



## Semi-natural habitat cover but not late season mass-flowering crops affect pollinator-plant networks in non-crop habitats

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### ABSTRACT

Plant-pollinator networks in agricultural landscapes are subject to high flower resources fluctuations due to mass-flowering crops cultivation. Mass-flowering crops can attract pollinators and alter community compositions in non-crop habitats, yet their impacts on plant-pollinator networks in non-crop habitats remain understudied. In this study, we investigated the effects of late-season mass-flowering red clover crops in 120 plant-pollinator networks in non-crop habitats during and after the clover bloom period in southern Sweden. Our findings show that late-season mass-flowering red clover crops did not impact the structure of plant-pollinator networks in non-crop habitats. On the other hand, plant-pollinator network structure in agricultural landscapes was predominantly affected by local flower richness and semi-natural habitat cover in the landscape. Semi-natural habitat (SNH) cover positively impacted network specialisation after clover bloom. Greater flower availability with increasing semi-natural habitat cover might increase the possibilities of pollinator species to focus on different resources to optimise foraging and avoid competition at time when flower resources are scarce in temperate landscapes (e.g. after clover bloom, late August). In line with this, both *Bombus terrestris* became more specialised in landscapes with high SNH cover after clover bloom. Specialisation may help reduce inter-individual and inter-specific exploitative competition for floral resources and thus favour coexistence in pollinator assemblages, especially in a context of agroecosystems, where flower resources are generally limited and fluctuating due to mass-flowering crop cultivation. In conclusion, our study underscores the robustness of plant-pollinator networks in non-crop habitats to shifts caused by mass-flowering crop cultivation and emphasises the critical role of semi-natural habitat preservation and flower richness in shaping plant-pollinator network structure in agricultural ecosystems.

### 1. Introduction

Agriculture and the associated losses of semi-natural habitats are major drivers of declines of flower resources and nesting habitats for pollinators (Schellhorn et al., 2015; Timberlake et al., 2019; Tuerlings et al., 2022). The loss of flowering resources in agricultural landscapes has a disproportionate negative impact on the abundance of specialised pollinator species, and this has implications for pollinator community compositions, and plant-pollinator networks structure (Kleijn et al., 2011; Tylianakis and Morris, 2017; Weiner et al., 2014). Plant-pollinator networks in agricultural landscapes tend to be dominated by crop-adapted and managed species (Fijen et al., 2019; Geslin et al., 2017), and are expected to be highly dynamic, due to seasonal changes

in flowering crop cultivation pattern (Chakraborty et al., 2021). Such characteristics have been assumed to lead to asymmetry and nestedness in plant-pollinator networks in agricultural landscapes (Ferreira et al., 2013), and contribute to the stability of these networks to land-use change (Memmott et al., 2004; Nielsen and Totland, 2014; Tiedeken and Stout, 2015). However, impacts of mass-flowering crops on plant-pollinator networks are highly crop dependent (Gay et al., 2024). In addition, the blooming of mass-flowering crops drastically affects the temporal availability of flower resources at the landscape scale in temperate regions (Holzschuh et al., 2011), influencing pollination in non-crop habitats (Stanley and Stout, 2014). However, their impact has seldom been investigated in networks outside of crop habitats (Magrath et al., 2018).

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Studies have shown that mass-flowering crop blooming can (a) attract pollinators and monopolise flower visits in the landscape, leading to dilution of pollinators in non-crop habitats adjacent to the mass-flowering crops (Grab et al., 2017; Holzschuh et al., 2016, 2011; Kovács-Hostyánszki et al., 2013); (b) alter the pollinator community composition in non-crop habitats (Beyer et al., 2021); and (c) have negative effects on the co-flowering non-crop plant species in the landscape (Cussans et al., 2010; Holzschuh et al., 2011; Magrath et al., 2017). Therefore, networks in non-crop habitats adjacent to blooming mass-flowering crops are expected to primarily lose common and generalist species which are the ones that form the core of their network (Thompson et al., 2021). Shifts in network composition can affect fundamental plant–pollinator networks properties, such as nestedness, modularity or degree distribution, in the non-crop habitats (Stanley and Stout, 2014; Vilà et al., 2009). Magrath et al. (2018) found that blooming oilseed rape crops attracted 8–35 % of the pollinator individuals away from the neighbouring grasslands, but that the plant–pollinator networks in these grasslands were resistant to this level of reductions. However, they also found that network changes in non-crop habitats could be triggered if > 50 % of pollinator individuals were attracted to the crop. Despite the potential impact from mass-flowering crops on plant–pollinator networks in non-crop habitats (Magrath et al., 2018), this link remains largely unexplored and plant–pollinator networks are neglected compared to other community structure measures such as richness. Plant–pollinator networks can inform on services, such as pollination, as well as their resilience to species loss, and this assessment is important when examining land-use impacts on biodiversity (Massol and Petit, 2013).

Mass-flowering crop bloom is characterised by short temporal pulses of high flower resource availability and low floral diversity. When in bloom, they significantly increase the amount of available floral resources at a location, and after blooming, they transform into a green desert with very few floral rewards. This sharp change in the amount of available floral resources can have an effect on pollinator density and foraging habitats (Beyer et al., 2021; Riggi et al., 2021), and potentially alter plant–pollinator network structure. As crop pollinators are attracted to remaining flower patches after the crop blooming ceases, concentration of generalists, crop-adapted pollinators in non-crop flowering habitats might increase the generalisation and connectance in the network or even temporarily exclude more specialised species from these patches. What also may happen is that individuals may broaden their diet (*individual generalisation*) or shift to other resources (*individual specialisation*), in response to increased competition for food (Bolnick et al., 2003; Fontaine et al., 2008; Kunin and Iwasa, 1996; Pornon et al., 2019). The balance between these two behaviours will influence network generality, connectance and nestedness after crop bloom.

Temporal effects of mass-flowering crop bloom on plant–pollinator networks in non-crop habitats have seldom been investigated. A notable exception is the study by Magrath and colleagues (2018), that found a lack of interactive effects between oilseed rape cover and bloom period on network structure and species roles within plant–pollinator networks. The lack of relationship may be partially explained by the fact that the open flowers of oilseed rape are attractive to widespread species, resulting in low individual and species losses and promoting high stability within the networks. In addition, oilseed rape flowers early in the season when flowering resources are abundant (Timberlake et al., 2019), potentially masking effect on network structure. For other crops, such as Fabacea, that flower late in the season when floral resources are scarcer in temperate regions (Timberlake et al., 2019), larger impacts on plant–pollinator networks in non-crop flowering might be visible.

