

# Resource gaps pose the greatest threat for bumblebees during the colony establishment phase

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## Abstract

1. A common management intervention to support declining wild pollinators is ‘pollinator planting’. However, despite years of inclusion in conservation initiatives, global pollinator declines continue.
2. Using the agent-based model BEE-STEWARD with two example species, *Bombus terrestris* (L. 1758) and *B. pascuorum* (Scopoli, 1763) (Hymenoptera: Apidae), we explore when during the year bumblebee resource demand is the highest and how that relates to seasonal changes in colony composition (numbers of eggs, larvae, pupae and adults). We then examine the impact of two-week periods of resource scarcity across the year. Finally, we explore how enhancement with early spring-blooming herbaceous species or trees changes colony survival and queen production.
3. In the United Kingdom, there is a previously under-appreciated ‘hungry gap’ for bumblebees in March–April, before the peak flight period, driven by the demands of larvae for protein and thermoregulation in the colony, rather than the number of adult bees.
4. A 2-week gap in forage availability during this period drives a 50%–87% drop in the production of daughter queens. Adding early-blooming species in the model had significant, positive, long-term effects on colony survival probability and daughter queen production.
5. Pollinator-planting initiatives in both national and international conservation schemes need to include plants that flower up to 1 month before the adults of target social pollinator species are apparent in the field, during the period that larvae dominate the colony. This approach is likely to increase colony survival and queen production, contributing towards halting and reversing global pollinator decline.

## KEYWORDS

agent-based model, BEE-STEWARD, foraging, nectar, pollen, pollinator planting

Matthias A. Becher and Grace Twiston-Davies contributed equally to this work and are co-first authors.

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## INTRODUCTION

Wild bees are important pollinators of crops and wild plants (Klein et al., 2003; Ollerton et al., 2011), but many wild bee species are in decline (Díaz et al., 2019; Goulson et al., 2008; Potts et al., 2010; Powney et al., 2019). Bee declines are largely a consequence of intensified farming practices and loss of habitat, particularly forage resources and nest sites (Baude et al., 2016; Carvell et al., 2006; Goulson et al., 2008; Jacobson et al., 2018; Mola et al., 2021; Timberlake et al., 2019). This suggests there has been an overall shift from a 'sweet world', where pollinators were mainly limited top-down by predators, parasites and disease (Sponsler et al., 2023) to a 'bitter reality' where pollinators are mainly limited bottom-up by floral resources (Roulston & Goodell, 2011).

Resource limitation for pollinators is a function of spatial, temporal and functional heterogeneity in the plant community. Although this has long been recognised, empirical studies of resource limitation have been limited by the difficulty of investigations at multiple spatial and temporal scales and across diverse functional groups of plants and pollinators (Horn et al., 2015). Studies have been further confounded by the challenges of accurately measuring fitness in the field (Sponsler et al., 2023). Thus Sponsler et al. (2023) suggest that the most basic question about pollinator use of spatio-temporally variable plant resources 'How does spatio-temporally transient resource limitation affect pollinator fitness?' remains unanswered. Similarly, Ogilvie and Forrest (2017) suggest that bee behavioural and reproductive responses to fluctuations in resource availability remain an area in critical need of investigation. Not only are investigations of pollinator resource use necessary for understanding pollinator fitness and developing conservation interventions, broader biological questions of plant and pollinator species competition and coexistence may be underpinned by resource use dynamics (Sponsler et al., 2023).

Interestingly, theory suggests that plant–pollinator resource use interactions may generate destabilising evolutionary feedbacks, wherein resource scarcity for pollinators is a result of visitation saturation for plants, and visitation saturation, in turn, drives reduced plant investment in nectar production, exacerbating resource scarcity; but also, if pollinators are not resource limited, plants may be under selection pressure to increase nectar production to compete for pollinators, further increasing available resources (Sponsler et al., 2023). Thus, plant–pollinator systems may tend towards extremes of high or low resource availability. Indeed, both excess and shortage of resources have been reported from empirical studies and may even occur at the same location over the course of a day or a season (Timberlake et al., 2021). In this case, the basic question about pollinator use of spatio-temporally variable plant resources may become 'When, where, and to what extent does spatio-temporally transient resource limitation affect pollinator fitness?' (Ogilvie & Forrest, 2017; Sponsler et al., 2023).

Based on the assumption that pollinator declines are due to floral resource limitation, one of the most common management interventions to support wild pollinators on agricultural land is to increase flowering plant diversity and abundance through 'pollinator planting'

(Gemmill-Herren et al., 2021; Kleijn et al., 2019; Timberlake et al., 2019). This approach is supported by both theoretical and empirical studies showing that mixed landscapes that provide abundant, continuous, early and season-long floral resources support larger bee populations and higher species richness (Guezen & Forrest, 2021; Kennedy et al., 2013; Ogilvie & Forrest, 2017). However, despite national and international planting and conservation initiatives, and programmes of agricultural reform based on this premise, pollinator declines continue (Redhead et al., 2022). This may be because there is mixed guidance on the identity and diversity of species to be planted. However, given the theory and empirical findings outlined above, perhaps an even more important information gap is the limited guidance on the seasonal timing of floral resources that should be provided to maximise conservation outcomes (Dicks et al., 2015; Nicholson et al., 2020). Indeed, planting floral resources without considering phenological coverage could amplify resource oscillations and drive perverse conservation outcomes (Ogilvie & Forrest, 2017; Sponsler et al., 2023; Timberlake et al., 2019).

In this study, we use the BEE-STEWARD agent-based model (Twiston-Davies et al., 2021), coded in Netlogo 5.3.1 (Wilensky, 1999), to investigate two questions for two bumblebee species, *Bombus terrestris* (L. 1758) and *B. pascuorum* (Scopoli, 1763): (Q1) 'When during the season, and to what extent, does spatio-temporally transient resource limitation affect bumblebee fitness?'. We hypothesise that the ability of a bumblebee colony to cope with a forage gap depends on (H1) the timing of the gap, and (H2) the colony composition (numbers of eggs, larvae, pupae and adults) (e.g. Horn et al., 2015). The second question is (Q2) 'Which plant species maximize the fitness benefit of pollinator planting for bumblebees on agricultural land?'. The advantage of using model simulations for this study is that forage availability can be systematically controlled, which is extremely difficult to achieve in the field (Horn et al., 2015), fitness can be accurately measured and the response of the populations over 10 years can be investigated in a relatively fast and cost-effective way.

To address Q1, H1, we explore when during the season most resources are consumed at a population level (Model Scenario 1) and what the impact of periods of resource scarcity is on the number of new queens produced (Model Scenario 2). We then address Q1, H2 by investigating how colony foraging is affected by colony composition (numbers of eggs, larvae, pupae and adults) (Model Scenario 3). Finally, we address Q2 by assessing seasonal resource availability and queen production over a 10-year period in a model agricultural landscape enhanced with five early-blooming herbaceous species (Model Scenario 4) or five early-blooming tree species (Model Scenario 5).

