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Research paper

Promoting diverse communities of wild bees and hoverflies requires a landscape approach to managing meadows

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ABSTRACT

There is ongoing concern regarding the observed decline in pollinator populations. Managing agricultural landscapes through agri-environment schemes (AES) supports biodiversity and could counteract pollinator population declines. We investigated whether alterations to current AES grassland mowing regimes would increase the abundance and species richness of wild bees and hoverflies. Furthermore, we investigated the response of different nesting and feeding guilds of wild bees and hoverflies, respectively, to these regimes. The three experimental mowing regimes were: (i) first cut not before 15 June, before the beginning of summer (Swiss AES management, control meadows); (ii) first cut delayed until 15 July (delayed meadows); (iii) as for control meadows but leaving 10–20% uncut as a refuge (refuge meadows). The rationale behind the delayed and refuge mowing regimes was extending the availability of floral resources for pollinators, while also providing refugia for species that may be directly impacted by mowing. Hoverflies and wild bees were collected in 2014 and 2015, respectively, using pan-trapping and sweep-netting, once before and once after the first cut. The two collecting methods showed contrasting results. While there was no difference in the abundance or richness of wild bees between the meadows when using pan traps, following the first cut, sweep-netting resulted in a higher abundance and richness of wild bees in delayed and refuge meadows compared to control meadows. Pan-trapping detected a higher abundance of hoverflies in delayed compared to refuge meadows, whereas sweep-netting detected a higher abundance in delayed and refuge compared to control meadows, after the first cut. Saprophagous hoverflies were more abundant in the control and delayed than refuge meadows following the first cut, when sampled with pan traps. Predatory hoverflies were more abundant and species rich in delayed and refuge compared to control meadows following the first cut, when sampled by sweep-netting. Our study demonstrates that simple alterations to a common AES grassland mowing regime can enhance populations of pollinators and natural enemies of crop pests. Furthermore, the contrasting response of the life-history guilds indicates that promoting heterogeneous management practices within the landscape is important for supporting diverse communities, and maintaining key ecosystem services such as pollination and biocontrol.

1. Introduction

The majority of flowering plant species, including wild species and agricultural crops, are reliant on animal pollination for reproduction (Klein et al., 2007; Ollerton et al., 2011). A recent global analysis has shown that managed pollinators (honeybees) are not an adequate substitute for wild pollinators (Garibaldi et al., 2013). Consequently, the reported decline in pollinator populations in many regions presents a worrying trend for the preservation of plant communities (Biesmeijer et al., 2006; Potts et al., 2010; Winfree, 2010). The decline of pollinator populations is often associated with anthropogenic changes to the landscape, in particular habitat loss and alteration through processes such as agricultural intensification (e.g. Kremen et al., 2002; Potts et al.,

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2010). Agricultural intensification leads to landscape homogenisation, along with additional pressures on biodiversity, such as the increased use of insecticides, herbicides and fertilisers (Tscharntke et al., 2005).

Agri-environment schemes (AES) were introduced in Europe in the early 1990s to counteract the decline in biodiversity by promoting semi-natural habitats that can maintain essential ecosystem functions (Kleijn and Sutherland, 2003; Albrecht et al., 2007; Scheper et al., 2013). Several studies have established that AES are more efficient at preserving biodiversity when compared to conventional, intensively managed meadows (Knop et al., 2006; Albrecht et al., 2007; Kohler et al., 2007; Scheper et al., 2013). However, the effectiveness of AES has often been debated, because the impacts on invertebrates, including pollinators are not as positive as expected (Kleijn and Sutherland 2003; Kleijn et al., 2006; Scheper et al., 2013). More recently, studies have tried to determine the causes of this moderate success (e.g. Batáry et al., 2011; Concepción et al., 2012). One cause might be the lack of landscape heterogeneity, since a great proportion of AES meadows are mown within a short time, depriving wild pollinators of resources in early summer. Benton et al. (2003) and more recently Garibaldi et al. (2014) highlighted the importance of spatial and temporal variation within AES to enhance wild pollinator populations and the ecosystem functions they provide.

Relatively simple alterations to meadow management regimes, such as the time of mowing, can increase landscape heterogeneity and have positive effects on the abundance and diversity of invertebrates (Cizek et al., 2012; Buri et al., 2013, 2014, 2016). For example, delaying the first mowing date could extend the temporal availability of resources, such as nectar, pollen, oviposition and nesting sites (Valtonen et al., 2006). Alternatively, leaving an uncut grass refuge on a portion of the meadow also serves to provide continuous resources and shelter (Weibull et al., 2000; Valtonen et al., 2006; Humbert et al., 2012), and has been demonstrated to increase the abundance of wild bees (Buri et al., 2014) and butterflies (Kühne et al., 2015; Lebeau et al., 2015; Bruppacher et al., 2016). Given that extensively managed grasslands are a widespread AES measure and among the most biodiversity-rich ecosystems in Europe (Veen et al., 2009), alteration to their management could have far-reaching impacts for improving their value for supporting diverse pollinator communities (Orford et al., 2016).