Red Clover (*Trifolium pratense*) is a common *Fabacea* crop in southern Sweden, flowering late in the season. Red clover is primarily pollinated by bumblebees (Goulson et al., 2005). Clover flowers are a high quality and highly rewarding source of pollen and nectar for bumblebees particularly for the less common long-tongued species (Goulson et al., 2015; Riggi et al., 2021). Therefore, cultivation of red clover might

alleviate the negative effects of loss of flowering resources on pollinators in agricultural landscapes (Riggi et al., 2021). As generalist pollinators preferentially visit the most abundant and/or rewarding resources in a given area, red clover could attract pollinators from the surrounding non-crop habitats and possibly disturb the plant–pollinator network structure in these habitats. After red clover crop bloom floral resources in the landscape are often low (Timberlake et al., 2019), and in temperate regions no other mass-flowering crops is flowering. This potentially increases the competition in the remaining non-crop flowering patches as pollinators concentrate in these habitats. Therefore, shifts in red clover mass-flowering resources could result in drastic changes in plant–pollinator network metrics like connectance, modularity, nestedness and specialisation; possibly affecting pollinator species survival and flower pollination in these habitats.

In this study, we investigated the effect of mass-flowering red clover crops on plant–pollinator networks in non-crop habitats both during and after red clover bloom. We did this by using data from 20 landscapes and 120 plant–pollinator networks. Our hypotheses were that red clover mass-flowering crop would affect pollinator communities' composition in non-crop habitats during bloom. This is a result from pollinators, particularly bumblebees, moving to forage in the clover fields during crop bloom in landscapes with these red clover crops (Riggi et al., 2021). This shift in pollinators' foraging behaviour is expected to increase connectance and decrease modularity, nestedness and specialisation of the plant–pollinator networks in the non-crop habitats during crop bloom. After red clover bloom, we expected crop foragers to shift foraging to non-crop habitats, thus decreasing connectance while increasing modularity, nestedness and specialisation of plant–pollinator networks in the non-crop habitats. In addition, because floral resource availability is assumed to increase with semi-natural habitat (SNH) cover, we expect plant–pollinator networks to be more nested, specialised and less connected (lower connectance) with increased amount of SNH cover in the landscape. Finally, we expected widespread species and red clover specialist species (e.g., long-tongue bumblebees), to shift their roles in the network between bloom periods in clover landscapes and becoming more of generalists (i.e. visiting more flower resources) after red clover bloom.

## 2. Material & methods

### 2.1. Study site and landscape design

Flowering plants and flower visitors were surveyed in 20 landscapes between June and August 2019 in the province of Skåne, in southernmost Sweden (Fig. S1). 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 peaking in July/August (Persson and 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 per m<sup>2</sup>: 236 ± 21 se, 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 ha of clover were cultivated in Skåne for seed production (76.5 %) and forage (23.5 %).

We selected 10 pairs of independent (> 4 km apart) circular landscapes with a radius of 2 km (Fig. S1, Riggi et al., 2021) (see Riggi et al., 2021 for field set-up). 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 centre (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 *Bombus terrestris* hives (no differences in honeybee abundances between clover and

control landscapes (Fig. S3), nor *Bombus terrestris/lucorum* abundances in clover fields were found between clover landscapes with and without bumblebee hives,  $p$ -value = 0.63). Each clover landscape corresponded to a control landscape with no red clover crops. Paired landscapes were selected to have a similar proportion of arable, SNH and early-season mass-flowering crops (Table 1).

## 2.2. Flower-visitors and flowers survey

We surveyed three 50 m long and 2 m wide flower-rich linear elements, from here onwards termed “non-crop” habitats, in each landscape. Transects were situated 0.5–2 km from the centre of the landscape. In each transect, flower-visiting insects were surveyed. All transects 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). New transects were surveyed after bloom as non-crop habitats that were flowering during clover bloom had ceased flowering after clover bloom due to flowering phenology. In each transect three plant characteristics were determined once during and once after clover blooming: floral area, flower species richness and floral dominance (see: Riggi et al., 2021). Flower metrics did not vary between clover and no-clover landscape (Table 1). Red clover was widespread but not dominant in the transects. Protocol, names and abundances of plant species in the transects are listed in Riggi et al. (2021).

Flower-visitor surveys were conducted on warm days ( $> 15\text{ }^{\circ}\text{C}$ ), between 10 am and 6 pm. Transects were slowly walked and all interactions between individual flower visitors and individual flowers were recorded. To avoid major impacts on populations, only a subset of bumblebees was collected to confirm identification. Overall, 17,966 flower visitor-flower interactions were recorded. Bumblebees (47.8 %) were identified to species level, except for the cryptic *B. terrestris* and *B. lucorum* species which were grouped. Lepidopterans (3.2 %) were identified as species when possible (except for some Aglais that were only identified to genus and some Polyommata subfamily). Diptera were categorised into syrphids (14.5 %) and other dipteras (0.9 %). Syrphidae were identified to species when possible or to genus, while other dipteras were grouped. Wasps (0.08 %) were categorised into: Digger wasp, Ichneumonidae and Social wasp. Non-*Bombus* bees were either solitary bees (0.3 %) or honeybees (31.7 %). Finally, other flower visitors included Coleoptera (1.3 %) and Damselfly (0.03 %). Table with taxonomic level and cumulative totals of each flower visitor group are available in the Supplementary material (Table S1). We identified most pollinators to species level, but some pollinators were only identified to genus, family or order (e.g. diptera). In order to minimise uncertainties that could arise from having multiple species aggregated in one node, we

classified individuals not assigned to species into morphospecies. Mutualistic networks tend to be more robust to taxonomic simplification than other network types, such as antagonistic networks (Rodrigues and Boscolo, 2020). The node resolution was consistent across sites, making the resultant networks comparable to each other (Hemprich-Bennett et al., 2021).

For each transect within each landscape we built bipartite pollinator–plant networks. Network-level and species-level metrics were calculated separately for surveys carried out during and post clover crop bloom, by pooling data across the two surveys per transect per bloom period. This created 120 networks across 20 landscapes during and after crop bloom. We used transect scale data, rather than aggregating the data at the landscape scale, to be able to assess the effect of local flower characteristics (richness, area, dominance) on network structure.

In order to assess how mass-flowering crops affect plant-pollinator interactions in non-crop habitats we calculated the following network-level metrics: weighted connectance, interaction evenness, network-level complementary specialisation (H2), modularity, and weighted nestedness (NODF) (Table 2). These metrics were selected because they capture some of the fundamental properties of a network, they are weakly correlated (Table S2) and have been previously successfully used to investigate the effect of flowering pulses on plant–pollinator network diversity (i.e. weighted connectance and interaction evenness) and their relative distribution of interactions (i.e. complementary specialisation, weighted nestedness, and modularity) (Kaiser-Bunbury and Blüthgen, 2015; Magrach et al., 2018). The weighted versions of connectance and nestedness were used to account for the effect of network size and species abundances on network metrics (Ballantyne et al., 2015; Magrach et al., 2018a). All metrics were extracted from ‘networklevel’ function in *bipartite* library. Modularity was calculated using the *cluster walk and fast greedy* algorithms using the package ‘igraph’. To assess if the values of the selected metrics were not random, we ran 1000 simulations of the matrices used to build the networks, with fixed marginal totals, using the *sample* function and checked if the measured values were outside of the 95 % confidence interval for each metric.

