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RESEARCH ARTICLE

Management of dry calcareous grasslands drives pollinator communities through availability of key forage plants

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Abstract

1. Dry calcareous grassland remnants play a key role in conserving European pollinators. In agricultural landscapes, agri-environmental schemes (AES; e.g., extensively managed meadows) and other semi-natural habitats (SNH; e.g., forests) can provide complementary resources. However, it remains unclear (i) how local factors (patch size and floral resource quality), landscape context (AES and SNH cover) and their interactions affect different pollinator groups, including rare species; (ii) which foraging plants are key to promote pollinators; and (iii) how local management (grazing vs. mowing) influences floral quality.
2. We surveyed wild bees, butterflies, hoverflies, and their interactions with flowering plants across 27 protected dry calcareous grasslands in Switzerland, spanning independent gradients of patch size, floral resource quality, and surrounding AES meadow and woody SNH cover.
3. Locally, patch quality (floral cover and species richness) was more important than patch size in promoting species richness of all pollinator groups and density of butterflies and wild bees. At the landscape-scale, woody SNH promoted wild bee density in focal calcareous grasslands, while butterfly richness decreased with increasing AES meadow cover, independent of local factors (no significant interactions).
4. Among 171 recorded flowering plant species, 58 were identified as key forage plants (i.e., species with disproportionately high pollinator visitor frequency or richness relative to flower cover), including 11 supporting rare pollinators. Key plants varied across pollinator group and season. While local management type did not affect flower cover, grazed sites supported, on average, 32% greater floral species richness than mown sites. Abundance weighted turnover of flowering species was greater among mown and grazed calcareous grasslands than among sites of the same management.
5. *Synthesis and applications*. Pollinator conservation in calcareous grasslands should prioritize enhancing local patch quality while promoting landscape heterogeneity, including woody SNH. To improve forage quality, our analytical approach supports targeted grassland management in selecting key forage plants, promoting complementary and diverse floral assemblages that support multiple pollinator

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taxa, including rare species, throughout the season. Extensive grazing can promote floral species richness, including key forage plants, whereas combining mowing and grazing across different patches of calcareous grassland better promotes beta diversity of floral resources.

KEYWORDS
Anthophila, conservation areas, extensively managed meadows, insect biodiversity, Lepidoptera, pastures, plant–pollinator networks, Syrphidae

1 | INTRODUCTION

Wild insect pollinators play a crucial role in ecosystem function and global food security (IPBES, 2016). While wild bees are among the most efficient crop pollinators, other pollinators such as hoverflies also contribute to pest control, and butterflies can serve as valuable bioindicators (Chaplin-Kramer et al., 2013; Greenleaf & Kremen, 2006; Khalifa et al., 2021; Rakosy & Schmitt, 2011). Diverse pollinator communities support plant population persistence, and the maintenance of biodiversity and stability of natural ecosystems (Katumo et al., 2022; Klein et al., 2007; Ollerton et al., 2011). Despite their importance, wild insect pollinators are facing global declines, primarily driven by human-induced land use change and associated habitat loss, fragmentation and degradation (Klein et al., 2018; LeBuhn & Vargas Luna, 2021; Potts et al., 2016). In particular, dry calcareous grasslands are one of the most species-rich semi-natural habitats in Europe, harbouring many endemic plants and red-listed invertebrate species (Carvell, 2002; WallisDeVries et al., 2002; Wilson et al., 2012). However, during the last century, an estimated 90% of the remaining habitat has been lost to agricultural intensification or abandonment, resulting in highly fragmented remnants (Krauss et al., 2010; Brückmann et al., 2010; WallisDeVries et al., 2002). When remnant patches are very small, they might fail to maintain strong and viable pollinator populations (Biegerl et al., 2025; Chase et al., 2020; Klaus et al., 2021).

In response to these challenges, there is growing recognition for the need to conserve, restore, and create habitats that support pollinators. In agricultural landscapes, the implementation of agri-environment schemes (AES) is, besides the maintenance of semi-natural habitats (SNH), among the most important measures to promote pollinators (Batáry et al., 2015; Kovács-Hostyánszki et al., 2017). Including a variety of these habitats in the landscape can provide important complementary resources for mobile species and build stepping stones for dispersal and colonization of focal habitat patches (Maurer et al., 2022; Bartual et al., 2019; Ganser et al., 2021; Albrecht et al., 2007). However, studies which have investigated pollinator responses to these habitat types have reported mixed outcomes, depending on pollinator group and landscape context (Kleijn et al., 2006; Lichtenberg et al., 2025; Neumüller et al., 2020; Biegerl et al., 2025; Luppi et al., 2018; Meyer et al., 2009). Moreover, their potentially important role in shaping pollinator communities within conservation areas situated in agricultural landscapes with varying amounts of AES and SNH areas remains largely unexplored. Therefore, comparing the responses of multiple pollinator taxa, with different ecological requirements and life history traits, to shared local and landscape factors is critical for both optimal management of conservation areas and the spatial implementation of AES interventions and maintenance of SNH areas.

Identifying key foraging plants, that is, those either disproportionately visited or supporting a high species richness, can aid in quantifying habitat quality and identifying management strategies to improve it. While some key plant lists exist for certain agricultural habitats (e.g., Kuppler et al., 2023; Russo et al., 2013; Sutter et al., 2017), they are often bee-focused and context dependent, whereas those targeting multiple pollinator groups, and rare species, in areas of conservation priority are lacking. Moreover, cutting regimes (i.e., grazing vs. mowing) may influence the quality of dry calcareous grasslands, including the availability of key plants for pollinators. Grazing can promote higher floral diversity through heterogenous feeding, while mowing may support community evenness through homogenous cutting (Tälle et al., 2016). On the other hand, increased nutrient input in grazed grasslands through animal excreta has also been associated with declines in plant diversity (Dickson & Foster, 2011). Since management can alter vegetation characteristics and thereby impact pollinator communities, an improved understanding of how different regimes impact floral resources could inform targeted interventions for improved habitat quality.

In this study, we surveyed wild bees, butterflies, and hoverflies and recorded plant–pollinator interactions across 27 dry calcareous grasslands in Switzerland along independent gradients of local and landscape factors to answer the following questions:

I. How do local factors (e.g., floral resource availability and patch size) and landscape-scale drivers (e.g., AES and SNH cover) affect the density and diversity of the different pollinator groups and their rare species?
II. Do local and landscape factors interact?, that is, are AES interventions in agricultural landscapes surrounding calcareous grassland remnants more or less effective if the latter are small and of poor floral resource quality?
III. What are the key floral resource plants in calcareous grasslands for each pollinator group and their rare species?
IV. How does management type (grazing or mowing) affect local floral quality in dry calcareous grasslands, and is beta diversity

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of flowering plants greater between mown and grazed sites than between sites under the same management?

2 | MATERIALS AND METHODS

2.1 | Study region and sampling sites

The study was conducted in 2022 across 27 dry calcareous grassland patches (hereafter referred to as sites) located throughout the northern half of the Swiss Plateau and Jura regions (cantons: Aargau, Basel, Bern, Jura, Schaffhausen, Solothurn, and Zurich) (see Figure S1). Sites were located within agricultural landscape mosaics dominated by agricultural permanent grasslands of different land use intensity, croplands and woody semi-natural habitats (WSNH; including hedges, forest, and sparse trees/shrubs). Focal sites were selected to maximize independent gradients of both local (focal patch size) and landscape-scale factors (amount of extensively managed AES meadows and WSNH in the landscape) (Figure 1). AES meadows are among the most widespread types of agri-environmental measures in Switzerland (BLW, 2023). The most important management prescriptions of the Swiss AES for extensively managed meadows are prohibition of any fertilizer applications and postponed mowing (no mowing before 15 June for the Swiss Plateau region) leading to overall decreased mowing intensity (one to two cuts per year) (Bundesrat, 2013; Huguenin-Elie et al., 2017; Knop et al., 2006). Intensively managed permanent meadows, in contrast, typically receive between 150 and 200 kg nitrogen per hectare and are generally mown up to five or six times per year (Huguenin-Elie et al., 2017), with the first cut already in May (Knop et al., 2006).

