

RESEARCH ARTICLE

Heathland pollinator communities are more strongly influenced by land management than by honeybee competition

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Abstract

1. Managed honey bees have the potential to compete with wild pollinators. Pollinator populations are also affected by land management such as grazing, but how this mediates competition with honeybees is not well understood. Many competition studies are short term, lack appropriate controls, or do not consider the impacts of hives on the interactions of whole plant–pollinator communities.
2. Our objective was to assess the effects of apiaries and two land management strategies (grazed/burned vs. regenerating) on wild plant and pollinator populations in upland heathlands. We used a landscape scale before–after control–impact experiment where apiaries were introduced to half of 20 sites, with the remainder left as controls. From May to September, we recorded at each site: (a) habitat structure and nectar phenology, (b) plant–pollinator network structure and (c) mass and protein:lipid ratio of pollen collected by bumblebees (which have high dietary overlap with honeybees).
3. We found that nectar phenology and pollinator community composition were strongly driven by land management. For example, grazed sites had 63% less nectar available to bumblebees in spring due to sheep browsing of *Vaccinium*, but supported more abundant and diverse fly communities in the summer, associated with increased grass cover and habitat heterogeneity. Whilst plant–pollinator network metrics were unaffected by apiary introductions, nestedness and pollinator robustness were lower at regenerating sites. The mass and protein:lipid ratio of bumblebee-collected pollen were consistent across treatments.
4. *Synthesis and applications.* Apiaries had modest impacts on heathland plant–pollinator communities, likely buffered by the abundance of *Calluna vulgaris* which provides 91% of landscape nectar during hive introductions. We recommend avoiding hive introductions outside of peak flowering periods and managing grazing in the spring to ensure nectar resources for emerging pollinators. Heathland management strategies that encourage habitat heterogeneity, such as conservation grazing, could support abundant and diverse pollinator communities that are more robust to disturbance such as hive introductions.

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KEYWORDS

beekeeping, competition, habitat management, plant–pollinator networks, pollination

1 | INTRODUCTION

Interspecific competition between species is a natural phenomenon, and an important driver of speciation and niche separation (Adams, 2010; Beans, 2014; Schluter, 1994). One of the most speciose guilds on Earth are pollinating insects, which together with the flowering plants they visit, make up a third of eukaryotic life on Earth (Sponsler et al., 2023). Pollinator species richness and abundance is key to maintaining plant communities and habitats worldwide (Kral-O'Brien et al., 2021; Potts et al., 2016). At the same time, an increasingly recognised threat to wild pollinators is the potential for competition with managed honey bees, which can increase competitive dynamics beyond natural levels. Research has largely focused on competition over floral resources via altered foraging behaviour, particularly regarding floral abundance or nectar supply (Cane & Tepedino, 2017; Henry & Rodet, 2018; Magrach et al., 2017; Valido et al., 2019). A key issue highlighted in reviews on this topic is the lack of landscape scale, community-wide studies that introduce hives to study sites and have adequate controls (Goulson, 2003; Iwasaki & Hogendoorn, 2022; Magrach et al., 2017; Mallinger et al., 2017; Paini, 2004). Studies that examine hive density and proximity, or whether pollinator behavioural changes translate into negative fitness impacts, are also limited (but see Henry & Rodet, 2018; Pasquali et al., 2025). In short, the mechanisms of honey bee–pollinator competition, and ‘thresholds of competition’ for hive density, are not well understood (Iwasaki & Hogendoorn, 2022).

A second key factor impacting on pollinator populations is habitat change. For example, management practices such as grazing can impact on floral resource availability by changing the assemblage and distribution of flowering plant species. Competitive impacts of managed honey bees are rarely assessed alongside other stressors such as habitat change (but see Herbertsson et al., 2016), despite evidence that stressors to pollinators rarely act in isolation and may interact synergistically (Lau et al., 2023; Vanbergen and The Insect Pollinators Initiative, 2013). Land management practices such as grazing or controlled burns can change the availability of microhabitats and floral resources for pollinators, however, how pollinator competition interacts with land management remains a recognised research need (Sponsler et al., 2023).

Upland heathlands, which cover 26% of Scotland's area (Office for National Statistics, 2023), are important for both wild pollinators and beekeeping, and are subject to diverse land management practices, with succession to woodland typically prevented in these habitats by burning and grazing. Heathlands are important for bumblebees, and a number of UK pollinator species are associated exclusively with *Calluna vulgaris* (Haysom & Coulson, 1998; Peters et al., 2008). Other pollinators in these habitats include Diptera, including many syrphids, some solitary bees, and Lepidoptera (Devoto et al., 2012). Managed honey

bees in Scotland commonly depend on mass-flowering crops such as oilseed rape and orchards (Gray et al., 2019; NatureScot, 2017), but when these are not in bloom, hives are relocated to heathlands during the flowering of ling heather (*Calluna vulgaris*) to ensure summer forage. This seasonal practice offers an opportunity to study how hive introductions and land management affect plant–pollinator community richness, abundance and foraging success at the landscape scale.

To date, no studies have assessed whether land management mediates pollinator competition via changes in nectar resources. Here, we assessed the combined effects of introduced apiaries and land management practices on wild pollinators, using a before–after control–impact design across a landscape. Sites were sampled from May–September, introducing apiaries to sites subject to two land management approaches ('grazed and burned' or 'regenerating') and compared with unmanipulated controls.

First, we quantified landscape habitat structure and nectar sugar provision at the sites. Habitat structure can strongly influence floral and insect communities (Jerrentrup et al., 2014; Vandvik et al., 2005), but the role of floral resources as a link between altered habitat structure and pollinator communities is not well explored (but see Gillespie et al., 2022, 2024). In brief, we predicted that land management type would explain variation in habitat structure and nectar sugar provision at sites, due to the effects of grazing on flowering plant assemblages (Lázaro et al., 2016; Wang & Hou, 2024).

Second, to assess changes in pollinator foraging behaviour in response to land management and apiary introductions, we compared plant–pollinator interactions among the sites. Honey bees can cause wild pollinators to forage on other plants due to resource competition (Henry & Rodet, 2018; Valido et al., 2019); therefore, we predicted that pollinators at sites with apiaries would shift or increase the breadth of their diets to include plants they previously did not interact with. In theory, this would result in measurable network changes such as broadly, an increase in the number of flower species visited by wild pollinators (increased links per species), a reduced separation between interaction groups in a network (modularity) or a greater overlap in the resources use between specialists and generalists (higher nestedness) (Valido et al., 2019). Third, we compared the mass, protein and lipid content of the pollen baskets (corbiculae) collected from bumblebees and honey bees, providing a more direct measure of the impacts of land management and apiaries on pollinator foraging success. The protein:lipid ratio of pollen is known to be important to pollinators, with *Bombus* species selecting for a higher lipid content and lower protein than *Apis* when foraging, due to their different life history traits (Vaudo et al., 2016, 2020). As bumblebees are known to maintain specific protein:lipid ratios in their pollen foraging across habitats and seasons (Timberlake et al., 2024; Vaudo et al., 2016, 2018), we predicted that macronutrient ratios would be maintained across treatments,

but that less pollen would be collected at apiary sites due to resource competition.

2 | MATERIALS AND METHODS

2.1 | Field site selection

The field experiment took place in upland heathlands in east Scotland (Figure 1a). Fieldwork was conducted at 20 independent field sites over an area of approximately 576,000 ha, and at each field site two 1-ha plots, 100 m apart, were surveyed. After consultation with collaborating landowners and beekeepers, 10 'apiary-free' sites were selected that had no known apiaries for 4 km in any direction, and no recorded history of beekeeping. The 10 'apiary' sites were used for seasonal commercial beekeeping, with at least 15 hives (mean 33.8 ± 16.7) placed on them during the heather bloom from mid-July until early September 2022. Sites were grouped into three distinct blocks based on geography and elevation (see Figure 1a), and within these blocks, the numbers of apiary-free and apiary sites were equal. Sites were an average of 393.5 m in elevation, and all within 221 (± 72) metres of each other.

The field sites were a minimum of two kilometres apart, a distance beyond the foraging range of most small-bodied bees and hoverflies (Greenleaf et al., 2007; Rotheray et al., 2014), maximising statistical independence of the data. Our data collection period spanned the 'pre-apiary' season from May to July and the 'during-apiary' season from July to September. The frequency of foraging honey bees is often found to increase with distance from the hive (Beekman & Ratnieks, 2000), with fewer honeybees foraging immediately next to the hive (Mallinger et al., 2017). However, previous studies have also found that competitive effects are stronger closer (<800 m) to the hive (Elbgami et al., 2014; Thomson, 2004, 2006). Therefore, at apiary sites, the two 1-ha sampling plots were located between 100 and 300 m from the apiary itself, to maximise the foraging pressure the plot would experience by honey bees. The study design made use of existing migratory beekeeping practices, and ethics approval was not required.