We conclude by discussing the practical implications of the study results for land management and pollinator conservation, particularly in the context of major national and international pollinator conservation schemes, including the United Kingdom Countryside Stewardship Program and Local Nature Recovery scheme, the United States Department of Agriculture Pollinator Habitat Initiative (USDA-PHI CP-42) and the European Union Pollinators Initiative.

## MATERIALS AND METHODS

All simulations were conducted using BEE-STEWARD (Twiston-Davies et al., 2021), a software tool that integrates the fully documented and validated Bumble-BEEHAVE and BEESCOUT models of bee colony growth, survival and landscape exploration (Becher et al., 2018). This group of models has been widely applied in research investigating the impact of disease and resource availability on bee colony success and in the development of land management recommendations (see <https://beehave-model.net/publications/>).

BEE-STEWARD has the capacity to simulate different types of forage patches with multiple flower species differing in nectar and pollen quality, quantity and availability. To do this, BEE-STEWARD imports a Habitats input file, detailing the abundance of each forage flower species in each habitat type (number of flowers per square metre, Table S1), and a Flower Species input file, detailing the nectar and pollen quality, quantity and availability for each forage flower species (Table S2). Each forage patch in the landscape is a homogenous mix of all forage flower species present in that forage patch. This is because the model applies a simplified representation of the forage patches where every flower species is a 'layer' across the forage patch rather than occupying a specific location within the forage patch. Bee foraging activity is modelled based on the detection probability of individual forage patches, a function of distance, and by attractiveness of the patch, a function of distance, handling time (affected by corolla depth and resource depletion) and sugar concentration. Foraging bees can only visit a single-flower species ('layer') of a forage patch on each trip.

Bumble-BEEHAVE is an agent-based computer model that takes a large number of biological processes into account. During spring, queens emerge from hibernation and have to find a suitable nest site. They then collect nectar and pollen from a complex, dynamic landscape and raise a first generation of brood. When the colony enters the social phase, workers take over foraging and brood care. Towards the end of the season, colonies may produce males and young queens, which will then mate and enter hibernation. In Data S2, we provide a 'visual guide' to give an overview of the modelled processes (Data S2: Understanding BEE-STEWARD), and a detailed model description following the ODD protocol (Overview, Design concepts, Details; Data S3: Bumble-BEEHAVE Model Description). The empirical basis for the model mechanisms and parameters that govern the queen's egg production, egg maturation to larvae, pupae and adults, nutritional requirements of all life stages, foraging behaviour and queen production are further detailed in Data S3 for Bumble-BEEHAVE (see SI5 (ODD protocol) and SI18 (Scheduling and Variables) in Becher et al., 2018). We use two bumblebee species, *B. terrestris* and *B. pascuorum*, as case-study pollinators because they are important pollinators of crops and wild plants (De Luca & Vallejo-Marín, 2013; Garibaldi et al., 2013) and represent a short-tongued, generalist and early-emerging species and a long-tongued, more specialist and later-emerging species, respectively. Moreover, unlike most pollinator species, there is sufficient information about their biology and resource use to enable us to build biologically realistic population models. In these simulations, we assume that, all else being equal, resources closer to a colony allow more energetically efficient foraging and are therefore more beneficial than those that are further away (Seeley, 1994; Wolf & Moritz, 2008). In real

landscapes, there may be other limiting factors such as predation or fragmentation that may affect foraging range with consequent energetic impact (Dramstad, 1996; Redhead et al., 2016), but in this model, we focus on the impact of resource availability in otherwise benign conditions. Thus, in this study, we do not model predation, or variation in landscape configuration or fragmentation, rather we focus on pollinator-planting species composition, which drives the quantity and timing of nectar and pollen production. This approach also reflects the fact that land owners usually have limited choice about where on their land to implement conservation interventions but can make choices about floral species composition in pollinator planting.

### Model Scenario 1: Bumblebee forage demand

#### Purpose

Determine the daily nectar and pollen collection at the population level at landscape carrying capacity (i.e., with strong intraspecific competition).

#### Setup

Single forage patch composed of a single, generic flower species, which provides a constant nectar and pollen flow (supports ca. 600 hibernating queens), 8 h foraging a day and 500 initial queens of either *B. terrestris* or *B. pascuorum* (see Gosterit & Gurel, 2016; Osborne et al., 2008). Duration: 10 years (3650 time steps). *N* Simulations (per species): 20 runs (replication  $N = 20$ ).

#### Output

Daily amount of nectar (in millilitres) and pollen (in grams) removed from the forage patch by the population in the last year of the simulation relative to the nectar and pollen available.

### Model Scenario 2: Two-week gaps in resource availability

#### Purpose

Determine which periods of forage supply are most critical to bee population size.

#### Setup

As for Scenario 1 (single forage patch, constant food availability, 8 h foraging a day, 500 initial queens), but a 2-week forage gap was applied. Two-week gaps were chosen because a previous study found that modelled forage gaps of 15 days provided useful results, whereas

gaps of 21 or 30 days caused colony failure regardless of the modelled treatment (Horn et al., 2015). In each iteration of the simulation, the 2-week gap was moved forward by 7 days so that the gap started on day 1, day 8, day 15, day 22, etc. in successive scenario runs. Duration: 10 years (3650 time steps). *N* Simulations (per species):  $51 \times 20 = 1020$  runs (replication  $N = 20$ ).

## Output

Number of hibernating queens after year 10.

## Scenario 3: Nectar and pollen demand related to the number of individuals at each life stage in the colony

### Purpose

Determine forage collection of a single bumblebee colony as colony composition changes.

### Setup

As for Scenario 1 (single forage patch, constant food availability, 8 h foraging a day) but only a single initial queen. To simplify data collection from the model, queens were forced to emerge on day 91 (as only one initial queen is present and seasonal effects [forage availability and weather] are constant, this only temporally shifts the colony dynamics and foraging patterns but does not alter them). Duration: 1 year (365 time steps). *N* Simulations (per species): 10,000 runs (replication  $N = 10,000$ ).

## Output

Daily amount of nectar (in millilitres) and pollen (in grams) removed from the forage patch by the colony and daily number of eggs, larvae, pupae and workers present.

