



Mass-flowering red clover crops have positive effects on bumblebee richness and diversity after bloom

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Received 1 October 2020; accepted 1 June 2021
Available online 7 June 2021

Abstract

Floral resource quantity in agricultural landscapes plays a key role in the persistence of wild pollinators. An equally important, but less investigated factor is how variation in floral resource availability over time, e.g. floral resource pulses, affects pollinator abundances and diversity. Despite the potential importance of late-season resource pulses for bumblebee reproduction, few studies have evaluated the effects of late-season mass-flowering crops on bumblebee abundances and diversity during and after crop bloom. We assessed how bumblebee abundances, diversity and traits associated with species rarity were affected by cultivation of late-season mass-flowering red clover grown for seed production. Bumblebees were surveyed in red clover fields and flower-rich field borders across 20 landscapes with or without a red clover field during and after crop bloom in southern Sweden. Bumblebee worker abundances were higher in clover fields compared to flower-rich borders in the surrounding landscape. There was no relationship between presence of clover fields and the abundance of males of social bumblebees, but more male cuckoo bumblebees were found in flower-rich borders in landscapes with clover following crop bloom. Mass-flowering red clover also had a positive effect on bumblebee species richness and diversity after crop bloom. Overall, clover had positive and lasting effects on less common bumblebees thereby sustaining higher bumblebee species richness after bloom. Cultivation of red clover has the potential, in combination with the management of flower-rich habitats, to benefit less common bumblebee species in temperate agroecosystems.

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Keywords: *Trifolium pratense*; *Bombus*; Insect conservation; Floral richness; Floral dominance; Floral area

Introduction

Understanding the factors that limit population sizes and species richness of pollinators in agricultural landscapes is critical in designing conservation schemes that ensure their survival. Limiting factors for wild pollinators include lack of floral resources (Timberlake, Vaughan & Memmott, 2019) and nesting sites, diseases, pesticide use, and competition with managed honeybees (Goulson, Nicholls, Botias &

Rotheray, 2015). The importance of floral resource quantity is well recognized for pollinators and is today an integral part in the design of agro-environmental schemes (Geppert et al., 2020; Marja et al., 2018). An equally important, but less investigated factor, is how temporal availability in floral resource, e.g. floral resource pulses, affects pollinators (Schellhorn, Gagic & Bommarco, 2015; Yang, Bastow, Spence & Wright, 2008).

Floral resource pulses are narrow periods of high flower availability followed by extended periods of low availability (Yang et al., 2008), and are commonplace in agroecosystems as a result of cultivation of mass-flowering crops

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(Eurostat, 2020). Mass-flowering crops can, according to the “landscape-moderated concentration and dilution hypothesis”, cause a transient dilution of pollinator density in non-crop habitats during the resource pulse (Tschamtko et al., 2012). A higher bee density generally found during bloom in and around the mass-flowering crop, indicates that pollinators aggregate at the pulsating resource (Holzschuh, Dormann, Tschamtko & Steffan-Dewenter, 2013; Rundlöf, Persson, Smith & Bommarco, 2014, 2018; Westphal, Steffan-Dewenter & Tschamtko, 2003). Persistence of bee species that forage on oilseed rape was found to be positively correlated with oilseed rape cover in the landscape, indicating also positive long-term effects of mass-flowering crops on bee populations (Woodcock et al., 2016). In addition to floral resource quantity, the timing of resource availability is important (Timberlake et al., 2019). For example, for social bumblebees, while abundant early-season resources can increase worker numbers, late-season resources are needed to enhance colony reproduction (queen and male production) and persistence (Hovestadt, Mitesser, Poethke & Holzschuh, 2019; Kallioniemi et al., 2017; Westphal, Steffan-Dewenter & Tschamtko, 2009; Williams, Regetz & Kremen, 2012). Therefore, to maintain bumblebee species in managed temperate landscapes, flowering resources are needed during early summer for colony growth and late summer for colony reproduction. In particular, in Sweden, bumblebee abundance has been found to be limited by floral resources mainly from midsummer and onward (Persson & Smith, 2013). Despite the potential importance of late-season resource pulses for bumblebee reproduction in temperate areas, few studies have evaluated the effects of late-season mass-flowering resource pulses during and after crop bloom (but see: Beyer et al., 2020; Kallioniemi et al., 2017).