In our study, we investigated the effect of a delayed mowing date and the presence of an uncut grass refuge on wild bee and hoverfly communities in extensively managed lowland grasslands. Although often overlooked and dismissed as less effective pollinators in comparison to bees (Jauker et al., 2012; Orford et al., 2015), flies (Diptera) and hoverflies (Diptera: Syrphidae) in particular are important pollinators for numerous wild plants and agricultural crops (e.g. Rader et al., 2009, 2016; Jauker et al., 2012). Furthermore, hoverflies show a diverse range of larval feeding modes, including predatory, saprophagous and phytophagous species (Rotheray and Gilbert, 1999). The predatory larvae of some species can provide effective biocontrol against crop pests, such as aphids (Tenhumberg and Poehling, 1995). While hoverfly populations can be supported by some AES measures such as wildflower strips (Haenke et al., 2009; Jönsson et al., 2015), we currently know very little about the effects of mowing on hoverfly populations. It is likely that hoverflies will respond differently to grassland management measures than wild bees. Previous studies have demonstrated that bee and hoverfly communities exhibit contrasting responses to landscape elements and structure (Jauker et al., 2009; Jönsson et al., 2015). Furthermore, bees and hoverflies strongly differ in their foraging strategy, with bees being central-place foragers, whereas hoverflies are not constrained by the need to provision a nest and may move more freely in the landscape (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Jauker et al., 2009). Furthermore, within pollinator taxonomic groups species may respond differently to habitat management or disturbance, due to variation in life-history traits (Williams et al., 2010). For example, above-ground nesting bees were more negatively affected by isolation from remnant native habitat and intensive agriculture than ground-nesting species (Williams et al., 2010).

We investigated whether i) leaving an uncut refuge when mowing, or delaying the first mowing date by one month would increase the abundance and species richness of wild bees and hoverflies, and ii) if life-history guilds would respond differently to these altered mowing regimes. The rationale behind the delayed treatment was to extend the availability of floral resources for pollinators, which may in turn lead to an increase in the abundance and diversity of pollinating insects. The refuge treatment is envisaged to provide some prolongation of resources, while also providing refugia for species that may be directly impacted by mowing (Humbert et al., 2012). We predicted that i) due to a longer duration of available resources, delaying the first mowing date will positively affect the abundance and species richness of wild bees and hoverflies and; ii) that uncut refuges and a delayed mowing date will favour species that require longer resource availability throughout the season, such as social bees like *Bombus*. In addition, we compared the pollinator community collected using two different sampling methods, pan traps and sweep-netting, to investigate the potential taxonomic bias that can result when using only one method (Hickman et al., 2001; Popic et al., 2013; Spafford and Lortie, 2013).

2. Materials and methods

2.1. Study sites

The study was conducted on 36 extensively managed hay meadows on the Swiss Plateau, a lowland region situated between the Jura Mountains and the Alps. A map of the study sites is presented in Appendix A of Buri et al. (2014). These 36 meadows were selected in 2010 when the experiment began, based on the following criteria: they had to be registered in the Swiss AES as biodiversity promoting areas since at least 2004, and the meadows had to be at least 0.3 ha in size (range: 0.3–1.7 ha; Table S1). The meadows were located between 390 and 833 m a.s.l. The meadows were clustered into 12 study sites (geographic replicates), separated by at least 5 km. Each of the 12 sites contained three experimental meadows, separated by at least 400 m, but within a radius of 3.5 km. A meadow was lost from the delayed treatment (see Section 2.2) in 2012.

2.2. Experimental design

Experimental mowing treatments were applied annually to the meadows since the initiation of the experiment in 2010. Within each site, three meadows were randomly allocated to one of three different mowing regimes: control (C-meadows), delayed (D-meadows), and refuge (R-meadows). The control regime is the conventional management of extensively managed meadows according to the Swiss AES regulations, where the first cut cannot occur before 15 June and no fertiliser application is allowed (Swiss Federal Council, 1998). D-meadows had a delayed first cut that did not occur before 15 July. R-meadows had the same management as C-meadows, but 10–20% of the meadow was left uncut as a refuge each time the meadow was mown. All meadows were cut between one and three times per year (mean ± SE; 2014, 1.82 ± 0.21; 2015, 1.87 ± 0.18). The mean number of cuts per year for each treatment regime was consistent from the initiation of the experiment in

2010, until the sampling took place in 2014 and 2015 (C-meadows, 1.88 ± 0.04; R-meadows, 2.1 ± 0.04; D-meadows, 1.5 ± 0.06).

2.3. Sampling of wild bees and hoverflies

Wild bees (Hymenoptera: Apoidea) and hoverflies were sampled using pan traps and sweep-netting. Sampling of hoverflies was conducted in 2014 and wild bees in 2015, four and five years after the initiation of the experimental mowing regimes. Each meadow was sampled twice during the season, using both methods, once before and once after the first cut (for C- and R-meadows). The first sampling session was from 23 May to 14 June in 2014 and 29 May to 9 June in 2015, and the second session was from 2 to 12 July in 2014 and 26 June to 14 July in 2015. The managed honeybee (*Apis mellifera*) was not included in the analysis.