Further, we calculated species-level metrics for pollinators to evaluate whether species changed their role within the networks during and after clover flowering. Species-level metrics were calculated for **a.** widespread species (*A. mellifera*, *B. terrestris*, *B. lapidarius*), and **b.** long-tongued bumblebee species known to benefit from clover after crop bloom (*B. hortorum*, *B. sylvarum* and *B. pascuorum* and *B. subterraneus*) (Riggi et al., 2021). These species were present across clover and control landscapes and bloom periods which made it possible to evaluate whether they changed their role within the networks. Species-level metrics described in Table 2 were extracted using the ‘specieslevel’ function in the ‘bipartite’ package (C. F. Dormann et al., 2009), the within-module degree ( $z$ ) and between-module connectivity ( $c$ ) were

**Table 1**

Landscape and local scale variables in landscapes with and without (control) clover. The 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 (includes oilseed rape) and throughout the season within 2 km radii (%). There were no significant differences in local nor landscape variables between clover and control landscapes (Riggi et al. 2021).

| Scale     | Variables                                   | Clover landscape |      |      | Control landscape |      |      |
|-----------|---------------------------------------------|------------------|------|------|-------------------|------|------|
|           |                                             | Mean $\pm$ SD    | Min  | Max  | Mean $\pm$ SD     | Min  | Max  |
| Landscape | Arable (%)                                  | 65.3 $\pm$ 17.5  | 42.6 | 91   | 71.9 $\pm$ 15.6   | 46.7 | 89.7 |
|           | SNH (%)                                     | 27.5 $\pm$ 18.2  | 5.5  | 58.5 | 27.8 $\pm$ 16.0   | 8.1  | 61.7 |
|           | Early MFC (%)                               | 8.7 $\pm$ 6.0    | 1.3  | 20.4 | 8.2 $\pm$ 4.9     | 2.9  | 17.7 |
|           | MFC (%)                                     | 11.6 $\pm$ 6.1   | 4.2  | 22.9 | 10.6 $\pm$ 5.4    | 4.9  | 19.4 |
| Local     | Floral area (m <sup>2</sup> ) – Bloom       | 4.5 $\pm$ 4.9    | 0.2  | 18.2 | 2.5 $\pm$ 2.5     | 0.2  | 7    |
|           | Floral area (m <sup>2</sup> ) - After bloom | 1.6 $\pm$ 1.7    | 0.09 | 6.3  | 1.4 $\pm$ 1.7     | 0.02 | 7.3  |
|           | Flower richness – Bloom                     | 14.6 $\pm$ 5.1   | 5    | 25   | 13.3 $\pm$ 5.1    | 3    | 27   |
|           | Flower richness - After bloom               | 8.8 $\pm$ 3.7    | 1    | 18   | 7.2 $\pm$ 3.2     | 1    | 13   |
|           | Floral dominance – Bloom                    | 0.3 $\pm$ 0.1    | 0.1  | 0.8  | 0.4 $\pm$ 0.2     | 0.08 | 0.9  |
|           | Floral dominance – After bloom              | 0.3 $\pm$ 0.2    | 0.03 | 1    | 0.4 $\pm$ 0.2     | 0.11 | 1    |

Network- and species-level metrics

**Table 2**  
Network-level and species-level metrics assessed and their ecological significance (modified from Magrath et al. (2018)).

| Network-level metrics                                        | Ecological significance                                                                                                                                                                                                                                                                                                                                                                                                              |
|--------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Weighted connectance                                         | Number of realised links among all possible links, weighted by their frequencies. It ranges from 0 to 1 and decreases with specialisation and network size (Bersier et al., 2002, van Altena et al., 2016).                                                                                                                                                                                                                          |
| Interaction evenness                                         | Higher numbers indicates a more even distribution of species interactions. The lower the evenness, the higher the specialisation in the network (C. F. Dormann et al., 2009).                                                                                                                                                                                                                                                        |
| Complementary specialisation                                 | Degree of network specialisation. Measures the deviation of interaction frequencies from a completely generalised network ( $H2 = 0$ ) to a completely specialised one ( $H2 = 1$ ) (Blüthgen et al., 2006).                                                                                                                                                                                                                         |
| Modularity                                                   | Represents the probability of showing more within-module than between module interactions, with 0 representing no within-module interactions and 1 represents only within-module interactions (Pons and Latapy, 2005).                                                                                                                                                                                                               |
| Weighted nestedness                                          | Specialisation asymmetry: the degree to which specialists interact with generalists. High nestedness is generally considered to increase network robustness in the face of perturbations. Estimated using the weighted NODF (Nestedness based on Overlap and Decreasing Fill) metric where a larger value indicates higher nestedness, with values ranging from 0 to 100 (Almeida-Neto et al., 2008; Almeida-Neto and Ulrich, 2011). |
| <b>Species-level metrics</b>                                 | <b>Ecological significance</b>                                                                                                                                                                                                                                                                                                                                                                                                       |
| Normalised degree                                            | Number of plant partners a pollinator has compared to the total pool of potential partners, ranges from 0 to 1 (C. Dormann et al., 2009).                                                                                                                                                                                                                                                                                            |
| Species-level specialisation                                 | Degree of species specialisation in networks. The level of exclusiveness of a species. Higher values indicate greater levels of specialisation or partner exclusiveness. It ranges from 0 to 1 (Blüthgen et al., 2006).                                                                                                                                                                                                              |
| Within-module degree (z) and between-module connectivity (c) | Number of links within modules for z (from 0 to 1) and between modules for c (from 0 to 1). <b>Module hubs</b> - highly connected species within their own module (high z, low c); <b>connectors</b> - species linking several modules (low z, high c); <b>network hubs or super generalists</b> - species with both a high z and a high c (Olesen et al., 2007).                                                                    |
| Nested-rank                                                  | Quantifies the generalism of a given species with increasing values for more specialist or rare species. It ranges from 0 (generalist) to 1 (specialist) (Alarcón et al., 2008).                                                                                                                                                                                                                                                     |

calculated using the 'Czvalues' function.

