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RESEARCH ARTICLE

Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes

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Abstract

1. The loss of floral resources is a leading cause of wild bee decline in agricultural landscapes, but little is known about the temporal aspects of floral resource limitation for both social and solitary bees. Understanding when floral resources are most needed is crucial for the optimal design of pollinator conservation measures.
2. We surveyed bees and flowers in 160 semi-natural habitat patches multiple times per year (May–July) for 5 years. We identified the seasonality of floral resources and wild bees and examined inter- and intra-annual patterns of floral resource limitation at both local and landscape scales.
3. Floral resource availability varied across years but generally peaked in late May, after which it declined and remained low through July.
4. Bumblebee and solitary bee abundances increased across the season, leading to stronger floral resource limitation for both groups later in the season. Bumblebee abundance was marginally positively associated with the cumulative amount of landscape-scale floral resources as well as the floral resources of the previous year. Solitary bee abundance was only predicted by local-scale floral resources.
5. *Synthesis and applications*: Our results indicate that agri-environmental management should target the provision of summer floral resources for both social and solitary bees. Local-scale enhancement of floral resources can likely benefit solitary bees, but bumblebees probably require the management of floral resources at the landscape scale. Increasing the floral resources and the flowering period of herbaceous habitats that cover large proportions of the landscape, such as pastures, has the greatest potential to improve summer floral resources for bees.

KEYWORDS
agri-environment, floral resources, landscape, phenology, pollinator conservation, resource limitation, wild bees

1 | INTRODUCTION

Agricultural intensification is a leading cause of decline in wild bees, a group of organisms that provide valuable pollination ecosystem services to farmland areas (Wagner, 2020). The loss of floral resources in agricultural landscapes plays a large role in this decline because bees rely almost exclusively on floral resources to complete their life cycles (Balfour et al., 2018; Carvell et al., 2006). Floral resources are lost when natural habitats are converted for agriculture but also due to altered management of agricultural areas, such as the transition from hay to silage production (Fitzpatrick et al., 2007). To counteract this decline, conservation measures in agricultural landscapes have aimed to increase floral resource availability (Albrecht et al., 2020). However, simplified landscapes not only have a reduced quantity of floral resources but also an altered phenology of resource availability (Mallinger et al., 2016), and how the timing of floral resource supply affects bee populations remains less understood (Timberlake et al., 2019). To promote species persistence in agricultural landscapes, it is important to identify the seasonality of floral resources and the organisms that rely on them so that conservation measures can be targeted at supplying resources when they are most needed (Schellhorn et al., 2015).

Bees can be influenced by floral resources at both local and landscape scales (Scheper et al., 2015), and these resources vary over time due to plant phenology and the composition and management of different habitats in the landscape (Cole et al., 2017; Maurer et al., 2022). Assuming bee populations are regulated by bottom-up forces such as resource provision, a positive relationship between bee abundance and resource quantity should indicate that these resources are a limiting factor (Steffan-Dewenter & Schiele, 2008). As both floral availability and bee populations vary phenologically, temporal mismatches could occur if floral resource availability does not meet the demand of bee populations (Timberlake et al., 2019), resulting in increased resource limitation, or stronger relationships between flowers and bees, at certain periods within a season (Figure 1). Previous research has identified periods when floral resources could be limiting bee populations; for example, bumblebee abundance has been shown to be predicted by landscape-scale September floral resources (Timberlake et al., 2021) and the presence of late-season mass-flowering clover in agricultural landscapes (Rundlöf et al., 2014). However, local and landscape floral resources can vary both within and across years. Despite the identification of resource limitations being crucial to conservation efforts, very little research has been done that examines these intra- and inter-annual relationships between floral resources and bees in general (Carvell et al., 2017; Guezen & Forrest, 2021; Timberlake et al., 2019), and even less is known about how different groups of bees differ in their responses on these time scales (Guezen & Forrest, 2021).

The sociality of a bee species likely affects its relationship with floral resources across time. Social bees build up colonies of workers before reproducing and have been shown to benefit from a continuous accumulation of resources to successfully grow (Hemberger et al., 2022). However, colonies have also been shown to successfully exploit pulses in floral resource availability, even under high temporal variability of these resources (Hemberger et al., 2020). Solitary bees often have shorter life cycles than social bees and instead rely on resource availability at specific moments within the season (Balfour et al., 2018), which may leave them more vulnerable to resource perturbations (Ogilvie & Forrest, 2017). Even relatively short mismatches in resource phenology (e.g. a few days) have been shown to cause severe fitness losses for solitary bees, impacting the population size of the following year (Schenk et al., 2018). Thus, both the total amount of floral resources available and the seasonality of these resources likely influence the ability of a landscape to support bee populations (Hemberger et al., 2020; Timberlake et al., 2021). We are only just beginning to understand these relationships for social bees (Hemberger et al., 2020; Timberlake et al., 2021), while very little work has been done on solitary bees (Guezen & Forrest, 2021), even though they make up the majority of species in temperate bee communities (Balfour et al., 2018).