Pan traps consisted of three coloured plastic bowls (white, yellow and blue, 13 cm diameter and 12 cm deep), filled with soapy water and fixed on a wooden pole just above the vegetation layer. Each meadow was sampled using three sets of pan traps (nine traps per meadow), forming an isosceles triangle (14 m base and 10 m sides; Fig. S1). The set of traps was positioned randomly in the meadow, but at least 10 m from the meadow edge to avoid edge effects (e.g. Knop et al., 2006). Pan traps were opened from 08:00 to 19:00 h for one day per sampling session. Specimens from the three sets of pan traps per sampling session were pooled for analysis.

Sweep-netting was conducted along two 30 m transects per meadow, positioned on either side of the isosceles triangle formed by the pan traps (Fig. S1). Each transect was sampled using one sweep per footstep (approximately 45 min to 1 h per meadow; Spafford and Lortie, 2013). Sampling of the R-meadows in the second session (following the first cut) was conducted with one transect in the cut area of the meadow and one in the uncut refuge. Wild bees were sampled similarly in the first session, but with two transects in each part of the R-meadows during the second session. Specimens from the two sweep-netting transects per sampling session were pooled for analysis.

Wild bees and hoverflies were sampled on dry, sunny days with ambient temperature above 15 °C, and low wind speed. The three meadows within each of the 12 study sites were sampled on the same day using the same sampling method, but pan-trapping and sweep-netting were conducted on different days (1–7 days apart) to avoid interference between the methods. Pan-trapping and sweep-netting was conducted at 2–3 sites per day, depending on weather.

The specimens were identified to species level where possible. Individuals that could not be identified to species were identified to the lowest possible taxonomic level. Furthermore, all species were assigned to life-history guilds; larval feeding guilds for hoverflies (Speight, 2014), and nesting guilds for wild bees (Amiet, 1996; Amiet et al., 1999, 2001, 2004, 2007). The main larval feeding guilds for hoverflies were predatory, saprophagous and phytophagous (Rotheray and Gilbert, 1999; Speight, 2014). The predatory guild primarily contains species that prey on aphids (Hemiptera: Aphididae) and other insects, such as coccids (Hemiptera: Coccidae; Rojo et al., 2003). Saprophagous species inhabit diverse micro-habitats, such as sap runs, tree rot holes, manure and silage (Rotheray and Gilbert, 1999). Bees were assigned to either ground nesting or above-ground nesting species. Bumblebees (*Bombus*

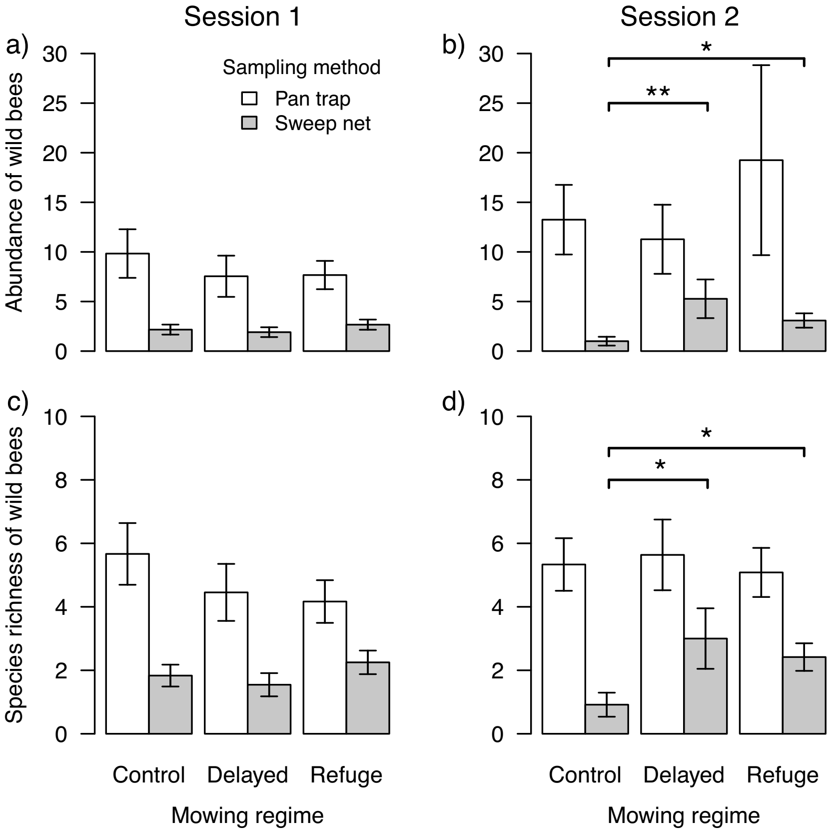

Fig. 1. Abundance (a, b) and species richness (c, d) of wild bees in response to the three different mowing regimes (control, delayed and refuge), collected by pan-trapping (white bars) and sweep-netting (grey bars). Stars represent significant differences determined by GLMMs: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Results presented are means ± SE.

spp. and *Psithyrus* spp.) were also treated separately and included in the relevant nesting guild.

