drop in species richness. If so, then our results would be conservative, meaning that the patterns observed might in reality be more marked than found in this study. It might also be that the short duration of our experiment (4 years) was not sufficient to provoke strong community changes in terms of species richness, which could occur over longer time periods (Birkhofer et al., 2015; Cole et al., 2005; Dauber et al., 2005).

4.2. Community response

The overall shift in community composition observed for both taxonomic groups was in line with our prediction that species composition of ground beetle and spider communities would change with the altered biotic and abiotic conditions created by our experimental gradient of intensification. Clearly, the main compositional differences were underlain by changes in relative species-specific abundances within these communities rather than changes in number of species *per se*, as this variable did not vary across treatments. The change in ground beetle communities might have been driven mainly by changes in habitat suitability as described above for changes in spider abundance. In effect, previous work has shown that vegetation architectural complexity is a significant driver of community assembly for both taxa, and that it even matters more than prey density for spider diversity (Greenstone, 1984; Luff and Rushton, 1989; Woodcock et al., 2007; Andrey et al., 2014). Further analyses of changes in species-specific functional traits along the intensification gradient would be needed to investigate the ecological mechanisms underlying the observed shifts in community composition.

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

Ground beetle community composition differed significantly between study sites. In contrast, spiders hardly showed any changes in species composition between study sites (there was only a weak significant effect on the Morisita-Horn index mentioned above). This is well depicted in the multivariate cluster projections (Fig. C2 in Supplementary material). The semi-natural grasslands that we used for our experiments were 2–45 km apart, and differed in elevation, soil type, exposition and productivity (Table 1). The reason for these diverging taxon-specific patterns may lie in the different dispersal capacities of these two groups of predatory invertebrates (Hendrickx et al., 2009). Small-sized and young spiders are highly mobile, relying mostly on aerial ballooning for dispersal (Bell et al., 2005). This mobility gives spiders the flexibility to vacate a locally disturbed or no longer suitable area, and to colonise a habitat patch that becomes suitable again, as typically encountered in hay meadows (Curry, 1994). This contrasts with the lower mobility of ground beetles, which are largely limited to ground level movement (Samu et al., 1999).

4.3. Conclusions and management recommendations

Our results indicate that, in mountain meadowlands, ground beetle and spider populations increased in the mid-term (4 years) under low and medium levels of management intensity, whereas species richness was not affected. Previous work using the same experimental setup has shown that Auchenorrhyncha abundance, biomass and species richness were likely maximized under a moderate management intensity (Andrey et al., 2016), whereas plant species richness and phylogenetic diversity were detrimentally affected under the highest management intensity (Lessard-Therrien et al., 2017). Hence, by combining the outcomes of this experiment, we can formulate recommendations for the management of hay meadows submitted to a double yearly mowing regime. Applying fertiliser and water inputs at 1/3–2/3 of the quantity that would be necessary to achieve the maximum local hay yield appears to be compatible with preservation of biodiversity-rich montane and subalpine grasslands.

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

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Appendices A to D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.08.025.

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