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Original Research Article

Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes

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ABSTRACT

For a diverse pollinator fauna it is important that pollen and nectar are available over the entire summer at spatially relevant scales. Semi-natural hay meadows are among the most important sources of flower resources for pollinators, but the resources are strongly affected by the timing of mowing. Management recommendations for hay meadows often prescribe late mowing on order to allow undisturbed flowering during most of the summer. Traditional practices, however, often include also earlier mowing. We investigate the link between the temporal variation of flower resources and traditional mowing practices of semi-natural hay meadows in a low-intensity agricultural landscape in Romania. In early August, we botanically surveyed meadows that were cut early, intermediately, or late in the season. We recorded all herb species, their phenological stage, and the number of reproductive units of each species. Data were analysed using DCA, LM and GLM. Plant species richness and composition are not affected by the time of mowing, but different sets of species flower in semi-natural grasslands with different mowing regimes. In August the proportion of species flowering and flower density are highest in the early-mown meadows due to re-flowering after mowing. Analyses of phenological stages indicate that late-mown meadows are the main pollen and nectar sources in July, whereas meadows mown early are the main resource from August to the end of the season. The results demonstrate that for pollinator conservation, heterogeneous mowing times within a landscape need to be encouraged when possible, and that strict focus on late mowing may lead to shortage of flower resources late in the summer. Studies of low-intensity agriculture has a great potential for learning about management methods that can be used in other parts of the world where traditional practices have been lost. Such studies can thereby contribute with important knowledge to manage global pollinator loss.

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1. Introduction

Semi-natural grasslands, i.e. hay meadows and pastures that are not intensely cultivated or fertilised, and mainly with spontaneously established flora, are among the most species-rich ecosystems in the world (Squires et al., 2018; Wilson et al., 2012). In addition to plant species richness, semi-natural grasslands are essential habitats for pollinators as they provide a high diversity of flower resources, both in time and space, as well as nesting sites (Holzschuh et al., 2007; Kovács-Hostyánszki et al., 2016; Öckinger and Smith, 2007). High plant diversity helps to ensure resources for pollinators throughout the season (Ebeling et al., 2008; Nicholls and Altieri, 2013).

In pre-industrial agriculture semi-natural grasslands constituted the nutrient base for production as they supplied fodder for the livestock, which in turn provided manure necessary for crop production (Grigg, 1974; Küster and Keenleyside, 2009; Lennartsson et al., 2016). With the agricultural revolution and a general intensification of agriculture, including the introduction of new techniques, mineral fertilisers, fossil fuels, and insecticides, the semi-natural grasslands largely became abandoned in favour of cultivated fodder. This caused a rapid decline in area of semi-natural grassland during the 19th and 20th century, especially in western Europe (e.g. Bignal and McCracken, 1996; Stanners and Bourdeau, 1995), which has caused a severe decline in abundance and diversity of plants and wild pollinators (Emanuelsson, 2009; IPBES, 2016; WallisDeVries & Van Swaay, 2009). Consequently, semi-natural grassland management is currently considered one of the core conservation activities for the conservation of biodiversity and pollinators, and several European countries have specific agri-environment schemes for increasing the area and quality of semi-natural grassland (Kleijn and Sutherland, 2003; Wehn et al., 2018).

Among the various types of semi-natural grasslands, hay meadows are often considered particularly important sources of nectar and pollen (hereafter denoted flower resources) because of their high flower richness before harvest (Buri et al., 2014; Hegland and Boeke, 2006; Pywell et al., 2005). The high plant diversity in hay meadows relies on regular mowing that reduces light competition (Aarssen, 1989), but the cutting constitutes a drastic disturbance to flower resources and also to several other ecological properties of the hay meadow, such as seed production (Lennartsson et al., 2012), host-plant availability for phytophages (Dahlström et al., 2008), and invertebrate mortality (Humbert et al., 2010). Therefore, determining an appropriate mowing regime is a key task for hay meadow conservation. The most common recommendation for mowing time is late mowing, for example in agri-environment schemes that normally prescribe threshold dates for the earliest permitted cutting date. These recommendations are based on the assumption that later mowing is favourable for biodiversity (Cizek et al., 2012; Dahlström et al., 2013; Humbert et al., 2012; Wehn et al., 2018) and that it mimics the traditional timing of mowing (Eriksson et al., 2015; Smith and Jones, 1991).

The general advantage of late mowing has, however, been questioned. It has been pointed out that EU subsidy regulations are risking homogenisation of EU grasslands, thus potentially counteracting the goal of increasing biodiversity (Cizek et al., 2012; Dahlström et al., 2013; Jakobsson and Lindborg, 2015; Wehn et al., 2018), and that traditional practices, historical and ongoing, may include considerable variation in mowing time of hay meadows (Eriksson et al., 2015; Iancu and Stroe, 2016).

For effective pollinator conservation, it is important to understand how mowing regimes of hay meadows in a landscape context can contribute to the availability of flower resources for pollinators (Bruppacher et al., 2016; Kühne et al., 2015; Valtonen et al., 2006). Late mowing can ensure undisturbed flower resources before the mowing, especially in the early half of the summer. Later in the summer, however, most plant species have finished flowering and the flower resource declines in spite of undisturbed conditions (Dahlström et al., 2008; Lennartsson et al., 2012). A few studies have demonstrated that early mown grasslands, in contrast, can be flower rich by the late summer due to re-flowering after cutting (Jantunen et al., 2007; Noordijk et al., 2009), but no systematic study has been made of the effect of mowing time on the abundance of flower resources over the season.