In this study, we examine the seasonality of floral resources in relation to bee abundance in order to identify temporally-related resource limitation in agricultural landscapes. Few studies have documented the seasonal variation in flower and bee communities (Balfour et al., 2018; Guezen & Forrest, 2021), and to our knowledge, none have investigated both intra- and inter-annual relationships between bee abundance and floral resources for both social and solitary bees at the landscape scale. To accomplish this, we surveyed wild bees and floral resources in 160 semi-natural habitat patches within an agricultural area multiple times per year for 5 years. We use these highly spatiotemporally replicated data to address three

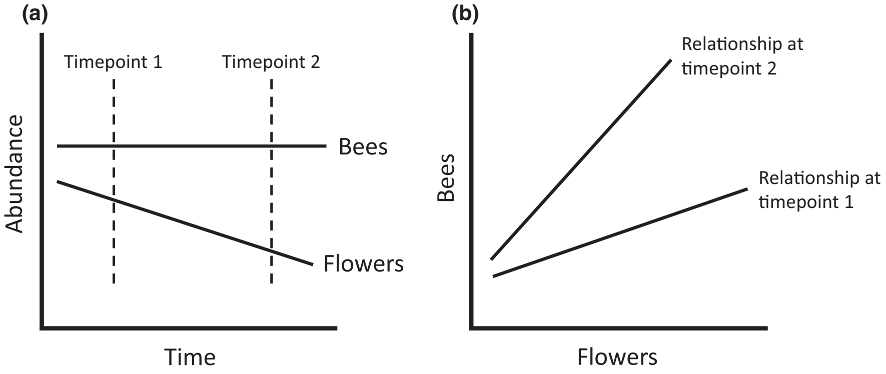

FIGURE 1 Possible temporal aspects of floral resource limitation on bee populations. If flowers and bees vary differently over time (a), then the strength of the relationship between them is expected to vary over time (b). Here, the bee-to-flower ratio increases over time (a), which increases resource limitation over time (b).

main research questions: (1) How do the floral resources provided by agricultural landscapes, and the abundance of social and solitary bees that rely on them, vary across the season? (2) Do relationships between local and landscape-scale floral resources and social and solitary bee abundance change across the season? (3) On which time scales (intra- and inter-annual) are social and solitary bees most limited by floral resource availability?

2 | MATERIALS AND METHODS

2.1 | Study design

In 2018, a landscape-level conservation initiative was started in the Geuldal area of south Limburg, the Netherlands (Figure 2) in an effort to improve existing semi-natural habitats for wild bees (boshommellandschap-geuldal.nl; for a general approach, see Kleijn et al., 2020). Approximately 60% of the area is covered by intensive agricultural land use (arable fields and permanent pastures, with almost no mass-flowering crops except for a small proportion of fruit orchards), but up to 13% consists of natural grasslands that are protected under the EU Natura 2000 conservation network, including 2% calcareous grasslands, a habitat that harbours high levels of biodiversity. The initiative targeted six habitat types that together comprise the majority of habitats valuable to wild bees in the area: field margins, hedges, extensively managed pastures, water retention sites, road verges and species-rich grasslands (calcareous grasslands). To monitor wild bees and floral resources, 160 survey sites were selected in an area of approximately 90 km^2, and have been surveyed three times per year (May, June and July) since 2018. Areal sites (all grasslands and water retention sites) are on average 1.7 ± 1.8 ha (mean ± SD; min = 0.05 ha, max = 9.7 ha), while linear sites are typically 1–2 m wide. The average closest distance between sites is 366 ± 383 m (mean ± SD; min = 19 m, max = 2766 m). From 2020, bee-friendly management, such as delayed or alternated mowing schedules, has been implemented on approximately 30% of the surveyed sites (see Table S1 in Supporting Information) to improve flower availability on the whole site, but these specific sites comprise only about 0.3% of the study area. Because we here explore general relationships between wild bees and flower cover and how these change over time, the effects of bee-friendly management are not investigated in this study. The data presented in this analysis are from 2018 to 2022 (15 survey rounds). Because it takes approximately 1 month to survey all sites included in the study, the study area is monitored virtually continuously during the survey period, allowing us to accurately model flower availability over time.