2.4. Statistical analysis

The two sampling sessions were analysed separately to investigate effects of the experimental mowing regimes before and after the meadows were first cut. To standardise the sweep-netting effort for wild bees in the R-meadows (second sampling session only, see Section 2.3. above) to the other mowing regimes, we halved the abundance of wild bees collected. Species richness was calculated by randomly subsampling individuals (without replacement) from the species present within the sweep net samples from each meadow, equal to the halved abundance for that meadow. This process was repeated 1000 times. The mean was used as the value for species richness. Mean and abundance were rounded up to the nearest whole number for the analysis.

We used generalised linear mixed models (GLMMs) with a Poisson distribution to test the effect of the mowing regimes on the abundance and species richness of wild bees and hoverflies. All models were performed in R (R Core Team, 2015) using the package 'lme4' (Bates et al., 2015). All models included mowing regime as a fixed factor, and site was included as a random factor. Following the analysis of the overall communities, we then conducted separate analyses for the abundance and species richness of each life-history guild. Models were constructed as for the general analysis. All models were visually checked for normal distribution of residuals. The presence of overdispersion was investigated by including an observation-level random factor in the model. This was then tested against a model without this factor, using ANOVA (Elman and Hill, 2009). If the test was significant, the observation-level random factor was retained in the model.

3. Results

We recorded a total (two sampling methods pooled) of 993 wild bees (103 bumblebees and 890 solitary bees) belonging to 67 species (eight individuals could not be identified and were excluded from analysis of species richness; Table S2), and 505 hoverflies from 42 species (Table S3). Twenty-seven wild bee species were caught only in the pan traps, whereas eight species were only caught by sweep-netting (Table S2). Nineteen hoverfly species were caught exclusively in the pan traps, whereas eight species were only caught by sweep-netting (Table S3).

3.1. Wild bee abundance and species richness

There were no significant differences in overall abundance or species richness of wild bees between the mowing regimes in the first sampling session (Fig. 1a, c; Table S3). There was also no significant difference in the abundance or species richness of wild bees caught in pan traps in the second sampling session (Table S4). However, the abundance and species richness from the sweep-netting samples were significantly higher in R- (3.1 ± 0.7 individuals, $P = 0.014$; 2.4 ± 0.4 species, $P = 0.023$) and D-meadows (5.3 ± 1.9 individuals, $P = 0.004$; 3.0 ± 1.0 species, $P = 0.012$), compared to C-meadows (0.9 ± 0.4 individuals, 0.9 ± 0.4 species; Fig. 1b, d; Table S4).

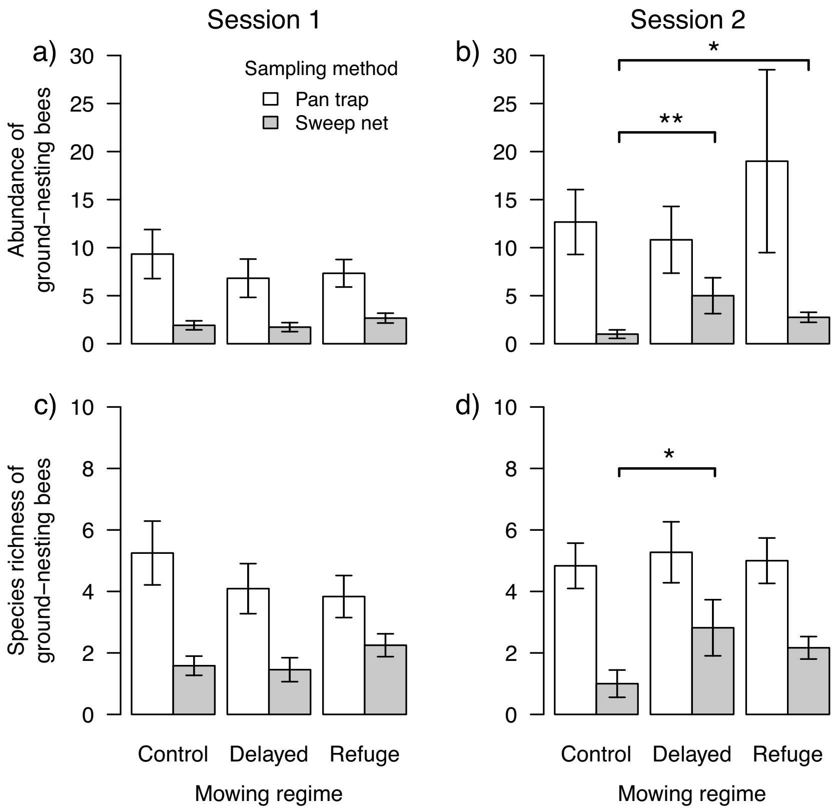

Fig. 2. Abundance (a, b) and species richness (c, d) of below-ground nesting bees in response to the three different mowing regimes (control, delayed and refuge), collected by pan-trapping (white bars) and sweep-netting (grey bars). Stars represent significant differences determined by GLMMs: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Results presented are means ± SE.