Local patch size and landscape-scale variables were measured and quantified using Geographic Information System (GIS; ArcGIS Pro version 10.7, ESRI), using publicly available Swiss land use layers (map.geo.admin.ch & geodienste.ch). Focal calcareous grassland patches were selected along a range of 0.3 ha to 24.5 ha. Landscape-scale amounts of land use types were measured as percentage cover within either 500 m (wild bees) or 1 km (hoverfly and butterfly) radius buffers from the centre of the focal patch. Taxon-specific radii were selected based on existing literature (Rivers-Moore et al., 2023; Rundlöf et al., 2008; Schirmel et al., 2018). All required permits for the collection of wild pollinators in dry calcareous grasslands were obtained from relevant cantonal authorities prior to fieldwork.

2.2 | Sampling of wild pollinators and plants

Standardized transect walks were conducted across three sampling rounds at each site from April to July 2022. Across rounds, the sampling order of each site varied among morning, noon or afternoon, and the exact location of transects within the focal grassland patch was randomly chosen during each visit. Surveys took place between 8:30 am and 5:30 pm on warm, dry days with low wind. All wild bees (no managed honey bees), hoverflies, and butterflies (including burnet moths), as well as plant–pollinator interactions (i.e., flower visits by pollinators) were recorded along 30 min constant-pace walks, pausing the clock during pollinator catching and processing, resulting in a total observation time of 81 h. Transects for

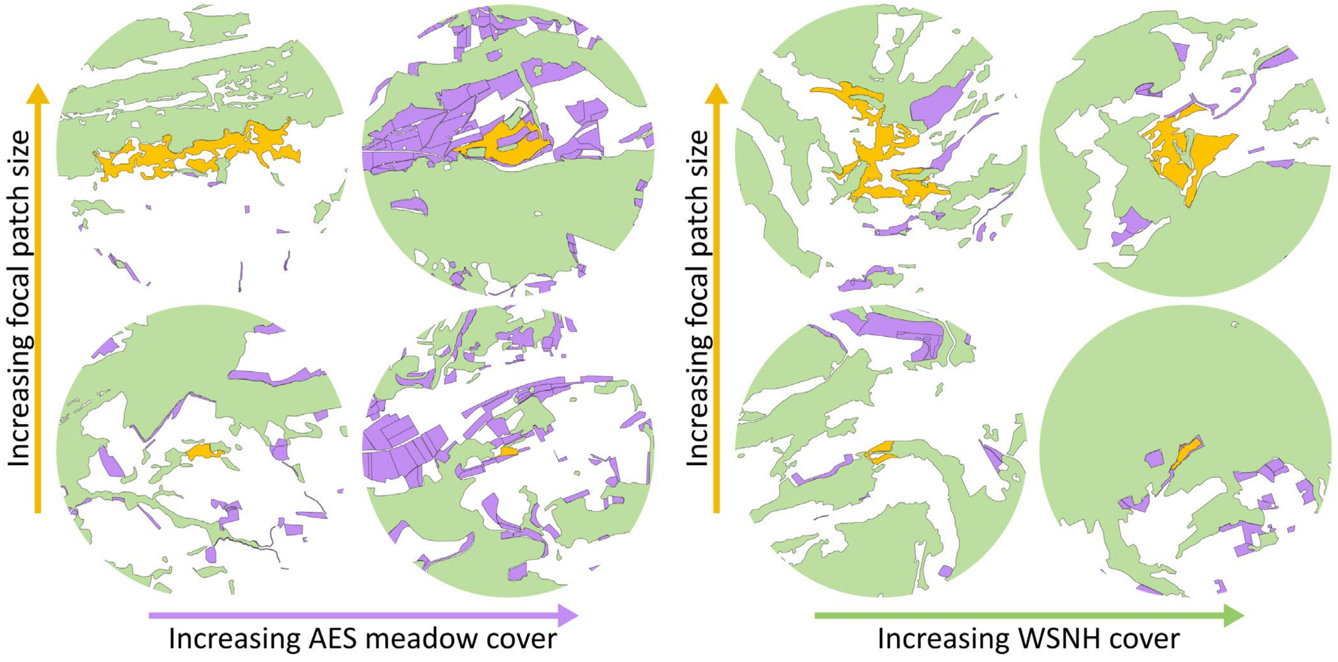

FIGURE 1 Graphical example of focal sites with independent local- and landscape-scale gradients. Central dry calcareous grassland focal patches ranging in size are shown in yellow, AES meadows and WSNH ranging in proportion in the surrounding agricultural landscape are shown in purple and green, respectively. Colour-associated arrows indicate increasing land use type cover.

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bees and hoverflies were 500 m long and 2 m wide (1000 m^2), while those for butterflies were performed separately over 600 m long and 5 m wide (3000 m^2) transects. Pollinators and flowering plants were either identified to species level in the field or were collected (photographed in the case of butterflies) and later sent for taxonomic identification by experts (see Acknowledgements). Cryptic butterfly species pairs, which could not be differentiated, are considered one species in our analyses (Guariento et al., 2023).

Identified pollinators were further classified as either 'rare' or 'non-rare' according to respective red list statuses in either the red list for Swiss bees (Müller & Praz, 2024), the red list for hoverflies Baden-Württemberg (Southern German region close/adjacent to the study region; Doczkal, 2000) or the Swiss red list for butterflies (Wermeille et al., 2014). Species listed as 'critically endangered', 'endangered', 'near threatened', 'vulnerable', 'regionally extinct' or similar threat levels (depending on the categorisation key), were considered as 'rare'. To assess flower cover, twenty-four 1 m^2 quadrats were randomly placed along each transect, within which the number and type of inflorescence were recorded for each flowering plant species. The total area covered by inflorescences across quadrats, calculated as a circle or an oval, depending on the species' inflorescence type (Ammann et al., 2024), was estimated and converted to flower cover percentage. Flower dimensions were gathered from: Maurer et al. (2024), D. Frey, L. Ammann, M. Albrecht. & M. Moretti (manuscript in preparation), info flora (https://www.infoflora.ch/fr/) and Naturegate (http://www.luontoportti.com/suomi/en/).