Some pollinator species have rather restricted activity times and are dependent upon available resources during that particular period (Minckley et al., 1994; Ogilvie and Forrest, 2017), and, typically, different assemblages of flower visitors follow each other during the vegetation season (e.g. Bosch et al., 1997; Sakagami and Matsumura, 1967). Other pollinator species, especially social species (e.g. bumblebees), are active throughout the season (Minckley et al., 1994). For species with a long activity period, it is important that pollen and nectar are available over the entire summer at spatially relevant scales (Bäckman and Tiainen, 2002; Persson and Smith, 2013; Westphal et al., 2009). A number of species are active only late, or have two flight periods, late and early. For example, of 75 butterflies, red-listed in Sweden and reproducing in semi-natural grassland, 30 species require nectar during early August and 12 species also in late August or later (Svensson, 1993). A study conducted in Romania identified 150 wild bee species (Kovács-Hostyánszki et al., 2016), many of which are bivoltine and known (at least in Britain) to fly as late as in September (Falk, 2015). Many bee species require considerable amounts of pollen for their reproduction, and reduction of flower resources by mowing in the activity period can have significant negative effects on the populations (Larsson and Franzén, 2007).

The supply of flower resources over the entire season is enhanced by high diversity of both flowering plants and habitats (Decourtye et al., 2010; Ebeling et al., 2011; Ebeling et al., 2008; Hegland and Boeke, 2006). Diversity of plants contributes to flower resources over time since different species flower at different occasions (Dahlström et al., 2008), and a diversity of habitats contributes to a complementary habitat use by pollinators at different times throughout the season (Mandelik et al., 2012).

In contrast to semi-natural grassland management based on strict agri-environment schemes, historical management methods for semi-natural grasslands varied both at local and regional scales, which led to structural heterogeneity of habitats in the landscape (Dahlström et al., 2013; Gustavsson, Dahlströ;m, Emanuelsson, Wissman and Lennartsson, 2011). Not least, the mowing time varied from year to year and from grassland to grassland depending on, among other things, the type of meadow, the duration of the mowing period, and the availability of labour (Burton and Riley, 2018; Dahlström et al., 2008). In order to unfold mowing regimes of the past, we need to understand how hay meadows and mowing management relate to the entire local agricultural system. In most of Europe, the management practices are nowadays relatively homogenous (Emanuelsson, 2009), but in a few regions, especially in east-central Europe, low-intensity farming practices and biodiverse semi-natural grasslands are still abundant and essential for agricultural production, and managed by a diversity of practices (Dahlström et al., 2013; Roleček et al., 2014; Sutcliffe et al., 2015). Although few studies on farmland biodiversity have been carried out in these regions (Archer et al., 2014; Sutcliffe et al., 2015), areas of low-intensity farming can be used as reference areas when designing sustainable biodiversity conservation in the rest of Europe where these types of landscapes have largely been lost (Egan, 2005; Gavin et al., 2015; Helldin and Lennartsson, 2007; Lennartsson, Westin and Crumley, 2018).

In this paper, we investigate the links between cutting date of hay meadows, traditional farming practices, and flower resources for pollinators in a highly biodiverse Romanian agricultural landscape in which the hay from meadows has a key function in the agricultural production. We address the following specific questions: How does different mowing times influence amount and composition of flower resources for pollinators throughout the season? How does late mowing, which is normally recommended in conservation management and agri-environment schemes, influence flower resources in hay meadows compared to traditional mowing regimes that also include earlier mowing?

2. Methods

2.1. Study area

This study was performed in an agricultural landscape in the village of Botiza in Maramureș in the Romanian Carpathians (47°40′05.30″N, 24°09′04.27″E). The study area is ca 200 × 900 m and situated along a northwest-facing slope 500–600 m a.s.l. (Fig. 1). The semi-natural grasslands have a dry to mesic species-rich vegetation containing several calciphilous species (Babai and Molnár, 2014; Dahlström et al., 2013). The study site belongs to the humid continental climate with heavy rainfalls, cool summers and frosty winters. The annual mean temperature is −7.58 °C, and annual precipitation is 829 mm (Fick and Hijmans, 2017). The local agriculture, which represents the typical traditional land-use system in the region, is based on animal husbandry and subsistence farming, complemented today by EU and governmental subsidies. The agricultural landscape is characterised by a mosaic of small parcels of low-intensity semi-natural hay meadows (hereafter denoted hay meadows), pastures, leys and cultivated fields (Fig. 1, Supplementary; (T Lennartsson et al., 2018; Lennartsson et al., 2016). Cultivated fields cover ca 11% of the village area, whereas semi-natural grassland, mostly hay-meadows, cover ca 56%. The hay meadows are generally small, 25% being smaller than 0.3 ha (Dahlström et al., 2013). Botiza has a few common pastures within the village and a high-altitude summer farm away from the village, at which the livestock stay during several months.