3.2. Wild bee nesting guilds

The most abundant bee nesting guild was the ground-nesting species (52 species, 952 individuals, 95.9% of the total community, including bumblebees), while above-ground nesting species were far less abundant (15 species, 41 individuals, 4.1% of the total community; Table S2). Overall, we recorded a total of 103 bumblebees from 11 species (nine *Bombus* and two *Psithyrus*, Table S2). Only the ground-nesting guild was abundant enough to perform the guild-level analysis (see Table S2).

In the first sampling session, there was no significant difference in the abundance or species richness of ground-nesting bees between the mowing regimes, for either sampling method (Fig. 2a, c; Table S5). In the second sampling session, there was no significant difference between the mowing regimes based on the pan-trapping results, for either metric (Table S5). In contrast, sweep-netting resulted in a significantly higher abundance in D- (5.0 ± 1.9 individuals, $P = 0.006$) and R- (2.8 ± 0.5 individuals, $P = 0.025$) compared to C-meadows (1.0 ± 0.4 individuals, Figure 2b Table S5), and higher species richness in D- (2.8 ± 0.9 species, $P = 0.025$) compared to C-meadows (1.0 ± 0.4; Fig. 2d, Table S5).

3.3. Abundance and species richness of hoverflies

There was no significant difference in the abundance of hoverflies caught in pan traps in the first sampling session, but sweep-netting resulted in a higher abundance of hoverflies in R- (1.8 ± 0.4, $P = 0.045$) compared to C-meadows (0.7 ± 0.3; Fig. 3a, Table S6). Species richness from pan traps was higher in D- (2.0 ± 0.4 species, $P = 0.022$) compared to R-meadows (0.8 ± 0.2 species; Fig. 3c, Table S6), while both experimental treatments did not differ from C-meadows. In comparison, there was no significant difference in species richness from the sweep-net samples (Fig. 3c, Table S6).

In the second sampling session, the abundance of hoverflies caught with pan traps was significantly higher in D- (7.6 ± 2.1 individuals, $P = 0.038$) compared to R-meadows (3.8 ± 0.9 individuals), while D- and R- did not differ from C-meadows (Fig. 3b, Table S6). For sweep-net samples, D- (5.3 ± 0.8 individuals, $P < 0.001$) and R- (4.2 ± 1.3 individuals, $P < 0.001$) had a significantly higher abundance compared to C- meadows (1.7 ± 0.5 individuals; Fig. 3b, Table S6). There was no significant difference in species richness of hoverflies caught by pan traps between the mowing regimes, in the second session (Table S4). However, species richness was higher in D- (2.9 ± 0.3 species, $P = 0.001$) compared to C-meadows (0.9 ± 0.3 species; Fig. 3d, Table S6).

3.4. Hoverfly larval feeding guilds

The most abundant hoverfly larval-feeding guild was the predatory species (21 species, 324 individuals, 64.2% of the total community), followed by the saprophagous (14 species, 146 individuals, 28.9%) and the phytophagous species (7 species, 35 individuals, 6.9%; Table S3). The phytophagous larval guild was not analysed due to the low total number of specimens.

In the first sampling session, there was no significant difference in the abundance of saprophagous hoverflies between the mowing regimes, with pan traps or sweep-netting (Fig. 4a; Table S7). In the second sampling session, the abundance of saprophagous hoverflies caught with pan traps was significantly lower in the R-