2.3 | Statistical analyses

To assess the impacts of local and landscape factors on wild pollinator density and species richness, generalized linear mixed-effects models (GLMMs) were run separately for each taxon and their subset of rare species using either Poisson distribution or, in cases of overdispersion, a negative binomial distribution. Local-scale explanatory variables included flower cover, flower species richness, and focal patch size, while landscape-scale variables included AES meadow and WSNH cover. To test for interactive effects of AES interventions in agricultural landscapes surrounding calcareous grassland remnants and local habitat quantity and quality, we included interaction terms among AES meadow cover and all local factors. Altitude and sampling round were included as covariates, and site ID was included as a random term to account for repeated transect rounds within sites. Prior to model fitting, we ensured no strong collinearity among explanatory variables (all Pearson correlation coefficients $|r| < 0.6$), and additionally assessed multicollinearity among predictors in the fitted models using variance inflation factors (all adjusted $\text{VIF} \leq 1.5$) (Graham, 2003). We also looked at sampling completeness for each pollinator group in relation to flower cover to ensure that any observed effects were not biased by differences in flower cover (all Pearson correlation coefficients $|r| < 0.4$). As there were only two individual hoverflies classified as rare, no separate models were fit for this category. Additionally, as some butterflies could not be identified to the species level in the field (82.4% identified to species level), a conservative approach was taken to assess species richness. To avoid overestimating species richness by double counting individuals of the same species that were identified to different taxonomic levels, we only considered individuals identified at higher taxonomic levels (either family, subfamily, tribe or genus) as distinct species, when no other individuals belonging to that taxonomic group were identified to species level at the same site.

To identify key flowering plant species that were visited by pollinators disproportionately more frequently than expected given their relative cover, we followed methods outlined in Sutter et al. (2017). Briefly, we used the recorded plant–pollinator interaction data, pooled across sites, to fit GLMMs using a negative binomial distribution, with the number of visits per flowering plant species as the response variable and flower cover as the explanatory variable, which was either log- or square-root transformed to improve model fit. Site ID was included as a random term. Models were run separately for each pollinator group and sampling round. The difference between the observed number of visits and the upper 95% confidence interval of the predicted relationship was calculated and then averaged per plant species. Plant species with positive average difference values were classified as key plant species (Figure 2).

To identify key plant species supporting a greater number of pollinator species than expected relative to their cover, we fit generalized linear models (GLMs) using either Poisson or Negative binomial distributions, separately for each of the three pollinator groups by using plant–pollinator interaction data pooled across sampling rounds and sites. The number of pollinator species visiting each flowering plant species was used as the response variable, with flower cover as the explanatory variable, with either a log- or square-root transformation to improve model fit. To account for potential differences in sampling completeness across different plant species and differences in regional pollinator species pools, we included the total number of visits each plant species received and the number of sites in which it was recorded as covariates. Plant species exceeding the upper 95% confidence interval of the relationship between flower cover and the number of pollinator species were considered as key plant species. To assess sampling completeness of plant–pollinator interactions, we used sample coverage, based on the coverage estimator of Chao and Jost (2012), as implemented within the R package iNEXT (Hsieh et al., 2016). Sampling of interactions pooled across sites, as used for the identification of key forage plants, reached high values of completeness for each pollinator group with 97% in butterflies, 82% in wild bees and 77% in hoverflies. Results of per-site sampling completeness of interactions are provided for the sake of completeness in Table S1, with a mean of 89% ± 11% per site for butterflies, 50% ± 18% for wild bees and 51% ± 28% for hoverflies. Finally, to investigate the importance of identified key plants on wild bee, butterfly, and hoverfly density and species richness, we additionally re-ran the local and landscape effect models using the cover and species richness of key plants identified for each associated pollinator group.

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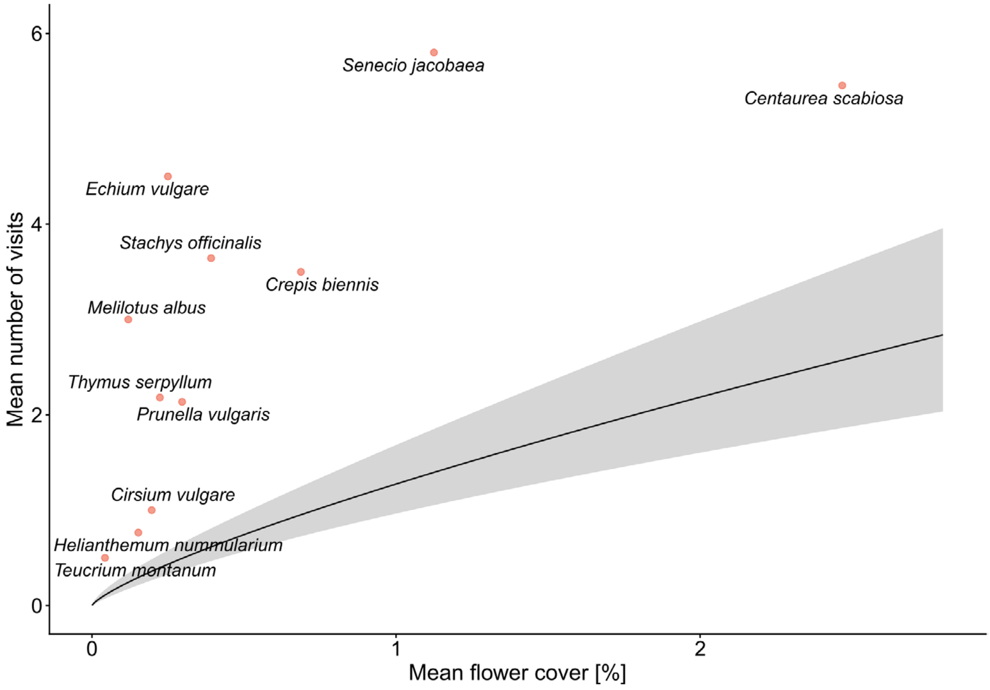

FIGURE 2 An example of key flowering plant species based on the relationship between flower cover and the number of wild bee pollinator visits, seen here during the third sampling round, with 95% confidence intervals indicated by grey shadows. Red points represent mean flower cover and mean number of visits per plant species. For visibility, only flower species with more visits than expected given their cover (key plants) are shown and labelled.

To assess the effects of management (mowing vs. grazing) on the local quality of dry calcareous grasslands for pollinators, we fit linear models with flower species richness, flower cover, and the cover and species richness of key plant species (based on number of visits and number of visitor species separately) per site and sampling round as response variables. An interaction term among management type and sampling round was initially included to assess potential temporal variation of management effects. However, as none of these interactions were statistically significant, they were dropped from the final models and all subsequent analyses were pooled across sampling rounds. Three sites that were managed by a combination of mowing and grazing were excluded from this analysis. All final models included management type as the explanatory variable and focal patch area as a covariate. When modelling flower cover, flower species richness was additionally included as a covariate, while flower cover was included as a covariate when modelling flower species richness. Finally, we assessed flowering plant beta diversity between sites of differing management types in comparison to sites of the same management type by calculating Jaccard (presence-absence) and Bray–Curtis (abundance-based) pair-wise dissimilarity matrices using the R package betapart (Baselga & Orme, 2012). Plant community nestedness and turnover were then analysed with multiple regression on distance matrices (MRM) including the geographic Euclidean distance across each pair of intervention patches as covariate (McLean et al., 2019). To identify plant species significantly associated with a particular management type, we performed a multilevel pattern analysis using the point biserial correlation coefficient within the package indicspecies (De Cáceres et al., 2011). To visualize these patterns and associations, we performed non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity using the R package vegan (Oksanen et al., 2022), and plotted resulting species scores in ordination space.

Model assumptions were validated visually according to the methods outlined in Zuur et al. (2009). To improve model convergence, all continuous explanatory variables were standardized. All statistical analyses were performed in R version 4.3.3 (R Core Team, 2024).