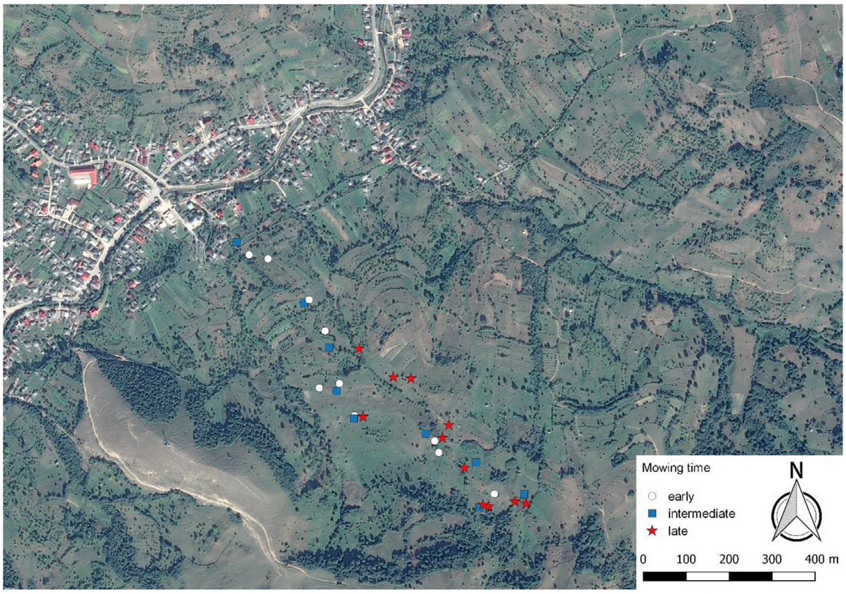

Fig. 1. The study area in Botiza, Romania, with the surveyed semi-natural hay meadows, being mown either early (white circle), intermediate (blue square), or late (red star). Map data: Google, CNES/Airbus. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In total there are 310 horses, 770 cattle, 1270 sheep and 270 goats that are primarily fed on semi-natural hay meadows and pastures (National Institute of Statistics, 2010).

Hay for livestock is harvested both from uncultivated hay meadows and from cultivated fields in rotation with other crops. The rotation in the fields includes periods with sown crops of vegetables, maize, potatoes, and fodder plants such as clover and alfalfa, alternating with ley periods of varying duration, having non-sown grassland vegetation that gradually turns into a more semi-natural state (Dahlström et al., 2013). The different types of hay sources are harvested at different times in order to optimise the amount and quality of hay, given the available labour and time for mowing. This creates a fine-scaled spatio-temporal variation of mowing. As a general mowing pattern, the cultivated (best) fodder is harvested first, in early June and then once or twice again later in the season. The young leys are mown in late June to early July, after which the mowing of old leys and hay meadows begins in mid-July and continues until the last meadows have been cut in September or even later. However, for practical reasons some hay meadows, being located close to young leys, are mown together with the ley, that is, in late June/early July. Sheep graze the hay meadows in early spring but autumn grazing in the meadows is rare due to the lack of fences, the extended mowing period, and the risk of destroying the numerous hay stacks that occur in the hay meadows. In this study, we focus on hay meadows that are mown at different occasions, either early mowing (mown in late June), intermediate (late July), or late mowing (after mid-August).

2.2. Data collection

We use number of flowering reproductive units of herb species and proportion of flowering species as indicators of flower resources (nectar and pollen) for pollinators.

We surveyed 9 hay meadows in 2015 and 31 hay meadows in 2016. The meadows were cut either around 25th of June (hereafter denoted early mowing), 20th of July (intermediate), or after mid-August (late mowing). In both years, the surveys were performed at the beginning of August, a couple of weeks before the latest meadows were mown. All meadows represent the same vegetation type, a dry-mesic, calcareous, herb-rich and species-rich type. The studied hay meadows were selected based on brief visual examination to represent this vegetation type and the three mowing times. As all hay meadows in the village, the selected ones were small (maximum 0.2 ha) and rather homogeneous in both structure and vegetation. In each meadow, we selected one survey plot, normally at the centre of the meadow and without paths, anthills shrubs, trees, or other deviations from the vegetation type.

In 2015, we investigated the abundance of flower resources for pollinators in hay meadows over the season and in relation to mowing date. Since we could not perform repeated sampling, we estimated the variation of flower abundance over the season based on phenological stage by the 1st of August (see Data analysis). We studied three early mown meadows, three with intermediate and three with late mowing. Within one plot of 2×1 m in each meadow we counted all reproductive units of each herb species. A reproductive unit was defined for each species as the smallest unit of reproductive organ (buds, flowers, and fruits) that could be readily recognised and counted in the field (Lennartsson et al., 2012). Each reproductive unit was assigned to one of five phenological stages: bud, flower, immature fruit, mature fruit, or old, dehisced fruit (modified from Losvik, 1991). Grasses and sedges are mainly wind pollinated and of little importance for pollinating insects and therefore not considered in this study.

In 2016, we performed a more comprehensive study of flower abundance in the late summer. On the 3rd of August we established one 1×1 m plot in each of 31 hay meadows of which ten were mown early, ten intermediately, and eleven late in the season (Fig. 1). These were a different set of meadows than surveyed in 2015 but within the same study area. For each herb species in each plot we counted the number of flowering reproductive units and registered the dominant phenological stage of the species based on which of the three classes bud, flower and fruit that were dominating among the reproductive units.

Survey of pollinators were not include in the study.