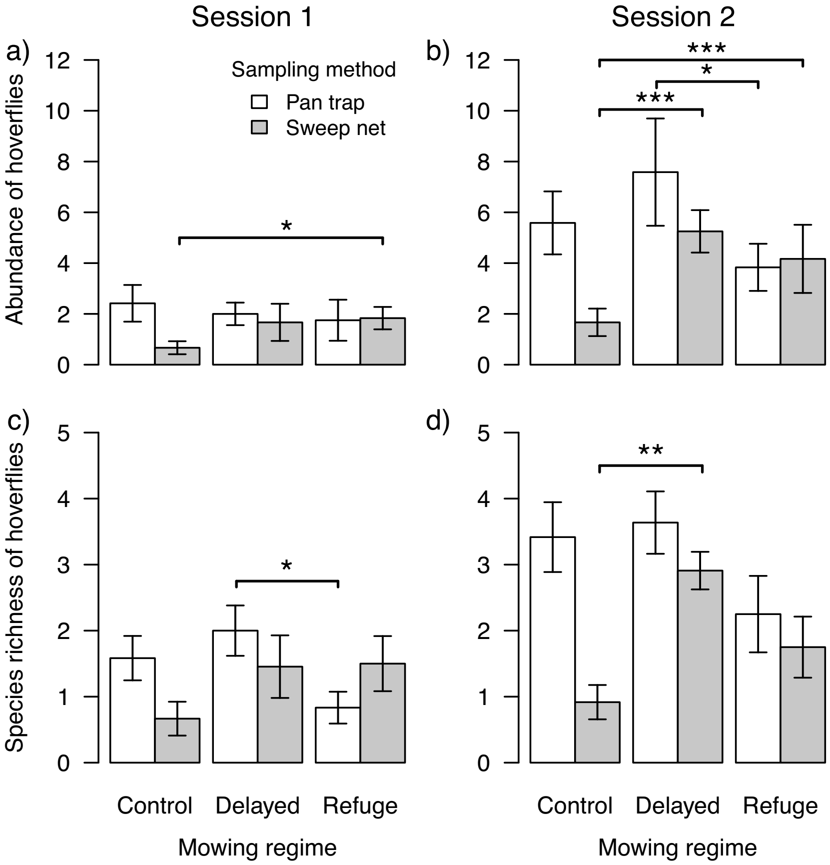

Fig. 3. Abundance (a, b) and species richness (c, d) of hoverflies in response to the three different mowing regimes (control, delayed and refuge), collected by pan-trapping (white bars) and sweep-netting (grey bars). Stars represent significant differences determined by GLMMs: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Results presented are means ± SE.

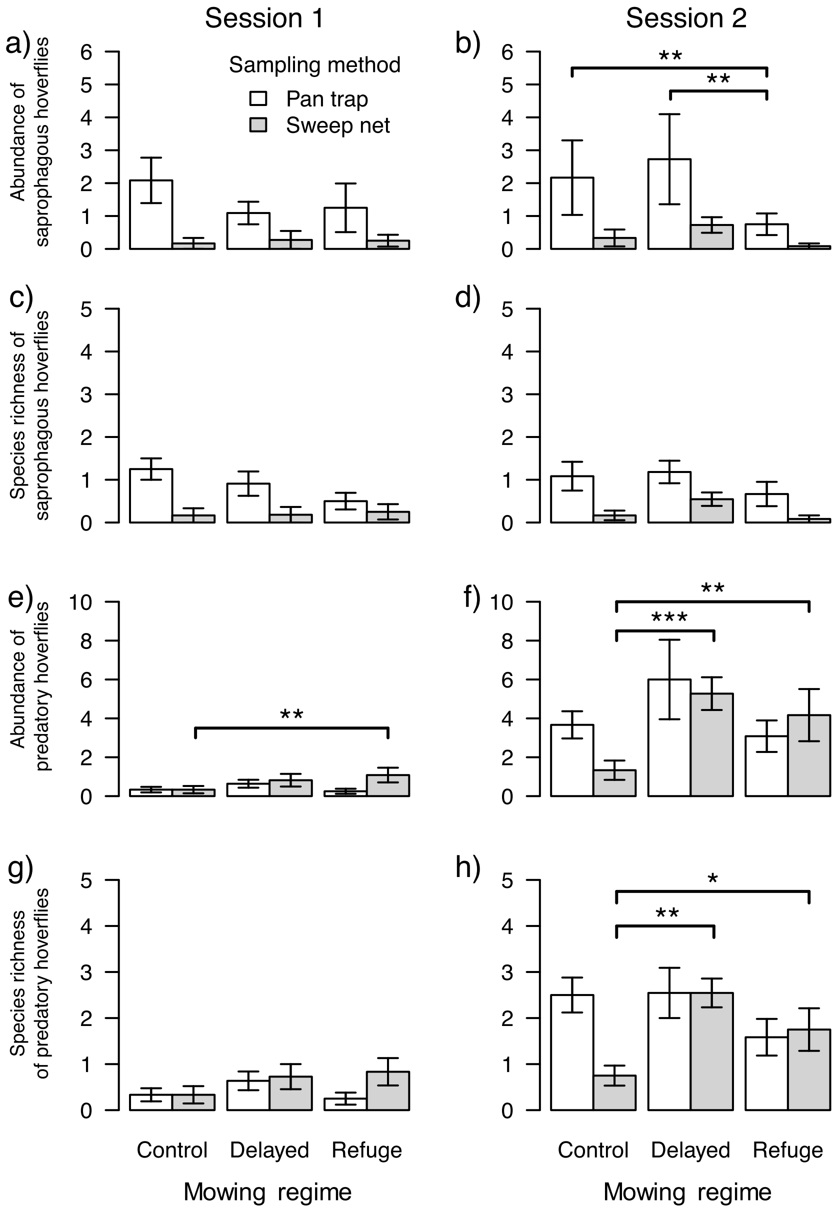

Fig. 4. Abundance and species richness of saprophagous (a-d) and predatory hoverflies (e-h) in response to the three different mowing regimes (control, delayed and refuge), collected by pan trapping (white bars) and sweep-netting (grey bars). Stars represent significant differences determined by GLMMs: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Results presented are means ± SE.