### 3. Statistical analyses

#### 3.1. Community analyses

Non-metric multidimensional scaling (NMDS) ordination was used to investigate differences in community composition of the flower-visitors community between landscapes with and without clover and between bloom periods. To evaluate differences between treatments a PERMANOVA was conducted using the 'betadisper' and 'adonis' functions with 999 permutations from the 'vegan' package (Oksanen et al., 2022), followed by the 'pairwise.adonis2' function to investigate post-hoc comparison including "landscape" as strata. When significant effects were found, indicator species analyses using the 'indicspecies' package were run to assess pollinators and flowers associations with

treatments (Cáceres et al., 2023). Pollinator community metrics (i.e. total abundance, richness, Pielou's evenness) were calculated using the 'vegan' package. Mixed effect models were used to investigate impact of clover presence in the landscape, bloom period and environmental variables on pollinator community metrics. Explanatory variables included mass-flowering crop treatment, bloom period and their two-way interaction, as well as SNH cover and local flower variables (richness, dominance and area). SNH cover and the local flower covariates (area, richness and dominance). Floral area, richness and 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). SNH cover was not correlated with local flower variables ( $\rho < 0.25$  for all combinations). We included transect nested within landscape as a random factor to account for non-independence of the repeated surveys carried out across bloom periods. Model assumptions were checked using diagnostic residual plots from 'DHARMA' package (Hartig and Lohse, 2020). Pollinator abundance was analysed using a negative binomial distribution, richness with a Conway-Maxwell Poisson distribution to account for overdispersion and evenness with a Gaussian distribution. Multicollinearity was not an issue for any models ( $VIF < 2$ ; Zuur et al., 2009). Additionally, the impact of mass-flowering crop presence and bloom was investigated for abundances of specific pollinator group when enough data was available. We simplified models using backward model simplification based on likelihood ratio tests (Zuur et al., 2009) keeping mass-flowering crop treatment and bloom period. Post-hoc tests using the 'emmeans' package (Lenth et al., 2021) were carried out. We estimated the marginal  $R^2$  of the models using 'r.squaredGLMM' (Nakagawa and Schielzeth, 2013). All analyses were done in R (R Core Team, 2020, version 3.6.2) using the 'glmmTMB' package (Brooks et al., 2017).

#### 3.2. Network level analyses

To evaluate whether there were changes in the plant-pollinator network structure (i.e., weighted connectance, interaction evenness, complementary specialisation, modularity and weighted nestedness, Table 2) between clover and control landscapes we used general linear mixed models. We built plant-pollinator networks for each transect, pooling the data from the two surveys per transect per bloom period. Fixed effects were: mass-flowering crop treatment (i.e. presence (MF, mass-flowering) and absence (C, control) of clover in the landscape), the proportion of SNH cover in the 2 km radius landscape (forest and pasture), flower area, flower species richness and flower dominance in the transect, and bloom period (during and after clover bloom), as well as the two-way interactions of crop bloom period with mass-flowering crop treatment. We included transect nested within landscape as a random factor to account for non-independence of the repeated surveys carried out across bloom periods.

#### 3.3. Species level analyses

In another set of models, we tested the effect of bloom period, mass-flowering crop treatment (MF versus C), SNH cover and local flower covariates (area, richness and dominance) on species level metrics: normalised degree, species-level specialisation, within and between-module connectivity, and nested rank (Table 2). We fitted one model per species-level metric for the dominant 3 species (*A. mellifera* (28.0 %), *B. terrestris* complex (33.7 %), *B. lapidarius* (6.6 %)) and four species of long-tongued bumblebee (*B. hortorum* (0.9 %), *B. sylvarum* (4.1 %) and *B. pascuorum* (2.0 %) and *B. subterraneus* (0.7 %) (Riggi et al., 2021). Fixed factors were the same as those included in the previous set of models. We further included the abundance of each pollinator species within the transect as an additional fixed factor as well as its interaction with bloom period. Transect nested within landscape was included as random effect.

We ran all combinations of models using the 'dredge' function in the



'MuMin' package with bloom period and species abundance in the species level analyses as fixed effects (Barton, 2018), and selected the best models based on the lowest second-order Akaike information criterion values (AICc). If more than one plausible model existed (i.e., when  $\Delta\text{AICc} < 2$  for more than one model, Burnham and Anderson, 2004) we computed average estimates for each variable across all models in which each variable was retained (full average). All analyses were performed in R 4.1.2 (R Development Core Team).

## 4. Results

### 4.1. Pollinator communities

Overall, 14,541 plant-pollinator interactions were recorded across 20 landscapes. Pollinator community composition per transect per landscape, significantly differed between both bloom period ( $R^2 = 5.8\%$ ,  $p = 0.001$ ) and landscape type ( $R^2 = 4.0\%$ ,  $p = 0.001$ ) (Fig. 1a). *Bombus rupestris* (est = 0.157,  $p = 0.002$ ) was associated with clover landscapes. There were no effects of mass-flowering crop presence nor blooming on overall pollinator per transect (Fig. 1b, Clover:  $p = 0.307$ ; Bloom:  $p = 0.305$ ), pollinator richness per transect (Fig. 1d, Clover:  $p = 0.835$ ; Bloom:  $p = 0.993$ ) and pollinator evenness (Fig. S2a, Clover:  $p = 0.867$ ; Bloom:  $p = 0.554$ ). Pollinator communities were affected by environmental variables, with total pollinator abundance positively related to flower dominance (Fig. 1c), pollinator richness positively related to flower richness (Fig. 1e) and evenness negatively related to flower dominance (Fig. S2b). When investigating specific pollinators abundances per transect, *Apis mellifera* (est  $\pm$  se =  $0.57 \pm 0.23$ ,  $p = 0.007$ ), *Bombus hypnorum* (est  $\pm$  se =  $0.73 \pm 0.28$ ,  $p = 0.009$ ) and hoverflies in the genus *Platycheirus* (est  $\pm$  se =  $0.72 \pm 0.23$ ,  $p = 0.002$ ) were more abundant and *B. terrestris* were less abundant in clover landscapes (est  $\pm$  se =  $-0.42 \pm 0.19$ ,  $p = 0.024$ ) (Fig. S3). *Bombus*

*lapidarius* (est  $\pm$  se =  $-0.46 \pm 0.18$ ,  $p = 0.013$ ) were more abundant after clover bloom, and *B. vestalis* (est  $\pm$  se =  $0.59 \pm 0.30$ ,  $p = 0.049$ ) and hoverflies in the genus *Platycheirus* (est  $\pm$  se =  $1.02 \pm 0.23$ ,  $p < 0.001$ ) were more abundant during clover bloom (Fig. S3). Flower communities at the transect scale differed during and after red clover bloom and between landscapes with or without clover (NMDS stress = 0.19, Fig. S4) No differences were found in floral area, richness and dominance between clover and control landscapes within bloom periods (Table S3).