2.3. Data analysis

To estimate the effect of mowing time on composition of herb species and the flower resources, we calculated three proxies using the data from 2016: i) total species composition of all species (presence/absence), ii) composition of species flowering (in bloom or not), and iii) composition of species flowering weighted by their number of flowering reproductive unit. The last proxy, composition of species flowering weighted by their number of flowering reproductive units, was used to indicate whether different species contributed to the flower resources in hay meadows mowed at different times. Such differences between species may be due to morphology (e.g. plant size and flower number) or capacity to re-flower after mowing. The proxies were developed by performing detrended correspondence analyses (DCA) and defined by the values (the plot scores) along the first DCA axis (Lepš; Šmilauer, 2003; Tuomisto, 2010). DCA axes are expressed in standard deviation (SD) units, which make comparisons across data sets possible (Feilhauer and Schmidtlein, 2009; Tuomisto, 2010). If the axis is > 4 SD units, there is a complete spatial turnover of species in the data which means that two or more plots do not have any common species. If the range of the first DCA axis was below 2, we considered the species composition to be similar across all hay meadows. If the range of the first DCA axis was above 2, we tested the effect of mowing time using the values of the first DCA axis as a dependent variable in a linear model (LM) with mowing time as a fixed factor. See further descriptions of the proxies in the companion Data in brief paper (Wehn et al., 2019).

To estimate the effect of mowing time on a) number of all species, number of flowering species, and number of flowering reproductive units, as well as b) proportion of species in each phenological stage (bud, flower, fruit), we analysed the data from the 2016 survey using generalised linear models (GLMs) with mowing time as a fixed factor and binomial (proportion data) or Poisson (count data) distributions. Overdispersion of the data was ruled out by applying quasi distributions when the models for number of flowering reproductive units and proportion of species in flowering and fruit stage were fitted. To estimate the effect of mowing time on the number of reproductive units in each phenological stage (data from 2015) we used nonparametric Kruskal Wallis Test.

The data from 2015 was used to assess differences in flower abundance over time between the mowing time categories. By assuming a two-week interval between each phenology stage (Lennartsson et al., 2012), we both hindcast and forecast the abundance of reproductive units per flower stage before and after the sampling date of 1st of August. An immature fruit was assumed to have been at the flowering stage two weeks earlier (i.e. July 15), a mature fruit four weeks earlier (July 1st), and so on. This analysis could only be done for the early and late mowing regimes, whereas in the intermediate meadows, which had recently been mown, we found too few reproductive units to enable hind- and forecasting of flower abundance. Because of the small sample size, the results were used only for a visual examination of flower abundance over time, in order to complement and explain the 2016 data.

The model fits of the LMs and GLMs were assessed by likelihood ratio tests by comparing (for each dependent variable) a full model including mowing time as a fixed factor, with a restricted model with only the intercept. If mowing time was significantly influencing a dependent variable, a post-hoc multiple comparison of means with Tukey contrasts was performed to assess differences between each mowing time category.

The DCAs were performed using Vegan 2.5—3 (Oksanen et al., 2013) in the R 3.5.1 software (R Core Team, 2015). The GLMs, LMs, likelihood ratio tests, Kruskal Wallis Test, and multiple comparisons were performed using the R 3.1.1 software (R Core Team, 2015).

For each species we calculated incidence of reproduction as the number of plots where the species was reproducing (in bud-, flowering- or fruit-stage) divided by the total number of plots in which the species was found.

3. Results

3.1. Species richness and species composition

In total, 80 herb species were found in the plots in the studied meadows, 70 in 2015 and 67 in 2016. The average number of species per plot ($n = 31$) for 2016 is 19.74 ($SD = 4.049$) and the number of species does not vary between the three mowing time categories (Table 1, Fig. 2a). Also species composition (based on presence/absence) does not vary much between the hay meadows, as indicated by the length of the DCA axis 1 which ranged across 1.8946 SD units.

3.2. Flower resources

The species composition of flowering species in early August differs more between mowing treatments than the overall species composition as indicated by the length of the DCA axis 1 based on data of species occurrence (1.8946 SD units) and the DCA axis 1 based on species flowering or not (3.6071 SD units, Table 1, Fig. 3a). This implies that even if all hay meadows have essentially the same species composition, a different set of species flowers by early August in meadows that are not yet mown compared to in meadows that have earlier been mown. The same result is obtained if we account for differences between species in number of flowers as indicated by the DCA axis 1 based on data on species flowering weighted by flowering reproductive units (4.3610 SD units, Table 1, Fig. 3b). The length of DCA axis 1 based on species flowering weighted by flowering reproductive units is longer than the length of the DCA axis 1 based on non-weighted species flowering or not, which indicates that different species provide different amounts of flowering reproductive units (= flower resources).

Table 1
Effects of mowing time (early, intermediate, late) in hay meadows on nine response variables of herb species in 2016. Response variables 1—2 are based on scores along the first detrended correspondence analysis (DCA) axes. 1—2 are estimated using linear models, 4—9 are estimated using generalised linear models. Test statistics are from likelihood ratio tests. See further descriptions of the modelling methods in the Data analysis.