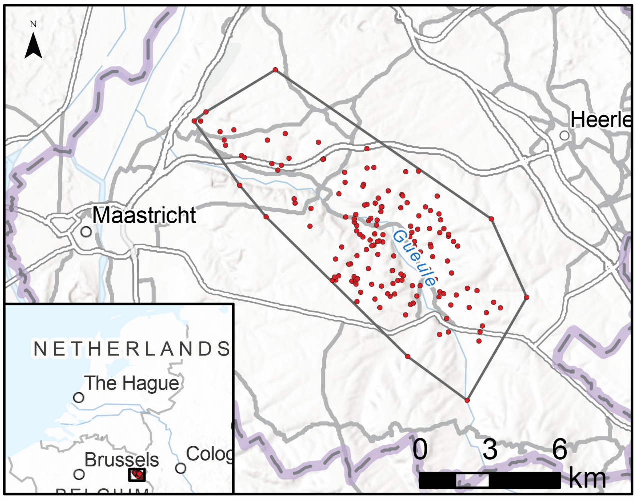

FIGURE 2 Study area in south Limburg, the Netherlands, with site points and a minimum convex polygon containing all sites.

Permits to carry out the surveys were provided by the nature conservation organizations Stichting Limburgs Landschap (Case number AL 07/15/01), Natuurmonumenten (Permission number ZL Prof. D. Kleijn/WUR 2021) and Staatsbosbeheer (agreement numbers 21074 & 23125) as well as by the waterboard Waterschap Limburg (document number 2021-D38644). No ethical approval was required for this study.

2.2 | Bee surveys

Wild bees were surveyed using the standardized transect method (Westphal et al., 2008). One 150 × 1 m fixed transect was demarcated at each site, and all wild bees encountered within the transect area in a period of 15 min were recorded or caught with an insect net for later identification. Catching and handling time were not included in the survey period. Surveys occurred on dry days with ≥15°C and with low winds and low cloud cover. In the Netherlands, *Bombus terrestris* and *Bombus lucorum* queens and workers cannot be separated without molecular techniques (Alferink et al., 2020) and were grouped into one *B. terrestris* complex.

2.3 | Floral resource surveys

Floral resources were surveyed after each bee inventory (or within ±2 days) according to the methods of Scheper et al. (2015). All forbs in flower within the transect area were identified to species using ObsIdentify and relevant keys (Heukels & Duistermaat, 2020), and all individual flowers for each species were counted in the entire 150 m^2 transect area. Asteraceae were counted as heads, and other composite flowers (e.g. umbels) were counted as heads and then multiplied by an average number of flowers per head. When flower numbers were large, they were estimated, for example by counting by factors of 10. Flower counts were multiplied by an average area per individual flower (per head for Asteraceae) for each species; total areas per species were then summed across all observed species, and the total flower area was divided by the transect area to calculate transect flower cover (%).

2.4 | Landscape flower cover calculation

To estimate landscape flower availability, we calculated the flower cover (%) in a 500 m buffer around each transect for each sampling day. We chose a 500 m buffer because this approximately corresponds to the average foraging distance of the largest bees considered in this study (Redhead et al., 2016). We adapted the formula used in Scheper et al. (2015):

$$\mathrm{LFC}\,(\%) = \frac{\sum_{i=1}^{n} \mathrm{PF}_i \times \mathrm{PA}_i}{100}$$

with PF_i being the average percentage flower cover in habitat type i on a given sampling day, PA_i the percentage area cover of habitat type i in the landscape, and n the total number of habitat types in the landscape. For each sampling day, PF_i was calculated by averaging all records of transect flower cover conducted on the three nearest sampling days for habitat type i. Flower cover values from transects where bee-friendly management was applied were excluded from these calculations because they are not representative of that particular habitat type and would lead to an overestimation of landscape flower cover for every other survey site. PA_i was calculated in ArcGIS Pro using defined land use classes (hedges, field margins, pastures and species-rich grasslands according to Bij12, 2021; water retention sites according to Waterschap Limburg, 2021) and by applying a 1 m buffer around all roads in the study area (road verges).

2.5 | Statistical analysis

Statistical analyses were conducted in R version 4.1.2 (R Core Team, 2021). First, we visualized how landscape flower availability changes across our study period by constructing generalized additive models for each study year with the mgcv package (Wood, 2017) using a gamma distribution with a log link. We used landscape flower cover as a response variable, growing degree days (temperature sums across days since January 1 with an average temperature ≥5°C) as a smoothed predictor variable and transect as a smoothed random effect term. We used degree days as an indicator of time in all analyses to account for differences in floral and faunal phenology between years. We selected the degree of smoothness (knots or k) for degree days ($k = 23$) by visually comparing models with $k \approx 0.3$ times the length of the time series (mean 60 sampling days per 3-month sampling period) according to the guidelines of Fewster et al. (2000). The mean trend across all years was modelled separately with year as an additional smoothed random effect term.