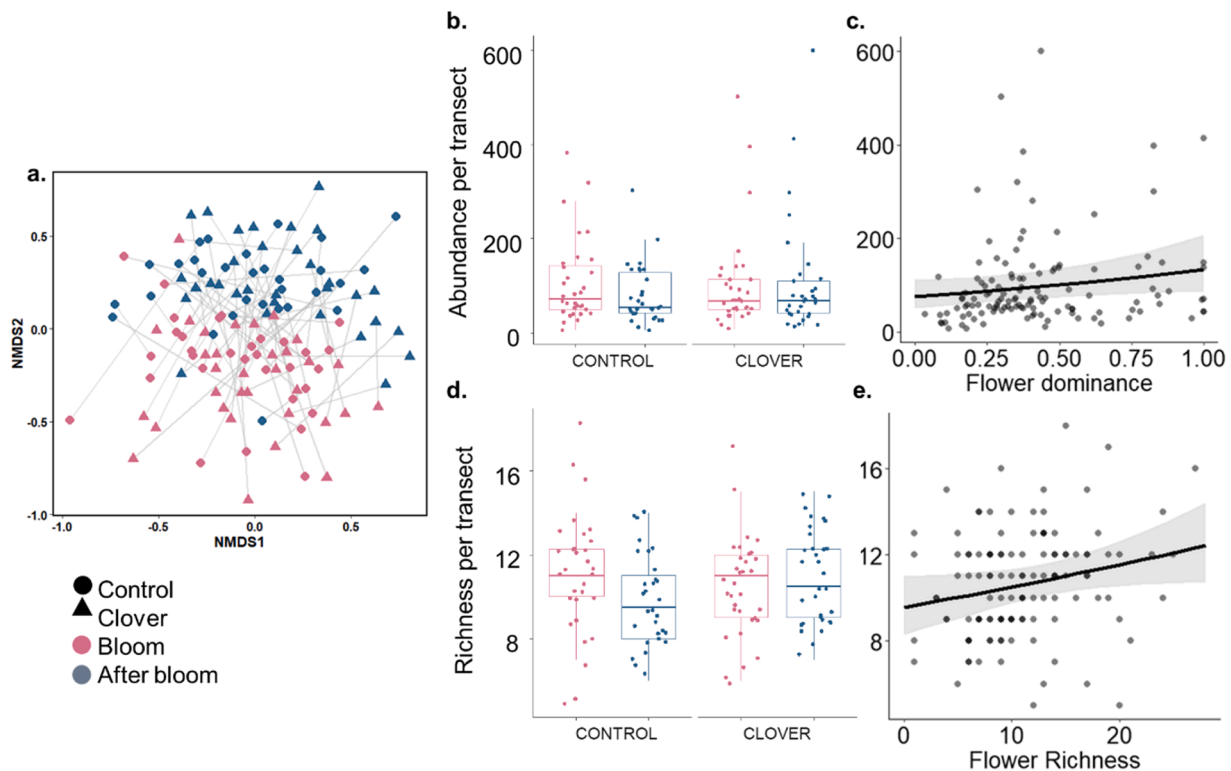
### 4.2. Network-level analyses

The examined networks had on average low connectance (i.e. realised interactions among all possible interactions, min = 0.08, max = 0.32), low to moderate levels of nestedness (i.e. generalist and specialist interactions, min = 0, max = 62.50), interaction evenness (i.e. distribution of interactions between species, min = 0.24 max = 0.72), and modularity (i.e. within module interactions, min = 0.01, max = 0.61), with moderate levels of complementary specialisation (Fig. S5, Table 3). Metrics differed from null model estimates, indicate that the measured metrics were non-random (Fig. S7). There was a general lack of

**Table 3**

Mean, standard error (se), minimum and maximum values (from the empirical data) for investigated network metrics.

| Variable                     | Mean $\pm$ Se    | Min - Max  |
|------------------------------|------------------|------------|
| Complementary specialisation | 0.46 $\pm$ 0.02  | 0.00–1.00  |
| Interaction evenness         | 0.55 $\pm$ 0.01  | 0.24–0.72  |
| Modularity                   | 0.27 $\pm$ 0.01  | 0.01–0.61  |
| Nestedness                   | 25.59 $\pm$ 1.32 | 0.00–62.50 |
| Connectance                  | 0.19 $\pm$ 0.00  | 0.08–0.32  |



**Fig. 1.** Pollinator community characteristics in relation to environmental variables: (a) NMDS plot of pollinator community composition dissimilarity at the transect scale between clover and control landscapes and between red clover bloom periods, lines connect landscape during and after clover crop bloom (stress = 0.20). Boxplots of (b) total pollinator abundances per transect and (d) pollinator richness per transect across treatments. Model predictions showing the relations between (c) flower dominance and pollinator abundance per transect (est  $\pm$  se =  $0.57 \pm 0.28$ ,  $p = 0.042$ ,  $R^2_{\text{marginal}} = 11.3\%$ ) and (e) between transect flower richness and pollinator richness per transect (est  $\pm$  se =  $0.009 \pm 0.004$ ,  $p = 0.043$ ).

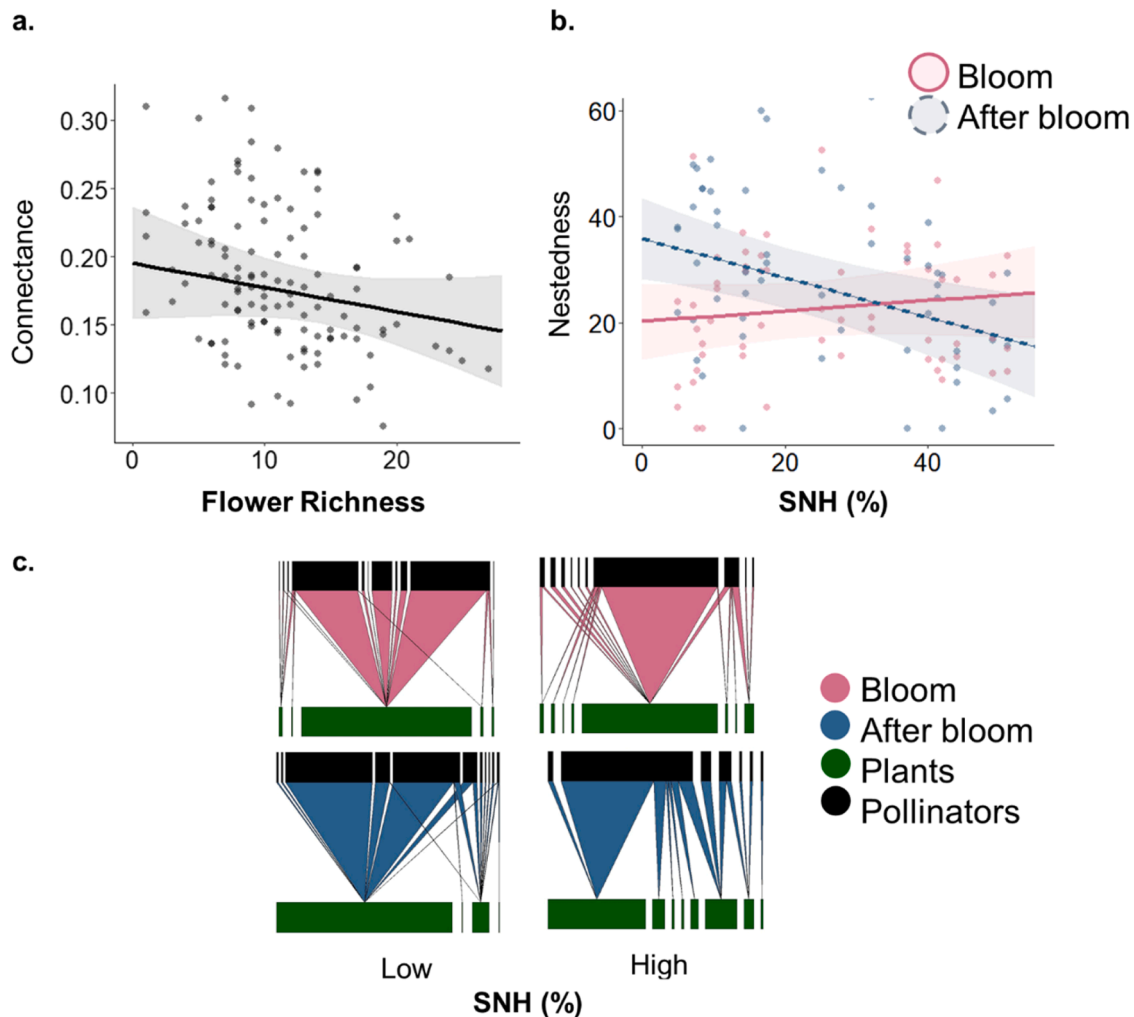
interactive effects between the presence of clover in the landscape and crop bloom period on the overall network structure (Table S4). Plant-pollinator network structure was affected by SNH cover in the landscape after crop bloom and local scale flower richness. Connectance in the network was negatively related to flower species richness, i.e. interactions between species were lower in flower rich areas ( $-0.002 \pm 0.001$ ,  $p = 0.03$ , Fig. 2) (Table S4). Networks in landscapes with more SNH cover were less nested (Fig. 2) and more specialised (i.e. a higher complementary specialisation (Bloom:  $\text{est} \pm \text{se} = -0.0004 \pm 0.002$ , CI  $-0.005/0.004$ ; After bloom:  $0.006 \pm 0.002$ , CI  $0.004/0.01$ ), Fig. S6) after the red clover bloom period.