## Scenario 4: Pollinator planting—herbs

### Purpose

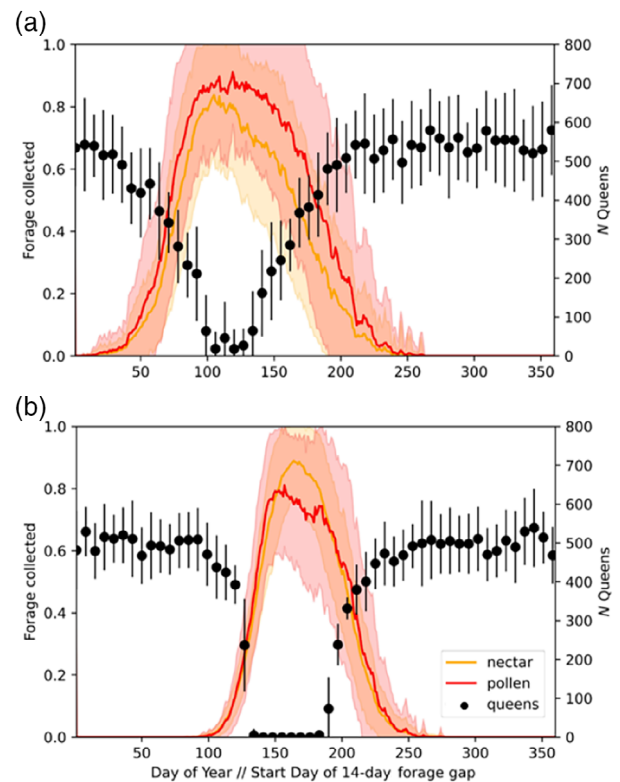
Determine the impact of early-flowering herb species on the maximal number of colonies, production of hibernating daughter queens and population survival.

### Setup

Eight hours foraging per day; 300 initial queens (*B. terrestris* or *B. pascuorum*). Duration: 10 years (3650 time steps). *N* Simulations

(per species): 20 simulations for the baseline and each of the 5 early-flowering species  $6 \times 20 = 120$  (replication  $N = 20$ ).

Scenario 4.1: The scenario uses a 52 ha model agricultural landscape based on a real farm landscape in the United Kingdom. The model landscape contains maize (42.5 ha), 'improved' grassland (ploughed, seeded and fertilised) (30.65 ha), unimproved grassland (3.09 ha), scrubland (0.91 ha) and hedgerow (8.16 ha) (species composition in Table S1). The fields are approximately average sized for England, and each field is separated from the next by a hedgerow, meaning the hedgerows are approximately evenly spaced across the model landscape (see basemap, Figure 1, in Twiston-Davies et al., 2021).



**FIGURE 1** Scenario 1: Colony nectar and pollen demand (left y-axis), and Scenario 2: Impact of 14-day forage gaps on queen production (right y-axis) for (a) *Bombus terrestris* and (b) *B. pascuorum*. Model Scenario 1 (left y-axis): A single food source was present, providing a constant amount of nectar and pollen on each day, and weather conditions allowed 8 h of foraging every day. We show nectar (yellow line) and pollen (orange line) collection ( $\pm$ SD) (relative to the daily available nectar or pollen) of a bumble bee population (all nests present in the model landscape) during year 10 of a 10-year simulation, when we assume that the simulation has reached landscape carrying capacity. On the left y-axis, 1 indicates that the bees are consuming all available resources (model replicates,  $N = 20$ ). Model Scenario 2 (right y-axis): The total number of hibernating queens produced by the end of the season if a two-week forage gap occurred, starting on a given date during the simulation. Forage gaps start on day 1 (January 1), day 8, day 15, day 22, etc. (model replicates per forage gap date,  $N = 20$ ).

Scenarios 4.2–4.6: Hedges are the United Kingdom landscape feature producing the most nectar per unit area (1% of farm area, 9.4% of total nectar production) and with the highest phenological continuity (Timberlake et al., 2019). Moreover, hedges are often already in place and land managers are accustomed to maintaining them. Thus, in Scenarios 4.2–4.6, we modify the model 4.1 landscape by adding 1 m<sup>2</sup> of full floral coverage of herbaceous ‘enhancement’ species per 100 m<sup>2</sup> of hedgerow (see Baude et al. (2016)). The enhancement species were cowslip (*Primula veris*), ground ivy (*Glechoma hederacea*), primrose (*P. vulgaris*), red campion (*Silene dioica*) or red dead-nettle (*Lamium purpureum*), providing % increase in nectar and pollen provision of between –1 and 1871 (Table 1; Figure 3; Data S1: Habitats and flower species input files details). The number of flowers added varied depending on the size of an individual flower for a given species. One square metre of basic or ‘un-enhanced’ hedgerow was removed from the model landscape for every 1 m<sup>2</sup> of enhancement planting added so that timing and quantity of floral resources may vary between treatments, but the area of hedgerow coverage is fixed. As the hedgerows in the model, landscape are distributed evenly across the farm (and the enhancement planting is along the hedgerows); the flight costs for forage trips to enhanced hedgerows in Scenarios 4 and 5 are low, whereas the resource benefits are high. Modelling exercises using landscapes with different spatial configurations of resources could have outcomes that differ in extent, due to travel costs, but we do not expect the outcomes to differ in type, because resources will still be required during the period before the peak flight season.

## Output

Daily availability of nectar (in millilitres) and pollen (in grams) from hedgerow forage patches, number of bumblebee colonies, number of adult queens each day and production of hibernating queens.

## Scenario 5: Pollinator planting—trees

### Purpose

Determine the impact of early-flowering trees on the number of colonies, production of hibernating daughter queens and population survival.

### Setup

Eight hours foraging a day; 300 initial queens (*B. terrestris* or *B. pascuorum*). Duration: 10 years (3650 time steps). *N* Simulations (per species): 20 simulations for each of the 5 early-flowering species  $5 \times 20 = 100$  (replication  $N = 20$ ).

Scenarios 5.1–5.5: The Scenario 4.1 landscape hedgerow is enhanced with one of five different woody species: blackthorn (*Prunus*

*spinosa*), cherry (*P. avium*), field maple (*Acer campestre*), hawthorn (*Crataegus monogyna*) or willow (*Salix caprea*). Hedgerow enhancement involved adding 1 m<sup>2</sup> of full floral coverage of woody ‘enhancement’ species (see Baude et al., 2016) per 100 m<sup>2</sup> of hedgerow. The number of flowers added varies depending on the size of an individual flower for a given species. One m<sup>2</sup> of basic or ‘un-enhanced’ hedgerow was removed from the model landscape for every one m<sup>2</sup> of enhancement planting added so that timing and quantity of floral resources may vary between treatments, but the area of hedgerow coverage is fixed.

## Output

Daily availability of nectar (in millilitres) and pollen (in grams) from hedgerow forage patches, number of bumblebee colonies and number of adult queens each day.

## Statistical analyses

Survival probability for *B. terrestris* and *B. pascuorum* was calculated as the proportion of simulation runs (from 20 random seeds) where adult queens survived to day 3650, for each of the 10 hedgerow enhancement treatments (Scenarios 4.2–5.5) and the baseline (Scenario 4.1). The maximum number of colonies in the final year and number of adult queens on the last day of the simulation of each replicate of each simulation was used to calculate the mean and standard error for those values.