Positive effects of mass-flowering crops tend to be temporary and pollinator trait-specific. Most studies on mass-flowering crops have investigated crops with open flowers easily accessible to generalist pollinators such as honeybees (Diekötter, Kadoya, Peter, Wolters & Jauker, 2010; Holzschuh et al., 2013, 2016; Jauker, Peter, Wolters & Diekötter, 2012; Westphal et al., 2003, 2009). This may explain why mass-flowering crops have been found to favor common generalist pollinators over more rare and specialized pollinators (Holzschuh et al., 2016; Westphal et al., 2009). Positive effects of early-season mass-flowering crops on solitary bee richness (Diekötter, Peter, Jauker, Wolters & Jauker, 2014; Jauker et al., 2012), and on early-colony growth of common generalist bumblebees have been found (Hovestadt et al., 2019; Westphal et al., 2009). However, this immediate effect has not been shown to translate to improved reproduction later in the season for the common *Bombus terrestris* (Westphal et al., 2009). In other bees, such as long-tongued bumblebees, studies have instead found a reduction in density with increasing amounts of early-season mass-flowering crops (oilseed rape) (Diekötter et al., 2010; Westphal et al., 2003). Long-tongued

bumblebees have suffered the greatest declines because of their more specialized pollen requirements, which rely on availability of long-tubed flowers, such as red clover (*Trifolium pratense*) (Goulson, Hanley, Darvill, Ellis & Knight, 2005). In addition to tongue length, the time of year at which queens emerge from hibernation correlates with bumblebee rarity, with greater declines in species with later emerging queens (Goulson et al., 2005). It has been suggested that restoring Fabaceae-rich grasslands, particularly containing red clover, would benefit the persistence of threatened bumblebee species (Goulson et al., 2005; Rundlöf et al., 2014). In addition to occurring in natural grassland habitats, red clover is widely cultivated in Europe and North America for forage and seed production (Boelt, Julier, Karagić & Hampton, 2015). Cultivation of late-season blooming red clover could have a positive effect on rarer bumblebee species. While landscape-scale positive effects of red clover have been found on abundances of the long-tongued bumblebee species *B. hortorum* and *B. subterraneus* during crop bloom (Rundlöf et al., 2014), it has not been examined whether these translate to increased species richness in clover landscapes and whether these positive effects are maintained after clover bloom.

We assessed how bumblebee abundance, richness, diversity, evenness and traits related to rarity and resource foraging in the community change in response to mass-flowering red clover during and after bloom. We hypothesized that in landscapes with mass-flowering red clover, pollinator abundances would be concentrated in the clover field during bloom leading to a transient dilution of bumblebee abundances in neighboring non-crop habitats. After clover bloom, we expected carryover effects of mass-flowering crops. Specifically, we hypothesized that after clover bloom, landscapes with mass-flowering clover crops would harbor higher abundances, more diverse bumblebee communities and benefit rarer bumblebee species in non-crop habitats compared to landscapes without mass-flowering resources. This is because, we expect late-season clover bloom in intensively farmed landscapes to enhance the growth and survival of more rare bumblebee species by reducing nutritional stress (Requier, Jowanowitsch, Kallnik & Steffan-Dewenter, 2020; Vanderplanck et al., 2019). Finally, we hypothesized that late-season mass-flowering clover would increase the abundance of sexuals (males and queens) after bloom.

Materials and methods

Study design and landscape context

The study was conducted between June and August 2019 in the province of Skåne, in southernmost Sweden (Fig. 1). The survey period was regarded as late-season based on the typical activity period of bumblebees in Scandinavia, with early species founding colonies in March/April, peaking in June, and late species founding colonies in May/June and

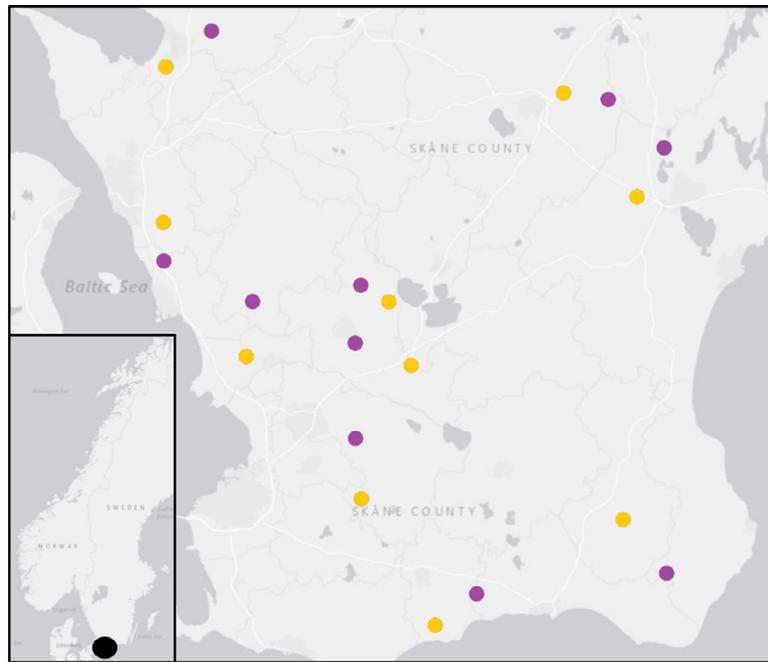


Fig. 1. Location of the study region in southern Sweden (55°59'43"N 13°26'30"E) and of selected landscapes with (purple) and without (yellow) red clover. Circles represent 2 km landscapes.