3 | RESULTS

We recorded a total of 1′085 wild bee individuals across 95 species (40.2±20.4 individuals and 14.4±4.7 species per site), 580 hoverfly individuals across 34 species (21.5±13.6 individuals and 5.4±2.7 species per site) and 10′668 butterfly individuals across 56 species (395±168 individuals and 20.3±5.9 species per site). These included 13 rare wild bee species, two rare hoverfly species and 17 rare butterfly species. We recorded 171 flowering plant species, 99 of which were visited by pollinators; in total for each pollinator group, we recorded 982 wild bee interactions (36.4±17.8 per site), 2′072 butterfly interactions (76.7±59.1 per site), and 376 hoverfly interactions (14.1±12.6 per site).

3.1 | Local and landscape effects

At the local scale, focal patch size of dry calcareous grasslands did not significantly affect the density or species richness of any of

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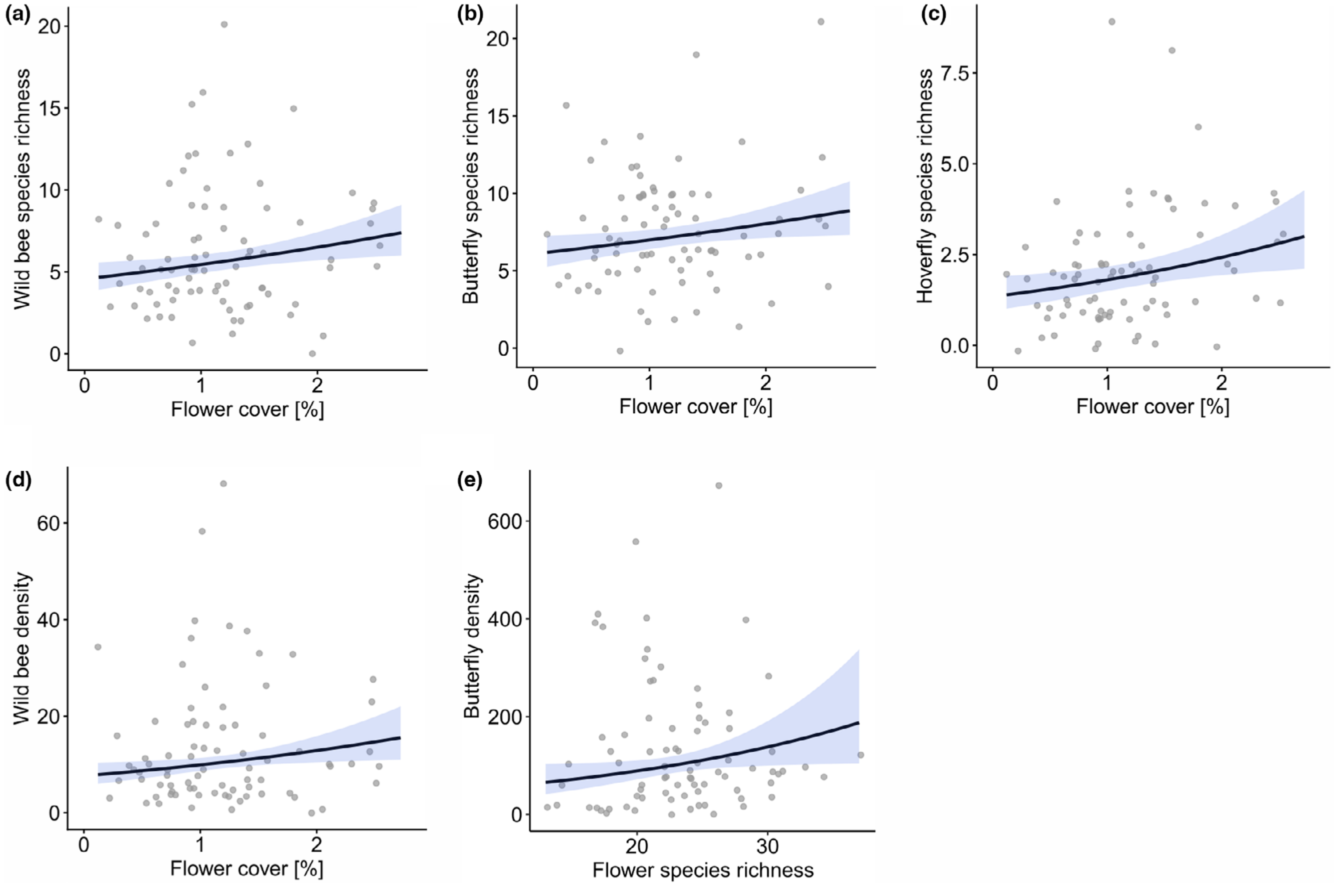

FIGURE 3 Effects of local patch quality on wild pollinator species richness and density. Relationship between flower cover and (a) wild bee species richness, (b) butterfly species richness, (c) hoverfly species richness, (d) wild bee density; (e) relationship between local flower richness and butterfly density. Blue shadows reflect 95% confidence intervals.

the pollinator groups (Table S2). Rather, these were more strongly influenced by local habitat quality. Specifically, increasing local flower cover had a positive effect on the density and species richness of both rare and overall wild bees, and on the species richness of butterflies and hoverflies (all *p*-values ≤0.034) (Figure 3a–d; Table S2; Figure S2). A positive trend was also detected for hoverfly density (Table S2). In contrast, only butterfly density was positively affected by increasing local floral species richness ($p = 0.030$) (Figure 3e; Table S2), while there were no significant effects on species richness or the density of either wild bees or hoverflies (Table S2).

Among local and landscape scales, no significant interactions were found between AES meadows and any of the local factors (flower cover, flower species richness or focal patch size) for any of the pollinator groups (Table S2). At the landscape-scale however, increasing amounts of WSNH in the landscape was positively related to wild bee density ($p = 0.035$) (Figure 4a; Table S2), and tended to be positively related to wild bee species richness, and both butterfly density and species richness (Table S2). In contrast, increasing amounts of AES meadows was negatively related to local butterfly species richness in dry calcareous grasslands ($p = 0.003$) (Figure 4b; Table S2), and marginally negatively related to rare butterfly density and wild bee species richness (Table S2). Density and species richness of all pollinator groups increased with progressing season (i.e., sampling round) (Figure S3; Table S2), except for rare wild bees, for which there was no significant sampling round effect (Table S2). Altitude negatively affected density and species richness of both rare and overall wild bees, and overall butterfly density, while being positively related to hoverfly species richness (Table S2).

3.2 | Key flowering plant species

Of the 171 recorded flowering plant species, 38 were identified as key forage species for wild bees, 14 for butterflies and 17 for hoverflies based on disproportionately high visitation rates (Figure 5). Key flowering species differed throughout the season for each pollinator group. However, *Crepis biennis* was consistently important for wild bees across all sampling rounds, and *Knautia arvensis* was consistently important for butterflies (Figure 5). No single flower species was consistently important for hoverflies throughout the season (Figure 5). However, *Echium vulgare* and *Valeriana officinalis* supported high numbers of visits across all three pollinator groups during peak season in May and June (Figure 5).