(0.8 ± 0.3) than in the C- (2.2 ± 1.1, $P = 0.007$) and D-meadows (2.7 ± 1.4, $P = 0.001$; Fig. 4b; Table S7), while sweep-netting showed no significant difference between the mowing regimes. There was no significant difference in species richness of saprophagous hoverflies between the mowing regimes for either method or session (Fig. 4c, d; Table S7).

There was no difference in the abundance of predatory hoverflies caught by pan-trapping, in either sampling session. Sweep-netting showed a significantly higher abundance of predatory hoverflies in R- (1.1 ± 0.3) compared to C-meadows, in the first sampling session (0.3 ± 0.2, $P = 0.041$) (Fig. 4e, Table S6). In the second sampling session, the abundance of predatory hoverflies caught by sweep-netting was significantly higher in D- (5.3 ± 0.8 individuals, $P < 0.001$) and R- (4.2 ± 1.3 individuals, $P = 0.002$) compared to C-meadows (1.3 ± 0.5 individuals, Fig. 4f, Table S8). There was no difference in the species richness of predatory hoverflies between the mowing regimes, with pan traps (Fig. 4g, h, Table S8). Sweep-netting showed a higher species richness in D- (2.5 ± 0.3 species, $P = 0.002$) and R- (1.8 ± 0.5 species, $P = 0.035$) compared to C-meadows (0.8 ± 0.2 species) in the second sampling session (Fig. 4h, Table S8).

4. Discussion

To maintain and improve the biodiversity of pollinators, agri-environment schemes should include management measures that target a wide range of taxa. In agreement with our predictions, we show that relatively simple alterations to common AES mowing regimes (delaying the first mowing date or leaving an uncut refuge) can have a positive effect on the local abundance and species richness of wild bees and hoverflies. Interestingly, we found little evidence in support of either the refuge or delayed regime being superior over the other. Rather, different life-history guilds of wild bees and hoverflies showed differing responses to the altered mowing regimes, demonstrating the importance of maintaining heterogeneous grassland management regimes in space to support diverse pollinator populations. In contrast to previous studies (Jauker et al., 2009; Jönsson et al., 2015), and our prediction, we found a similar response to the altered mowing regimes for both hoverflies and wild bees. Furthermore, conclusions differed depending on the sampling method employed (pan-trapping or sweep-netting), confirming the importance of using multiple methods when sampling insect communities (Hickman et al., 2001; Popic et al., 2013; Spafford and Lortie, 2013).

Sampling method strongly influenced the interpretation of the effects of the three mowing regimes. For example, following the first cut of the C- and R-meadows (second sampling session), sweep-netting showed a higher abundance of wild bees and hoverflies in D- and R-meadows, compared to C-meadows, and higher species richness in D- compared to C-meadows. In contrast, pan-traps showed no significant difference in abundance or species richness between the regimes for wild bees, and only a higher abundance of hoverflies in D- compared to R-meadows. The contrasting results are likely to be an artefact of the methods themselves. Pan-trapping has the potential to attract food-foraging insects from the surrounding landscape, a factor that is likely to be particularly pronounced after the meadows have been mown, whereas sweep-netting is more likely to sample insects using the meadow (Hickman et al., 2001; Popic et al., 2013; Spafford and Lortie, 2013). This may be particularly pronounced in landscapes with varying amounts of semi-natural vegetation in the surrounding landscape. For example, Kennedy et al. (2013) demonstrated that the amount of high-quality habitats in the surroundings was the most important factor affecting wild bee communities in agroecosystems. Therefore, sweep-netting is more likely to represent an accurate estimate of the community and population responses to the mowing regimes, especially when comparing meadows displaying different vegetation stages like during our second sampling session. We shall therefore hereafter focus mostly on the results of sweep-netting.

The higher abundance and species richness of bees and hoverflies in R- and D-meadows in the second sampling session, compared to C-meadows is likely to result from the experimentally prolonged availability of resources, such as nectar and pollen. Previous research has highlighted the value of refuges for promoting the abundance of wild bees (Buri et al., 2014) and butterflies (Kühne et al., 2015; Bruppacher et al., 2016). The provision of floral resources by delaying mowing or leaving an uncut refuge can be particularly important in agro-ecosystems later in the season, as floral resources may often be limited, either due to cessation of flowering in some species, or management practices, such as large-scale mowing (Scheper et al., 2014; Requier et al., 2015). While Buri et al. (2014) investigated the effect of these mowing regimes on wild bee communities in 2011, this study only utilised pan-trapping. Here, we build upon the previous study by incorporating pan-trapping and sweep-netting, which gives a more accurate representation of on-field effects. In contrast to Buri et al. (2014), we found no effect of mowing regime on wild bee abundance prior to the first cut. Alternatively, we found similar results in the second sampling session, with R- and D-meadows having a higher abundance than C-meadows. However, our results were not significant for pan-trapping, but for sweep-netting. Furthermore, while Buri et al. (2014) found no effect of the mowing regimes on wild bee species richness following the first cut by using pan traps, we showed that sweep-netting resulted in a higher species richness in R- and D- compared to C-meadows. This may indicate that sweep-netting, or a combination of the two methods provides a more accurate measure of the local bee community. The differences between the results of the two studies could possibly arise from inter-annual variation in bee abundance. This may also be reflected by the generally lower number of specimens captured in our study in 2015, compared to Buri et al. (2014) in 2011. For example, it is known that bee populations can display significant spatio-temporal variation in abundance and community composition between years (e.g. Potts et al., 2009).