peaking in July/August (Persson & Smith, 2013; Rundlöf et al., 2014). Red clover seed fields flower between late June and early August peaking in July in the region (mean clover inflorescence density/m²: 236 ± 21se, see: Rundlöf et al., 2014) and therefore represent a late-season flower resource. The province is dominated by agricultural land, mostly cereals (40%), and to a lesser extent, flowering crops (12%) and pastures (15%). In 2019, 5800 hectares of clover were cultivated in Skåne for seed production (76.5%) and forage (23.5%).

We selected ten pairs of independent (> 4 km apart) circular landscapes with a radius of 2 km (Fig. 1 and see

Appendix A: Fig. A.1). The 2 km landscape radius was selected because bumblebees are expected to mainly be foraging within this scale (Rundlöf et al., 2014). One landscape in each pair contained a mass-flowering red clover field grown for seed in the center (mean field size (ha): 11.6 ± 3.9sd). As it is common practice to supplement mass-flowering crops with beehives, each clover field had honeybee-hives nearby and seven fields also had six *B. terrestris* hives (no differences in *B. terrestris/lucorum* abundances in clover fields were found between clover landscapes with and without bumblebee hives (p-value = 0.63; see Appendix A: Fig. A.2). To each clover

Table 1. Landscape and local scale variables in each landscape type (MF – mass-flowering with clover field; C – landscape without clover field). Local transect data were measured from the linear elements (LEs). Data presented are the mean, standard deviation (SD) and minimum and maximum for each variable. Abbreviation: SNH – Semi-natural habitat within 2 km radii (%), MFC – Mass-flowering crops flowering early and throughout the flowering season within 2 km radii (%). There were no significant differences in local nor landscape variables between MF and C landscape (see Appendix A).

Scale	Variables	MF landscape			C landscape		
		Mean±SD	Min	Max	Mean±SD	Min	Max
Landscape	Arable (%)	65.3 ± 17.5	42.6	91	71.9 ± 15.6	46.7	89.7
	SNH (%)	27.5 ± 18.2	5.5	58.5	27.8 ± 16.0	8.1	61.7
	Early MFC (%)	8.7 ± 6.0	1.31	20.4	8.2 ± 4.9	2.9	17.7
	MFC (%)	11.6 ± 6.1	4.2	22.9	10.6 ± 5.4	4.9	19.4
Local	Floral area (m ²) - Bloom	4.5 ± 4.9	0.24	18.16	2.5 ± 2.5	0.27	7
	Floral area (m ²) - Post bloom	1.65 ± 1.70	0.09	6.39	1.4 ± 1.7	0.02	7.3
	Flower richness - Bloom	14.6 ± 5.1	5	25	13.3 ± 5.1	3	27
	Flower richness - Post bloom	8.8 ± 3.7	1	18	7.2 ± 3.2	1	13
	Floral dominance - Bloom	0.3 ± 0.1	0.17	0.82	0.4 ± 0.2	0.08	0.9
	Floral dominance - Post bloom	0.3 ± 0.2	0.03	1	0.4 ± 0.2	0.11	1

landscape corresponded a control landscape with no red clover crops (see Appendix A: Fig. A.1). Paired landscapes were selected to have similar proportion of arable land and of early-season mass-flowering crops (Table 1, see Appendix A). Land-use data on the proportion of arable and semi-natural habitats in each 2 km landscape was extracted from the Swedish National Ground Cover Data (Naturvårdsverket 2018). Data on the proportion of early-season mass-flowering crops in 2019 within each 2 km landscape was extracted from the Land Parcel Identification System (Swedish Board of Agriculture 1:10,000). Proportion of early-season mass-flowering crops was selected because it is known to impact bumblebee dynamics (Riedinger, Renner, Rundlöf, Steffan-Dewenter & Holzschuh, 2014), in addition late-season mass-flowering crops proportion was confounded with the treatment (landscapes with or without red clover field).