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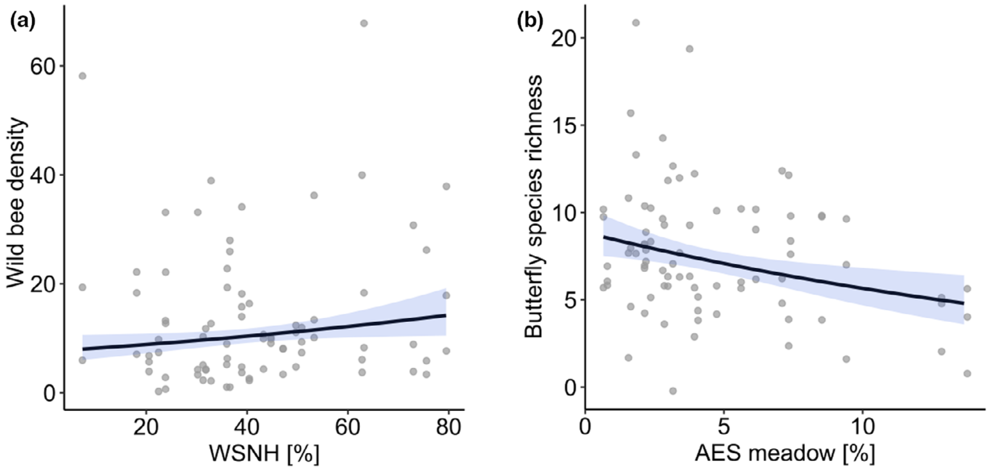

FIGURE 4 Effects of landscape-scale factors on wild pollinator species richness and density. Relationship between woody semi-natural habitats (WSNH) and (a) wild density. (b) Relationship between agri-environment scheme (AES) meadows and butterfly species richness. Blue shadows reflect 95% confidence intervals.

When considering flower species based on the number of supported pollinator species, 18 key forage plant species were identified for wild bees (Figure 6a; Figure S4), with *K. arvensis* supporting the highest number of wild bee species (22 supported species). Of the 18 key plant species, *K. arvensis*, *Dianthus cathusianorum*, *Centaurea scabiosae* and *Onobychis vicifolia* also supported rare wild bee species (Figure 6a). Eight plant species were important floral resources for a high number of butterfly species (Figure 6b; Figure S4), with *Trifolium pratense* supporting the greatest species richness (14 supported species). Of these key species, *Buphthalmum salicifolium* supported three rare butterfly species, while *Hypochaeris radicata*, *Origanum vulgare*, *Stachys officinalis*, and *Sanguisorba minor* also supported one rare butterfly species each (Figure 6b). For hoverflies, 12 key flowering plant species were identified (Figure 6c; Figure S4), with *Leontodon hispidus* supporting the greatest number of hoverfly species (eight supported species). *T. pratense* was also important for hoverflies and supported one of the two rare hoverfly species, while *Helianthemum nummularium* supported the other (Figure 6c).

When considering key plants that promote high pollinator density and species richness simultaneously, we identified 11 important plant species for wild bees, five for butterflies and four for hoverflies. However, no overall key plant species was shared among the three pollinator groups (Table S3).

Comparisons of local and landscape effect models run with key plants or with total plant cover and richness resulted in similar model fits and explanatory power across pollinator groups. Models run with all plants had slightly lower AIC values and slightly higher pseudo-R^2 values, indicating better fit and explained variance for overall wild bee density and species richness. They also showed higher pseudo-R^2 values with equal AIC values for overall butterfly density, but higher AIC values for rare wild bee density. Models run with key plants provided equal or slightly better fit and explained variance for rare wild bee species richness, rare butterfly density, both overall and rare butterfly species richness, and hoverfly density and species richness (Table S4).

3.3 | Management effects on local patch quality

Local management, either mowing or grazing, had no significant effect on the cover of local floral resources, whether it be the overall floral cover, or the cover of key plant species. However, grazed areas supported a higher number of flowering plant species for overall plant richness and the richness of both key plant metrics (Figure 7a). Analyses of plant community beta diversity revealed that Jaccard nestedness was significantly higher between sites of different management types than among sites of the same management type ($p=0.001$; Figure 7b), with meadows harbouring a subset of plant species found in pastures. While Jaccard turnover was not significant, the Bray–Curtis (abundance-based) balanced variation (i.e., abundance turnover) was significantly higher between different management types than across sites of the same management ($p=0.012$; Figure 7c). Further, multilevel pattern analysis revealed that while most plants were not significantly associated with either management type, six flowering plant species were significantly associated with meadows (five of which are key plants), while 19 were significantly associated with pastures (including seven key plants) (all p-values <0.05; Figure 7d).

4 | DISCUSSION

4.1 | Local and landscape effects

At the local scale, the quality of dry calcareous grasslands, particularly flower cover, was more important than patch size in supporting the density and species richness of wild bees, hoverflies and butterflies. Notably, flower cover was also the only factor to benefit rare wild bees, increasing both their density and species richness. These positive effects of patch quality are in line with our expectations, as increasing floral richness and cover provide additional pollen and nectar resources, increase the likelihood of suitable host

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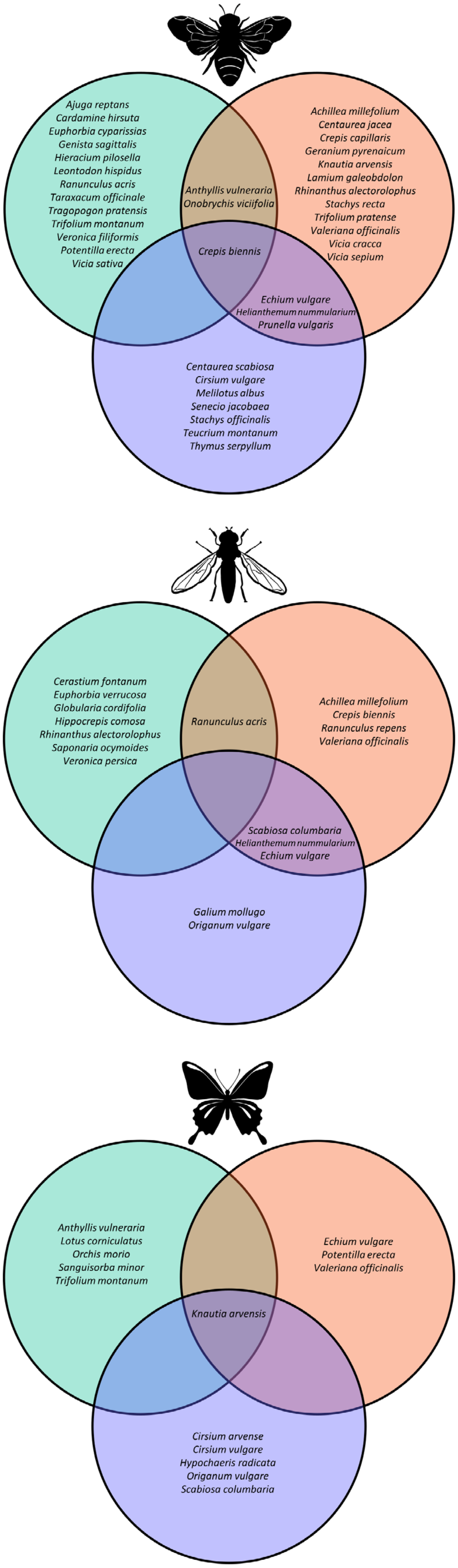

FIGURE 5 Temporal variation and overlap of key plant species based on pollinator visitation frequency, pooled across sites, per sampling round for wild bees (top), hoverflies (middle) and butterflies (bottom). Coloured circles indicate sampling rounds: Green—round 1, orange—round 2, and purple—round 3.

plant presence, and potentially reduce competition among pollinators (Doublet et al., 2022; Lichtenberg et al., 2025). These findings also corroborate findings of studies highlighting the critical role of flower availability across a range of pollinator taxa and rare species (Luppi et al., 2018; Meyer et al., 2009; Neumüller et al., 2020). In some cases, such as with wild bees, flower resources have even been shown to determine the local carrying capacity (Fijen et al., 2025).