Response variable	Residual deviance	Residual df	p	Explained deviance (%)
1. Species composition $_{\text{species flowering}}$	12.586	28	<0.001	42.57
2. Species composition $_{\text{species flowering weighted by flowering reproductive unit}}$	21.935	28	<0.001	44.62
3. Number of species	25.449	28	0.502	5.15
4.Number of species in flower stage	32.9	28	<0.001	52.38
5. Number of flowering reproductive units	1324.2	28	0.002	42.83
6. Proportion of species in bud stage	37.6	28	0.001	37.85
7. Proportion of species in flower stage	42.6	28	<0.001	50.46
8. Proportion of species in fruit stage	56.7	28	<0.001	56.68

df = degrees of freedom.

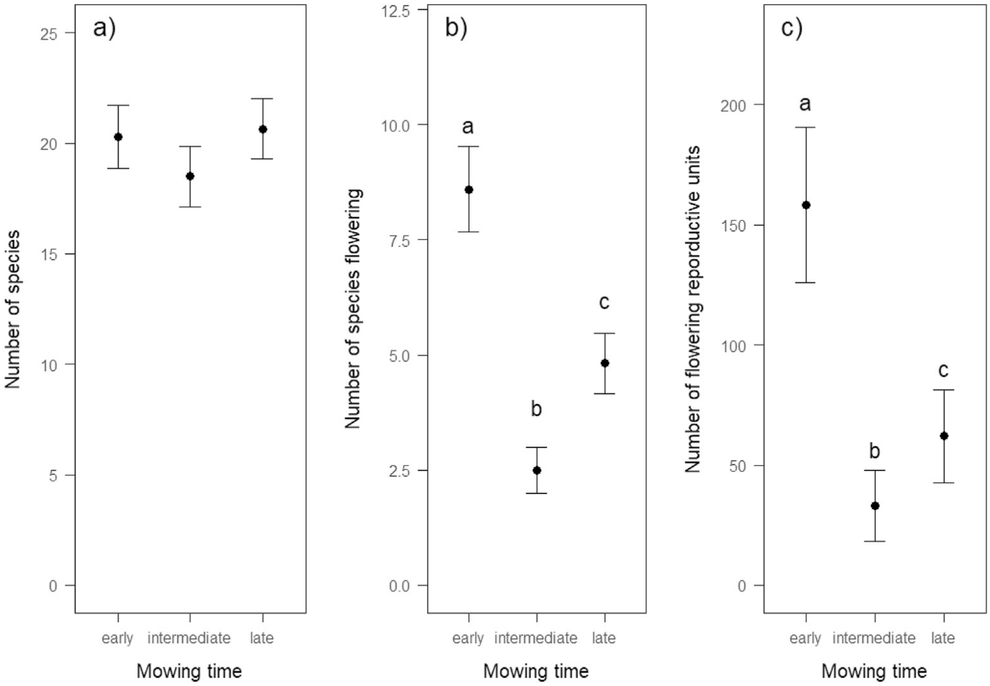

Fig. 2. Estimated means and standard errors for a) species richness, b) number of species in the flowering stage, and c) number of flowering reproductive units in semi-natural hay meadows (n = 31) with varying mowing times (early, intermediate, late). Different letters showed significantly different ($p < 0.05$) numbers between the mowing time categories in Tukey multiple comparison tests (only included when there is significant variation among mowing times).