Ten field sites were subject to grazing by sheep and/or deer, and were part of a landscape managed using 'muirburn' (Gill & Groves, 1981), where patches of heather are burned every 15 years or so to provide habitat for driven grouse shooting. These were classed as 'grazed/burned' sites. The other 10 sites were located on land that was not subject to burns and had little to no grazing pressure due to

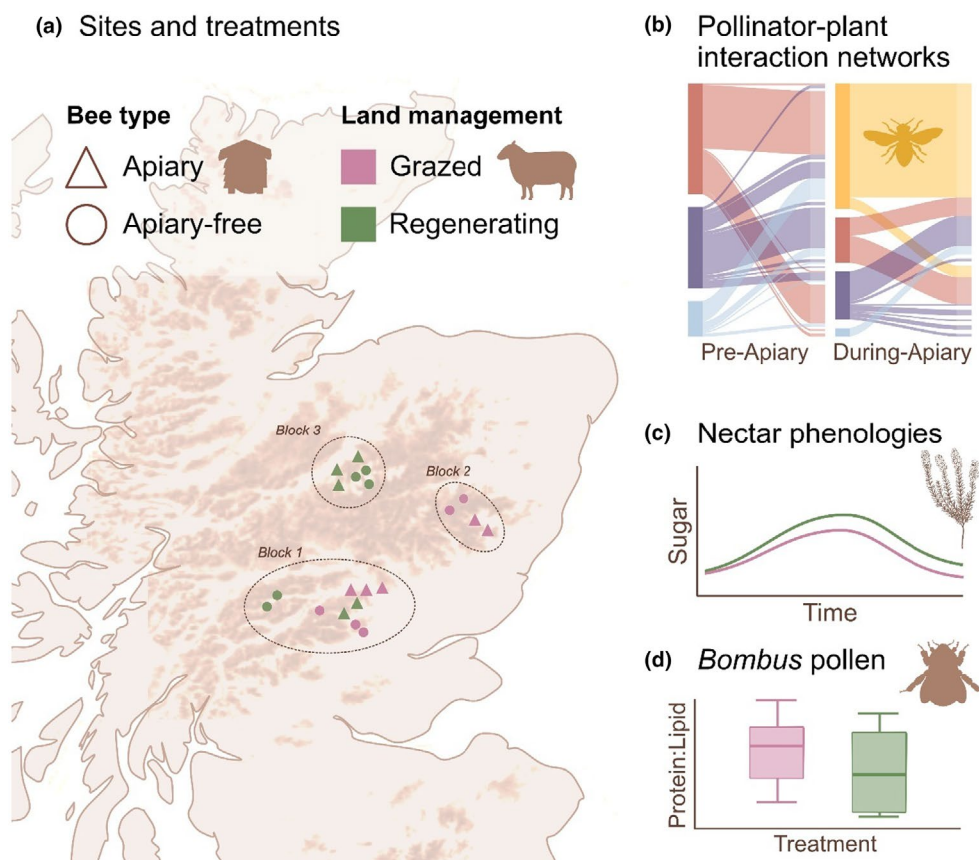


FIGURE 1 A map of 20 field sites in Scotland (a), and the three kinds of data collected (b,c,d): (a) The types and locations of the 20 field sites. Treatment is shown by the shape of each point, and land management by the colour. (b) Example plant–pollinator interaction data for one site. Each network contains data from four surveys, the left network before apiary introductions, and the right network during apiary introductions. Yellow links show plant visits made by honey bees. (c) A conceptual plot of seasonal nectar sugar production between two sites. (d) A conceptual comparison of the protein:lipid ratio of pollen collected by bumblebees between two treatments.

fencing or deer culling. These were classed as 'regenerating' sites. The resulting four combinations of apiary treatment and land management types were replicated with five sites each, leading to 20 plots overall, split into three blocks (see [Figure 1a](#)). According to landowner records, the time since the last burn at the 10 'grazed/burned' sites was 3–10 years, and at 'regenerating' sites was 10–20 years. Regarding grazing pressure, all 'grazed/burned' sites were exposed to sheep year-round; 'regenerating' sites had no sheep, but two sites had low densities of roe deer. Whilst both grazing and burning pressures were continua, on average, the 'grazed/burned' sites were disturbed more frequently than the 'regenerating' sites.

It was important to account for habitat variation in the landscape surrounding each field site, first to account for any unexpected variation within treatments, and second to assess how land management affected habitat structure and heterogeneity - factors which can strongly influence floral and insect communities (Jerrentrup et al., 2014; Vandvik et al., 2005). To do this, landscape classification models were created based on the Red-Green-Blue (RGB) pixel values and run on the most recently available aerial imagery for a 500 m area around each site (EDINA Aerial imagery, 2022). A 500 m area was used as most small insects forage within this dispersal range (Greenleaf et al., 2007; Rotheray et al., 2014). RGB pixel values are commonly used to develop landscape classifications for spatial analysis from aerial imagery, for example, Mattupalli et al. (2018) and Baek et al. (2024). Details of the landscape classification models and habitat composition of the sites are provided in [Supporting Information, Figures S1 and S2](#).

The percentage cover of the different land classes (e.g. heather, grass, water) and metrics of 'connectance' and 'interspersed juxtaposition' were then produced for each site area using the '*landscapemetrics*' package in RStudio v.3.2.2. (R Core Team, 2019). These metrics are considered robust indices for measuring, respectively, the connectivity and patchiness of a landscape, compared with other metrics (Wang et al., 2014). The connectance index measures the number of connected patches of each habitat type relative to the total number of patches in a landscape, whilst interspersed juxtaposition measures the extent to which different landcover types are intermingled across a landscape, that is, the fragmentation (Wang et al., 2014).

2.2 | Habitat structure and nectar production

To compare the provision of nectar sugar for pollinators between the two land management types, and to ensure nectar provision was comparable between the apiary and apiary-free sites, we recorded the flowering phenology at the sites from May–September ([Figure 1c](#)). At each site, a floral survey of both 1-ha plots was conducted an average of once per fortnight from May 4th to September 20th. Four 50 m transects were surveyed in each plot, 20 m apart. Every 10 m along each transect, the number and species of individual inflorescences in a 1 × 1 m quadrat were recorded. Inflorescences of grasses (Poaceae) were excluded from the surveys as they do not produce nectar. Individual flowers were either counted using a tally-counter, or flower

frequency was calculated by multiplying inflorescences by the mean number of flowers per inflorescence. Floral data from the 20 quadrats (4 transects × 5 quadrats) from the two plots at each field site were pooled, covering 40 m² each site each survey.

By combining the mean nectar sugar production per 24 h for each plant species with floral abundance data, the amount of nectar available at each site from May to September could be calculated, as previously done by Baude et al. (2016), Tew et al. (2022), and Timberlake et al. (2019). The nectar production data came from published databases (Baude et al., 2016) and the nectar production of four additional flowering species not included in the published databases was collected following Baude et al.'s (2016) protocol. These species were *Pinguicula vulgaris*, *Polygala vulgaris*, *Genista anglica* and *Pedicularis sylvatica*; nectar measurements provided in [Table S1](#). For these species, standing nectar per inflorescence was measured using microcapillary tubes after flowers had been bagged for 24 h, and the values used in the analyses were the mean amount of sugar (μg/24 h) produced per species. Using the mean value per species to model landscape nectar is the same approach as used in other nectar quantification studies such as (Baude et al., 2016; Timberlake et al., 2021; Tew et al., 2023).

2.3 | Plant-pollinator interaction networks

To compare pollinator foraging behaviour across the treatments, we collected plant-pollinator visitation data during fortnightly surveys. During each survey, a 30 min timed walk was carried out through each 1-ha plot, totalling 60 min per site. During the surveys plant-pollinator interactions were recorded, defined as an insect making contact with the reproductive plants of a flower, as per (Dicks et al., 2002). For each interaction, the plant and insect species were recorded, and the individual was caught and pinned for later identification by a taxonomist. Clocks were stopped during insect handling, ensuring sampling time was consistent across surveys. Surveys were carried out on dry days above 12°C and with wind speed below 10 m/s, between 09:00 and 18:00. Repeated surveys for all plots were carried out at a different time of day (between 09:00–12:00, 12:00–15:00 or 15:00–18:00) to account for temporal variation in pollinator behaviour and provision of pollen and nectar, as per (Gibson et al., 2011).

Plant-pollinator interaction data for each site were pooled into two periods: 'pre-apiary' and 'during-apiary' ([Figure 1b](#)). When comparing the structure of the plant-pollinator networks, honey bee interactions were removed from the data, thus we are comparing changes in the behaviour of just wild pollinators at the sites rather than including the foraging behaviour of honeybees in our networks. We used this approach because including honey bee interactions substantially affects network metrics, but may reflect the treatment intensity, rather than changes in wild pollinator behaviour. Honey bee records in our networks were separately used to assess their dietary overlap with wild pollinators and the success of our apiary-free control treatment.

The following six network indices were measured for each site and period:

1. *Plant and Insect richness*: The number of species of flowering plants and pollinators present in the network. A decline in richness would suggest that honey bee introductions reduce the diversity of wild pollinators, for example through competitive exclusion, displacement from flowers or reduced fitness leading to population declines.
2. *Links per species*: The mean number of interactions made by each species in the network. If wild pollinators experience resource competition with honey bees, they may broaden their diets to include additional plants. This behavioural shift would appear as an increase in links per species.
3. *Connectance*: The proportion of possible interactions realised in the network. An increase in connectance indicates that species behave in a more generalised way, for example, if wild pollinators are displaced from preferred plants and begin visiting a wider array of floral species.
4. *Shannon diversity of interactions*: A measure of the diversity of plant–pollinator interactions in the network, taking into account the proportion represented by each type of interaction. An increase in Shannon diversity at sites with honey bees would indicate that wild pollinators diversify their foraging, resulting in novel or more evenly distributed interactions across plant species.
5. *Nestedness*: A measure of the structure of species interactions within the network, where in a fully nested network, specialist species interact with subsets of the flowers used by the most generalist species. If honey bees dominate key floral resources, specialist pollinators may be forced onto other plants, potentially reducing nestedness.
6. *Robustness*: The mean likelihood of a species extinction given the random removal of links from the network, that is the ability of the network's functionality to withstand species loss. Competition from honeybees may reduce the redundancy of interactions if wild pollinators lose access to key plants, so a reduction in robustness would indicate that the community is more vulnerable to disturbance.

2.4 | Mass and macronutrients of pollen collected by bumblebees

Whilst we can infer pollinator competition through behavioural changes observed in plant–pollinator networks, changes in the mass or nutrients of collected pollen provide a more direct measure of the impact of apiaries on bumblebee fitness. During each survey, bumblebees and honey bees with pollen baskets (corbiculae) had both baskets removed, air-dried and frozen. These samples were then weighed, with one corbicula from each individual used to measure protein content, and the other used to measure lipid content, based on the protocol of Vaudo et al. (2020) and adjusted for use with 1 mg pollen samples. The intertegular distance (ITD) of each individual bee was also measured to account for the effect of body size on foraging effort. For each sample, the mean protein and lipid concentration values from three subsamples were used to calculate the protein to lipid ratio (P:L ratio).

2.5 | Statistical analysis

To compare the availability of nectar across treatments over the field season, generalised additive mixed models (GAMMs) were used, with day modelled using a thin-plate spline with degree of smoothing selected via generalised cross-validation, with land management type included as a fixed effect and site as a random effect. The starting model also included an interaction between day and land management type, leading to separate smoothed relationships in each management type. Candidate models were created through starting with the full model including the treatment and interaction term, removing the terms sequentially, and then compared using values generated by Akaike's information criterion, with the model with the lowest AIC value selected for each site type. All models with the best fit used a gamma error family and log link function. All modelling, analysis and plotting was done using RStudio v.3.2.2. (R Core Team, 2019), using ggplot2 and mgvc (Wood, 2011) packages.