#### 4.3. Species-level analyses

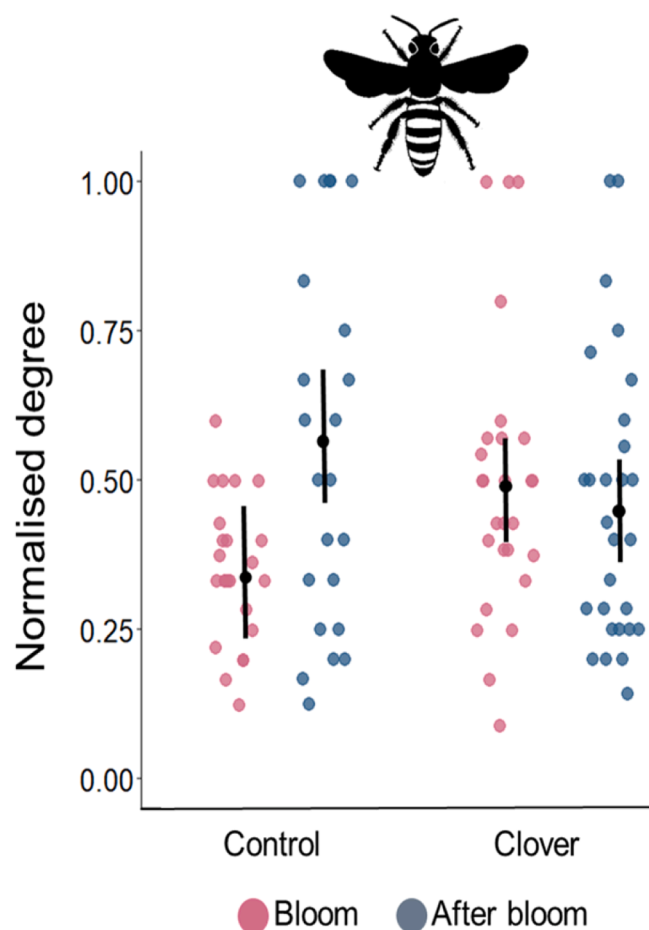
Because of low abundances, within-module degree and/or between-module connectivity could not be assessed for *B. hortorum*, *B. pascorum*, *B. sylvarum* and *B. subterraneus*, as model assumptions were not met (Table S4). Overall changes in species roles within plant-pollinator networks were mostly driven by bloom period, local scale flowers' characteristics and SNH cover (Table S4, Table S5). The exception was *A. mellifera*, which used a lower proportion of available plants (i.e. lower normalised degree) during clover bloom in non-clover landscapes

compared to after bloom ( $C_{\text{Bloom}} - C_{\text{After}} -0.22 \pm 0.06$ ,  $p = 0.005$ ) and this was marginally lower compared to during crop bloom in clover landscapes ( $C_{\text{Bloom}} - MF_{\text{Bloom}} -0.16 \pm 0.06$ ,  $p = 0.079$ ) (Fig. 3). Local and landscape variables affected bumblebee species-level network metrics (Table S4). *B. terrestris* used a lower proportion of available plants with an increase in transect-scale flower richness (normalised degree:  $-0.01 \pm 0.005$ ,  $p = 0.040$ ) and with more SNH cover after crop bloom (Fig. 4a). *B. terrestris* specialisation increased with flower richness ( $0.013 \pm 0.004$ ,  $p = 0.002$ ) and declined with SNH cover during bloom (Fig. 4b). Furthermore, *B. terrestris*, interactions with a close and limited group of species increased with flower dominance (within-module degree,  $1.11 \pm 0.39$ ,  $p = 0.005$ ), while interactions with species outside this group (between-module connectivity) declined with flower dominance in the period after bloom (Fig. 4c). *B. hortorum* used a lower proportion of the available plants with an increase in flower richness (normalised degree:  $-0.01 \pm 0.004$ ,  $p = 0.016$ ). *B. sylvarum* specialisation increased with flower richness after clover bloom (Fig. 4d). With increased flower richness in the landscape *B. pascorum* used a lower proportion of the available plants (normalised degree:  $-0.013 \pm 0.004$ ,  $p = 0.002$ ).

On average we found low values for both between (c) and within-module (z) connectivity for the bumblebee species (Table S5), with



**Fig. 2.** Models' estimates and schematics of the interactive effect of flower richness and SNH cover on network metrics during (pink, solid lines) and after (blue, dashed lines) red clover bloom. (a) Weighted connectance was negatively related to flower richness. Weighted nestedness was (b) negatively related to SNH cover after crop bloom (Bloom:  $0.07 \pm 0.13$ , CI  $-0.18/0.33$ ; After bloom:  $-0.40 \pm 0.13$ , CI  $-0.67/-0.13$ ). Shaded bands represent 95 % confidence intervals (CI) obtained from 1000 iterations, with fixed marginal totals, of the original network matrices. (c) bi-partite network layout of plant-pollinator networks in one "low SNH cover" (site 35\_C, 7 % SNH) and one "high SNH cover" (site 27\_C, 44 % SNH) landscape during and after bloom.