Bumblebee and flower survey

We surveyed three 50 m long and 2 m wide flower-rich linear elements (LEs) in each landscape. LEs were selected based on having long-tube flowers, high floral abundance and richness and ease of access. Transects were situated 0.5–2 km from the center of the landscape. In each flower-rich LE, flower-visiting bumblebee workers, queens and males were surveyed. In addition, a 50 m long and 2 m wide survey transect was established in each clover field, parallel and at 10 m from a field edge. All transects in LEs were surveyed four times, twice during red clover bloom (21 June – 22 July) and twice after (16 July – 28 August) (overlap in the dates between bloom and after bloom was due to slight differences in red clover bloom phenology between fields). Transects in clover fields were surveyed for bumblebees twice during red clover bloom only. New flower-rich LEs were surveyed after bloom as LEs that were flowering during clover bloom had ceased flowering after clover bloom. In each LE transect three plant characteristics were determined once during and once after clover blooming: floral area, flower species richness and floral dominance (Table 1). Red clover was widespread but not dominant in the LEs. Protocol, names and abundances of plant species in the LEs are listed in Appendix B.

Bumblebee surveys were conducted on warm days (> 15 °C), between 10am and 6pm. To avoid major impacts on bumblebee populations, no queens were collected but determined to species in the field. Due to high numbers of bumblebees foraging ($n = 8603$) only a subset were collected to measure traits and confirm identification ($n = 3110$); for specimens identified in the field ($n = 5493$) it was not feasible to assign caste with certainty, except for *B. lapidarius*. These individuals were identified to species but not to caste and included in the analyses for overall bumblebee abundances, richness, diversity and functional traits, which were not caste-specific. For bumblebee species richness and abundance, we present results for males and workers separately

and combined (i.e. including specimens of unknown caste) to investigate effects of mass-flowering clover within population and at the population level.

Bumblebee traits

Categorical traits on colony size, queen emergence, and nest type were compiled from the literature (Arbetman, Gleiser, Morales, Williams & Aizen, 2017; Persson, Rundlöf, Clough & Smith, 2015; Rundlöf, Lundin & Bommarco, 2018). Tongue length and body size (measured as intertegular distance (ITD)) were directly measured on six field-collected individuals per caste per species whenever possible. All selected traits respond to landscape simplification (Persson et al., 2015) and are associated with bumblebee rarity, with smaller body (ITD), longer tongue, aboveground nesting, late queen emergence and smaller colony sizes associated with less widespread species (Goulson et al., 2005). Tongue length and body size are particularly relevant traits for resource acquisition. Species with long tongues are more restricted to feed on flowers with long corollas (Heinrich, 1976). Body size of bees is in general positively related to their foraging range (Greenleaf, Williams, Winfree & Kremen, 2007), and may affect their ability to utilize resources in the landscape. Traits for each species and correlation among traits are presented in Appendix C. Community weighted means (CWM) were calculated for each trait in each transect. For categorical traits, we coded the traits as dummy variables and transformed each trait level into a binary vector (0/1). To test whether mass-flowering resources had an effect on intraspecific body size (Persson & Smith, 2011), bumblebee ITD was measured on all collected workers of the most common species *B. terrestris/lucorum* ($N = 145$) and *B. lapidarius* ($N = 103$) from both the clover and the LE transects in clover landscapes (see Appendix C).

Data analysis

We performed two separate sets of analyses (see Appendix A: Fig. A.1). In the first analysis, we tested for differences between clover fields and LE habitats within landscapes in which a clover field was present during clover bloom. For these analyses, data was averaged per habitat (clover field and LE). Tested response variables were: bumblebee abundances - all (including specimens that were not assigned to a caste) and males and workers; species richness, species diversity (Shannon index), Pielou's community evenness index (Spiesman, Bennett, Isaacs & Gratton, 2017), *B. terrestris* and *B. lapidarius* ITD, CWM of the categorical traits (aboveground nest, early queen emergence, and small colony size) and the continuous traits (body size (ITD) and tongue length). Because of insufficient data, abundances of cuckoo bumblebees ($n = 40$) and queens ($n = 5$) were not

Table 2. Best fitting models results presenting the estimate (Est.), the standard error (SE), the P-value and the marginal R^2_m for the bumblebee community and trait variables in relation to habitat type (clover field (CLO) or linear element (LE)) and floral area in the clover landscapes during clover bloom. Significant results ($p < 0.05$) are in **bold**. Abbreviation: ITD – Intertegular distance (cm).