To test whether sampling effort reflected true species richness at sites, Chao1 estimates of floral and insect species richness were generated for each site for the whole season and compared with observed species richness (Table S2). The assemblages of flowering plants at the 20 sites were compared using non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarities to assess underlying variability in floral abundance and richness across sites and periods ('pre-apiary' and 'during-apiary') (Figure S3). GAMMs were used to model the observed floral abundance and insect visits per survey from May to September for all 20 sites, with land management as a fixed effect and site as a random effect. The SE around the means was fitted using thin-plate smoothing splines for plotting.

Plant–pollinator network metrics were compared among apiary and land management treatments, using generalised linear models (GLMs) and generalised linear mixed models (GLMMs) in the *lme4* package in R (Bates et al., 2015). The difference between the pre-apiary and during-apiary periods was calculated for each metric and site, and this change was used as the dependent variable. Fixed effects were apiary treatment, land management type, and, where it improved the predictive power of the model, their interaction. To assess the impact specifically of habitat structure on network metrics, models were made with either percentage grass cover, habitat connectance, or interspersed juxtaposition as fixed variables alongside beetype. These habitat structure metrics were not included within the same model as land management type, due to non-independence, as grazing/burning is likely to impact on habitat structure. The three site 'Blocks' were considered as a random effect but only included in models where this explained additional variance to the fixed effects. All candidate models including interactions terms were compared using values generated by Akaike's information criterion, and the model with the lowest AIC value selected.

Finally, to compare the mass and macronutrient composition of pollen collected by bumblebees across treatments, we ran GLMMs using the *lme4* package in R, including apiary treatment and land management type as fixed effects and site as a random effect. Dependent variables were pollen basket (corbicular) mass and pollen protein:lipid

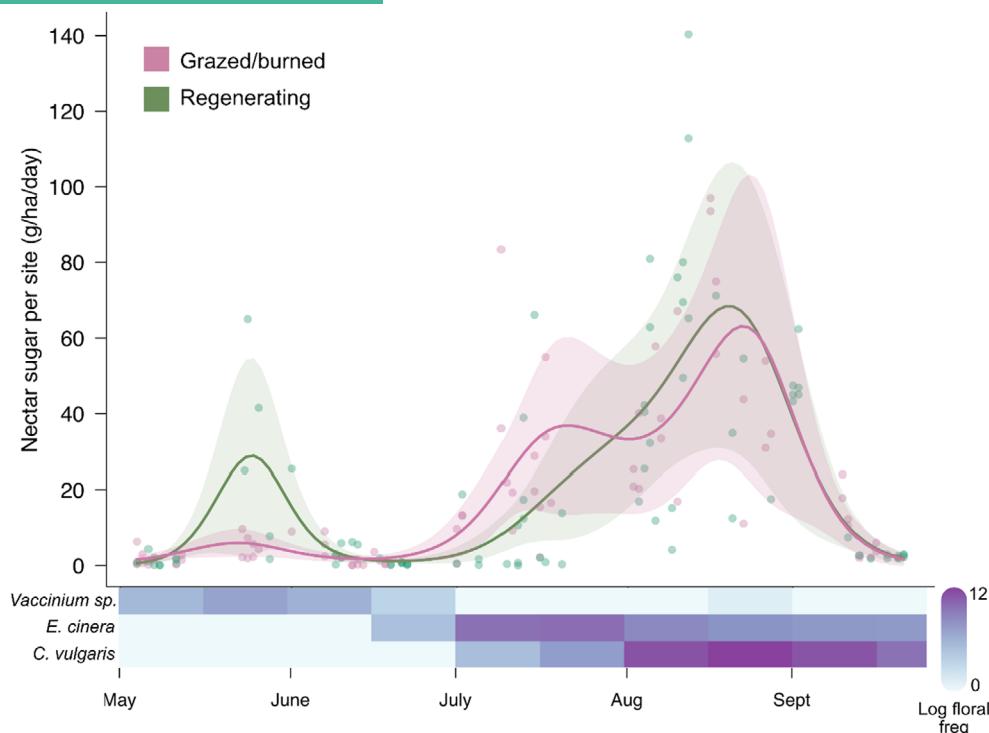


FIGURE 2 Landscape nectar sugar phenology from May to September 2022; surveys for grazed/burned sites are shown in purple, and regenerating sites are shown in green. A spline curve is applied to the data using a GAMM model for the two land management types, with shaded regions representing standard error. The phenologies of the three plant species which contributed 80% of annual landscape nectar are shown below the graph, with log floral abundance shown using a heatmap.

ratio. To account for the impact on foraging effort due to body size variation across castes and species, pollen mass was weighted by the intertegular distance (ITD/mm) of each bee.

3 | RESULTS

3.1 | Habitat structure and nectar production

From May to September 2022, a total of 1280 transects were walked at the 20 sites, and 1,629,659 individual floral units were recorded from 54 plant species. Over the whole season, there was no significant difference in total nectar sugar production between the land management types (GAMM, $t = -0.251$, $p = 0.802$), however, GAMMs run using data collected during the *Vaccinium* flowering period showed that regenerating sites had significantly more *Vaccinium* flowers (GAMM, $t = 2.209$, $p = 0.048$), and subsequently produced significantly more nectar (on average 16 ± 4.2 g/ha/day) than grazed/burned sites during this time (GAMM, $t = 3.79$, $p = 0.001$). Nectar phenology was significantly non-linear (GAMM, $F_{7,7} = 39.09$, $p < 0.001$), with peaks in nectar corresponding with the flowering of nectar-rich *Vaccinium* species early in May, and *Calluna vulgaris* in August (Figure 2). Over the whole season, the two land management types were not significantly different in floral abundance (GAMM, $t = -0.245$, $p = 0.807$), nor floral species richness (GAMM, $t = -1.393$, $p = 0.166$), see Figure S4. Instead, the clearest difference in habitat

cover between land management types was percentage grass cover, with grazed/burned sites on average having $18.24\% (\pm 8.0)$ more grass cover than regenerating sites (LMM, $t = -2.279$, $p = 0.035$, Figure 3). Habitat connectance was significantly higher at regenerating sites (LMM, $t = -2.276$, $p = 0.044$), whilst interspersed juxtaposition was lower (LMM, $t = 2.577$, $p = 0.019$, Figure 3). Details of the landscape classification models can be found in Supporting Information, Figures S1 and S2.

3.2 | Plant-pollinator interaction networks

A total of 5115 plant-pollinator interactions were recorded at the 20 field sites among 58 plant species (four more plant species than recorded in the floral surveys) and 405 pollinator species (Figure 4b). Of these interactions, 713 were made by honey bees, comprising 38.1% of all visits to flowers at sites with apiaries. The percentage of visits at apiary-free sites made by honey bees was 0.003%, comprising six records at one site. Honey bees showed dietary overlap with 98% of co-occurring wild insect taxa, or 162 species. Chao1 estimates of sampling completeness showed that 55.9% of insect species and 96.1% of plant species present in the landscape were observed in the networks (for full results see Table S2). Just six plant species received 85.1% of all insect visits (Figure 4a). These were *Calluna vulgaris* (43% of visits), *Potentilla erecta* (16.1%), *Erica cinera* (11.8%), *Galium saxatile*

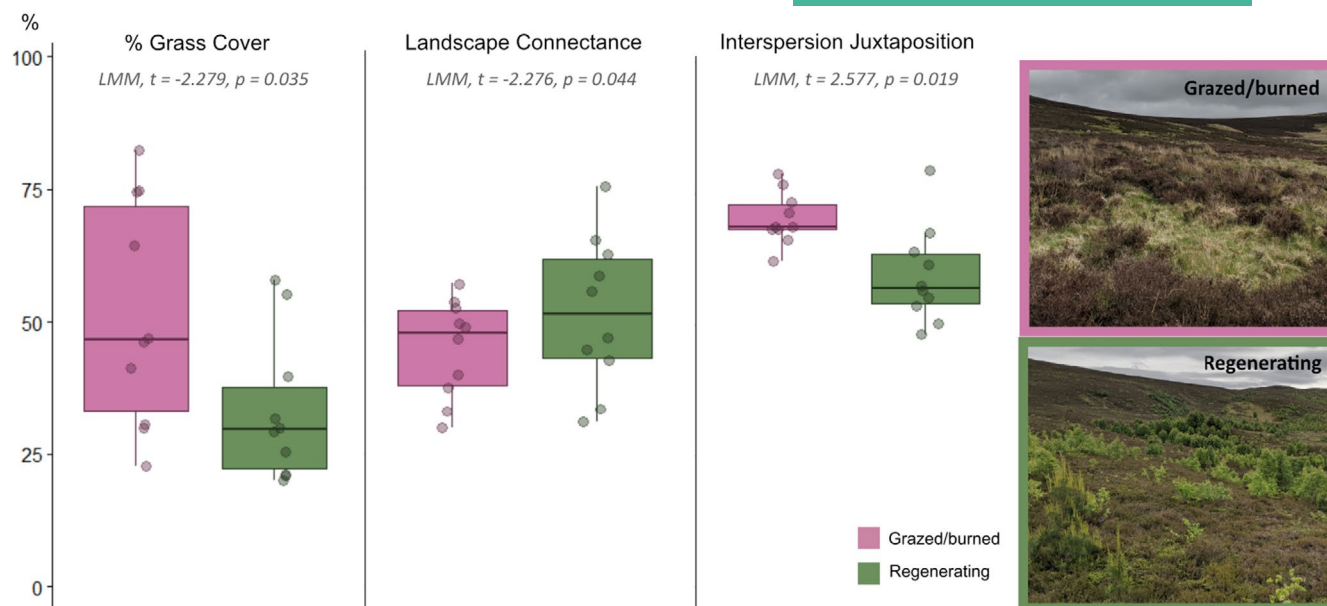


FIGURE 3 Plots describing the habitat structure at the sites showing significant differences in percentage grass cover, landscape connectance and interspersion juxtaposition between the two land management types. Images show typical site vegetation cover for the two site types.