Next, we used a multi-model inference approach to evaluate the effects of local and landscape-scale flower availability on bee abundances across time. Multi-model inference accounts for 'model selection uncertainty' (Burnham & Anderson, 2004) by considering a set of models that support the data well according to a threshold of AIC, which is generally more appropriate for landscape-scale ecological studies than traditional hypothesis testing. We used transect-level bumblebee (truly eusocial) and solitary bee abundances as response variables in two separate generalized linear mixed models. While certain non-*Bombus* species in our study area exhibit some social life strategies, we have grouped all non-*Bombus* species here for simplicity and together refer to them as solitary bees. *Apis mellifera* was excluded from these models because it is managed in our study area. To model both intra- and inter-annual effects, the response variables of bee abundances were limited to data from 2019 to 2022, since no previous-year flower data was available for bee abundances recorded in 2018.

To test which temporal aspect of floral resources is most relevant and how the effect of floral resources on bee abundances changes across the season, we included degree days in interaction with five different estimates of floral resources (Table 1) in order to account for both intra- and inter-annual responses to floral resources. We considered measures of cumulative resources across the season, which are relevant to long-season bees (e.g. bumblebees) (Carvell et al., 2017; Malfi et al., 2022), and resources at the flight time of bee measurements, which are relevant to short-season bees (e.g. most solitary species; Van der Meersch et al., 2022).

We additionally included the interaction between local and landscape flower cover in our models to control for a possible moderating effect of landscape resources on local resources (Scheper et al., 2015). We included forest cover in the surrounding landscape as a covariate because many trees and understorey plants provide floral resources unmeasured by our surveys. The habitat type in which transects were located was also included as a covariate to reflect differences in nesting resources.

Models were constructed using glmmTMB (Brooks et al., 2017) with a negative binomial distribution. All flower variables were log transformed prior to analysis due to right-skewness. All continuous predictor variables were then scaled by subtracting the mean and dividing by the standard deviation (i.e. z-scores) to standardize beta coefficients and allow the interpretation of main effects in the presence of interaction terms. The random effects of transect and year were crossed to account for repetition within and across years. Model residuals, zero inflation and temporal and spatial autocorrelation were checked using the DHARMa package (Hartig, 2022), and collinearity was checked using the performance package (Lüdecke et al., 2021). Models displayed residual heteroskedasticity, meaning that the model assumption of equal variances was violated. To remedy this, we explicitly modelled unequal variances using the individual predictor variables that contributed to the heteroskedasticity (Zuur et al., 2009), which in glmmTMB is done with a dispersion formula (Brooks et al., 2017). We additionally used an Ornstein–Uhlenbeck correlation structure to model temporal autocorrelation across the entire dataset. No significant spatial autocorrelation or zero inflation was present in the models. Global model formulas are presented in Table S2.

We constructed candidate model sets from our global models using the MuMIn package (Barton, 2022). We excluded from

TABLE 1 Floral resource variables used as model fixed effects.

Variable	Time	Calculation
Transect flower cover	At time of sampling	Direct survey
Landscape flower cover (LFC)	At time of sampling	See Section 2.4
Cumulative LFC	Up to time of sampling	Summed LFC across all previous sampling days
Last year average LFC	Around time of sampling in the previous year	Mean LFC at approximately same period in the previous year (within 150 degree days, encompassing ~2 weeks)
Last year cumulative LFC	All sampling days of the previous year	Summed LFC across all sampling days of the previous year

these sets models that contained any combination of the four estimates of landscape flower cover, because these variables were highly correlated (model vifs >3). If any predictor variable was excluded from a candidate model, it was concurrently excluded from the dispersion formula. To evaluate the effects of the chosen predictor variables, conditional model averaging ('natural average method', Burnham & Anderson, 2004) was performed on a set of best-candidate models with ΔAICc <4. We opted for conditional model averaging as opposed to full model averaging ('zero method') since landscape flower cover variables were prevented from being present in models together, and assigning zeroes for these absent beta coefficients would be a misrepresentation of our model selection approach.

Figures were constructed using the ggplot2 (Wickham, 2016) and viridis (Garnier et al., 2021) packages.

3 | RESULTS

In total, 8987 bumblebees, 8801 solitary bees and over 32.8 million individual flowers were recorded over the 5 years of monitoring. The most common bumblebee species recorded were *Bombus lapidarius* (*n* = 3787), *Bombus pascuorum* (*n* = 2656) and *B. terrestris* complex (*n* = 1728), which accounted for 90.9% of all bumblebee individuals. The most common solitary bee species recorded were *Lasioglossum pauxillum* (*n* = 1693), *Halictus scabiosae* (*n* = 1229), *Halictus quadricinctus* (*n* = 442) and *Andrena florea* (*n* = 442), which accounted for 43.2% of all solitary bee individuals. Lists of all bee and flower species recorded are presented in Tables S6 and S7.