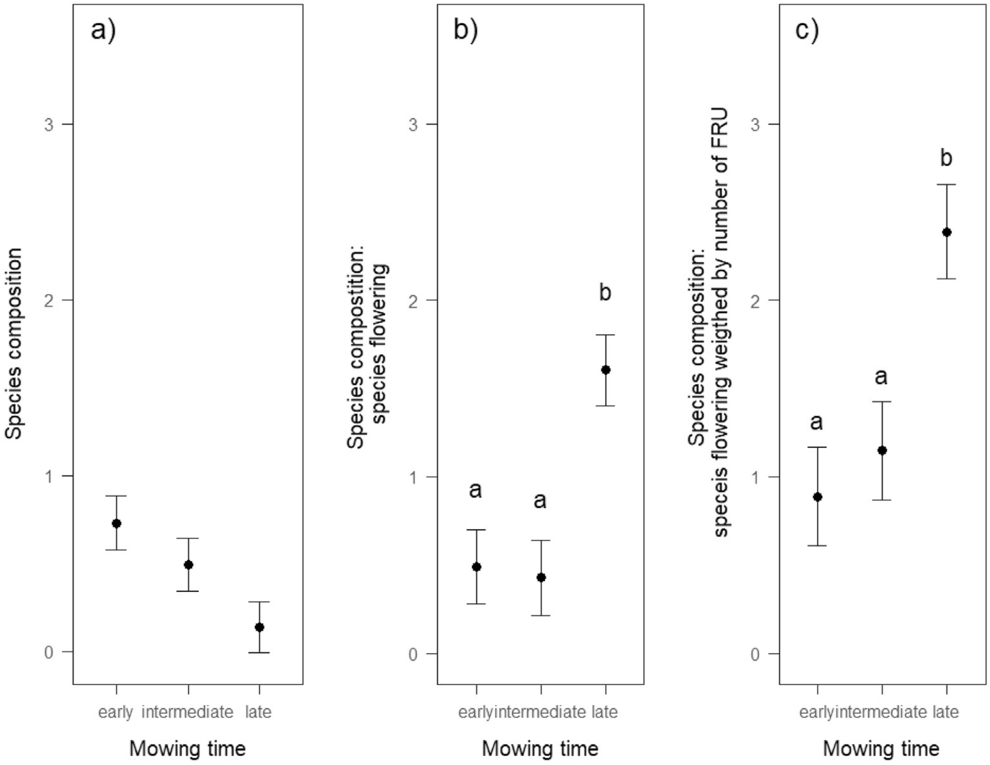

Fig. 3. Estimated means and standard errors for the proxies of a) total speceis composition, b) composition of species flowering (in bloom or not), and c) composition of species flowering weighted by their number of flowering reproductive unit, in semi-natural hay meadows (n = 31) with varying mowing times (early, intermediate, late). Species composition data are plot scores along the first detrended correspondence analysis (DCA) axis. Different letters showed significantly different ($p < 0.05$) numbers between the mowing time categories in Tukey multiple comparison tests (not included when range of the first DCA axis was below 2).

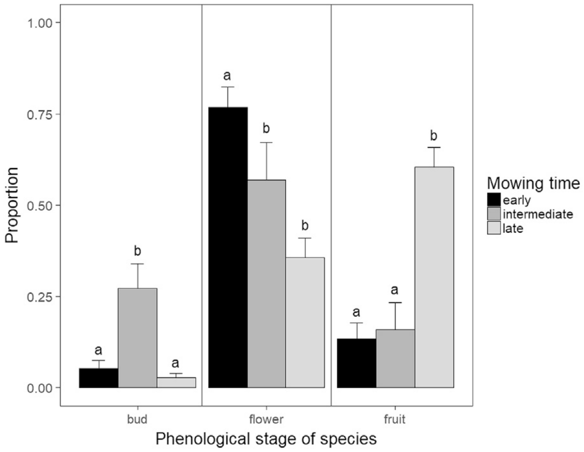

Fig. 4. Estimated means and standard errors for proportion of herb species within the phenological stages: bud, flower and fruit in semi-natural hay meadows (n = 31) in hay meadows with different mowing times (early, intermediate, late) by 3 August 2016. Bars with different letters are significantly different (p < 0.05) among mowing time within phenological stage in a Tukey multiple comparison test.

By early August, the three mowing time categories have different proportions of species in the bud, flower, and mature fruit phenological stages (Table 1). Hay meadows with late mowing have the highest proportion of species in the fruit stage while early-mown meadows have the highest proportion of species in the flowering stage (Fig. 4, Table 1). Early-mown hay meadows have also the highest number of reproductive units in the phenological stages flower ($\chi^2 = 7.2$, $p = 0.027$) and bud ($\chi^2 = 7.32$, $p = 0.026$), while late mowing have the highest number of immature ($\chi^2 = 7.2$, $p = 0.027$), mature ($\chi^2 = 7.2$, $p = 0.027$) and old fruits ($\chi^2 = 7.45$, $p = 0.024$) (Fig. 5). By 1st of August about 87% of the reproductive units were in flower or bud stage in early-mown meadows, compared to ca. 18% in late-mown meadows, indicating a vigorous re-flowering after early mowing.

Number of species flowering and number of flowering reproductive units in early August are highest in the hay meadows mown early and lowest in the hay meadows with intermediate mowing time (Table 1; Fig. 2b and c).

An extrapolation of the density of flowering reproductive units, assuming a two-week interval between each phenological stage, indicates that late-mown hay meadows are the main source of flower resources in July, whereas meadows mown early have considerably more flower resources from around 1 August onwards (Fig. 6). The flower resources in early mown meadows were due to re-growth after mowing. Of the 67 taxa found in the early mown meadows in 2016, 31 had reproductive units in early August, and thus re-flowered after mowing. Several of these species had about the same incidence of flowering in early as in late mowing (e.g. *Daucus carota, Euphrasia rostkoviana, Knautia arvensis*, *Trifolium medium*), whereas other species reproduced somewhat less commonly (>25% less) in early mown than in late mown meadows, indicating a lower tolerance to cutting (e.g. *Betonika officinalis*, *Campanula patula*, *Leucanthemum vulgare*). A few species, in contrast, showed higher incidence of reproduction (>25% higher) in early than in late mown meadows (e.g. *Leontodon autumnalis, Lotus*

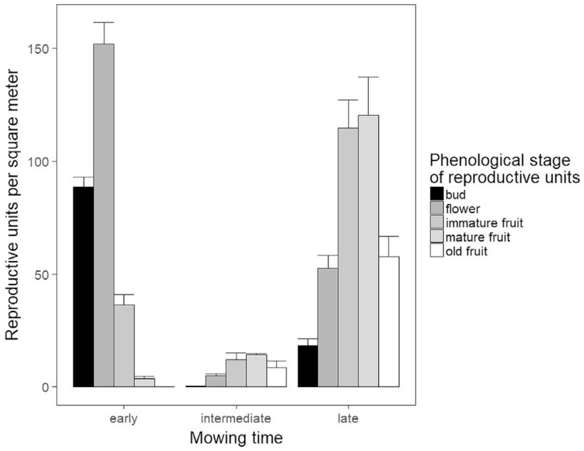

Fig. 5. Mean number and standard error of reproductive units at different phenological stages (bud, flower, immature, mature and old fruits) by 1 August 2015 in hay meadows (n = 9) with different mowing times (early, intermediate, late).