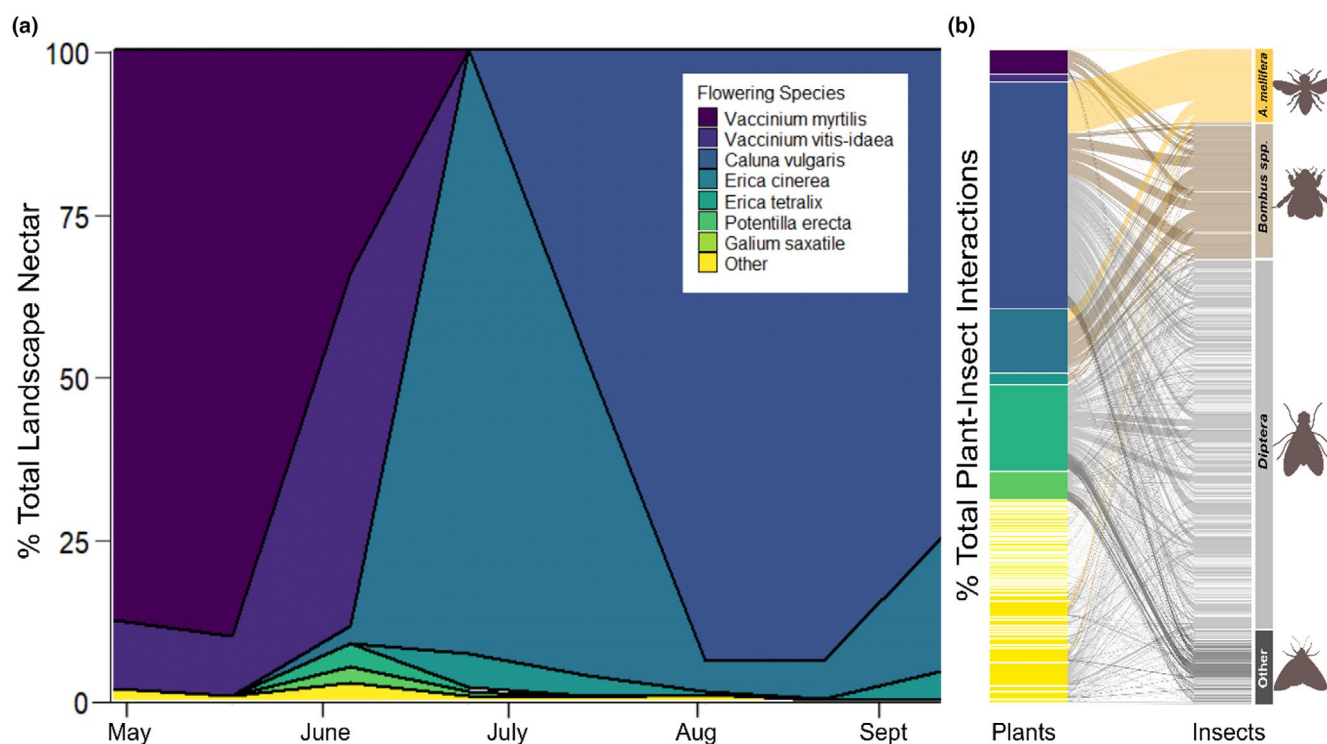


FIGURE 4 (a) Proportional contributions to landscape nectar supply through time by different plant species, and (b) a plant–pollinator network showing proportional contributions to all species interactions by different plant and insect taxa.

(5.6%), *Vaccinium myrtillus* (4.5%) and *Ranunculus acris* (4.1%). The remaining 14.9% of visits were made to 52 other plant species. Notably, 30% of insect visits were made to plant species that together contribute 2% of annual landscape nectar (Figure 4a). The nine most common insect taxa in the networks made up 41% of visits. These were *Apis mellifera* (13.9%), *Bombus lucorum*/

terrestris (7.5%), *Bombus monticola* (7.3%), *Bombus jonellus* (4.1%), the hoverflies *Melanostoma scalare* (3.1%) and *Episyrphus balteatus* (2.4%), and the ant *Formica lemni* (2.8%). The two most common insect orders were Diptera (51.4%) and Hymenoptera (45%). Lepidoptera and Coleoptera together contributed just 3.6% of the visits. Lists of the most abundant plant and insect

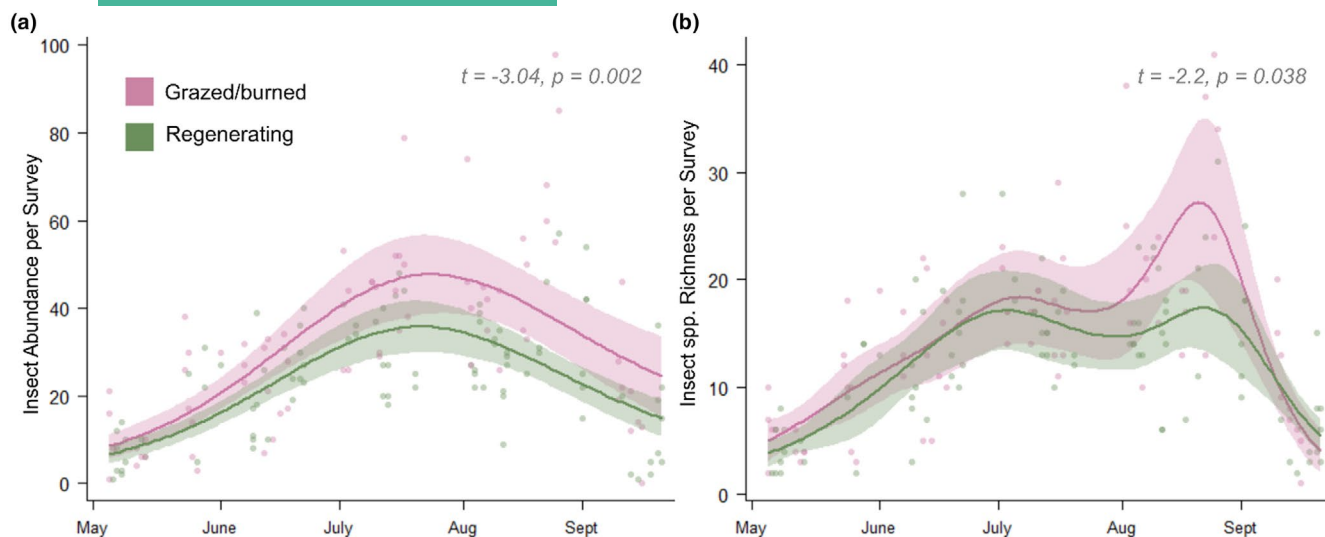


FIGURE 5 (a) insect abundance and (b) insect richness per survey from May to September 2022. Surveys for grazed/burned sites are shown in purple, and regenerating sites are shown in green. Splines generated by the generalised additive mixed models $\pm$ standard error are shown for both land management types.

species in the interaction networks are provided in [Supporting Information \(Table S3\)](#).

Grazed/burned sites were significantly higher in insect species richness (GAMM, $t = -2.2$, $p = 0.038$) and abundance (GAMM, $t = -3.04$, $p = 0.002$) compared with regenerating sites (Figure 5). However, no difference in insect abundance or richness was found between apiary and apiary-free treatments (abundance: GAMM, $t = 1.103$, $p = 0.272$, richness: GAMM, $t = 2.57$, $p = 0.10$).

When hives were present at apiary sites, honey bees contributed an average of 32.1% ($\pm 6.9\%$) of interactions in the networks. However, the presence of honeybees at sites did not result in significant changes in species abundance, richness, links per species, connectance, Shannon diversity of interactions, number of plant species visited, nor network robustness (see Table S4). However, nestedness was lower at apiary sites compared with apiary-free sites (GLMM, $e = -0.12$, $p = 0.04$), with the strongest effect at regenerating sites with apiaries (GLMM, $e = -0.43$, $p = 0.04$). Including the interaction between interspersed juxtaposition and apiaries was also found to improve model fit for nestedness (GLMM, $e = -1.04$, $p = 0.05$); interspersed juxtaposition also improved model fit for pollinator robustness (GLM, $e = -0.006$, $p = 0.008$). Overall, 42.2 (± 26.2)% of mean total variance was explained by the models; and of this variance, 18.6 (± 17.5)% could be accounted for by apiaries alone, and 20.7 (± 34.6)% by land management type alone.

3.3 | Mass and macronutrients of pollen collected by bumblebees

A total of 205 bumblebee corbiculae (pollen baskets) were collected for macronutrient analysis, 111 from apiary sites and 94 from apiary-free sites; 101 from grazed/burned sites and 104 from regenerating sites. The mean protein: lipid ratio in samples was 1.44 (± 0.17), and

mean pollen mass (ITD/mg) was 6.51 (± 0.72). Pollen protein: lipid ratio was not affected by apiary treatment (GLMM, $t = 1.51$, $p = 0.13$), nor by land management type (GLMM, $t = 1.30$, $p = 0.19$); rather, as expected, bumblebees maintained consistent protein: lipid ratios across all treatments and periods (Figure 6b). No difference in *Bombus* body size was found across all treatments and periods (GLM, $t = -0.53$, $p = 0.59$). The relative mass of *Bombus corbiculae* compared with bee body length was not significantly different between apiary treatments (GLMM, $t = -1.84$, $p = 0.06$), nor land management types (GLMM, $t = -0.84$, $p = 0.39$). Figure 6a.

In addition, 108 corbiculae from honey bees were analysed. Pollen mass per individual was significantly higher than for *Bombus* spp. (Wilcoxon rank-sum test, $W = 4771.5$, $p < 0.0001$), and pollen protein: lipid ratio was significantly lower (Wilcoxon rank-sum test, $W = 7747$, $p = 0.00013$), Figure S5.

4 | DISCUSSION

Our findings suggest that, within this heathland system of migratory beekeeping, land management plays a greater role in shaping wild pollinator communities than resource competition from managed honey bees. Whilst apiaries had moderate impacts on plant-pollinator networks, these effects were modest and did not result in changes in the mass or macronutrient content of pollen collected by bumblebees. In contrast, land management influenced multiple aspects of the ecosystem, including habitat structure, spring nectar provision, and insect abundance and richness. Notably, the moderate impact of apiaries on pollinator networks occurred at regenerating sites, indicating that impacts of hives may depend on underlying habitat structure and floral phenology. In what follows, we explore these findings and their implications for landscape management for wild pollinator conservation.