3.1 | Seasonality of floral resources and bee abundance

Visualizations of landscape floral resource seasonality during the study period demonstrated that, in most years, landscape flower cover peaked in spring (Figure 3). On average, the maximum landscape flower cover was 0.1% and occurred around 575 degree days or approximately late May. In early summer, landscape flower cover dropped and, in some years, recovered slightly, with some smaller peaks in mid- to late summer. The low point in mean landscape flower cover (0.036%) was nearly three times lower than the season peak and occurred around 865 degree days or approximately mid-June.

Bee abundances were positively predicted by degree days (Figure 4), meaning that during the study period, abundances increased as the season progressed for both bumblebees and solitary bees. For example, a transect with 1% flower cover had on average 3.4 bumblebees and 2.9 solitary bees early in the study period, but 8.3 bumblebees and 5.2 solitary bees late in the study period (Figure 5).

3.2 | Limitation of floral resources over time

Both bumblebee and solitary bee abundances were positively predicted by local flower cover, and this was the largest effect within both model sets (Figure 4; Table S3). Furthermore, the relationship between local flower cover and bee abundance changed during the course of the study period (flower cover * degree days interaction), with relationships becoming more pronounced across the season (Figure 5). Local flower cover, degree days and their interaction featured consistently across both candidate model sets (with the exception of one solitary bee model; Tables S4 and S5).

3.3 | Intra- and inter-annual effects of landscape floral resources

Landscape flower cover variables featured less consistently in models compared to local flower cover and did not predict solitary bee abundance, as the effect sizes for these variables were overall low (Figure 4b). There was no evidence for interaction effects between landscape flower cover variables and degree days. Cumulative landscape flower cover featured in the best-candidate model predicting bumblebee abundance (Table S4), and the model-averaged effect size for this variable showed a generally positive relationship with bumblebee abundance (Figure 6a), although the 95% confidence interval marginally overlapped zero (Figure 4a). The average landscape flower cover of the previous year also showed a marginally positive effect on bumblebee abundance (Figure 6b), although this effect size was slightly lower compared to that of cumulative landscape flower cover (Figure 4a). Landscape flower cover marginally interacted with local flower cover to predict bumblebee abundance (Figure 4a), with the relationship between local flower cover and bumblebee abundance

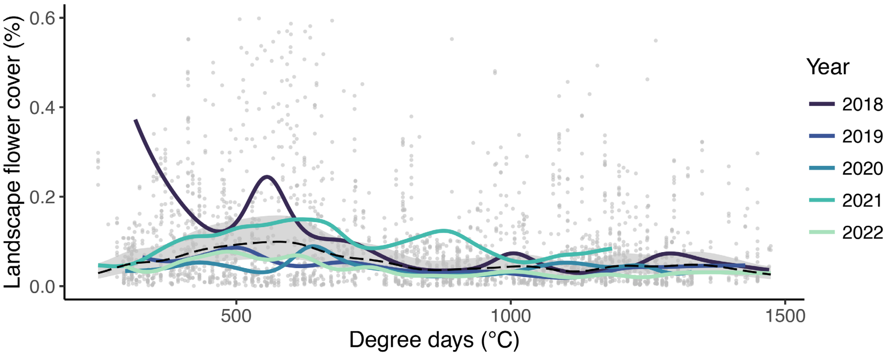

FIGURE 3 Predictions for landscape flower cover (%) from May through July, back-transformed from the log scale. The dashed line represents mean values across all years, with a 95% confidence interval. Points represent raw data; some high-value points (>0.6%) have been obscured for considerations of scale. For predictions against Julian day, see Figure S1.

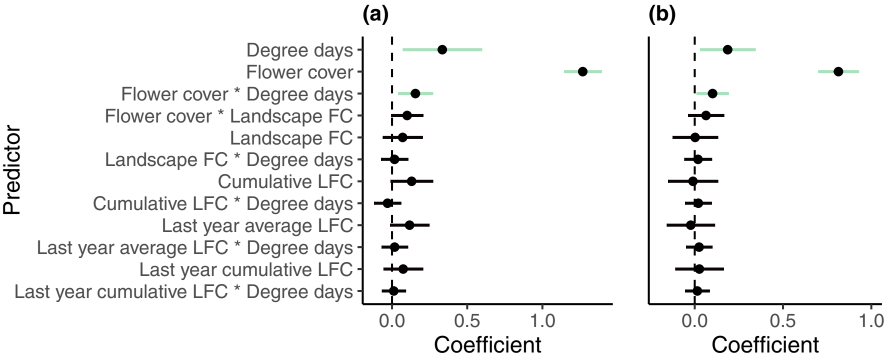

FIGURE 4 Model-averaged beta coefficients and 95% confidence intervals for (a) bumblebee and (b) solitary bee abundance. Light confidence intervals do not overlap zero. FC, flower cover; LFC, landscape flower cover. All model-averaged beta coefficients, including forest cover and habitat types, are listed in Table S3.