As ground-nesting species comprised the majority of the bees collected (95.9%; Table S1), the response of this guild to the mowing regimes reflected the results for the overall bee community. It is estimated that there are approximately 610 wild bee species in Switzerland. Approximately 76% (445 spp.) are assumed to build nests and the others are cleptoparasitic. Of those that build nests, 73% (approximately 325 spp.) nest below ground, while the other 27% (120 spp.) are either above-ground nesting, or their nesting biology is unknown (http://http://www.wildbienen.de/). The low abundance of above-ground nesting species may have been due to the general dramatic negative effect of modern agricultural matrices and practices, as this guild has been shown to be sensitive to isolation from remnant natural habitat and agricultural intensification (Williams et al., 2010).

The dominant hoverfly larval guild was the predatory species, which are often abundant in agricultural landscapes (Frank, 1999; Haenke et al., 2009, 2014; Meyer et al., 2009). Following the first cut, this guild had a significantly higher abundance and species richness in D- and R-meadows compared to C-meadows when sampled with sweep-netting. Delayed and R-meadows maintain the sward for longer in the season compared to C-meadows, which may in turn maintain prey populations, thus benefitting predatory species (see Buri et al., 2016). Small predatory species, such as *Melanostoma* spp. and *Platycheirus* spp. were dominant in the sweep-netting samples. These species also include a high proportion of pollen in their diet, particularly from wind pollinated plants, such as grasses and plantains (Branquart and Hemptinne, 2000). Therefore, we assume that R- and especially D-meadows harbouring a high abundance of tall grasses could provide vital pollen resources for these species at a time when most of the grasslands within the agricultural matrix have been mown. Saprophagous species were more abundant in R- than D-meadows, as detected by pan-trapping. In comparison to bees, hoverflies are not constrained by the need to provision offspring and thus are relatively free to move in the landscape in search of suitable resources (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Jauker et al., 2009). The higher abundance of saprophagous species in R- than D-meadows may have resulted from these flies searching for floral resources in the regenerating vegetation (Lebeau et al., 2015). The generally low abundance of saprophagous species in the landscape may be due to a limitation of larval habitats, as many of these species require moist microhabitats in which to lay their eggs (Rotheray and Gilbert, 1999).

Our results indicate a higher abundance of wild bees and hoverflies in D- and R-meadows following the first cut could be partly due to a short-term concentration effect; resulting from animals moving to these relatively resource rich patches from mown areas (see Kleijn et al., 2011). However, we show a higher abundance of predatory hoverflies in R- compared to C-meadows, prior to the first cut, which may indicate a cumulative effect (i.e. carry-over effect induced by the application of the experimental mowing regimes in previous years) in the long term, and not just within the same season. In other words, the alternative mowing regimes may have a long-lasting positive effect on local hoverfly populations.

5. Conclusions and management recommendations

We demonstrated that altered mowing regimes, such as a delaying the first mowing date or leaving an uncut refuge has positive effects on wild bee and hoverfly communities and populations. Refuge and D- meadows supported an increase in abundance (up to +68% and +81%) and species richness (up to +69%

and 70%) of hoverflies and wild bees, respectively Therefore, our study provides evidence that this relatively simple management technique could benefit pollinator populations in extensively managed grasslands. Spill-over of pollinators from extensively managed meadows may provide pollination services to adjacent crops (e.g. Albrecht et al., 2007). The delayed mowing regime provides a prolonged period of resource availability for pollinators at an otherwise resource limited time (Requier et al., 2015). Interestingly, overall wild bee and hoverfly communities responded similarly to the experimental mowing regimes. However, there were differences in the responses of the life-history guilds. Therefore, we recommend delaying the first possible mowing date of current AES meadows and any extensively managed grassland structures such as ditch banks and road verges to 15 July, or leaving an uncut refuge if mown earlier. The two alternative mowing regimes tested here affected the wild bee and hoverfly communities in different but complementary ways. Therefore, we recommend implementing both delayed mowing dates, and leaving uncut grass refuges. If properly implemented at the landscape scale, such a spatio-temporally heterogeneous management regime will enhance wild bee and hoverfly communities and populations, and may have positive impacts on pollination services and biocontrol of insect pests in the surrounding landscape (Jönsson et al., 2015; Tschumi et al., 2015, 2016).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.01.037.

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