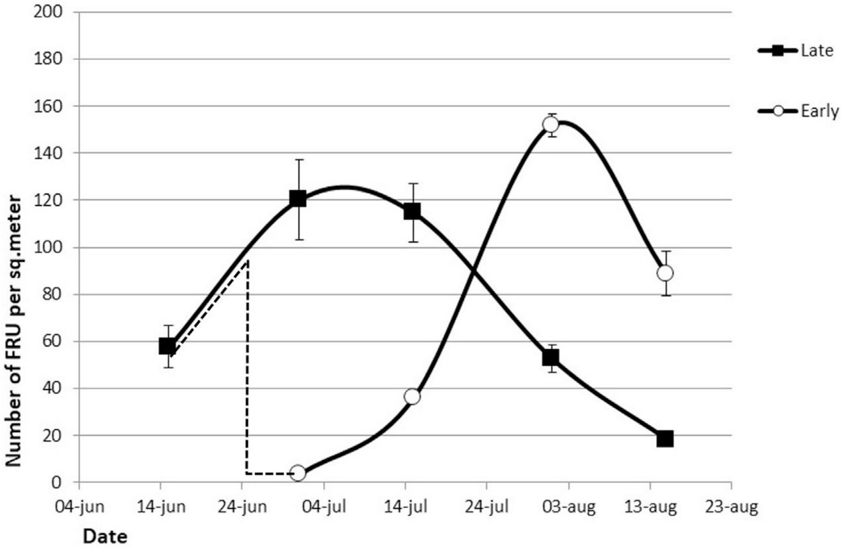

Fig. 6. Estimated density and standard error of flowering reproductive units (FRU) in semi-natural hay meadows (n = 6) mown in late June (Early) and after mid-August (Late). The solid lines indicate flower density based on field data from 2015, see text. The dashed line indicates how FRU density is affected by the early mowing (July 24). Smoothed curve through means of three plots per mowing regime. Hay meadows with intermediate mowing times are not included because too few reproductive units were available to enable FRU density estimates.

corniculatus, Peucedanum oroselinum, Plantago major, Polygala vulgaris and *Trifolium repens*). A detailed description of species composition and species flowering in each mowing time are in the companion Data in Brief paper (Wehn et al., 2019).

4. Discussion

This study shows that temporal variation in mowing of hay meadows within a landscape enhances flowering throughout the summer, thus providing more continuous flower resources for pollinators. Late mowing is important for providing flower resources in June and July, whereas re-flowering in early-mown hay meadows provides flower resources from August and later in the season. By early August, meadows that were mown around 25 June had three times as many flowers per area unit as the meadows that were not yet mown. This difference becomes larger later in the season since the flower resources in late-mown meadows decline during August when most plant species finish their reproduction (Dahlström et al., 2008; Lennartsson et al., 2012).

The study was performed in one of the few regions in Europe were low-intensity and heterogeneous farming practices are still in use (Dahlström et al., 2013; Roleček et al., 2014; Sutcliffe et al., 2015) A previous study from Romania has shown positive effects of semi-natural habitats, including hay meadows, on most groups of pollinators (Kovács-Hostyánszki et al., 2016). Our study showed, in addition, that heterogenous mowing times in a landscape increase availability of flower resources throughout the season. In Europe, pollination of several crops and wild plants rely on diverse pollinator communities including managed honeybees (*Apis mellifera* L.) (Potts et al., 2010), wild bees (Hymenotera: Apoidea), butterflies (Lepidoptera), hoverflies (Diptera: Syrphidae), and other insect groups (Garibaldi et al., 2013; Kleijn et al., 2015). These groups are affected differently by the scale of management and the resulting distribution, diversity, and quantity of flower resources within landscapes (Bommarco et al., 2010; Ekroos et al., 2013; Kremen et al., 2007). Differences depend on pollinator traits such as dispersal capacity, movement pattern, specialisation, length of active flight season, and host plant needs (Aarvik et al., 2009; Asher et al., 2001; Gathmann and Tscharntke, 2002), highlighting the importance of flower diversity and heterogeneous management times throughout the season for maintaining diverse pollinator communities.

In the studied landscape, the early mown hay-meadows are the main source of flower resources in August and later. Late mown hay meadows, and, occasionally, arable field with alfalfa and clover provide pollen and nectar in the early summer. The arable fields are all cut early and subsequent cuts prevent these crops from re-flowering (Westin and Lennartsson, pers. obs). Also the semi-natural pastures are poor in flower resources in the late summer, because of high grazing pressure from May to October. Consequently, the pollinators depend largely on the early mown hay meadows later in the season.

Undisturbed plants reach peak of flowering in July (Dahlström et al., 2008; Lennartsson et al., 2012), whereas plants that have been cut re-flower later. Hence, flower resources in the late summer and autumn can be enhanced by early mowing that trigs re-flowering, an observation also made by others (Jantunen et al., 2007; Noordijk et al., 2009) The study of Noordijk et al. (2009), which included a survey of flower visitors, also found that these flower resources were very important for pollinators late in the growing season.