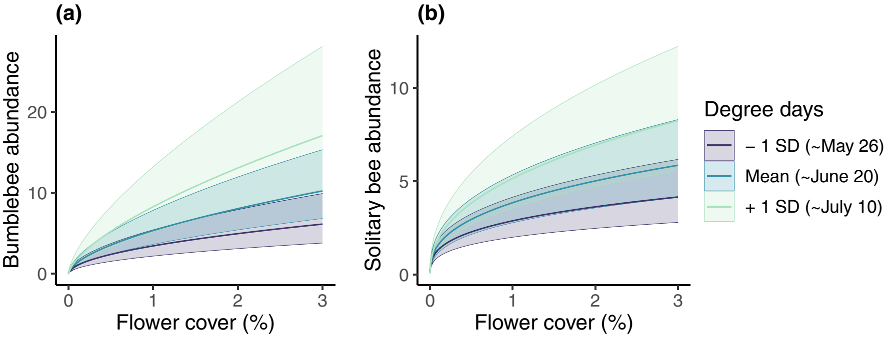

FIGURE 5 Predictions and 95% confidence intervals for the effect of local flower cover on (a) bumblebee and (b) solitary bee abundance at low (−1 SD), mid (mean) and high (+1 SD) levels of degree days, back-transformed from the log scale. Approximate calendar days are shown in parentheses. Predictions are from the best model in each candidate set.

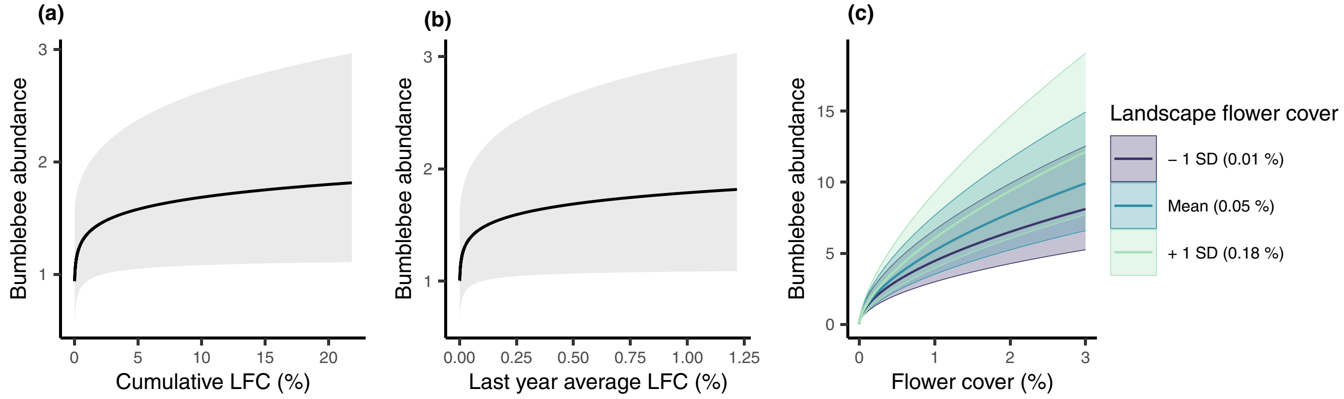

FIGURE 6 Predictions and 95% confidence intervals for the effects of (a) cumulative landscape flower cover, (b) average landscape flower cover of the previous year and (c) local flower cover at different levels of landscape flower cover on bumblebee abundance, back-transformed from the log scale. Landscape flower cover mean and SD were calculated on the log scale, with back-transformed values shown in parentheses. Predictions were made from the best models in the candidate set that contained each specific predictor (models 1, 3 and 2, respectively; see Table S4). LFC, landscape flower cover.

becoming more pronounced in landscapes with higher flower cover (Figure 6c).

4 | DISCUSSION

Landscape floral resources varied across and within years but generally peaked in late spring and showed little to no recovery in summer. However, both bumblebee and solitary bee abundances increased across the season, leading to increased limitation by local floral resources from spring to summer. Bumblebees, but not solitary bees, were marginally predicted by landscape floral resources, in particular the cumulative amount of floral resources available across the season. These findings largely suggest a temporal mismatch in floral resource supply and bee abundance, which has not been previously demonstrated for the whole bee community. They furthermore indicate that conservation management should target the increase of summer (i.e. late June and July) floral resources for both bumblebees and solitary bees, despite the differences in responses to landscape-scale floral resources between these two groups.