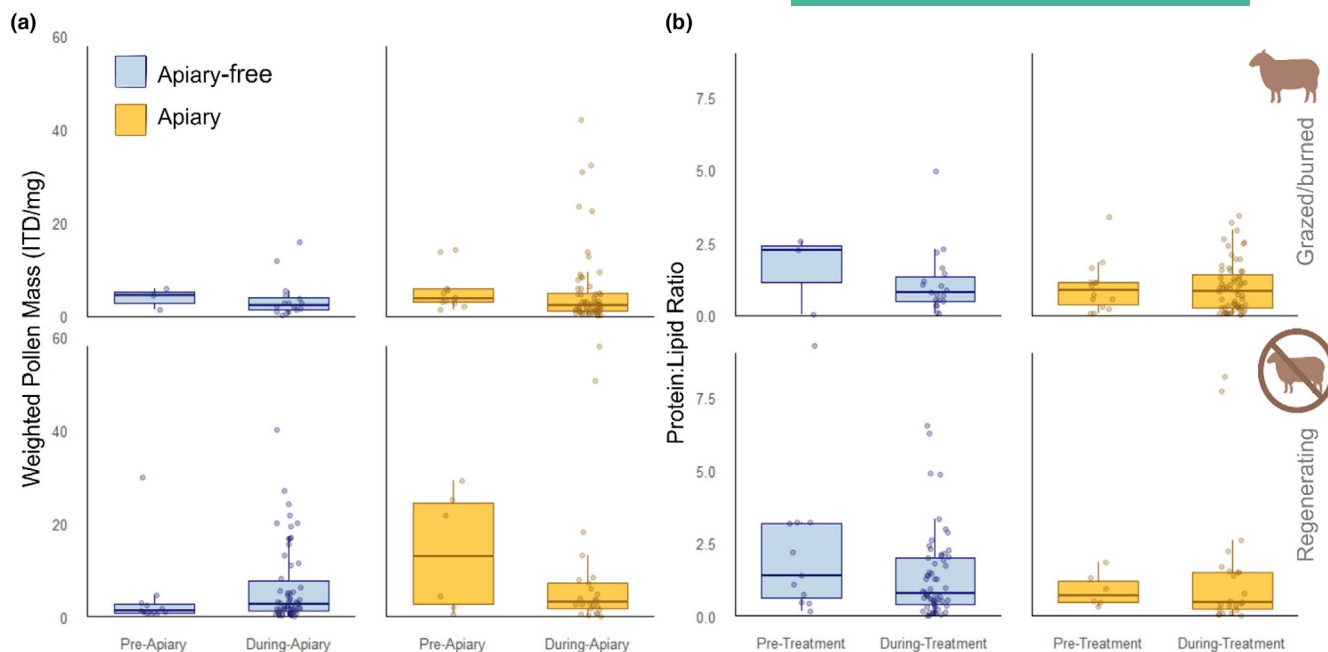


FIGURE 6 Boxplots comparing (a) the relative mass (ITD.mm/mg.pollen) and (b) the Protein: Lipid ratio of pollen baskets collected by individual bumblebees between apiary and land management treatments, before and during apiary introductions. No significant differences were detected between any categories.

4.1 | Habitat structure and nectar production

We found that nectar phenology was strongly affected by land management, with 63% less nectar on average produced at grazed/burned sites in spring. This is likely due to the impact of sheep at these sites, which browse on *Vaccinium* new growth including flowers. This has potentially acute implications for queen bumblebees emerging from hibernation, which in heathlands rely almost entirely upon *Vaccinium* for nectar at this time of year (Moquet et al., 2015). During May surveys, over 98% of available nectar was produced by *Vaccinium* species (see Figure 4), and 93% of flower visits by *Bombus* were to *Vaccinium*. The loss of this floral resource due to spring grazing is therefore important to consider when managing livestock in heathlands.

Whilst both land management types hosted similar plant communities, our habitat classification models showed that grazed/burned sites had significantly more grass, and had less connected, more interspersed land cover than the regenerating sites. In other words, these sites were more heterogenous in their vegetation cover than regenerating sites. We found that Diptera abundance and diversity was higher at grazed/burned sites, and to a smaller extent increased habitat fragmentation also explained this. Such habitat heterogeneity has been linked to more abundant and diverse pollinator populations, where a diversity of vegetation structures provides a wider variety of niches and resources for insects (Sinclair et al., 2024). Other factors potentially driving Diptera assemblage at burned/grazed sites are that grass flowers are important sources of pollen for many Diptera groups (e.g. Orford et al., 2016), and the increased abundance of livestock in these sites is likely to offer niches for animal and dung-associated species. Whilst regenerating field sites generally supported smaller and

less diverse pollinator communities later in the season, it is important to note that these heathlands are transition habitats, where burning and grazing practices have only ceased in the last 10–20 years. Thus, the heterogeneity and plant communities will continue to change as these habitats succeed towards woodland.

4.2 | Plant–pollinator interaction networks

Many studies assessing pollinator competition using plant–pollinator networks retain honeybee records in network analyses (e.g. Dáttilo et al., 2022; Pasquali et al., 2025; Valido et al., 2019), which is appropriate when honey bee density is unknown or when dietary overlap and interaction patterns are the primary focus. However, when assessing behavioural responses of wild pollinators to hive introductions, removing honey bee records allows network changes driven by wild pollinators to be isolated, rather than simply reflecting treatment intensity of hive introductions. Because including or excluding honeybees can substantially alter network metrics analyses (explored in Worthy et al., 2024), it is crucial that decisions should be justified.

Contrary to our hypothesis, with the exception of nestedness, the plant–pollinator network metrics at the field sites were not significantly affected by the introduction of honey bees, despite their accounting for a third of plant–pollinator visits to sites on average. This is in line with Worthy et al. (2024), who found that shifts in network structure were only detectable when honeybees themselves were included in the analysis. In addition to having lower insect richness and abundance, we found that when apiaries were present, regenerating sites and lower habitat ‘fragmentation’ (interspersed

juxtaposition) were associated with lower nestedness and pollinator robustness. Interspersion is comparable to fragmentation or mixing of habitat types, which leads to increased density of habitat edges. This has been linked to robustness in plant–pollinator networks due to the increase in available microclimates that edges in mixed habitats provide (Grass et al., 2018; Ren et al., 2023). High nestedness in networks is associated with stability and resilience (Bascompte et al., 2003; Thébault & Fontaine, 2010), therefore, the slight reduction in nestedness of plant–pollinator interactions found at regenerating sites with apiaries suggests that these sites were perturbed, resulting in a less cohesive, more partitioned network with potentially a lower redundancy of interactions. A reduction in nestedness and robustness could make plant–pollinator communities more susceptible to other forms of disturbance, such as extreme weather events, land use change and invasive species (Grass et al., 2018; Ramos-Jiliberto et al., 2018; Wang et al., 2023; Weiner et al., 2014).

4.2.1 | Mass and macronutrients of pollen collected by bumblebees

The protein:lipid ratio of collected pollen was significantly lower for bumblebees than for honeybees, a finding reflecting the differing life histories of the two genera and widely reported in the literature (Vaudo et al., 2016, 2018, 2024). However, no significant differences in mass or protein: lipid ratios of pollen collected by bumblebees were found across treatments or periods, suggesting limited resource competition between honey bees and bumblebees in these habitats. Whilst our plant–pollinator network methods cannot directly measure competition because they assess behaviour rather than fitness, pollen nutrition provides more direct evidence of fitness impacts as it provisions bumblebee offspring and influences colony success. For instance, reduced protein can lower larval survival, and nutritional stress increases susceptibility to disease (Roger et al., 2017; Roulston & Cane, 2002).

Because this landscape offers few alternative floral resources, competitive effects may not appear as network re-wiring due to there being no alternative plants for pollinators to switch to. If this were the case, we would also expect to see reduced pollen collection from *Bombus* species, but this was not detected. Although reviews (Thomson & Page, 2020) and recent work (Page et al., 2024) suggest that introduced honey bees can alter wild pollinator nutrition in resource-poor habitats, we did not detect similar effects. Bumblebees may serve as sensitive indicators of competition, as large-bodied species are particularly vulnerable due to their high energetic demands (Henry & Rodet, 2018) and have strong floral overlap with honeybees (Iwasaki & Hogendoorn, 2022). Therefore, the absence of detectable changes in pollen mass or nutritional quality suggests that floral resources were not limiting these habitats.

Bumblebees are known to regulate their protein: lipid intake across habitats and seasons, in line with our findings (Vaudo et al., 2016, 2018). Although some studies report smaller bumblebees near apiaries

and others report the opposite (Burns et al., 2025), we did not observe bumblebee body size differences between apiary treatments.

4.3 | Limitations and future directions

It is important to note that whilst we detected negligible changes in the foraging behaviour of wild pollinators, even at a proximity to hives that maximises honey bee foraging pressure, we cannot say how 'robust' wild pollinator populations are to apiary introductions in these landscapes. For example, whether competition would occur given more limited resource availability (e.g. during a drought year), at higher hive densities, or whether disease transmission is an issue, remains unexplored. Nevertheless, by monitoring realistic densities under normal conditions, our results offer evidence of the normal impact of honey bees on wild pollinators in these habitats.

A perennial challenge in pollinator competition research is that whilst shifts in foraging behaviour can signal competitive pressure on pollinators, they are not direct measures of competition because they do not capture impacts on wild pollinator fitness. Collecting true fitness data is challenging, and the lack of such data is a recognised limitation in the field (Iwasaki & Hogendoorn, 2022; Sponsler et al., 2023). Future work should therefore prioritise capturing pollinator fitness indicators, for example through multigenerational population monitoring, or physiological measurements of managed 'wild' pollinator species such as introduced bumblebee colonies. The breadth of data offered by plant–pollinator networks could then be used alongside fitness data to offer insights into how fitness may be impacted via changes in foraging behaviour.