For the following calculations, only those random seeds where adult queens survived to day 3650 were used: number of adult queens per simulation on the last day of the simulation (Day 3650, e.g., in hibernation), maximum number of colonies per simulation in the last year of the simulation (Day 2285–3650).

To determine whether there was a significant difference between the baseline (Scenario 4.1) and Scenarios 4.2–4.6 or 5.1–5.5, a two-tailed Student’s or Welch’s *t*-test was run for each treatment compared with the baseline. The choice of Student’s or Welch’s *t*-test depended upon the results of an *f*-test for equal variances (Table S7).

## RESULTS

### Model Scenario 1: Bumblebee forage demand is highest march to June

Scenario 1 shows population-level bumblebee colony demands for nectar and pollen over the season when there is no temporal variation in floral resources. In this scenario, *B. terrestris* forage collection starts to rise in February (Day of Year [DoY]: 32), peaks in April (DoY: 91) and May (DoY: 121) and falls in July (DoY: 182) and August (DoY: 213). *B. pascuorum* forage collection starts to rise in April, peaks in June (DoY: 152) and falls in July and August (Figure 1).

**TABLE 1** Results of Scenarios 4 and 5: Bumblebee colony number, production of hibernating queens and population survival probability in relation to the timing and quantity of pollen and nectar production in the model hedgerow.

Planting	Flowers per square metre of hedgerow in 4.1					<i>B. terrestris</i>					<i>B. pascuorum</i>				
	Flowers per square metre added to hedgerow	Nectar (L) (%) <sup>a</sup>	Pollen (kg) (%) <sup>†</sup>	Max no. colonies (mean)	No. Queens (mean)	Srv <sup>b</sup> %	Max no. colonies (mean)	No. Queens (mean)	Srv %	Max no. colonies (mean)	No. Queens (mean)	Srv %			
													Flowers per square metre added to hedgerow	Nectar (L) (%) <sup>a</sup>	Pollen (kg) (%) <sup>†</sup>
4.1 Baseline landscape	5.31	53.42	102.81	15.14 (2.96)	118.29 (17.06)	35	47.67 (3.91)	201.06 (18.53)	90						
4.2 Cowslip	0	60.17 (13)	117.20 (14)	21.21 (3.16)	158.57 (22.96)	70	42.26 (3.94)	170.21 (15.18)	95						
4.3 Ground ivy	0.06	194.33 (264)	150.52 (46)	58.15 (4.86) <sup>d</sup>	538.20 (42.25) <sup>d</sup>	100	38.74 (43.52)	172.42 (19.52)	95						
4.4 Primrose	0	57.10 (7)	113.62 (11)	17.83 (3.04)	144.00 (35.19)	30	46.37 (3.24)	198.95 (14.71)	95						
4.5 Red campion	0	58.01 (9)	101.60 (–1)	20.43 (1.45)	120.00 (22.98)	35	42.05 (3.51)	206.32 (18.20)	95						
4.6 Red dead-nettle	0.10	1053.09 (1871)	226.05 (120)	821.65 (13.47) <sup>d</sup>	8124.60 (109.40) <sup>d</sup>	100	161.75 (8.12) <sup>d</sup>	813.75 (38.18) <sup>d</sup>	100						
5.1 Blackthorn	0.93	59.90 (12)	104.60 (2)	17.20 (3.93)	160.80 (41.33)	25	46.05 (3.69)	201.16 (18.82)	95						
5.2 Cherry	0	137.32 (157)	107.39 (4)	231.90 (9.38) <sup>d</sup>	1878.00 (64.19) <sup>d</sup>	100	71.00 (5.28) <sup>f</sup>	277.20 (16.09) <sup>f</sup>	100						
5.3 Field maple	0	218.55 (309)	1102.87 (973)	428.85 (11.30) <sup>d</sup>	3165.00 (87.64) <sup>d</sup>	100	72.10 (5.94) <sup>f</sup>	270.55 (23.57) <sup>f</sup>	100						
5.4 Hawthorn	0.44	1002.87 (1777)	159.10 (55)	46.53 (3.96) <sup>d</sup>	430.11 (35.59) <sup>d</sup>	95	67.95 (5.29) <sup>f</sup>	315.35 (24.10) <sup>d</sup>	100						
5.5 Willow	1.28	141.64 (165)	518.96 (405)	32.75 (2.60) <sup>f</sup>	289.20 (25.17) <sup>d</sup>	100	41.70 (4.46)	191.80 (20.15)	100						

Note: Outcomes are shown as maximum number of colonies in the final year of the simulations (Max colonies), number of adult Queens at year 10 (only for runs where there are Queens in hibernation on day 365) (Queens), likelihood of population survival to year 10 (defined as the percentage of simulations that result in Queens in hibernation on day 365) (Srv %). Numbers in bold indicate and increase of the hibernating queens in comparison to the initial population (i.e., 300) or 100% survival probability. Nectar and pollen production is based on number of flowers per square metre from (Baude et al., 2016), except for cherry, maple and willow, for which the model uses nectar and pollen production per square metre from (Agatz et al., 2019). Cherry, maple and willow are given an arbitrary flower count value of '1.00' in the model and Table 1.

<sup>a</sup>%<sup>†</sup> = % increase in nectar or pollen above the baseline landscape.

<sup>b</sup>Srv = % chance of population surviving.

<sup>c</sup>Data on flowers per square metre for *Primula veris* were not available in (Baude et al., 2015), so the data *P. vulgaris* were used as a proxy.

<sup>d</sup>Significance (*p*) comparing treatment to baseline landscape  $\leq 0.001$ .

<sup>e</sup>Nectar and pollen production per square metre from (Agatz et al., 2019). These species were given an arbitrary flower count value of '1.00'.