4.1 | Seasonality of floral resource availability

We observed a lull in floral resources in mid-June, semblant of a 'June gap' (Timberlake et al., 2019), which is a natural phenomenon (Balfour et al., 2018) but is also largely driven by mowing schedules in our study area. However, there was little summer recovery in floral resource availability. Though the majority of herb species have flowering peaks in late summer (Balfour et al., 2018), the alteration and management of agricultural landscapes over decades of intensification, for example the disappearance of late-flowering habitats like calcareous grasslands and the frequent cutting of existing grasslands for production, likely have reduced summer floral resources (Fitzpatrick et al., 2007). Our results show that there is a general scarcity of summer floral resources in agricultural areas, indicating that the concept of the 'June gap' may not adequately capture the extent of temporal resource limitation for bees. Furthermore, our floral resource phenology is largely aligned with that recorded in British agricultural landscapes (Timberlake et al., 2019), which suggests that our findings are generalizable to other pasture-dominated agricultural areas.

While floral resources varied greatly within the year, there were also differences between years that were most likely driven by weather conditions. The summer of 2021 saw extreme rainfall (June and July 285.9 mm; long-term average 144.6 mm; Koninklijk Nederlands Meteorologisch Instituut (KNMI), 2022), which was reflected by the relatively high and long-sustained floral availability, whereas 2022 was overall dry (May–July 124.6 mm; long-term average 204.6 mm; Koninklijk Nederlands Meteorologisch Instituut (KNMI), 2022) and consequently had relatively low floral availability throughout the season. This suggests that floral resources in managed semi-natural habitats, even when cut in spring or summer, can recover in summer given sufficient rainfall.

4.2 | Increased limitation of floral resources over time

Both bumblebee and solitary bee abundances followed a largely opposite pattern compared to the average availability of floral resources, since they increased as the season progressed. While this is an intuitive finding for bumblebees, which grow colonies of workers before reproducing, it is seldom demonstrated for solitary bees, which exhibit high temporal species turnover (Rollin et al., 2015). However, a greater diversity of solitary bees are late fliers, possibly due to patterns in floral diversity (Balfour et al., 2018), which could explain why their abundance increased over the season. While the relationship between local flower cover and bee abundance could represent a concentration effect (Roulston & Goodell, 2011), the fact that adding more resources to a habitat patch increases the abundance of bees found there suggests that the carrying capacity of a habitat is determined by its quality, and thus that floral resources are limiting to bees in a habitat. Under this assumption, the opposing temporal trends of flower cover and bee abundance suggest that the supply and demand of floral resources are not well matched and that floral resources are more limiting later in the season. This most likely explains the increasing strength of the relationship between flowers and bees across the season. While previous studies have detected some indications of late-season resource limitation in bumblebees (Rundlöf et al., 2014; Timberlake et al., 2021), our results demonstrate this pattern for the first time for solitary bees. These findings support the hypothesis that the loss of late-season floral resources has contributed to the disproportionate extinction of late-flying bee species (Balfour et al., 2018; Hofmann et al., 2019) and may help explain why late-flying bumblebee species are more vulnerable to decline (Fitzpatrick et al., 2007; Persson et al., 2015). While our study period covered the main flight period of bees, it did not include early spring and late summer, so we cannot comment on how these periods, which can be especially important to certain species (Timberlake et al., 2021), would contribute to the temporal trends in resource limitation.

4.3 | Intra- and inter-annual effects of landscape floral resources

Our results showed marginal support for relationships between landscape floral resources and bumblebee abundance, but not solitary bee abundance. Bumblebee abundance was marginally positively associated with cumulative landscape flower cover and the average landscape flower cover of the previous year, which could suggest the presence of both intra- and inter-annual resource dynamics. This was largely expected because bumblebee colonies benefit from an accumulation of resources over time (Hemberger et al., 2022; Malfi et al., 2022), but survival and establishment are also dependent on the resources available to colonies from the previous year (Carvell et al., 2017). Since our study area does not contain arable mass-flowering crops, landscape flower cover is primarily determined by the cover of permanent forms of land use, such as pastures. This means that spatial variation in landscape flower cover is largely stable within and between years. While this makes it difficult to conclude which temporal aspect of landscape floral resources best determines bee abundances, it lends simplicity to management strategies in that bumblebees could be limited by overall landscape floral resource provision across the season. Solitary bees, which include species that overwinter as both brood and adults and thus might respond to both intra- and inter-annual resource dynamics, were only affected by local-scale floral resources. Most solitary bees, which are typically smaller than bumblebees, have shorter foraging ranges (e.g. <300 m; Kendall et al., 2022), which likely explains why no relationships with landscape resources were detected. This could indicate that solitary bee abundances are primarily limited by local-scale resources.