Re-flowering after mowing depends on tolerance mechanisms of the plants, including reserves of meristems and resources for regrowth (Crawley, 1997). Perennials can be expected to be more tolerant to damage than annuals, especially species with pronounced resource storage in tap roots, such as *Daucus carota, Pimpinella saxifraga,* and *Tragopogon pratensis*, which flowered after early mowing (Wehn et al., 2019). Very few annuals were found in the plots, but one, *Euphrasia rostkoviana*, showed high tolerance to early mowing. Undamaged plants of *E. rostkoviana* in late-mown hay meadows produced on average 7.6 reproductive units per square metre, compared to 87.5 units in the early-mown hay meadows (Wehn et al., 2019). Although these data are for the plot level and not for individual plants, the result suggests that mown plants of *E. rostkowiana* may produce more reproductive units than undamaged plants. Such overcompensation following damage has been reported from a few monocarpic herbs, including other *Euphrasia* (Huhta et al., 2003), and has been suggested to be an adaptation to mowing or grazing (Lennartsson, Ramula and Tuomi, 2018; Lennartsson et al., 1997). Regrowth is triggered by the damage and may be favoured by reduced light competition in early mown, compared to late mown meadows (Lennartsson and Oostermeijer, 2001).

Successful reproduction and seed rain may be important determinants of species composition in grasslands because the abundance of many species have been shown to be seed limited (Hellström et al., 2009; Turnbull et al., 2000). If the timing of mowing influences plant reproduction differently across species, mowing time could be expected to differentiate the species composition of hay meadows. No such differentiation was found in this study, which may be due to the fact that most species reproduced in both late and early mown meadows (but at different times), and that the mowing time of a certain meadow may vary between years.

Late mowing is frequently promoted in conservation and agri-environment schemes (Dahlström et al., 2013; Iancu and Stroe, 2016; Wehn et al., 2018), and has also been subject to considerable more research than early mowing, (see, e.g., the meta-analysis by Humbert et al., 2012). However, studies comparing early and delayed mowing indicate that early mowing has little negative effects on plant species richness (Humbert et al., 2012), although some grassland plant species, e.g. early-flowering species, may be disfavoured by early grassland disturbance (Blažek and Lepš, 2015; Lennartsson et al., 1997; Reisch and Poschlod, 2009). Furthermore, the large variation of mowing practices in historical land-use (Eriksson et al., 2015; T Lennartsson et al., 2018; Poschlod & WallisDeVries, 2002) suggests that a strict use of late mowing in conservation will lead to more homogenous land-use practices compared to those practices that originally formed the grassland habitats. Negative effects of early mowing may be found in ground nesting grassland birds (Green et al., 1997; Strebel et al., 2015), and phytophagous insects (Miller and Gardiner, 2018). Timing of mowing or grazing can also have opposing effects on habitat quality for feeding resources compared to nesting resources. For instance abandonment reduce flower resources but cab increases availability of nesting holes (Steffan-Dewenter and Leschke, 2003). .For example, a Swedish study of 75 red-listed butterflies showed that by 1 July, about half of the species were still confined to their host plant as egg, larva, or pupa. By mid-August, 22% of the species remained on their host-plants, and by early September only circa 10% (Dahlström et al., 2008). On the other hand, 12 of the red-listed butterflies used their host-plants from August onwards, and such species can be considered to be favoured by early mowing and disfavoured by late disturbance. The phenology of insects and plants vary with climate between regions, and the timing of management therefore needs to be locally adapted (Baumgärtner and Hartmann, 2000; Bühler and Schmid, 2001).

Most likely, in landscapes with high abundance of semi-natural grasslands, such as the one studied, early mowing of a certain proportion of the hay meadows is not a problem for the insect populations, but contributes positively to nectar and pollen resources over the season. For both plant species and vegetation types, the temporal variation of flowering and flower resources are usually considered intrinsic characteristics (Dahlström et al., 2008; Decourtye et al., 2010; Mandelik et al., 2012), but this study shows that the flowering time of plants and thus the supply of flower resources in semi-natural grasslands over time can be strongly influenced by management such as mowing. The same habitat with the same species composition can provide nectar and pollen during different times depending on whether and when the vegetation is cut. This result has two important implications for the design of semi-natural grassland management regimes for conservation of species dependent on pollen and nectar resources.

First, that the supply of flower resources throughout the summer can be enhanced by increasing the diversity of mowing times in the semi-natural grasslands. Such a management may be considerably easier to achieve in fragmented and grassland-poor landscapes than to increase the diversity of habitats, or the plant species diversity in the habitats. In regions where little semi-natural grassland is left, we recommend to mow parts of each meadow at different times and vary which part every year, or to mow other herb-rich semi-natural grassland habitats in the nearby surroundings, such as road verges and field margins (Jantunen et al., 2007) earlier and later than the time of mowing in the hay meadows.

The second implication is that the ecological as well as cultural importance of diverse mowing times needs to be acknowledged and promoted in landscapes where such variation still exists, such as the Romanian mountainous agrarian landscapes. Studies of low-intensity agricultural systems have a great potential for informing about the ecological significance of traditional and heterogeneous management methods, of importance for other parts of the world where such variation has been lost. With proper knowledge about the mechanisms involved in the response of species to a management regime, results from one region may be translated to other regions, considering similarities and differences between regions (Helldin and Lennartsson, 2007). We believe that this and other studies in low-intensity agricultural regions can contribute with important knowledge for counteracting global pollinator loss as well as loss of grassland biodiversity in general.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:https://10.1016/j.gecco.2019.e00619.

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