While some studies identified local patch size as a key supporter of pollinator richness and density (e.g., Biegerl et al., 2025), its limited role here may reflect the high availability of other suitable habitats in the surrounding landscape (Krämer et al., 2012), with most of our study sites containing >15% cover of AES meadows and WSNH. In line with this, Fijen et al. (2025) and Bishop et al. (2025) found that increasing habitat quantity is more effective in simple landscapes, whereas the importance of habitat quality increases with greater habitat quantity. Moreover, larger patches might not necessarily offer proportionally higher floral quality (floral density and species richness per area), for instance, we found no correlation between patch size and either flower richness or cover within standardized transects in our study system. Although patch size did not translate into higher pollinator density per unit area, assuming comparable densities, larger patches would still be expected to support greater total abundances at the patch scale simply due to a larger area. Accordingly, even very small patches may support abundant pollinators when they are of high enough quality and embedded in a landscape with high proportions of accessible habitats (Albrecht et al., 2007; Boetzl et al., 2021; Riva & Fahrig, 2022).

Across local and landscape scales, we found no interaction effects between AES meadow cover and local habitat variables (patch size, flower cover or species richness) for any pollinator group. This suggests that AES meadows did not disproportionately compensate for small or poor-quality local patches in supporting pollinator populations, nor did they complement them, e.g., by complemental flowering periods. On the one hand, AES meadows are most effective in homogenous, intensely managed landscapes (Scheper et al., 2013), thus the relatively high AES and SNH cover in our landscapes may have masked their additional benefits. On the other hand, the lack of interaction effects may also be attributed to similar management regimes (e.g., cutting times and no fertilizer) among both AES meadows and the focal dry calcareous grassland patches, leading to similar resource provision and ultimately limiting the ability of AES meadows to function as temporal refuges during floral resource gaps (Knauer et al., 2026; Timberlake et al., 2019).

Alone, increasing AES meadow cover in the landscape had a negative effect on butterfly species richness, with similar negative trends observed for wild bee species richness and rare butterfly density. While this could reflect low habitat suitability, subsequently

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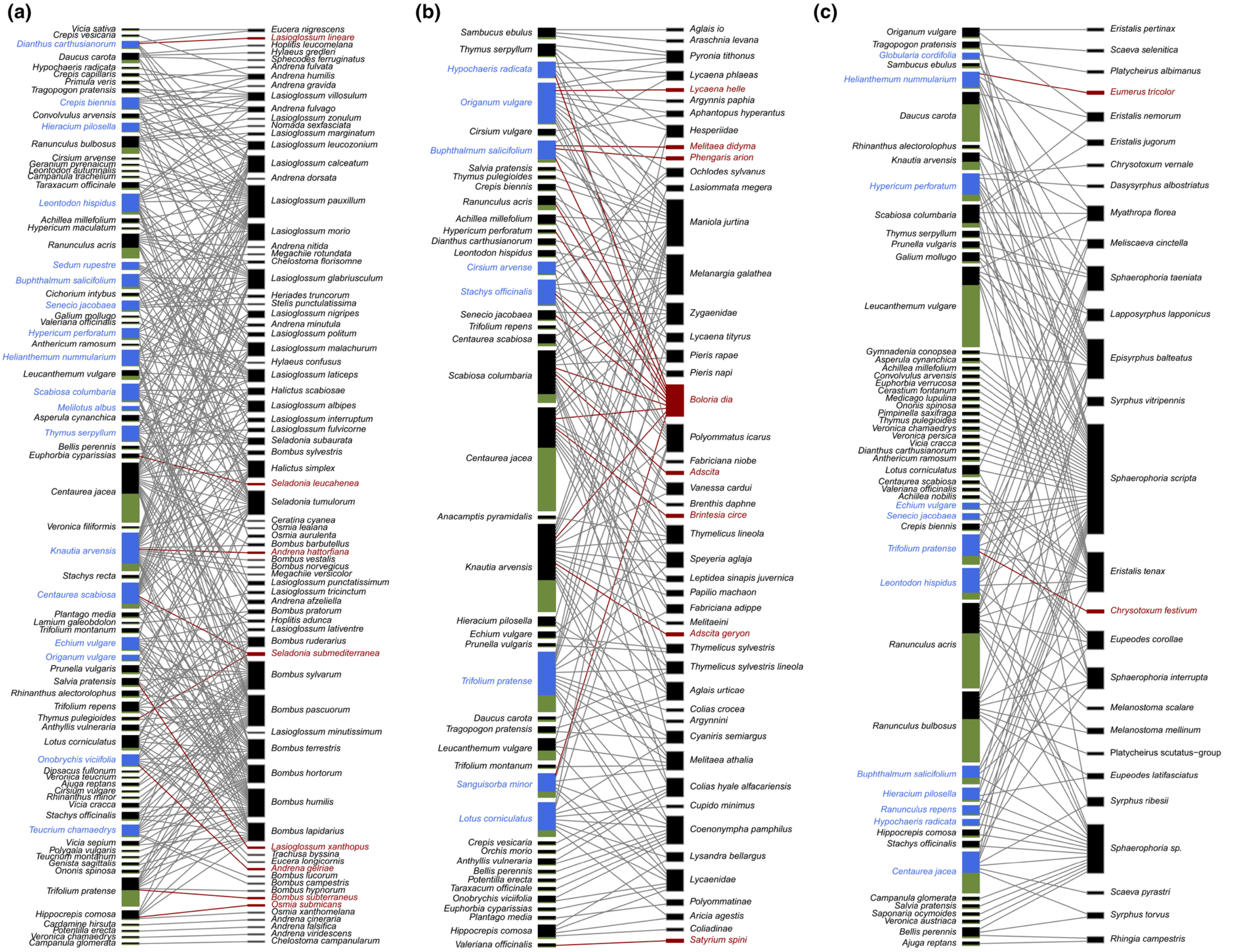

FIGURE 6 Plant–pollinator (flower visitation) interactions for each pollinator group across all sampling rounds. (a) wild bees (b) butterflies, and (c) hoverflies. Key forage plants based on disproportionately high numbers of supported pollinator species considering the flower cover are highlighted in blue, rare pollinator species in red, the flower cover is indicated by proportional green rectangles and black rectangles are proportional to the number of species interactions.

leading to reduced populations throughout the landscape (Luppi et al., 2018), perhaps a more likely explanation is that of a dilution effect (Holzschuh et al., 2016; Tscharntke et al., 2012). In this case, some pollinator species are drawn to, or more specialized on, the additional resources provided by nearby AES meadows, leading to lower observed richness in focal patches. However, since we did not assess pollinator communities or floral resources in the surrounding habitats, we are unable to confirm either mechanism here.

In contrast, increasing WSNH in the landscape positively influenced wild bees, with a similar positive trend observed for butterflies. Woody habitats have previously been found to support local wild bees, particularly in the early and late seasons (Neumüller et al., 2020). Such habitats can offer complementary feeding resources, nesting sites, overwintering habitat and nest building materials (Ammann et al., 2024; Meyer et al., 2009; Eeraerts & Isaacs, 2023; Schirmel et al., 2018; Timberlake et al., 2019; Neumüller et al., 2020), which can benefit local populations, particularly when they are situated near the focal patches. By increasing microhabitat availability and landscape heterogeneity, WSNH can enhance pollinator communities and provide refuge from disturbances, such as mowing (Luppi et al., 2018). While WSNH, such as hedgerows, can also benefit butterflies by providing nectar, shelter from wind, and thermal microclimates (e.g., Aviron et al., 2023), which can be particularly important during larval development, we might not have captured the full impacts of WSNH on butterflies since we sampled only during the adult stages.