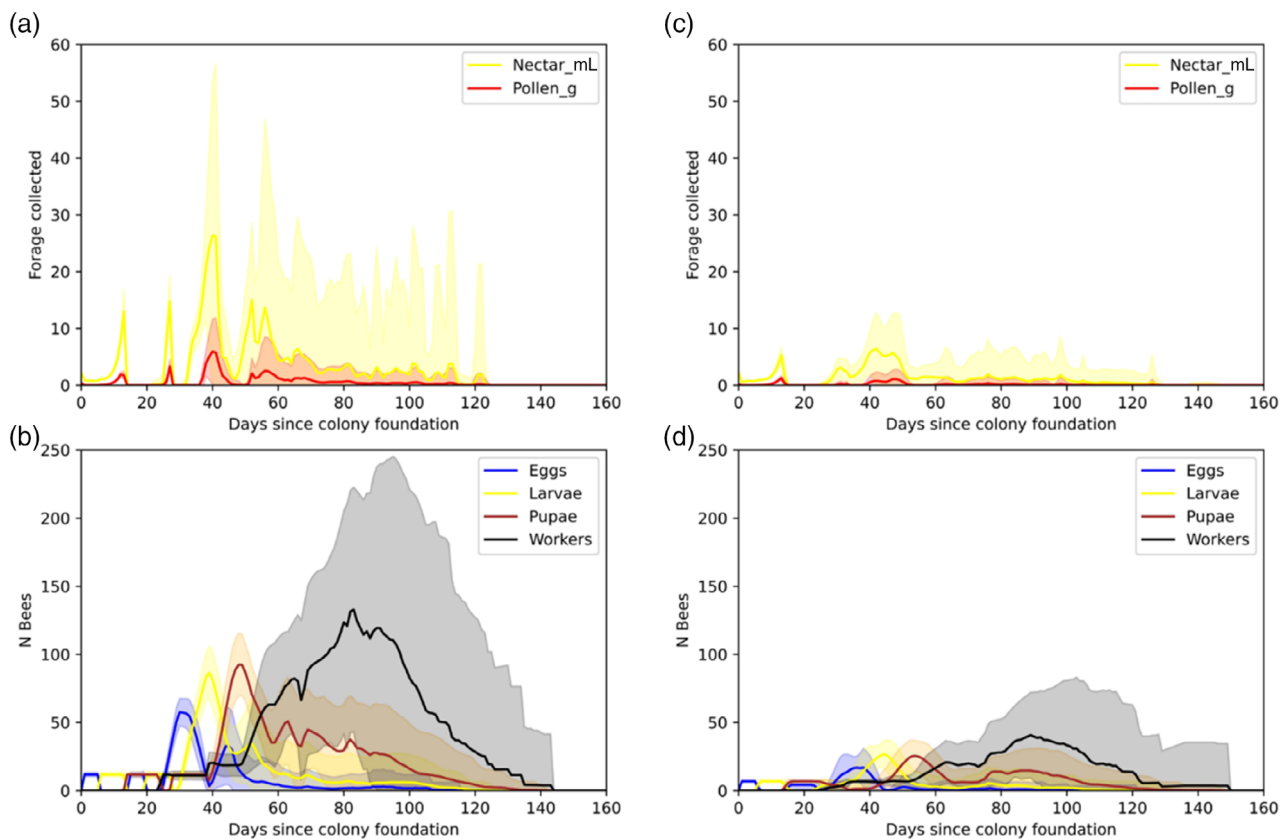
<sup>f</sup>Significance (*p*) comparing treatment to baseline landscape  $\leq 0.05$ .

## Model Scenario 2: Two-week gaps in resource availability during March to June have the greatest impact on new queen production

Scenario 2 tests the impact of two-week ‘forage gaps’ with zero forage availability during year 10 of the simulations. Results of the forage gap simulations were quantified in terms of queen production, a measure of long-term population persistence. Although forage gaps during autumn and early winter did not affect the hibernating queen population, forage gaps between February and August had a striking impact. For *B. terrestris*, the most critical period was March (DoY: 60) to May: a two-week gap in forage provision in March or April lead to a ~50% or ~87% (respectively) drop in bumblebee queen production for the following season, and a gap starting on 7 May (DoY: 127) resulted in a 97.5% drop in queen production for the following season. For *B. pascuorum*, the most critical period was April to June: a two-week gap in forage provision in April lead to a ~50% drop in bumblebee queen production for the following season, and a gap any time between 21 May (DoY: 141) and 25 June (DoY: 176) resulted in a 100% drop in queen production and extinction of the population (Figure 1).

## Model Scenario 3: Nectar and pollen demand is driven by the number of larvae

Scenario 3 investigates which life stage (eggs, larvae, pupae or adults) drives pollen and nectar demand during the colony lifespan. The simulations show that the demand for nectar and pollen is mainly driven by the presence of larvae and not by the number of adult workers, which explains the high colony demand in March–April (Figure 1), prior to the presence of large numbers of adult workers (Figure 2). Note that in the Bumble-BEEHAVE model, a *B. terrestris* colony transitions from the ‘founding stage’ to the ‘social phase’, when the first cohort of eggs have matured to adults, after approximately 26 days; depending on foraging results. This is in line with published empirical values (e.g. Rotheray et al., 2017) and reflects the fact that the model mechanisms and parameter values are based on published empirical data (e.g., Cnaani et al., 2000; Moerman et al., 2017) (see Data S3: S15, ODD protocol; Becher et al., 2018). Correlation of foraging activity and the number of individuals at each life stage found the following  $R^2$  values: *B. terrestris*: Nectar foraging against eggs, 0.06; larvae, 0.71; pupae, 0.15 and adults, 0.04. Pollen foraging against eggs, 0.01; larvae, 0.51; pupae, 0.10 and adults, 0.05. *B. pascuorum*: Nectar



**FIGURE 2** Forage collection and colony composition for a single colony for (a and b) *Bombus terrestris*; and (c and d) *B. pascuorum*. (a and c) Nectar (yellow line, mL) and pollen (orange line, g) collection ( $\pm$ SD) by a single colony. Data were collected over 10,000 model replicates. Here, we show the average nectar and pollen collection of surviving colonies at a given time step. (b and d) The number of bees at each developmental stage at each time step ( $\pm$ SD). Brood stages are comprised of males and worker- and queen-destined females. Adult males and queens are not included in the count of adult workers because in the model they immediately leave the colony.

foraging against eggs, 0.19; larvae, 0.86; pupae, 0.09; and adults, 0.03. Pollen foraging against eggs, 0.01; larvae, 0.62; pupae, 0.05 and adults, 0.01.

#### Model Scenario 4: Ground ivy or red dead-nettle help to fill the March–April ‘hungry gap’

Scenario 4 investigates bumblebee colony number and production of hibernating queens in relation to the timing and quantity of pollen and nectar production in a 52-hectare model agricultural landscape based on a real farm landscape in the United Kingdom. The baseline model landscape contains maize (9.48 ha), ‘improved’ grassland (ploughed, seeded and fertilised) (30.65 ha), unimproved grassland (3.10 ha), scrubland (0.91 ha) and hedgerow (8.16 ha) (species composition in Table S1) (Scenario 4.1).

Adding ground ivy (Scenario 4.3) or red dead-nettle (4.6) to the model landscape increased survival probability for *B. terrestris* populations from 35% to 100% and produced a total number of adult queens in year 10 greater than 300, the number of initial queens. Adding red dead-nettle (4.6) increased *B. pascuorum* survival probability from 90% to 100% and also produced a total number of adult queens in year 10 greater than 300 (Table 1). Adding red dead-nettle also significantly increased the number of colonies and the number of adult queens for both *B. terrestris* and *B. pascuorum* in the last year of the simulation compared to the baseline (*t*-test,  $p < 0.0001$ ).