Dependent variables		Habitat type (LE > CLO)		
		Est. \pm SE	P-value	R^2_m
Abundance	All	-41.2 ± 10.17	0.003	0.46
	Workers	-8.8 ± 2.10	0.002	0.48
	Males	1.64 ± 0.36	0.001	0.38
Community	Species count All	-0.17 ± 0.38	0.66	0.01
	Species count Workers	-0.82 ± 0.24	0.008	0.37
	Species count Males	0.70 ± 0.21	0.009	0.27
	Shannon diversity	0.50 ± 0.08	<0.001	0.54
	Evenness	0.44 ± 0.07	0.001	0.73
Traits	Tongue length	0.037 ± 0.009	0.002	0.47
	Aboveground nesting	0.25 ± 0.02	<0.001	0.8
	Late emergence	0.11 ± 0.02	<0.001	0.34
	Small colony	0.09 ± 0.01	0.003	0.41
	ITD	-0.02 ± 0.003	<0.001	0.77
	<i>B. terrestris/lucorum</i> ITD	-0.02 ± 0.009	0.009	0.05
	<i>B. lapidarius</i> ITD	-0.02 ± 0.008	0.005	0.07

tested. The explanatory variable included in the models was habitat type (clover field or LE). We included landscape ID as a random effect in all models. Linear mixed effects models were used to test all response variables (Table 2).

In the second analysis, we tested for differences in bumblebee variables between the LEs in landscapes with and without a red clover field, and raw data collected per transect per sampling round were used. Differences were tested during and after red clover bloom in separate models. In addition to the response variables investigated in the first analysis, we tested differences in abundance of cuckoo bumblebees ($n = 112$) after crop bloom, while queen abundance data was too sparse ($n = 42$) to analyze. The explanatory variables included in the models were: landscape type (with or without clover), proportion of early-season mass-flowering crops in the landscape (early MFC: oilseed rape) and semi-natural habitat (SNH: forests, pastures), and local floral resources (area, richness and dominance) in the LEs. To avoid overfitting the model and convergence issues we only tested for interactions between landscape types (with and without clover) and floral resources amount (local floral area and proportion of early MFC in the landscape). Floral area, floral richness and floral dominance were all included in the model as they were not correlated (during bloom: $\rho < 0.4$; after bloom: $\rho < 0.3$ for all combinations). The proportions of SNH and early MFC were negatively correlated ($\rho = -0.67$), but since the variance inflation factor was < 2 both variables were included in the models. Early MFC and SNH proportions were not correlated to local flower variables ($\rho < 0.25$ for all combinations). We included sampling round nested within landscape nested within paired landscape as a random effect in all models. Linear mixed effects models ('nlme' package) were used to test all response variables except species richness and abundances

which were analyzed using generalized mixed effect models with a Poisson distribution and an individual level random effect to improve residual fit and account for overdispersion ('lme4' package). Appendix D describes the structure of each model.

All analyses were done in R (R Core Team, 2020, version 3.6.2). Model simplification was done using the function 'dredge' ('MuMIn' package (Bartoń, 2020)) to get the model with the lowest AIC. Residual plots were used to assess linear model assumptions and a variance structure ('varIdent') was specified to address heteroscedasticity. The 'DHARMA' package was used to visualize the residuals for the generalized linear mixed models and test for overdispersion (Hartig & Lohse, 2020).

Results

Bumblebee foraging habitats

Bumblebee abundance was higher in clover compared to LEs in landscapes with a clover crop (Fig. 2A, Table 2). However, the difference between these habitats depended on caste, with higher abundance of workers in clover but more males in LEs. There were no differences in overall bumblebee species richness between habitats, but differences were detected between castes with higher worker species richness in clover and higher male species richness in LEs. Bumblebee diversity and community evenness were higher in LEs than in clover field (Fig. 2B and C).

Traits associated with rarity (smaller body, longer tongue, aboveground nesting, late queen emergence and small colony size) were positively related with LE habitats (Fig. 2D,