Interestingly, we found no landscape-scale effects on hoverflies. This may be due to their diverse and complex life histories, particularly during the larval stages, which can depend on specific habitat factors that may not have been captured in this study since we only focused on adults (Meyer et al., 2009; Schirmel et al., 2018). Additionally, hoverflies are not central place foragers, and many adult species are polylectic (Branquart & Hemptinne, 2000), making them less reliant on any single habitat type. Rather, heterogeneous landscapes that

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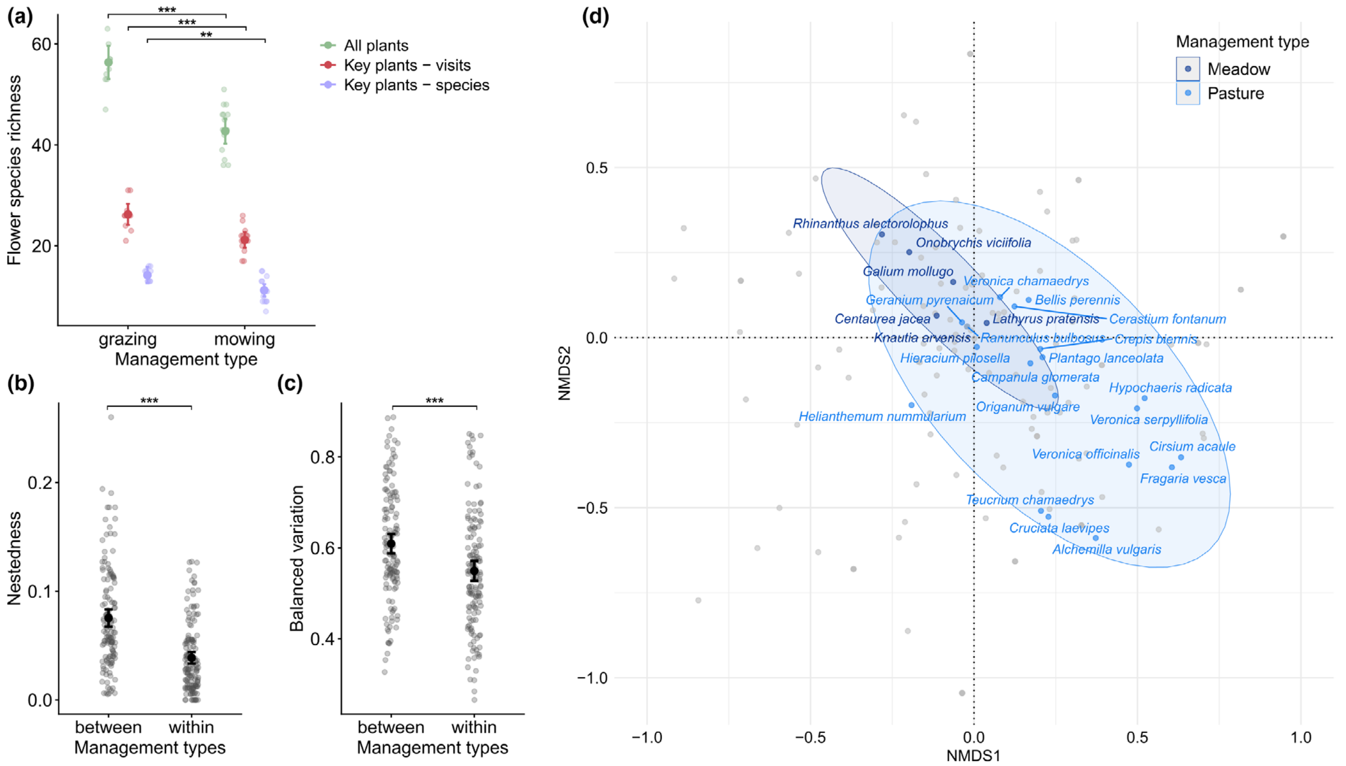

FIGURE 7 Effects of management (mowing or grazing) on flowering plant communities. (a) Estimated mean flower species richness of grazed or mown dry calcareous grasslands, (b) Jaccard nestedness of plant species among sites of the same management type and among sites of different management types, (c) Bray–Curtis balanced variation (turnover) of plant species cover among sites of the same management type and among sites of different management types, (d) Non-metric multidimentional scaling (NMDS) ordination based on Jaccard dissimilarity. Ellipses represent 95% confidence intervals for plant species significantly associated with a management type, based on point biserial correlation analyses. Only names for significantly associated plants ($p < 0.05$) are shown. Bar and asterisk indicate significant differences among management types, *** for $p \leq 0.001$, ** for $p < 0.01$ in (a), (b) and (c).

can support the varying larval and adult requirements are likely most effective to sustain hoverfly communities (Biegerl et al., 2025; Meyer et al., 2009; Schirmel et al., 2018). It is important also to note that we only recorded two rare hoverfly species, further emphasizing the need to better understand the drivers of hoverfly diversity and density to conserve these important, yet often overlooked pollinators and the ecosystem services they provide.

4.2 | Key flowering plant species

Our analyses of plant–pollinator visitation interactions identified key flowering plant species in dry calcareous grasslands for three important wild insect pollinator groups in Switzerland. While several plant species identified as key forage species here align with findings for Central European (Pietrzak & Pabis, 2025) or Irish agricultural grasslands (Larkin & Stanley, 2023), various SNH (Sutter et al., 2017), or sown flower strips or fields (Kuppler et al., 2023; Warzecha et al., 2018), (e.g., *Origanum vulgare*, *Echium vulgare*, *Centaurea* spp., *Trifolium* spp., *Ranunculus* spp.), we also identified key species that were not highlighted in other studies despite being present. In some cases, species classified as having low visitor richness elsewhere (e.g., *Vicia sativa*, *Prunella vulgaris* or *Achillea millefolium* in Kuppler et al., 2023) emerged as key foraging resources in our studied calcareous grasslands. Beyond differences in habitat context, these discrepancies may be linked to analytical differences, for instance Larkin and Stanley (2023) and Warzecha et al. (2018) utilized species strength, a network metric that emphasizes community-wide dependencies, to identify important forage plant species, whereas our method identifies plants visited disproportionately relative to their flower cover, as our objective was to identify preferred plant species while accounting for their floral availability.

Our findings for the different pollinator groups bees, butterflies and hoverflies corroborate evidence for bees (Kuppler et al., 2023) that key plants are highly variable across the season. Key plants with disproportionately high visitation frequencies differed throughout the season, while only a few remained important across multiple time points. This temporal turnover in key plant species may be linked to a number of factors, such as phenological matching among plants and pollinators, differences in dispersal ability of pollinators limiting their access to alternative resources, or the availability and quality of alternative resources in the local plant community and the surrounding landscape (Corbet, 2000). While the few key plant species used at multiple timepoints should be prioritized, the limited overlap underscores the importance of resource complementarity in dry calcareous grasslands to ensure continuous nectar and pollen supply throughout the season for different pollinator taxa, especially during periods when other floral resources are scarce or unavailable (e.g., post-mowing) (Ammann et al., 2024; Langlois et al., 2020).