Whilst the protein: lipid ratio of pollen is a useful measure of nutrition that has been shown to drive decisions in bee foraging, pollen is a highly complex substance, containing a variety of compounds beneficial or detrimental to different aspects of bee development (Furse et al., 2023; Roger et al., 2017; Vanderplanck et al., 2014). Analysis of micronutrients, rather than simply protein and lipid content, could therefore reveal other changes in nutrition as a result of apiary introductions.

For consistency with other landscape-scale nectar models, we used the mean nectar value per species in our analyses. However, this ignores the natural variation in nectar provision among individual plants, which can vary with temperature, water availability, age and time of day (e.g. Bertazzini & Forlani, 2016; Herrera et al., 2006). Looking forward, Bayesian modelling approaches (which can retain and propagate variation in models, rather than requiring single-point estimates) offer an option for integrating the variability of nectar provision into landscape-scale models (Kéry & Royle, 2016).

We used 500m as a buffer distance for habitat analysis as most small flying insects disperse within a few 100m (Greenleaf et al., 2007; Rotheray et al., 2014), however, it would be useful to see how other distances might explain our data. Lastly, here we only considered the effects of apiaries on day-flying insects, and so assessing impacts on nocturnal pollinators such as moths remains a pressing research gap.

4.4 | Policy and management implications

An important management finding was that grazed/burned sites had greatly reduced spring nectar availability, due to sheep grazing on *Vaccinium* species. This resource is particularly important for emerging *Bombus* species in April and May. We therefore recommend limiting early-season grazing in heathlands to conserve this nectar source; avoiding spring grazing could increase *Vaccinium* nectar availability to bumblebees by an average of 63%.

Commercial hives in European heathlands are typically introduced during the *Calluna vulgaris* flowering period, when floral resources are most abundant. Our results suggest that this practice likely reduces the potential for competition with wild pollinators, as 91.45% of annual landscape nectar production occurred during this bloom period. We recommend that introducing apiaries outside the *Calluna* flowering season should be avoided, as the likelihood of resource competition is likely to increase when floral resources are less abundant, particularly in early spring. Together, these findings highlight how floral phenology can influence resource limitation, and subsequently competition between pollinators.

The higher pollinator abundance and diversity observed at grazed/burned sites were driven primarily by *Diptera* species, and previous research has shown that habitats created by grazing can benefit *Diptera* families associated with open and disturbed areas (Jerrentrup et al., 2014). However, excessive grazing can reduce habitat heterogeneity, floral resources and insect diversity, as illustrated by the decline in spring *Vaccinium* nectar observed here. Our findings therefore support the Intermediate Disturbance Hypothesis, suggesting that moderate disturbance can benefit pollinator communities whilst excessive disturbance may be detrimental in grazed landscapes (Lázaro et al., 2016; Ma et al., 2017; Sinclair et al., 2024; Wang & Hou, 2024). We therefore recommend management approaches that maintain habitat heterogeneity, such as targeted conservation grazing, as strategies to balance pollinator conservation with wider heathland restoration objectives.

We found pollinator abundance, diversity, robustness and network nestedness are positively associated with grazing/burning and habitat interspersed, highlighting the importance of landscape heterogeneity. These findings are particularly relevant given the recent implementation of the Scottish Wildlife Management and Muirburn Act (2024), which restricts burning on heathland without a licence (Scottish Parliament, 2024). Although muirburn has traditionally been used to maintain patchy landscapes of young *Vaccinium* for grouse and to improve grazing for livestock, intensive burning and grazing have also been linked to biodiversity loss, soil erosion and increased wildfire risk (Lilly et al., 2009; Pakeman et al., 2019; Shewring et al., 2024). Hence, the bill has important implications for habitat heterogeneity and its effects on heathland plant and pollinator populations.

Heathlands are important forage habitats for commercial honeybees across Europe (Henry & Rodet, 2018; Jensen et al., 2005; Olmeda et al., 2020) and in other heathland-type habitats such as in Australia (Benecke, 2003; Keith et al., 2014), South African Fynbos (Hepburn, 1991) and Chilean matorral (Lobos et al., 2022). At the same time, these habitats support diverse wild pollinator communities

(Descamps et al., 2015; European Environment Agency, 2025; Medel et al., 2018; Melin et al., 2014; Wawrzyczek et al., 2024). Whilst concerns about hive overstocking are recognised in the 2020 EU Habitat Action Plan (Olmeda et al., 2020), the potential impacts of managed honeybees on wild pollinators are not mentioned in the 2017–2027 Pollinator Strategy for Scotland (NatureScot, 2017). Our study therefore helps to address an important evidence gap to help to inform hive management for pollinator conservation in these landscapes.

5 | CONCLUSION

Overall, we find that honey bees have limited effects on the flower visitation behaviour and pollen foraging of wild pollinators in upland heathlands, whereas land management is a strong driver of habitat structure, floral resource availability, and pollinator communities. Our results suggest that the extent of pollinator competition is strongly influenced by habitat management and floral phenology, highlighting the importance of considering honeybee impacts within a broader landscape context. By integrating pollinator networks, pollen nutrition, and landscape-scale nectar modelling, we provide a comprehensive assessment of floral resource competition in heathlands and identify practical mitigation measures, including avoiding grazing and apiary introductions during spring. To the best of our knowledge, this is the first study to use landscape-scale nectar modelling to assess competition between managed honeybees and wild pollinators.

AUTHOR CONTRIBUTIONS

Maisie F. Brett and Jane Memmott conceived and designed the experiment, Maisie F. Brett established the field sites, Maisie F. Brett and Lis Mijares collected the data, Maisie F. Brett and Lisa Mijares analysed the data, Ian P. Vaughan advised on data analysis, and Maisie F. Brett and Jane Memmott led the writing of the manuscript.

CONFLICT OF INTEREST STATEMENT

Ian Vaughan is an Associate Editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data are available through Dryad digital repository (<https://doi.org/10.5061/dryad.v6wwpzhc5>, Brett et al., 2026).

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REFERENCES

- Adams, D. C. (2010). Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders. *BMC Evolutionary Biology*, 10(1), 72. <https://doi.org/10.1186/1471-2148-10-72>

- Baek, W.-K., Lee, M.-J., & Jung, H.-S. (2024). Land cover classification from RGB and NIR satellite images using modified U-net model. *IEEE Access*, 12, 69445–69455. <https://doi.org/10.1109/ACCESS.2024.3401416>
- Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530(7588), 85–88. <https://doi.org/10.1038/nature16532>
- Beans, C. M. (2014). The case for character displacement in plants. *Ecology and Evolution*, 4(6), 862–875. <https://doi.org/10.1002/ece3.978>
- Beekman, M., & Ratnieks, F. L. W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology*, 14(4), 490–496. <https://doi.org/10.1046/j.1365-2435.2000.00443.x>
- Benecke, F. S. (2003). *Commercial beekeeping in Australia: A report for the Rural Industries Research and Development Corporation*. RIRDC.
- Bertazzini, M., & Forlani, G. (2016). Intraspecific variability of floral nectar volume and composition in rapeseed (*Brassica napus* L. var. oleifera). *Frontiers in Plant Science*, 7, 288. <https://doi.org/10.3389/fpls.2016.00288>
- Brett, M. F., Mijares, L., Vaughan, I. P., & Memmott, J. (2026). Data from: Heathland pollinator communities are more strongly influenced by land management than by honey bee competition. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.v6wwpzhc5>
- Burns, K. L. W., Herbertsson, L., & Stanley, D. A. (2025). Honeybee hive density has consequences for foraging bumblebees in Irish heathlands. Preprint. <https://doi.org/10.1101/2025.03.07.642004>
- Cane, J. H., & Tepedino, V. J. (2017). Gauging the effect of honey bee pollen collection on native bee communities: Apis pollen depletion and native bees. *Conservation Letters*, 10(2), 205–210. <https://doi.org/10.1111/conl.12263>
- Dáttilo, W., Cruz, C. P., Luna, P., Ratoní, B., Hinojosa-Díaz, I. A., Neves, F. S., Leponce, M., Villalobos, F., & Guevara, R. (2022). The impact of the honeybee *Apis mellifera* on the organization of pollination networks is positively related with its interactive role throughout its geographic range. *Diversity*, 14(11), 917. <https://doi.org/10.3390/d14110917>
- Descamps, C., Moquet, L., Migon, M., & Jacquemart, A. L. (2015). Diversity of the insect visitors on *Calluna vulgaris* (Ericaceae) in southern France heathlands. *Journal of Insect Science*, 15(1), 130. <https://doi.org/10.1093/jisesa/iev116>
- Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning ecological restoration of plant–pollinator networks: Understanding network restoration. *Ecology Letters*, 15(4), 319–328.
- Dicks, L. V., Corbet, S. A., & Pywell, R. F. (2002). Compartmentalization in plant–insect flower visitor webs. *Journal of Animal Ecology*, 71(1), 32–43. <https://doi.org/10.1046/j.0021-8790.2001.00572.x>
- EDINA Digimap. (2022). Data provided by University of Edinburgh. <https://digimap.edina.ac.uk/>
- Elbgami, T., Kunin, W. E., Hughes, W. O. H., & Biesmeijer, J. C. (2014). The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. *Apidologie*, 45(4), 504–513. <https://doi.org/10.1007/s13592-013-0265-y>
- European Environment Agency. (2025). *Protecting and restoring Europe's wild pollinators and their habitats*. Publications Office. <https://data.europa.eu/doi/10.2800/6525185>
- Furse, S., Koch, H., Wright, G. A., & Stevenson, P. C. (2023). Sterol and lipid metabolism in bees. *Metabolomics*, 19(9), 78. <https://doi.org/10.1007/s11306-023-02039-1>
- Gibson, R. H., Knott, B., Eberlein, T., & Memmott, J. (2011). Sampling method influences the structure of plant–pollinator networks. *Oikos*, 120(6), 822–831. <https://doi.org/10.1111/j.1600-0706.2010.18927.x>
- Gill, A. M., & Groves, H. R. (1981). Fire regimes in heathlands and their plant–ecological effects. In *Heathlands and related shrublands* (pp. 61–84). Elsevier.
- Gillespie, M. A. K., Baude, M., Biesmeijer, J., Boatman, N., Budge, G. E., Crowe, A., Davies, N., Evans, R., Memmott, J., Morton, R. D., Moss, E., Murphy, M., Pietravalle, S., Potts, S. G., Roberts, S. P. M., Rowland, C., Senapathi, D., Smart, S. M., Wood, C., & Kunin, W. E. (2022). Landscape-scale drivers of pollinator communities may depend on land-use configuration. *Philosophical Transactions of the Royal Society B*, 377(1853), 20210172. <https://doi.org/10.1098/rstb.2021.0172>
- Gillespie, M. A. K., Baude, M., Biesmeijer, J., Boatman, N., Budge, G. E., Crowe, A., Davies, N., Evans, R., Memmott, J., Morton, R. D., Moss, E., Potts, S. G., Roberts, S. P. M., Rowland, C., Senapathi, D., Smart, S. M., Wood, C., & Kunin, W. E. (2024). Flowering plant communities mediate the effects of habitat composition and configuration on wild pollinator communities. *Functional Ecology*, 38(12), 2576–2594. <https://doi.org/10.1111/1365-2435.14666>
- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 1–26. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132355>
- Grass, I., Jauker, B., Steffan-Dewenter, I., Tschamtkke, T., & Jauker, F. (2018). Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. *Nature Ecology & Evolution*, 2(9), 1408–1417. <https://doi.org/10.1038/s41559-018-0631-2>
- Gray, A., Brodschneider, R., Adjlane, N., Ballis, A., Brusbardis, V., Charrière, J. D., Chlebo, R., F. Coffey, M., Cornelissen, B., Amaro da Costa, C., Csáki, T., Dahle, B., Danihlík, J., Dražić, M. M., Evans, G., Fedoriak, M., Forsythe, I., Graaf, D., Gregorc, A., ... Soroker, V. (2019). Loss rates of honey bee colonies during winter 2017/18 in 36 countries participating in the COLOSS survey, including effects of forage sources. *Journal of Apicultural Research*, 58(4), 479–485. <https://doi.org/10.1080/00218839.2019.1615661>
- Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153(3), 589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Haysom, K. A., & Coulson, J. C. (1998). The Lepidoptera fauna associated with *Calluna vulgaris*: Effects of plant architecture on abundance and diversity. *Ecological Entomology*, 23(4), 377–385.
- Henry, M., & Rodet, G. (2018). Controlling the impact of the managed honeybee on wild bees in protected areas. *Scientific Reports*, 8(1), 9308. <https://doi.org/10.1038/s41598-018-27591-y>
- Hepburn, H. R. (1991). The cape honeybee and the fynbos biome. *South African Journal of Science*, 87, 70–73.
- Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, 17(7), 609–616. <https://doi.org/10.1016/j.baae.2016.05.001>
- Herrera, C. M., Pérez, R., & Alonso, C. (2006). Extreme intraplant variation in nectar sugar composition in an insect-pollinated perennial herb. *American Journal of Botany*, 93(4), 575–581. <https://doi.org/10.3732/ajb.93.4.575>
- Iwasaki, J. M., & Hogendoorn, K. (2022). Mounting evidence that managed and introduced bees have negative impacts on wild bees: An updated review. *Current Research in Insect Science*, 2, 100043. <https://doi.org/10.1016/j.cris.2022.100043>
- Jensen, A. B., Palmer, K. E. L. I. E. A., Boomsma, J. A. C. O. B. U. S. J., & Pedersen, B. O. V. (2005). Varying degrees of *Apis mellifera ligustica* introgression in protected populations of the black honeybee, *Apis mellifera mellifera*, in northwest Europe. *Molecular Ecology*, 14(1), 93–106. <https://doi.org/10.1111/j.1365-294X.2004.02399.x>