In the model landscape, there are 8.16 ha of hedgerow (81,600 m<sup>2</sup>), and 1 m<sup>2</sup> of the enhancement species was added per square metre of hedgerow, so 816 m<sup>2</sup> (0.15% of the farm area) of ‘enhanced hedgerow’ were added and 816 m<sup>2</sup> of ‘baseline hedgerow’ were removed. Thus, the simulated intervention is realistic in that it does not remove land from agricultural production. However, the enhancement species are added as ‘1 m<sup>2</sup> of full floral coverage’. The ‘full floral coverage’ values are red dead-nettle: 928 flowers/m<sup>2</sup> (SD, 538;  $n = 7$ ) and ground ivy: 734 flowers/m<sup>2</sup> (SD, 418;  $n = 15$ ) (Baude et al., 2016), and the % increase in nectar and pollen production are  $n: 1871, p: 120; n: 246, p: 46$ , respectively (Table 1). These values may be higher than would realistically be found on an average farm. In addition, it may be more labour intensive to establish and maintain the enhancement species than the hedgerow which they replace.

Adding *Primula* species (primrose) or red campion to the model hedgerow had a null or negative impact on *B. terrestris* population survival compared with the baseline. This is due to the smaller number of flowers per square metre, the lower % increase in nectar and pollen production compared with red dead-nettle and ground ivy and the long corolla tubes of these species. The ‘full floral coverage’ values for these species are red campion: 227 flowers/m<sup>2</sup> (SD 139,  $n = 10$ ) and *Primula*: 247 flowers/m<sup>2</sup> (Table S6 in Baude et al., 2016; *Primula* % increase in nectar compared with baseline: 7, pollen: 11; red campion nectar: 9, pollen: –1; Table 1; corolla lengths 13 and 30 mm, respectively). The longer corolla tubes mean that in the model, short-tongued *B. terrestris* benefits less from these species compared with species with shorter corollas. Cowslip (another *primula* species),

however, increased colony survival from 35% to 70% potentially due to the smaller corolla tube length of 8 mm. In the field, *B. terrestris* has been recorded ‘nectar robbing’ from species with long corolla tubes (Leadbeater & Chittka, 2008); however, this behaviour is not included in the BEE-STEWARD model. Therefore, the model is likely to underestimate the potential benefit of long-corolla flower species for short-tongued bumblebees.

Overall, these results indicate that providing strategic areas of flowering species that flower early (e.g., red dead-nettle: March–October, ground ivy: March–May), produce large numbers of flowers per square metre, provide abundant nectar and pollen per flower and have corolla tube lengths appropriate to the target pollinator species is likely to have positive impacts on colony survival and queen production.

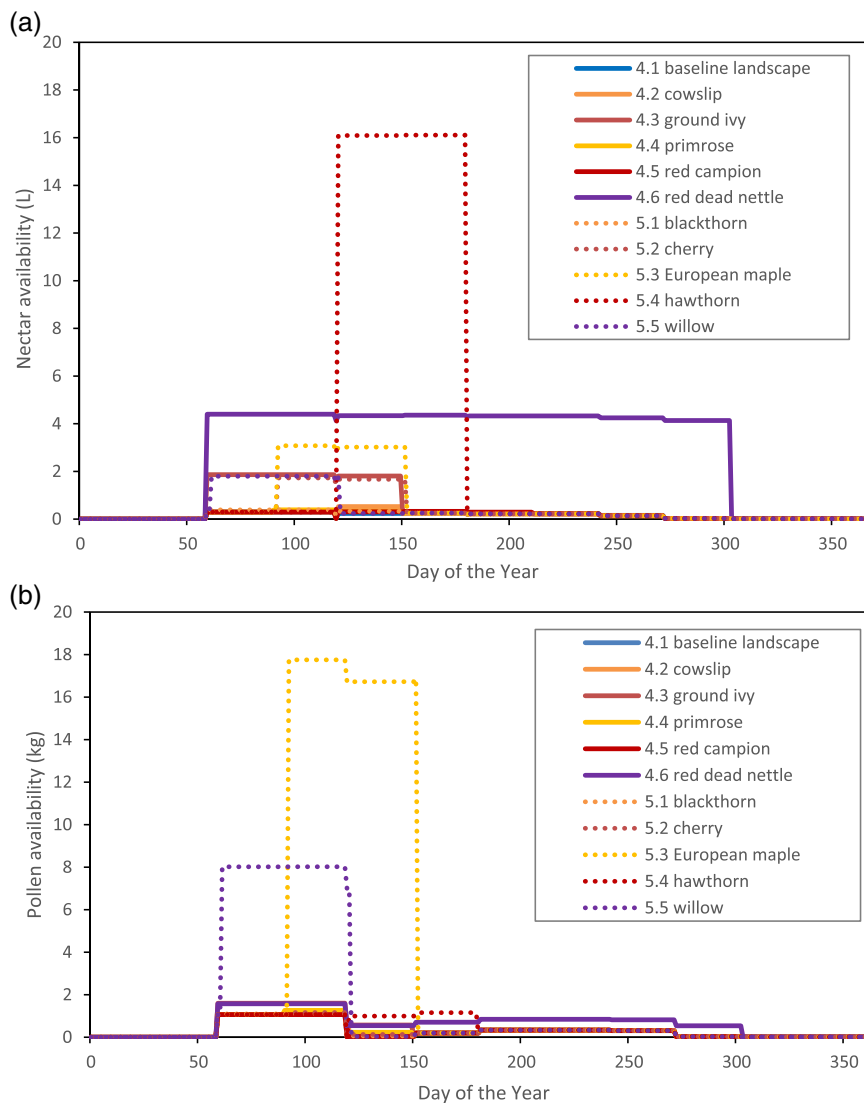
#### Model Scenario 5: Adding maple or *Prunus* species to hedgerows helps to fill the March–April ‘hungry gap’

Scenario 5 investigates bumblebee colony number and production of hibernating queens in relation to the timing and quantity of pollen and nectar production in the same 52-hectare model agricultural landscape used in Scenario 4. As for Scenario 4, hedgerow enhancement involved adding 1 m<sup>2</sup> of full floral coverage of ‘enhancement species’ (see Baude et al., 2016) per 100 m<sup>2</sup> of hedgerow. However, Scenario 5 uses five woody species: blackthorn, cherry, field maple, hawthorn and willow (Scenarios 5.1–5.5 in Table 1; Figure 3, Data S1: Habitats and flower species input files details). We ran a specific set of Scenarios for woody species because these hedgerow tree species provide important quantities of pollen and nectar during the critical March–May foraging period: (Table 1; Table S2).