Key plants supporting high numbers of pollinator species often differed from those based on visitation frequency. Building on the method of Sutter et al. (2017), which focused on visitation frequency, this second approach allowed us to additionally identify plant species that support high pollinator diversity, including rare taxa of conservation concern, rather than those that may support only the most abundant pollinators. Of the 171 recorded plant species, 16% supported disproportionately higher pollinator richness, and 6% also supported rare species. In particular, *Buphthalmum salicifolium* was identified as key across all pollinator groups, including three rare butterfly species, likely owing to its bright colour, open floral morphology and easily accessible nectar. Maintaining key plants that support multiple pollinator groups, and their rare species in particular, through targeted management interventions could be a pragmatic conservation strategy. Additionally, such generalist plant species can support complex community stability and contribute to network resilience (Biella et al., 2019; Zografou et al., 2020). However, high resource overlap could also lead to increased competition, and the large number of taxon-specific key plants, found here and in previous studies (Larkin & Stanley, 2023; Warzecha et al., 2018), further suggests that effective resource provision includes functionally complementary resources (Blüthgen & Klein, 2011). Such differences in key plants are likely linked to the wide variety of pollinator life histories and the different morphological compatibilities among pollinators and flowers, ultimately highlighting the need for clear conservation targets and tailored action plans that include key flower species for multiple taxa, particularly rare and specialist species.

In general, our model comparisons suggest that key plants do indeed play an important role in promoting pollinators, particularly for hoverflies and for butterfly species richness, including rare species. However, the slightly lower AIC and higher pseudo-R^2 values of models run using all flowering plants for overall wild bees, and the higher pseudo-R^2 values for overall butterfly density, indicate that other abundant plant species still contribute to promoting additional pollinators.

4.3 | Management effects on local patch quality

Comparisons of extensive grazing and mowing in dry calcareous grasslands revealed that, while total local flower cover was similar between both management regimes, grazing supported significantly greater floral species richness than mowing (approximately 32%), including greater species richness of key plants (approximately 27% and 24% based on supported species and visitation frequency, respectively). Beta diversity analyses further revealed that meadows tended to harbour a subset of the species found in pastures, and while total cover was similar across management types, the identity of abundant flowering plants differed.

These differences are likely because grazing is a form of selective disturbance, combining selective feeding with trampling and droppings, subsequently leading to increased habitat heterogeneity and possibly reduced interspecific competition among plants by promoting openness throughout the growing season (Davies, 2001; Rook & Tallowin, 2003; Tälle et al., 2016). While trampling creates open gaps that facilitate the establishment of low-growing species and those with larger seeds, the grazing animals themselves can additionally act as vectors for seed dispersal, subsequently improving chances of seedling emergence (Rysiak et al., 2021; Tälle et al., 2016). In contrast, mowing is a form of non-selective disturbance that can lead to trait-determined plant communities, favouring species that can establish and grow quickly after cutting. This uniform effect often leads to homogenization of vegetation structure and composition (Lepš, 2014), therefore leading to a subset of the plants found in pastures, but with differently abundant species.

Despite these compositional differences, mowing and grazing resulted in similar total floral cover, a key characteristic of calcareous grasslands affecting all pollinator groups in our study. This may be because both management types reduce biomass and suppress dominant vegetation, which may boost flowering species by providing better access to essential resources, such as light (McCain et al., 2010). Our findings therefore align with previous studies in showing that both mowing and grazing can be valuable, despite their different ecological outcomes (e.g., Reutimann et al., 2023; Rysiak et al., 2021; Schlapfer et al., 1998; Tälle et al., 2016).

Taken together, these results suggest that because mowing or grazing can influence the turnover of flowering plant species abundance across sites, including some key forage plants, variation in management type across calcareous grassland patches appears to be an effective strategy to promote high beta diversity of important flowering plant species at landscape and regional scales (Guariento et al., 2023; Knauer et al., 2026; Rysiak et al., 2021). Nonetheless, our findings highlight the need to prioritize the conservation of pastures under extensive grazing, as their cover continues to become increasingly rare despite their role in supporting florally diverse and heterogeneous habitats for pollinators.

4.4 | Synthesis and applications

Our study across 27 dry calcareous grasslands in Switzerland highlights that conservation efforts should focus on improving local-scale patch quality while promoting landscape-scale heterogeneity to best support diverse pollinator communities. In landscapes with high AES and SNH cover, such as our study region, management efforts should prioritize maintaining the quantity while enhancing the quality of existing dry calcareous grassland patches, particularly through increased floral resources. However, in simple landscapes with little SNH, the focus should be on achieving a higher SNH cover (ideally ≥20%) to sustain pollinator populations (Fijen et al., 2025, Garibaldi et al., 2021). Given the varying responses among pollinator groups to landscape-scale habitats, our results indicate that the promotion of different SNH types, such as WSNH and AES meadows, may be crucial to meet the various spatial and temporal needs of diverse pollinator communities.

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Beyond simply increasing floral resources, our plant–pollinator interaction-based analyses underscore the need for targeted promotion of key forage plants to better support diverse and complimentary pollinator communities. However, the scarcity of universally important plant species across pollinator taxa and throughout the season suggests that relying on a narrow set of 'pollinator friendly' flowers may not be an effective method to promote pollinators, especially for supporting rare or specialized species. Therefore, beyond prioritizing overlapping key plants that support multiple taxa and provide foraging resources throughout the season (e.g., *Buphthalmum salicifolium*, *Knautia arvensis* and *Echium vulgare*), *and* 'double' key plants that support high pollinator density and species richness (e.g., *Helianthemum nummularium* or *Lotus corniculatus*) (Table S3), we recommend additionally promoting species which uniquely support pollinator groups and their seasonal needs. In other words, efforts should aim to promote phenologically complementary and functionally diverse floral assemblages to ensure continuous and complimentary resources that meet the needs of multiple pollinator groups throughout the season, including rare species. For instance, through local habitat management, our results indicate that extensive grazing may be an effective strategy to promote floral species richness, including key plants, and potentially habitat heterogeneity. However, our findings also highlight that throughout the landscape, an integrated approach combining both grazing and mowing appears to be an effective strategy to enhance beta diversity of flowering plant diversity, including key foraging plants for pollinators.

Implementing the above-mentioned management recommendations is likely to benefit not only diverse pollinator communities, but also the essential pollination services they provide.

AUTHOR CONTRIBUTIONS

Gabrielle McLaughlin and Matthias Albrecht conceived the ideas; Gabrielle McLaughlin, Anina Knauer and Matthias Albrecht designed the methodology; Gabrielle McLaughlin collected the data; Gabrielle McLaughlin and Anina Knauer analysed the data; Gabrielle McLaughlin led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Digital Repository https://doi.org/10.5281/zenodo.20283557 (McLaughlin et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of the 27 sampling sites in Switzerland. Circle size is proportional to the focal patch size (in hectares).

Figure S2. Effects of local patch quality on rare wild pollinator density and species richness.

Figure S3. Effect of sampling round on wild pollinator density and species richness.

Figure S4. Overlap of key flower species based on the number of supported species among the three taxa.

Table S1. Sampling completeness (proportion) of plant–pollinator interactions per site and pollinator group, estimated with the coverage-based estimator of Chao and Jost (2012) as implemented in the iNEXT R package (Hsieh et al., 2016).

Table S2. Summary results of generalized linear mixed effect models (GLMMs) testing the importance of local and landscape-scale habitat factors on the density and species richness of different pollinator groups.

Table S3. Table of all recorded flower species across all sites and sampling rounds.

Table S4. Summary results of generalized linear mixed effect models (GLMMs) testing the importance of local and landscape-scale habitat factors on the density and species richness of different pollinator groups, using key plants for each pollinator group instead of all flowering plants.

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