**Fig. 3.** Model prediction showing normalised degree (proportion of available plants used) for *A. mellifera*. The normalised degree was lower in control landscapes without clover compared to landscapes with clover during the period during (pink) but not after (blue) clover bloom.

none of the dominant species acting as a network hub i.e., being highly linked species within their own module (with  $c > 0.63$  and  $z > 2.5$ , Olesen et al., 2007). Nested rank (the specialist value of the species) showed lower values for the dominant species (*A. mellifera*, *B. terrestris* complex and *B. lapidarius*) (Table S5).

## 5. Discussion

### Mass-flowering red clover cultivation does not affect network structure in non-crop habitats

Despite differences in pollinator communities between clover and non-clover landscapes, plant-pollinator networks were not affected by cultivation of late-season mass-flowering red clover crops. In previous work done in the same systems, mass-flowering clover crops resulted in a temporary dilution of bumblebees in non-crop habitats during red clover bloom, and in higher bumblebee species richness and diversity in the red clover landscapes after crop bloom (Riggi et al., 2021). Therefore, changes in plant-pollinator network structure between clover and non-clover landscapes were anticipated. However, network structure in non-crop habitats remained constant between landscapes with and without clover cultivation. It is possible that the impact of red clover crop bloom on pollinator communities was not strong enough to trigger significant changes in the plant-pollinator networks. Indeed, despite shifts in bumblebee and honeybee abundances due to clover bloom (Fig. S3), overall pollinator abundance, richness and evenness did not differ between clover and control landscapes nor bloom periods (Fig. 1). We found that network connectance decreased with flower richness

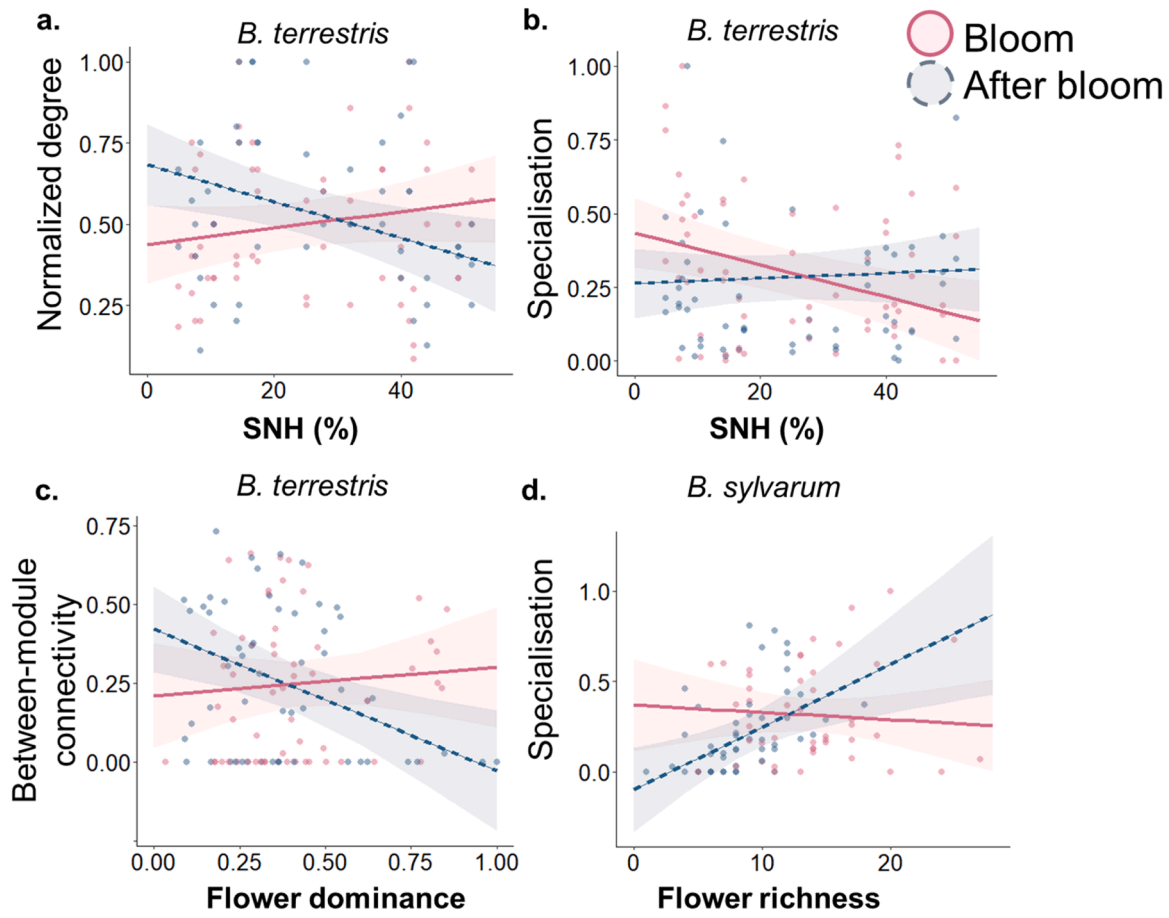
(Fig. 2a). It is well documented that network connectance decreases when the number of nodes increases in plant-pollinator networks (Olesen and Jordano, 2002). Increased network complexity (i.e. low connectance, modular and nested network structure) is hypothesised to lead to higher network robustness against disturbances (Ebeling et al., 2011). Our results are consistent with previous findings that plant-pollinator network structure in non-crop habitats are robust to early-season mass-flowering crop resource shifts in oilseed-rape systems (Magrach et al., 2018). Together these findings indicate that plant-pollinator interactions in non-crop habitats in temperate agricultural landscapes are robust to patchy and seasonally fluctuating mass-flowering crop resources.

### 5.1. Low complexity of plant-pollinator networks in agro-ecosystems

The networks in our study were characterised by low connectance (i.e. realised interactions among all possible interactions), low nestedness (i.e. generalist and specialist interactions), low interaction evenness (i.e. distribution of interactions between species), and low modularity (i.e. within module interactions), as well as moderate levels of complementary specialisation (Table 3). These characteristics, indicate that networks were dominated by few generalist species, which appear to be typical of plant-pollinator networks in agricultural landscapes (Chakraborty et al., 2021; Gay et al., 2024; Proemans et al., 2024; Redhead et al., 2018). Networks are indeed expected to be less specialised in disturbed ecosystems, as these select for species capable of readily utilising a wide array of resources (Devictor et al., 2008; Soares et al., 2017; Vázquez and Simberloff, 2002). In line with this, honeybees and *B. terrestris*, both generalist pollinator species that form large colonies, were the dominant pollinators in our systems (Fig. S3). Previous pollinator surveys in the same region indicate that communities were dominated by generalist *Bombus* species and that increasing landscape complexity did not benefit species richness in the region (Olsson et al., 2023). Low regional species pool diversity could explain the low variability in plant-pollinator networks. Increasing taxonomic resolution and surveys effort over the season as well as collecting pollen from flower visitors to assess interactions, would allow to identify more specialised plant-pollinator interactions and possibly detect more subtle shifts in network structure due to mass-flowering crop resources pulses (Avalos et al., 2023).