- Jerrentrup, J. S., Wrage-Mönnig, N., Röver, K.-U., & Isselstein, J. (2014). Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. *Journal of Applied Ecology*, 51(4), 968–977. <https://doi.org/10.1111/1365-2664.12244>
- Keith, D. A., Lindenmayer, D., Lowe, A. J., Russell-Smith, J., Barrett, S. R., Enright, N. J., Fox, B. J., Guerin, G. R., Paton, D., Tozer, M., & Yates, C. (2014). Heathlands. In *Biodiversity and environmental change: Monitoring, challenges and direction*. CSIRO publishing.
- Kéry, M., & Royle, J. A. (2016). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS*. Elsevier/AP, Academic Press is an imprint of Elsevier.
- Kral-O'Brien, K. C., O'Brien, P. L., Hovick, T. J., & Harmon, J. P. (2021). Meta-analysis: Higher plant richness supports higher pollinator richness across many land use types. *Annals of the Entomological Society of America*, 114(2), 267–275. <https://doi.org/10.1093/aesa/saaa061>
- Lau, P., Sgolastra, F., Williams, G. R., & Straub, L. (2023). Editorial: Insect pollinators in the Anthropocene: How multiple environmental stressors are shaping pollinator health. *Frontiers in Ecology and Evolution*, 11, 1279774. <https://doi.org/10.3389/fevo.2023.1279774>
- Lázaro, A., Tscheulin, T. H. O. M. A. S., Devaldez, J. E. L. L. E., Nakas, G. E. O. R. G. I. O. S., & Petanidou, T. H. E. O. D. O. R. A. (2016). Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecological Entomology*, 41(4), 400–412. <https://doi.org/10.1111/een.12310>
- Lilly, A., Grieve, I. C., Jordan, C., Baggaley, N. J., Birnie, R. V., Futter, M. N., Higgins, A., Hough, R., Jones, M., Noland, A. J., Stutter, M. I., & Towers, W. (2009). *Climate change, land management and erosion in the organic and organo-mineral soils in Scotland and Northern Ireland*. Scottish Natural Heritage Commissioned Report No.325. Scottish Natural Heritage.
- Lobos, I., Silva, M., Ulloa, P., & Pavez, P. (2022). Mineral and botanical composition of honey produced in Chile's central-southern region. *Food*, 11(3), 251. <https://doi.org/10.3390/foods11030251>
- Ma, J., Huang, X., Qin, X., Ding, Y., Hong, J., du, G., Li, X., Gao, W., Zhang, Z., Wang, G., Wang, N., & Zhang, Z. (2017). Large manipulative experiments revealed variations of insect abundance and trophic levels in response to the cumulative effects of sheep grazing. *Scientific Reports*, 7(1), 11297. <https://doi.org/10.1038/s41598-017-11891-w>
- Magrath, A., González-Varo, J. P., Boiffier, M., Vilà, M., & Bartomeus, I. (2017). Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution*, 1(9), 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>
- Mallinger, R. E., Gaines-Day, H. R., & Gratton, C. (2017). Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PLoS One*, 12(12), e0189268. <https://doi.org/10.1371/journal.pone.0189268>
- Mattupalli, C., Moffet, C. A., Shah, K. N., & Young, C. A. (2018). Supervised classification of RGB aerial imagery to evaluate the impact of a root rot disease. *Remote Sensing*, 10(6), 917. <https://doi.org/10.3390/rs10060917>
- Medel, R., González-Browne, C., & Fontúrbel, F. E. (2018). Pollination in the Chilean Mediterranean-type ecosystem: A review of current advances and pending tasks. *Plant Biology*, 20(S1), 89–99. <https://doi.org/10.1111/plb.12644>
- Melin, A., Rouget, M., Midgley, J. J., & Donaldson, J. S. (2014). Pollination ecosystem services in south African agricultural systems. *South African Journal of Science*, 110(11/12), 9. <https://doi.org/10.1590/sajs.2014/20140078>
- Moquet, L., Mayer, C., Michez, D., Wathelet, B., & Jacquemart, A. L. (2015). Early spring floral foraging resources for pollinators in wet heathlands in Belgium. *Journal of Insect Conservation*, 19(5), 837–848. <https://doi.org/10.1007/s10841-015-9802-5>
- NatureScot. (2017). *Pollinator Strategy for Scotland 2017–2027*. Scottish Government.
- Office for National Statistics (ONS). (2023). *Scotland natural capital accounts: 2023*. Released 15 June 2023, ONS website, statistical bulletin. ISBN: 978-1-80525-868-1.
- Olmeda, C., Šeffrová, V., Underwood, E., Millan, L., Gil, T., & Naumann, S. (2020). *EU Action plan to maintain and restore to favourable conservation status the habitat type 4030*. European Commission. <https://www.ecologic.eu/17537>.
- Orford, K. A., Murray, P. J., Vaughan, I. P., & Memmott, J. (2016). Modest enhancements to conventional grassland diversity improve the provision of pollination services. *Journal of Applied Ecology*, 53(3), 906–915. <https://doi.org/10.1111/1365-2664.12608>
- Page, M. L., Francis, J. S., Müller, U., & Williams, N. M. (2024). Wildflower plantings and honeybee competition impact nutritional quality of wild bee diets. *Journal of Applied Ecology*, 61(12), 3104–3113. <https://doi.org/10.1111/1365-2664.14813>
- Paini, D. R. (2004). Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review. *Austral Ecology*, 29(4), 399–407. <https://doi.org/10.1111/j.1442-9993.2004.01376.x>
- Pakeman, R. J., Fielding, D. A., Everts, L., & Littlewood, N. A. (2019). Long-term impacts of changed grazing regimes on the vegetation of heterogeneous upland grasslands. *Journal of Applied Ecology*, 56(7), 1794–1805. <https://doi.org/10.1111/1365-2664.13420>
- Pasquali, L., Bruschini, C., Benetello, F., Bonifacio, M., Giannini, F., Monterastelli, E., Penco, M., Pesarini, S., Salvati, V., Simbula, G., Skowron Volponi, M., Smargiassi, S., van Tongeren, E., Vicari, G., Cini, A., & Dapporto, L. (2025). Island-wide removal of honeybees reveals exploitative trophic competition with strongly declining wild bee populations. *Current Biology*, 35(7), 1576–1590.e12. <https://doi.org/10.1016/j.cub.2025.02.048>
- Peters, A., Foster, A. P., & Barker, G. (2008). *National trust conservation directorate nature conservation evaluation: Studland, dorset*. National Trust.
- Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540(7632), 220–229. <https://doi.org/10.1038/nature20588>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Foundation for Statistical Computing. <https://www.R-project.org/>
- Ramos-Jiliberto, R., Moisset de Espanés, P., Franco-Cisterna, M., Petanidou, T., & Vázquez, D. P. (2018). Phenology determines the robustness of plant–pollinator networks. *Scientific Reports*, 8(1), 14873. <https://doi.org/10.1038/s41598-018-33265-6>
- Ren, P., Didham, R. K., Murphy, M. V., Di Zeng, X. S., & Ding, P. (2023). Forest edges increase pollinator network robustness to extinction with declining area. *Nature Ecology & Evolution*, 7, 393–404. <https://doi.org/10.1038/s41559-022-01973-y>
- Roger, N., Michez, D., Wattiez, R., Sheridan, C., & Vanderplanck, M. (2017). Diet effects on bumblebee health. *Journal of Insect Physiology*, 96, 128–133. <https://doi.org/10.1016/j.jinsphys.2016.11.002>
- Rotheray, E. L., Bussière, L. F., Moore, P., Bergstrom, L., & Goulson, D. (2014). Mark recapture estimates of dispersal ability and observations on the territorial behaviour of the rare hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae). *Journal of Insect Conservation*, 18(2), 179–188. <https://doi.org/10.1007/s10841-014-9627-7>
- Roulston, T. H., & Cane, J. H. (2002). The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). *Evolutionary Ecology*, 16(1), 49–65. <https://doi.org/10.1023/A:1016048526475>
- Schluter, D. (1994). Experimental evidence that competition promotes divergence in adaptive radiation. *Science*, 266(5186), 798–801. <https://doi.org/10.1126/science.266.5186.798>
- Scottish Parliament. (2024). *Wildlife Management and Muirburn (Scotland) Act 2024* (asp 15). ISBN: 978-0-10-590418-2.