Adding maple to the model hedgerows (Scenario 5.3) had the biggest impact on the number of adult *B. terrestris* queens produced over a 10-year period. Maple has been shown to be an important early forage resource for *Bombus* species, including *B. terrestris* (Bertrand et al., 2019; Kämper et al., 2016; Matsui, 1991; Uruguchi & Kubo, 2005), and in our simulations, it shifted *B. terrestris* survival percentage in the final year, year 10, from 35% in the baseline Scenario 4.1% to 100% in Scenario 5.3, and the mean number of hibernating queens from 17 to 88. The next most beneficial hedge tree was cherry (Scenario 5.2), and then hawthorn (Scenario 5.4) (Table 1). All tested tree species except blackthorn significantly increased the number of colonies and the number of adult queens in the last year of the simulation compared to the baseline for *B. terrestris* (colonies, *t*-test,  $p < 0.001$  for maple, cherry, hawthorn and willow) and all but willow and blackthorn for *B. pascuorum* (colonies, *t*-test,  $p < 0.01$ , for maple, cherry and hawthorn).

Overall, *B. terrestris* had lower numbers of colonies and adult queens as well as lower survival probability in each scenario compared with *B. pascuorum*. This is likely due to the fact that *B. pascuorum* emerges later in the season than *B. terrestris*. During *B. pascuorum*’s critical May–July foraging period, there is a variety of forage available in the baseline landscape (Scenario 4.1).





**FIGURE 3** Nectar (a) and pollen (b) produced per day in each of the Scenarios 4.1–5.5.

**DISCUSSION**

Model Scenarios 1 and 3 show that for two example spring-emerging bumblebees, *B. terrestris* and *B. pascuorum*, colony forage demand begins in early spring, March and April, and is driven by the number of larvae, not adults. This is valid for both resources, nectar and pollen, as protein from the pollen is needed by the larvae for growth, whereas the majority of energy from the nectar is required for thermoregulation of the brood. Although for both species colony forage collection appears to be driven by the number of larvae, there are differences in total forage collection and colony composition between the species. These differences may be explained by the fact that in the BEE-STEWARD model, which uses reported empirical values, *B. pascuorum* colonies are smaller than *B. terrestris* colonies (Brian, 1952; Dornhaus & Chittka, 2005; Knight et al., 2005; Nasir et al., 2019; Spaethe & Weidenmüller, 2002; Velthuis & van Doorn, 2006; Zaragoza-Trello et al., 2021), and *B. pascuorum* individuals are smaller

than *B. terrestris* individuals (Goulson & Stout, 2001; Peat et al., 2005), which may mean that *B. pascuorum* needs less food per individual. Moreover, although *B. pascuorum* is classed as a long-tongued species, whereas *B. terrestris* is classed as a short-tongued species, in the model, there is overlap in tongue length because the model uses the published range of tongue length values (*B. pascuorum*: 7.3–11.6 mm, *B. terrestris*: 6.9–11.1 mm; Twiston-Davies et al., 2021).

In Scenario 2, we find that for *B. terrestris* and *B. pascuorum*, lack of forage availability during March and April leads to a, respectively, 50%–87% and 50%–100% drop in queen production for the following season. In support of these results, numerous previous studies have found that early season forage is important for colony success (e.g. Guezen & Forrest, 2021; Rotheray et al., 2017; von Königslöw et al., 2022; Westphal et al., 2009; Williams et al., 2012), and gaps in floral resource availability reduce bee abundance and nest survival, even for social species that have nectar and pollen reserves (Hemberger et al., 2023; Nicholson et al., 2020; Timberlake

et al., 2019). Other studies have found that late season forage was the best predictor of their bumblebee success measures, but those studies differ in important ways from the study presented here. For example, Timberlake et al. (2021) found that late season forage predicted mid-season colony density, but forage in March was measured in the same year as colony density in June–July. Thus, they were not measuring the impact of early season forage on queen production for the following season, as in our study. Furthermore, they explain that variation in floral resources between farms in March was low so would be unlikely to be a significant explanatory factor in their analyses (Timberlake et al., 2021). Similarly, Rundlöf et al. (2014) found that the presence of late season red clover increased the recorded numbers of males and queens, whereas semi-natural grassland and ‘early-flowering’ (May) oil seed rape did not increase the number of queens and only increased the number of males when in combination with red clover. However, it is important to note that the semi-natural grassland in their study had a low density of flowers and was expected to serve as nesting, rather than foraging, habitat. In addition, in contrast to our study, they did not measure forage availability during March–April, when early season bumblebees found colonies in the study region. We note that some bumblebee species display plasticity in foraging behaviour, which could buffer the colony against forage resource gaps (Maebe et al., 2021), but whether phenological or behavioural shifts could entirely eliminate the impact of resources gaps is an open area of research.

Various previous studies have shown that forage provision during the larval stage affects the adult size achieved by the larvae, which in turn affects adult foraging efficacy and total colony resource provision through the season (Horn et al., 2015; Nicholson et al., 2020). Despite this knowledge, conservation efforts to date have largely targeted the later season, social stage of the bumblebee lifecycle, when there are many mature adults, rather than focusing on the demands of the early season, founding stage, when there are high resource demands from the larvae (e.g. Sarro et al., 2021). The resulting lack of forage during the founding stage likely affects colony success, but no previous work that we are aware of has specifically quantified the potential drop in colony survival or queen production due to early season forage shortage (but see Rotheray et al., 2017). Together the results from Scenarios 1, 2 and 3 indicate that forage availability during the colony founding stage is a critical, and previously under-appreciated, factor in colony success. Forage gaps may be even more severe in reality than we find in the model, as bees tend to forage from a variety of food sources in order to fulfil their needs for essential amino acids and other nutrients. This level of nutritional detail is not taken into account in the model, largely because the nutritional data for most flower species is not available (Hendriksma et al., 2019; Vaudo et al., 2016). As a result, times when bees suffer from deficits in at least one essential amino acid may occur more often than the more general resource deficits in the model, and widen the identified forage gap.

Scenario 5 found that adding maple, cherry or hawthorn to the hedgerows in the model landscape significantly increased the number of queens produced over the 10-year model cycle. Hawthorn is the 25th most nectar-productive species in the United Kingdom (kg/ha/

year, Baude et al., 2016), but of the species in our model it provides the second largest quantity of nectar per square metre (Table 1), and was therefore expected to have an important impact. The addition of hawthorn did significantly increase the number of colonies and adult queens in year 10, although it did not increase *B. terrestris* survival probability to 100%, unlike maple and cherry. This may be because hawthorn mainly flowers May through June, at the end of the critical March–May period (Figure 3). Interestingly, blackthorn did not have a positive impact on survival probability of *B. terrestris*, despite blooming early in the season. This appears to be because of low nectar and pollen production per flower, and low numbers of flowers per square metre coverage compared to other species such as hawthorn (hawthorn produces nearly 8 times more flowers per square metre and 20 times more nectar compared with blackthorn; Baude et al., 2016). In the model, food sources providing low resources can have a negative impact as foraging becomes energetically inefficient. This effect may be exaggerated in the model compared with real-world foraging.