### 5.2. SNH cover impacts network- and species-level specialisation

As expected SNH cover affected network structure, however, the effect depended on crop phenology. We found that network specialisation increased and nestedness declined with SNH cover after clover crop bloom (Fig. 2, S6), indicating that overall species narrowed their diet and that less species interacted with the same resources with increasing SNH cover after clover bloom. Other studies showed that SNH cover in the landscape is associated with more diverse habitats and flower resources for pollinators to forage on, affecting pollinator communities and species foraging behaviour (Martínez-Núñez et al., 2022). The positive relationship between SNH and network specialisation after clover bloom might be due to resource partitioning in landscapes with greater non-crop resources and SNH in the landscape (Lami et al., 2021; Riggi et al., 2023; Schoener, 1974). Greater flower availability with more non-crop habitat cover might increase the possibilities of generalist pollinator species to focus on different resources to optimise foraging and avoid competition at time when flower resources are scarce (e.g. after clover bloom) (Morán-López et al., 2022; Timberlake et al., 2019). In line with this hypothesis, *B. terrestris* normalised degree declined with increasing SNH cover, after clover bloom (Fig. 4). Indicating that this generalist pollinator species became more specialised in landscapes with high SNH cover after clover bloom. This effect was, however, somewhat reversed during clover bloom as *B. terrestris* specialisation decreased with SNH cover (Fig. 4). A large diet breadth



**Fig. 4.** Bumblebee species-level network metrics response to local and landscape variables during (pink, solid lines) and after (blue, dashed lines) red clover bloom. For *B. terrestris*: (a) normalized degree (nd) (Bloom:  $0.002 \pm 0.002$ , CI  $-0.001/0.006$ ; After bloom:  $-0.004 \pm 0.002$ , CI  $-0.008/-0.0005$ ) was negatively related to SNH after crop bloom; (b) specialisation (d') was negatively related to SNH cover during red clover bloom (Bloom:  $-0.005 \pm 0.001$ , CI  $-0.009/-0.001$ ; After bloom:  $0.0008 \pm 0.001$ , CI  $-0.003/0.004$ ); and (c) between-module connectivity (c) was negatively related to flower dominance after the crop bloom period (Bloom:  $0.07 \pm 0.17$ , CI  $-0.27/0.41$ ; After bloom:  $-0.36 \pm 0.15$ , CI  $-0.66/-0.06$ ). For *B. sylvarum* (d) specialisation (d') increased with flower richness after crop bloom (Bloom:  $-0.0070.009 \pm 0.0090.008$ , CI  $-0.0026/0.012$ ; After bloom:  $-0.034 \pm 0.01$ , CI  $-0.052/-0.017$ ). Shaded bands represent 95 % confidence intervals (CI).

may allow *B. terrestris* individuals to respond to less abundant and diverse flower resources later in the season, when clover ceased flowering. On the other hand, long- and medium tongued bumblebees, such as *B. hortorum*, *B. sylvarum* and *B. pascorum*, foraged on a lower number of available flower species with increasing flower richness (Table S4), which is in line with their more specialised diet breadth (Goulson et al., 2008). *B. sylvarum* became more specialised with increasing flower richness after clover bloom only (Fig. 4), suggesting a more flexible foraging behaviour during clover bloom. Specialisation and complementarity may help reduce inter-individual and inter-specific exploitative competition for floral resources and thus favour coexistence in pollinator assemblages, especially in a context of agroecosystems, where flower resources are generally limited and fluctuating due to mass-flowering crop cultivation (Bolnick et al., 2003). Investigations into the species of pollen carried by pollinators across flower resource gradients would shed light on drivers of pollinators' shifts in diets (Avalos et al., 2023; Pornon et al., 2019).

### 5.3. Wild pollinator species-specific roles are not affected by mass-flowering clover cultivation

Contrary to our hypothesis, mass-flowering clover crops did not affect wild pollinator species' role in the network. Consistent with previous finding, wild pollinator species-specific roles in the network were mostly affected by pollinator density, and local flower resources, such as flower diversity and dominance (Table S4) (Fontaine et al., 2008;

Magrath et al., 2018; Morán-López et al., 2022). *Apis mellifera* was the only species to change its role in response to the presence of clover in the landscape, with a marginally lower normalised degree in landscapes without clover during crop bloom (Fig. 3). This indicates that *A. mellifera* visited fewer flower species, relative to the available species pool, in non-clover landscapes. *Lamium purpureum* and *Phacelia tanacetifolia* were two flower species that associated strongly to landscapes without clover (Fig. S4). Both flowers are highly attractive to *A. mellifera* as they produce large quantities of pollen or nectar. Therefore, *A. mellifera* individuals might have preferentially foraged on these more rewarding flower species in non-clover landscapes, thus decreasing their normalised degree in the networks. Honeybee hives were present in clover landscapes, while there were no differences in honeybee abundances between clover and control landscapes (Fig. S3), we cannot exclude that hives might have affected honeybees' foraging behaviour. Further studies investigating individual foragers' pollen richness are required to understand how individual specialisation on different floral resources affect networks (Avalos et al., 2023; Pornon et al., 2019). We could not assess species-specific role shifts for species that rarely occurred; however, we can hypothesise that changes in dominant pollinators' role in the network might also affect less widespread species interactions (Valido et al., 2019).

We found no evidence that late season red clover crop bloom impacts plant-pollinator network structure in non-crop habitats in our study area. SNH cover and flower communities in the agricultural landscape mediated plant-pollinator network structure in non-crop habitats more



than mass-flowering crop resource pulses. SNH cover was associated to higher specialisation of interaction networks after clover ceased flowering. Increasing specialisation may help reduce inter-individual and inter-specific competition for non-crop flower resources at a time of the season when these resources are limited. While further studies are needed to understand how individual pollinators shift their foraging behaviour in response to mass-flowering crops resource availability, our results indicate that pollinators species-role and interaction networks are little affected by red clover mass-flowering crop resources. Increasing the amount of SNH cover in the landscape and local flower richness will likely benefit less-widespread pollinators, and buffer pollinator communities against resource shifts due mass-flowering crop cultivation. To comprehensively understand the impact of early-season mass-flowering crops on plant-pollinator interactions later in the season, and to evaluate the importance of non-crop flowering resources throughout the season, further investigations of plant-pollinator networks across the cropping season will be essential.

### Statement on inclusion

Our study brings together authors from a number of different countries, and research disciplines. Authors were engaged with the research to ensure that the diverse sets of perspectives they represent was considered.

### CRediT authorship contribution statement

**L.G.A. Riggi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **T.S.M. Teixeira:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Å. Berggren:** Writing – review & editing, Conceptualization

### 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

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.109455](https://doi.org/10.1016/j.agee.2024.109455).

### Data availability

Data to support the findings for this study is available on Zenodo repository ([10.5281/zenodo.14258179](https://doi.org/10.5281/zenodo.14258179)).

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