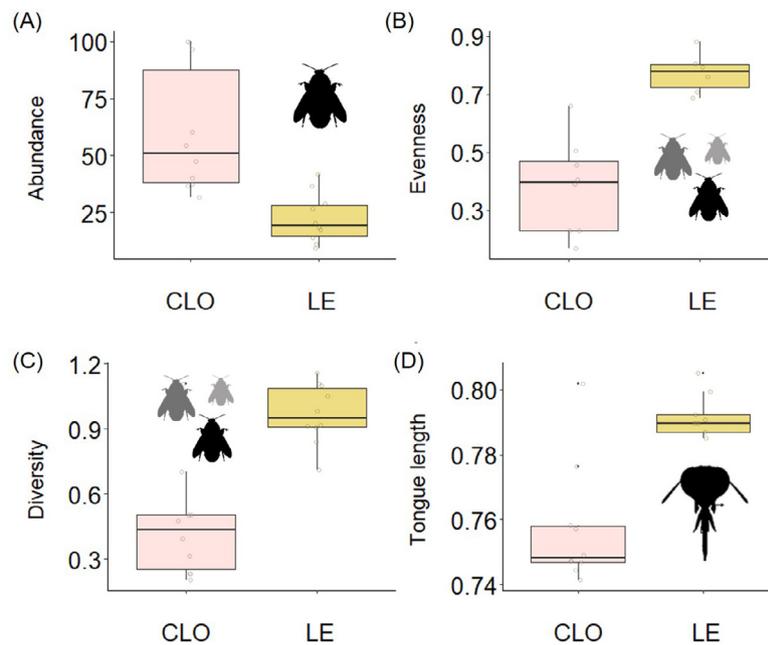


Fig. 2. Relationship between foraging habitat and bumblebee (A) abundance, (B) evenness, (C) diversity and (D) CWM tongue length. Abbreviations: CLO – clover and LE – linear element habitats.

Table 2). Intraspecific traits were also affected by habitat, with larger workers of *B. lapidarius* and *B. terrestris/luccorum* in clover fields.

Impact of landscape resource pulses

When comparing bumblebee communities between LEs in landscapes with or without clover during crop bloom, LEs in landscapes with red clover had lower overall bumblebee abundance, bumblebee worker abundance and worker richness (Fig. 3A). Overall bumblebee species richness and diversity did not differ between landscapes. Community evenness was higher in LEs in landscapes with clover and decreased with increasing flower dominance (Fig. 3B). After clover bloom, bumblebee abundances overall and within castes, did not differ between landscapes (see Appendix D). There was a positive relation between bumblebee worker abundance and flower area, but only in clover landscapes (see Appendix E). Overall bumblebee abundance was positively related to flower area and was negatively related to floral richness, and abundance of males was negatively related to proportion of SNH in the landscape (see Appendix D). Abundance of cuckoo bumblebees was higher in LEs in clover landscapes and were negatively related to proportion of SNH in the landscape (see Appendix D). Bumblebee species richness and diversity were higher in LEs in landscapes with clover (Fig. 3C and D).

During bloom, CWM traits did not differ between landscape type. Traits related to rarity (smaller body, longer tongue, aboveground nesting and late queen emergence) were negatively related to flower dominance (see Appendix

D). Late queen emergence was also negatively related to proportion of early mass flowering crops in the landscape. After clover bloom traits associated with rarity (longer tongue, aboveground nesting and smaller colony sizes) tended to be associated with presence of clover in the landscape. Traits associated with rarity were also positively related to flower richness (smaller body, late queen emergence, longer tongue and small colony sizes) or SNH (aboveground nesting) and negatively related to flower area (body size, late queen emergence and small colony sizes).

Discussion

In agreement with previous studies in both early (Hanley et al., 2011; Herrmann, Westphal, Moritz & Steffan-Dewenter, 2007; Westphal et al., 2003) and late (Rundlöf et al., 2014) season mass-flowering crops, we found that mass-flowering crop blooming was attractive for bumblebees. Bumblebee workers were on average three times more abundant in clover fields during bloom compared to flower-rich LEs. We did not find an effect of late mass-flowering crop on the abundance of males of social bumblebees as hypothesized and previously detected in red clover (Rundlöf et al., 2014). Instead, our results show that mass-flowering red clover was positively related to bumblebee species richness and diversity in the landscape after bloom.

Bumblebee foraging habitats

One well-documented consequence of mass-flowering crops on bumblebees is an increased abundance in and