Since local flower cover became increasingly limiting over time, one might expect the same relationship for bumblebees and landscape flower cover, but this was not present in our findings. We did, however, observe a marginal positive interaction between local and landscape flower cover, meaning bumblebees could be concentrating on resource-rich patches in landscapes with greater overall resources and therefore likely greater overall bumblebee populations. Different species within the bumblebee community might respond differently to landscape-scale resources depending on their foraging strategies and ranges (Westphal et al., 2006). For example, *B. terrestris* and *B. lapidarius*, which made up 61% of our bumblebee observations, prefer to exploit large, concentrated resource patches (Walther-Hellwig & Frankl, 2000). The foraging behaviour of these common species could thus influence the distribution of bumblebee densities across a landscape, which might explain why relationships with landscape-scale resources were overall weaker compared to relationships with local floral resources.

4.4 | Management implications

Overall, our results suggest that increasing summer floral resources in agricultural landscapes has the potential to release resource limitation for both social and solitary bee populations. For solitary bees, tailored local-scale habitat improvements that increase summer resources, such as sowing preferred wildflowers in field boundaries (von Königslöw et al., 2022), are likely beneficial. Bumblebees, however, could require increased landscape-scale resource availability. Small-scale agri-environment schemes such as wildflower strips contribute very little to the overall floral resource availability in agricultural landscapes (Baude et al., 2016), so significant increases in landscape floral resources require measures that target large, pre-existing forms of land use. In the mixed farming landscapes of our study area, the dominant land use type that provides resources to bees is pasture (Figure S2), which consequently contributes the most to landscape floral resource availability (Figure S3) and thus also to the variation in floral resource availability within the year. Increasing summer floral availability in pastures would likely require delayed or alternated mowing (Pywell et al., 2011) in order to extend the flowering period. Alternatively, legumes such as *Trifolium repens*, *T. pratense* and *Medicago sativa*, which are among the top 10 species contributing to July flower cover in our study area (Table S8), can be sown in pastures to benefit bumblebees (Baude et al., 2016; Beye et al., 2022). These recommendations can be applied to other pasture-dominated landscapes, but as our landscapes largely do not contain mass-flowering crops, these crops likely need to be taken into account in management strategies in arable-dominated landscapes. Future research should focus on identifying how much of an increase in floral resources is needed to release resource limitation for wild bees, because while some efforts have been made to answer this question (Dicks et al., 2015; Timberlake et al., 2021), our knowledge is still limited to a small subset of the bee community.

AUTHOR CONTRIBUTIONS

Gabriella A. Bishop, Thijs P. M. Fijen, Ivo Raemakers and David Kleijn conceived the ideas and designed the methodology; Gabriella A. Bishop, Thijs P. M. Fijen, Ivo Raemakers, Ruud J. M. van Kats and David Kleijn collected the data; Gabriella A. Bishop analysed the data; Gabriella A. Bishop 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 no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via Zenodo https://doi.org/10.5281/zenodo.7890518 (Bishop et al., 2023).

STATEMENT ON INCLUSION

This study is part of a conservation project in south Limburg, the Netherlands that involves researchers, municipalities, nature conservation organizations, farmers and water management boards. The project is designed collaboratively, and results are shared regularly with all stakeholders.

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SUPPORTING INFORMATION

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

Table S1. Number of sites per habitat type included in the study, and the subset in which bee-friendly management was implemented in 2022.

Table S2. Global model formulas for bumblebee and solitary bee abundances*.

Table S3. Model-averaged beta coefficients and 95% confidence intervals for bumblebee and solitary bee abundances*.

Table S4. Beta coefficients, delta AICc, and model weights for candidate models predicting bumblebee abundance.

Table S5. Beta coefficients, delta AICc, and model weights for candidate models predicting solitary bee abundance.

Table S6. All bee species recorded and their total abundances.

Table S7. All flower species recorded.

Table S8. The top ten flower species that contribute most to midsummer (July) flower cover, in order from greatest to least.

Figure S1. Predictions for landscape flower cover (%) from May through July (plotted against Julian day), back-transformed from the log scale.

Figure S2. Coverage of habitat types in the surrounding 500 m radius of each study site, ordered from smallest to largest.

Figure S3. Contribution of habitat types to landscape flower cover (LFC) in the surrounding 500 m radius of each study site, ordered from smallest to largest (mean ± SE).

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