- Shewring, M. P., Wilkinson, N. I., Teuten, E. L., Buchanan, G. M., Thompson, P., & Douglas, D. J. T. (2024). Annual extent of prescribed burning on moorland in Great Britain and overlap with ecosystem services. *Remote Sensing in Ecology and Conservation*, 10(5), 597–614. <https://doi.org/10.1002/rse2.389>
- Sinclair, J. S., Buchner, D., Gessner, M. O., Müller, J., Pauls, S. U., Stoll, S., Welti, E. A. R., Bässler, C., Buse, J., Dziok, F., Enss, J., Hörrn, T., Künast, R., Li, Y., Marten, A., Morkel, C., Richter, R., Seibold, S., Sorg, M., ... Haase, P. (2024). Effects of land cover and protected areas on flying insect diversity. *Conservation Biology*, 39, e14425. <https://doi.org/10.1111/cobi.14425>
- Sponsler, D., Iverson, A., & Steffan-Dewenter, I. (2023). Pollinator competition and the structure of floral resources. *Ecography*, 2023(9), e06651. <https://doi.org/10.1111/ecog.06651>
- Tew, N. E., Baldock, K. C. R., Morten, J. M., Bird, S., Vaughan, I. P., & Memmott, J. (2023). A dataset of nectar sugar production for flowering plants found in urban green spaces. *Ecological Solutions and Evidence*, 4(2), e12248. <https://doi.org/10.1002/2688-8319.12248>
- Tew, N. E., Baldock, K. C. R., Vaughan, I. P., Bird, S., & Memmott, J. (2022). Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens. *Journal of Applied Ecology*, 59(3), 801–811. <https://doi.org/10.1111/1365-2664.14094>
- Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329(5993), 853–856. <https://doi.org/10.1126/science.1188321>
- Thomson, D. (2004). Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology*, 85(2), 458–470. <https://doi.org/10.1890/02-0626>
- Thomson, D. M. (2006). Detecting the effects of introduced species: A case study of competition between *Apis* and *Bombus*. *Oikos*, 114(3), 407–418. <https://doi.org/10.1111/j.2006.0030-1299.14604.x>
- Thomson, D. M., & Page, M. L. (2020). The importance of competition between insect pollinators in the Anthropocene. *Current Opinion in Insect Science*, 38, 55–62. <https://doi.org/10.1016/j.cois.2019.11.001>
- Timberlake, T. P., Vaughan, I. P., Baude, M., & Memmott, J. (2021). Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *Journal of Applied Ecology*, 58(5), 1006–1016. <https://doi.org/10.1111/1365-2664.13826>
- Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, 56(7), 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Timberlake, T. P., de Vere, N., Jones, L. E., Vaughan, I. P., Baude, M., & Memmott, J. (2024). Ten-a-day: Bumblebee pollen loads reveal high consistency in foraging breadth among species, sites and seasons. *Ecological Solutions and Evidence*, 5(3), e12360. <https://doi.org/10.1002/2688-8319.12360>
- Valido, A., Rodríguez-Rodríguez, M. C., & Jordano, P. (2019). Honeybees disrupt the structure and functionality of plant-pollinator networks. *Scientific Reports*, 9(1), 4711. <https://doi.org/10.1038/s41598-019-41271-5>
- Vanbergen, A. J., & The Insect Pollinators Initiative. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, 11(5), 251–259. <https://doi.org/10.1890/120126>
- Vanderplanck, M., Moerman, R., & Rasmont, P. (2014). How does pollen chemistry impact development and feeding behaviour of polylectic bees? *PLoS One*, 9(1), e86209. <https://doi.org/10.1371/journal.pone.0086209>
- Vandvik, V., Heegaard, E., Måren, I. E., & Aarrestad, P. A. (2005). Managing heterogeneity: The importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology*, 42(1), 139–149. <https://doi.org/10.1111/j.1365-2664.2005.00982.x>
- Vaudo, A. D., Dyer, L. A., & Leonard, A. S. (2024). Pollen nutrition structures bee and plant community interactions. *Proceedings of the National Academy of Sciences of the United States of America*, 121(3), e2317228120. <https://doi.org/10.1073/pnas.2317228120>
- Vaudo, A. D., Farrell, L. M., Patch, H. M., Grozinger, C. M., & Tooker, J. F. (2018). Consistent pollen nutritional intake drives bumble bee (*Bombus impatiens*) colony growth and reproduction across different habitats. *Ecology and Evolution*, 8(11), 5765–5776. <https://doi.org/10.1002/ece3.4115>
- Vaudo, A. D., Patch, H. M., Mortensen, D. A., Tooker, J. F., & Grozinger, C. M. (2016). Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. *Proceedings of the National Academy of Sciences*, 113(28), E4035–E4042. <https://doi.org/10.1073/pnas.1606101113>
- Vaudo, A. D., Tooker, J. F., Patch, H. M., Biddinger, D. J., Coccia, M., Crone, M. K., Fiely, M., Francis, J. S., Hines, H. M., Hodges, M., Jackson, S. W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E. D., Vanderplanck, M., Yip, E., Leonard, A. S., & Grozinger, C. M. (2020). Pollen protein: Lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects*, 11(2), 132. <https://doi.org/10.3390/insects11020132>
- Wang, L., Li, J., Wang, T., & Liao, J. (2023). A positive complexity-stability relationship emerges in pollinator-plant-consumer tripartite networks disturbed by plant invasion. *Ecological Modelling*, 484, 110461. <https://doi.org/10.1016/j.ecolmodel.2023.110461>
- Wang, W., & Hou, F. (2024). Grazing modified the effects of insect on Plant in Grassland: A meta-analysis. Preprint. <https://doi.org/10.2139/ssrn.4872975>
- Wang, X., Blanchet, F. G., & Koper, N. (2014). Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in Ecology and Evolution*, 5(7), 634–646.
- Wawrzyczek, S. K., Davis, R. A., Krauss, S. L., Hoebee, S. E., Ashton, L. M., & Phillips, R. D. (2024). Pollination by birds, non-flying mammals, and European honeybees in a heathland shrub, *Banksia cataglypta* (Proteaceae). *Botanical Journal of the Linnean Society*, 206(3), 257–273. <https://doi.org/10.1093/botlinnean/boae024>
- Weiner, C. N., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2014). Land-use impacts on plant-pollinator networks: Interaction strength and specialization predict pollinator declines. *Ecology*, 95(2), 466–474. <https://doi.org/10.1890/13-0436.1>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: Estimation of Semiparametric Generalized Linear Models. *Journal of the Royal Statistical Society. Series B, Statistical Methodology*, 73(1), 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Worthy, S. H., Acorn, J. H., & Frost, C. M. (2024). Biodiversity measures of a grassland plant-pollinator community are resilient to the introduction of honey bees (*Apis mellifera*). *PLoS One*, 19(10), e0309939. <https://doi.org/10.1371/journal.pone.0309939>

SUPPORTING INFORMATION

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

Note S1. Methodology for landscape classification models.

Figure S1. An example of a 'Grazed/Burned' 500m site area, with predicted land cover classifications.

Figure S2. The relative contributions of the six land cover classes to each 500m site area, (a) between the two land management types, and (b) per site. The largest land cover type, grass, covered a significantly greater area at grazed/burned sites.

Figure S3. Two non-metric multidimensional scaling (NMDS) plots showing (a) insect assemblages and (b) floral assemblages per site, for different periods, land management types and apiary treatments. We used permutational analyses of variance to assess differences in assemblage among treatments, based on Bray–Curtis dissimilarities. Floral assemblages did not significantly differ from one another (PERMANOVA: $F=1.447$, $R^2=0.015$, $p=0.185$), however, insect assemblages differed between land management types in the 'during' period (PERMANOVA: $F=1.572$, $R^2=0.033$, $p=0.036$), marked with an asterisk.

Figure S4. (a) Floral abundance and (b) Floral spp. richness per survey from May to September. Grazed/burned sites are shown in purple, and regenerating sites are shown in green. Splines generated by the generalised additive mixed models $\pm$ SE are shown for both site types.

Figure S5. Plots comparing metrics for *Apis* and *Bombus* individuals showing the (a) relative weight and (b) protein: Lipid ratio of pollen collected per bee.

Table S1. Nectar sugar measurements for 4 additional plant species.

Table S2. Floral and Insect species accumulation curves and Chao1 values.

Table S3. Insect and Plant Species lists.

Table S4. Results of GLMMs looking at changes in network metrics between apiary treatments, land management types and habitat structure metrics. The model family is gaussian in all cases; 'interaction evenness' and 'nestedness' use a log link. Site block is included as a random effect where this improved the model predictive power, see formulas for details.

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