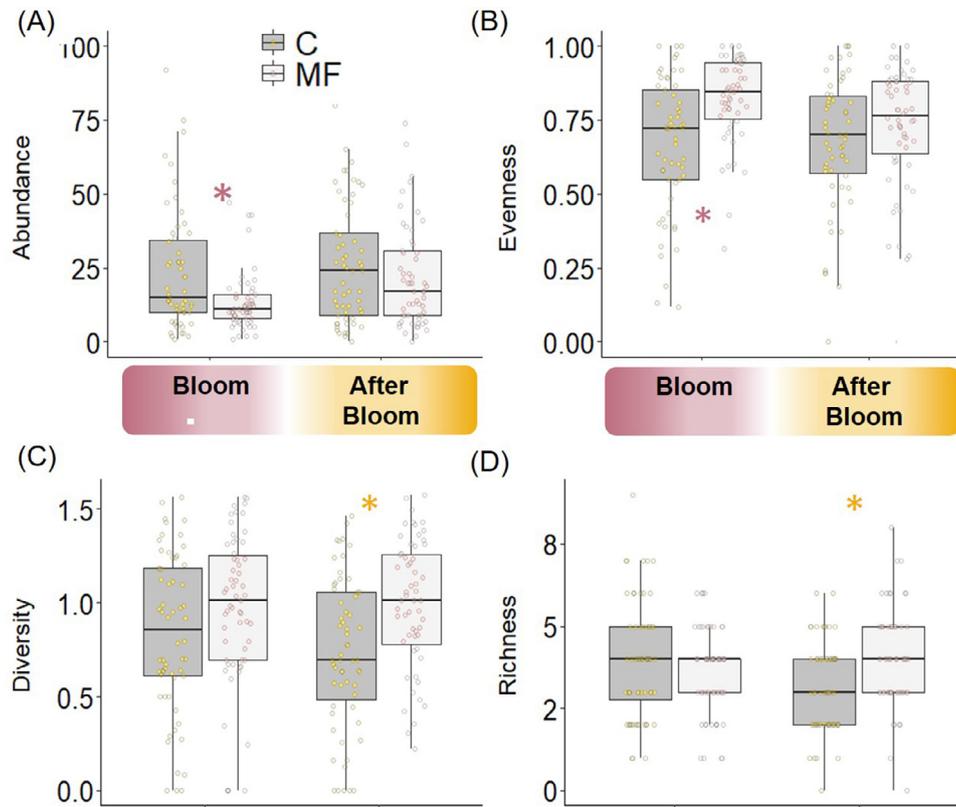


Fig. 3. Landscape scale effects of clover during and after bloom on (A) abundance, (B) evenness, (C) diversity and (D) richness of bumblebees in the linear elements. Significant differences are shown with (*). Abbreviations: Landscape with (MF) and without (C) a clover field.

around mass-flowering crops during crop bloom (Hanley et al., 2011; Herrmann et al., 2007; Westphal et al., 2003). We detected such relationship, with on average 172% more bumblebees visiting clover fields than LEs. We also found that bumblebee worker abundances during clover bloom was higher in LEs in landscapes without clover. This indicates a potential shift in bumblebee density in clover landscapes during clover bloom due to aggregation of bumblebees in the clover field. Rundlöf et al. (2014) also found higher densities of bumblebees in mass-flowering clover fields than in the field borders during mass-flower crop bloom, and the attractiveness of red clover to bumblebees is well known (Goulson et al., 2005). Consequently, our results support the hypothesis that cultivation of mass-flowering crops leads to a temporary dilution of bumblebees in non-crop habitats and an increase in the mass-flowering crops during the resource pulse (Holzschuh et al., 2016; Yang et al., 2010). Foraging habitat preferences of bumblebees are caste-specific. We found higher abundance and species richness of workers in clover fields, but not for males. These dissimilarities in foraging habitats are likely due to differences in patrolling behavior (i.e. territorial and mate searching behavior) (Rundlöf et al., 2014) and feeding habits between castes (Roswell, Dushoff & Winfree, 2019). While workers forage for both pollen and nectar for the colony, males forage for nectar and patrol for mating. For this reason workers are likely better at exploiting mass-flowering plant

species than males (Fijen, Scheper, Boekelo, Raemakers & Kleijn, 2019).

Clover fields were predominantly visited by bumblebee species with traits associated with common species – larger body, shorter tongue, belowground nesting, early queen emergence and larger colony size. This indicates that mass-flowering clover resources are preferentially used by dominant bumblebee species. When comparing LEs between landscapes with and without clover, no differences in CWM traits were found during clover bloom, suggesting that the influence of clover on traits associated with common bumblebees is localized to the clover field. In addition, larger-bodied workers of *B. terrestris/lucorum* and *B. lapidarius* were found in clover fields compared to LEs in clover landscapes. Bumblebee body size can be an indication of food availability, where smaller bumblebees are produced in areas with low availability of resources (Persson & Smith, 2011), but could also be related to movement potential, with larger individuals being able to forage over longer distances (Greenleaf et al., 2007). As clover blooms late, after the growth phase of the bumblebee colony, our results are more likely to be a consequence of mass-flowering red clover crops attracting large bumblebee workers of common species from distant nesting sites. If workers come to forage on clover fields from far away sites, this may explain why we did not find higher male abundances in mass-flowering landscapes after clover bloom as expected.