This study, like other modelling studies, has limitations in comparison to field studies; most notably, the necessary simplification of landscape composition and organismal biology and behaviour. We note, for example, that the absolute numbers of bees predicted by the model might not reflect values found in the field because of the lack of competition with other flower visiting insects and unlimited number of potential nest sites, and, unlike in the model, the exact timing of resource demand in the field will vary with annual weather conditions and other factors. However, modelling approaches have the advantage of being able to systematically control forage availability, accurately measure fitness, and investigate organism response over long time periods in a relatively fast and cost-effective way. Moreover, the model used in this study, BEE-STEWARD, is the most thoroughly parameterized and mechanistically rich pollinator model available (Becher et al., 2018). Future simulations could provide more nuanced results by adding combinations of plant species to the model simulations, rather than adding one species at a time, and by reducing the forage available rather than removing it altogether in the periods of forage gap. Overall, none of the model limitations that we are aware of invalidate our finding that resources are most needed when the bulk of larvae needs feeding. Given the urgent need for interventions to stop and reverse pollinator declines (Díaz et al., 2019; Goulson et al., 2008; Potts et al., 2010; Powney et al., 2019), we suggest that the results presented here can not only guide future field experiments, but also have practical implications for land management and pollinator conservation interventions now.

Most national and international pollinator conservation schemes and pollinator-planting initiatives refer to ensuring that forage is available early in the season. However, most recommended forage mixes begin to bloom when adult pollinators are abundant and apparent in the landscape (e.g. Mottershead & Underwood, 2020; USDA, 2013). For colony-forming pollinators, that peak flight period is after the start of high forage demand within the colony. Planting schemes that begin to provide forage only when there are large numbers of adults are hence missing a critical period of forage requirement when the colony is dominated by larvae and the adults are not yet abundant. Increased

emphasis on temporal breadth of resource provision in pollinator planting is likely to increase the diversity of species served by pollinator planting and increase colony survival and queen production even for species already benefitting from pollinator planting (e.g. Rotheray et al., 2017). Below we offer specific recommendations regarding resource provision guidance in the United Kingdom Countryside Stewardship Program and Local Nature recovery scheme, The USDA-PHI and the European Union Pollinators Initiative.

In the United Kingdom, conservation interventions on agricultural land are guided by the Countryside Stewardship Program (CSP) of the Department for Environment, Food and Rural Affairs (DEFRA, 2023). Eight of the Countryside Stewardship Options (CSOs) are designed to maximise pollen and nectar quantity and quality (Redhead et al., 2022), but the temporal dynamics of floral resources have received less consideration (Nicholson et al., 2020). Only one of the pollinator-focused CSOs includes a species that flowers in March (DEFRA, 2023), and only 3 of the 13 'phenologically important' species identified by Timberlake et al. (2019) are included in the CSOs (Table S3). Thus, there remains a 'hungry gap' in March–April, even on farms fully engaged in the UK-CSP. This shortage of floral resources in March–April may be contributing to UK pollinator declines (42% of bee species and 27% of hoverflies declining between 1980 and 2013; Powney et al., 2019) and may be limiting the success of UK agri–environment schemes (Nicholson et al., 2020; Rotheray et al., 2017; Timberlake et al., 2019). As the understanding of pollinator needs and resource gaps in the United Kingdom grows, tools are becoming available to support decision making in land management methods and planting species (see, e.g., <https://app4future.org.uk/>).

The USDA, Farm Service Agency CP-42 PHI (IPBES, 2016; Koh et al., 2015) specifies that land managers use a minimum of three species that bloom during April–June 15 (USDA, 2013). The critical early spring period we have identified is not emphasised in this system where April–June 15 is grouped as a single period and March is not included at all. The efficacy of the PHI is likely to be increased by emphasising temporal breadth of resource provision and abundance of early spring flowers, while recognising that 'early spring' comes at different times across the latitudinal gradient of the United States.

The European Union Pollinators Initiative (EU-PIP) (European Commission, 2018) provides specific guidance to allow wild plants to flower during the pollinator flight season and to cut grass or graze in early spring and/or autumn to allow for flowering during the summer (2020). These recommendations do not place an emphasis on early spring forage, and the cutting recommendations are likely to reduce early spring forage in favour of summer forage. Thus, as for the CSP and the PHI, an increased emphasis on temporal breadth of resource provision, and specific provision in the early spring, is likely to increase the efficacy of the EU-PIP.

## CONCLUSIONS

Our study has identified a previously under-appreciated period of critical colony resource demand during the founding stage, when the colony is dominated by larvae and adult bees are not yet abundant or

even apparent in the landscape. In our model, lack of resources during this critical period has catastrophic consequences for colony survival probability and queen production, and increases the probability of population extinction.

In the United Kingdom, approximately 3% of pollinating insect taxa (aculeate wasps, bees, butterflies and hoverflies) have peak adult flying periods in April, 14% in May and 21% in June (Balfour et al., 2018). Of this 38% of UK pollinating insect taxa, those that are colony-forming are likely to have high resource demands during March–May, a month before their peak flying period when there are large numbers of larvae and few adults. There are similarly early pollinator species in North America (Bartomeus et al., 2011; Lanterman et al., 2019) and Europe (Duchenne et al., 2020). For these early spring pollinators, lack of emphasis on early season floral resources is likely to be limiting the success of pollinator conservation initiatives such as the UK-CSP, USDA-PHI and the EU-PIP.

Scenarios 4 and 5 show that hedgerow enhancement with early-blooming species, especially ground ivy, red dead-nettle, maple, cherry, hawthorn and willow, can help to meet early forage demand. This approach may be especially useful because, although there is strong evidence for the ecological and agricultural benefits of establishment of wildflower strips, they are amongst the practices most disliked by farmers due to the opportunity costs associated with the loss of cropped area (Kleijn et al., 2019; but see Pywell et al., 2015). Focusing interventions on increasing nectar and pollen provision from existing hedgerows during critical foraging periods could be appealing to land managers and provide important conservation outcomes for pollinators.

## AUTHOR CONTRIBUTIONS

**Matthias A. Becher:** Conceptualization; methodology; software; investigation; writing – original draft; data curation. **Grace Twiston-Davies:** Conceptualization; methodology; software; investigation; writing – original draft; data curation. **Juliet L. Osborne:** Conceptualization; methodology; investigation; writing – original draft. **T. A. Lander:** Conceptualization; methodology; investigation; writing – original draft.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

BEE-STEWARD input files that were edited for the experiments can be found in the University of Exeter Repository (<https://doi.org/10.24378/exe.5047>).

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## SUPPORTING INFORMATION

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

**Data S1.** Habitats and flower species input files details.

**Data S2.** Visual guide—understanding BEE-STEWARD.

**Data S3.** Bumble-BEEHAVE—model description.

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