Impacts of landscape resource pulses

We expected mass-flowering crops to increase the abundances of bumblebees in the landscape after crop bloom (Williams et al., 2012). However, no effect of late or early mass-flowering crop area in the landscape was detected on bumblebee abundance after clover bloom. Based on experimental evidence that bumblebee colony growth is greater when food supply is constant rather than pulsed (Hemberger et al., 2020), we suggest that the lack of bumblebee numerical response to mass-flowering clover in our study could be due to a deficit of floral resources between the mass-flowering of early and late crops in the study area (Beyer et al., 2020; Timberlake et al., 2019). Lack of mid-season (June) mass-flowering crops (e.g. faba bean) may have led to a resource bottleneck earlier in the season, in particular for the widespread species with larger colonies (*B. lapidarius* and *B. terrestris/lucorum*). Interestingly, higher abundances of cuckoo bumblebees, mostly males, were found in landscapes with clover after bloom. Previous experiments on commercial *B. terrestris* colonies have found positive correlations between social parasitism and mass-flowering resource availability of oilseed rape (Carvell, Rothery, Pywell & Heard, 2008). Our study provides the first field indication that mass-flowering crops increase the reproductive success (males) of cuckoo bumblebees.

During clover bloom, we found a positive relationship between the proportion of early mass-flowering crops and CWM late queen emergence. This may be from that *Bombus hortorum* and *B. subterraneus*, the dominant species associated with this trait, may have preferentially nested in areas with high cover of oilseed rape. After clover bloom, despite lower densities for some long-tongued bumblebees (*B. hortorum*) (see Appendix F), several traits associated with rarity in bumblebees (long tongue, aboveground nesting and small colony sizes) were marginally ($p < 0.1$) associated with landscapes containing clover. This indicates a positive correlation after bloom between mass-flowering resources and less common bumblebees. A positive association between clover and less common bumblebee species is also supported by higher bumblebee species richness and diversity in clover landscapes after bloom. High richness of bumblebees in the spring have been found to be associated to high cover of late mass-flowering crops in the previous year (Kallioniemi et al., 2017). This is likely due to higher bumblebee reproduction in the previous year (Rundlöf et al., 2014). Our results partially support these findings and are congruent with the hypothesis that late-season flowering resources can be a bottleneck for reproduction and survival of bumblebees, particularly so for less common species. Less common species may have benefitted from mass-flowering clover resources in the landscape during bloom, with lasting and more visible effects after clover bloom, when resources were scarcer and bumblebees concentrated in the LEs.

Effect of non-crop resources at the local and landscape scale

At the local scale, our study shows that the benefits of flower resources for bumblebees may not be a simple ‘more is better’. During bloom, floral dominance was negatively related to traits associated with rarity. High floral dominance during bloom, with one or two flowering species providing most of the resources in a patch, may have benefited the most generalist and common bee species, leading to competitive exclusion of rarer bumblebees. After clover bloom there were fewer flowers blooming in the LEs. The bumblebee abundances were then higher in patches with a greater floral area. Patches with high floral area attracted widespread species (i.e. larger body, earlier emergence and larger colony) to the patch that might have competitively excluded less dominant species in these patches. Importantly, we also found that higher floral richness after clover bloom can support less common species, which confirms that diverse plant communities benefit a wider range of bee species (Kallioniemi et al., 2017).

After clover bloom, we found CWM aboveground nesting to be positively associated with semi-natural habitats which confirms that these habitats are important sites for bumblebee nesting. This is clear particularly for *Bombus sylvarum* and *B. subterraneus*, the dominant species in this category (see Appendices B and F). It is difficult to interpret the negative relation between semi-natural habitat and abundances of males of both social and cuckoo bumblebees. One possibility is that males aggregate in the SNH habitats rather than in the LE habitats in landscapes with high SNH and we therefore did not sample them.

Conclusions

Understanding how land-use practices affect wild pollinators is central to maintain biodiversity in agricultural landscapes. It has been suggested that mass-flowering crops should be considered as part of agri-environmental schemes to improve pollination services in agricultural landscapes (Westphal et al., 2003). Our results indicate that the benefits of mass-flowering crops such as clover on bumblebee abundances are localized to the mass-flowering crop with little spill-over effects in neighboring semi-natural habitats. In addition, it is likely that bumblebees forage over large distances when high quality resources such as clover are present. Interestingly, the presence of a mass-flowering resource had positive effects on less common bumblebees seen by higher species richness and diversity after bloom. Our results indicate that bees who profit from high floral dominance, such as *B. lapidarius* and *B. terrestris/lucorum*, would directly benefit from an expansion of red clover mass-flowering crops. Less common bumblebee species that

benefit from diverse floral communities may also benefit from red clover cultivation due to increased colony survival. However, our results indicate that red clover cultivation cannot substitute naturally occurring species-diverse flower areas in the landscape as these habitats support less widespread bumblebee species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to Tiago Souto Teixeira and Caroline Lindgren Svensson without whom the fieldwork would not have been possible. We thank Maj Rundlöf who provided useful criticism of the manuscript. This project was funded by the Swedish research council Formas (2016-00361) to Prof. Anna Jansson.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.06.001.

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